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A new melobesioid alga *Synarthrophyton chejuensis* sp. nov. (Corallinales, Rhodophyta), including comparison with *Mesophyllum cystocarpideum*

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J.H. KIM, H. CHUNG, D.S. CHOI AND I.K. LEE. 2004. A new melobesioid alga *Synarthrophyton chejuensis* sp. nov. (Corallinales, Rhodophyta), including comparison with *Mesophyllum cystocarpideum. Phycologia* 43: 501–520.

Synarthrophyton chejuensis (Corallinales, Rhodophyta) is newly described from Korea and represents the first northern hemisphere species of that genus. It differs from other known species of *Synarthrophyton* in having the following combination of features: it has thalli that are thin, foliose, discoid, more or less proliferously lobate, and lamellate with numerous horizontally to vertically oriented layers of branches. The thalli are partially attached to the substrate. Mature tetra- or bisporangial conceptacles have flat or moundlike pore plates, and usually two or more conceptacles are joined. The pore plates are composed of filaments of four or five cells along with an epithallial cell. The pore canal is lined by filaments with cells similar in size and shape to the cells of other filaments making up the pore plate. Korean plants belonging to *S. chejuensis* previously had been misidentified as *Lithothamnion cystocarpideum* or *Mesophyllum cystocarpideum*, but a reexamination of the type of *M. cystocarpideum* has shown that it is specifically distinct from *S. chejuensis*. A detailed morphological and anatomical account of *S. chejuensis* is provided, and the value of several characters used to distinguish species within *Synarthrophyton* is discussed.

INTRODUCTION

The genus *Synarthrophyton* Townsend (Corallinales, Rhodophyta) is known to include seven species, all from the southern hemisphere (Townsend 1979; May & Woelkerling 1988; Woelkerling & Foster 1989; Mendoza *et al.* 1996; Keats & Chamberlain 1997; Keats & Maneveldt 1997). During ecological studies of the whitening of nongeniculate corallines in Korean coastal waters (Chung *et al.* 1998), plants possessing the generic characteristics of *Synarthrophyton* were found subtidally at Cheju Island. Further investigations led to the conclusions that these plants represented a species distinct from others so far placed in *Synarthrophyton,* and they appeared conspecific with Korean and Japanese plants to which the names *Lithothamnion cystocarpideum* Foslie or *Mesophyllum cystocarpideum* (Foslie) Adey had been applied by Masaki (1968), Park (1977, 1980) and Yoshida (1998). It became clear from an examination of the type of *M. cystocarpideum,* however, that the type was not conspecific with Korean or Japanese plants to which the name had been applied, and that it did not belong to *Synarthrophyton.* No other name for the Cheju Island material or the misidentified plants of *M. cystocarpideum* was found, and thus these collections appeared to represent an undescribed species of *Synarthrophyton* and the first species of the genus to be described from the northern hemisphere. The present study provides an account of *Synarthrophyton chejuensis* sp. nov. and a reassessment of the type of *M. cystocarpideum,* from New Zealand.

MATERIAL AND METHODS

Field collections were made using SCUBA in the coastal zone of Cheju Island and along the southern and eastern coasts of Korea. The type specimen of *M. cystocarpideum* was obtained from Trondheim (TRH) (Holmgren *et al.* 1990). Thalli were air-dried or fixed in 5% formaldehyde–seawater and stored in a 70% ethanol : 10% glycerol : 20% distilled water solution. For sectioning, plants were decalcified with 1% HNO_3 (in 5% formalin–seawater), stained in 1% aqueous toluidine blue, dehydrated through an ethanol series and then embedded in LR White resin (Woelkerling 1988). Sections 6–12 μm thick were then cut with a steel knife on a microtome (Reichert–Jung, Nussloch, Germany), flattened by wetting with a drop of Histo-clear clearing agent and mounted in Polymount (Polysciences, Warrington, PA, USA). For scanning electron microscopy (SEM), specimens were rinsed in demineralized water and air-dried. Observations and photographs were made using Olympus (Venox-T and BH-2; Olympus, Tokyo, Japan) and Zeiss (Axioskop; Zeiss, Göttingen, Germany) microscopes. Drawings were made directly from prepared slides using a Zeiss microscope equipped with a drawing tube. Fractures and whole thalli were mounted on double-sided adhesive tape, coated with gold and examined in a Philips SEM 515 at 25 kV (Philips, Eindhoven, The Netherlands).

Cell measurements followed the method adopted by Keats & Chamberlain (1997), whereas conceptacle measurements used the system of Adey & Adey (1973). We used the thallus terminology of Chamberlain (1990) and the morphological terminology of Woelkerling *et al.* (1993).

All specimens examined and illustrated (apart from the holotype *M. cystocarpideum* from TRH) are housed at the Korea Polar Research Institute (KOPRI).

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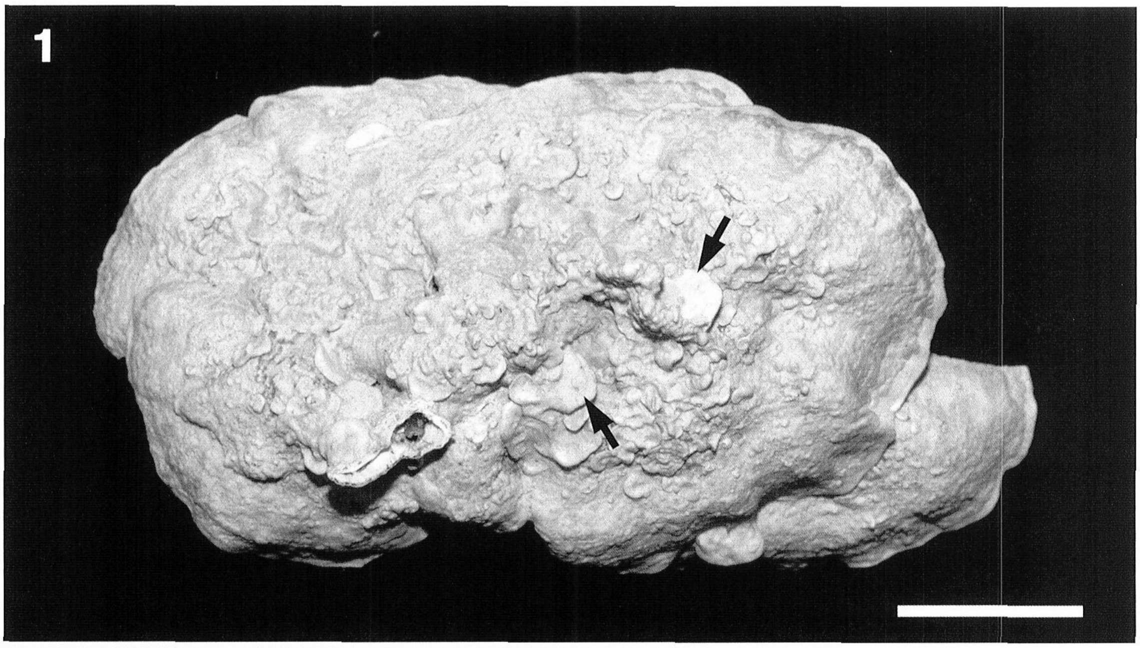

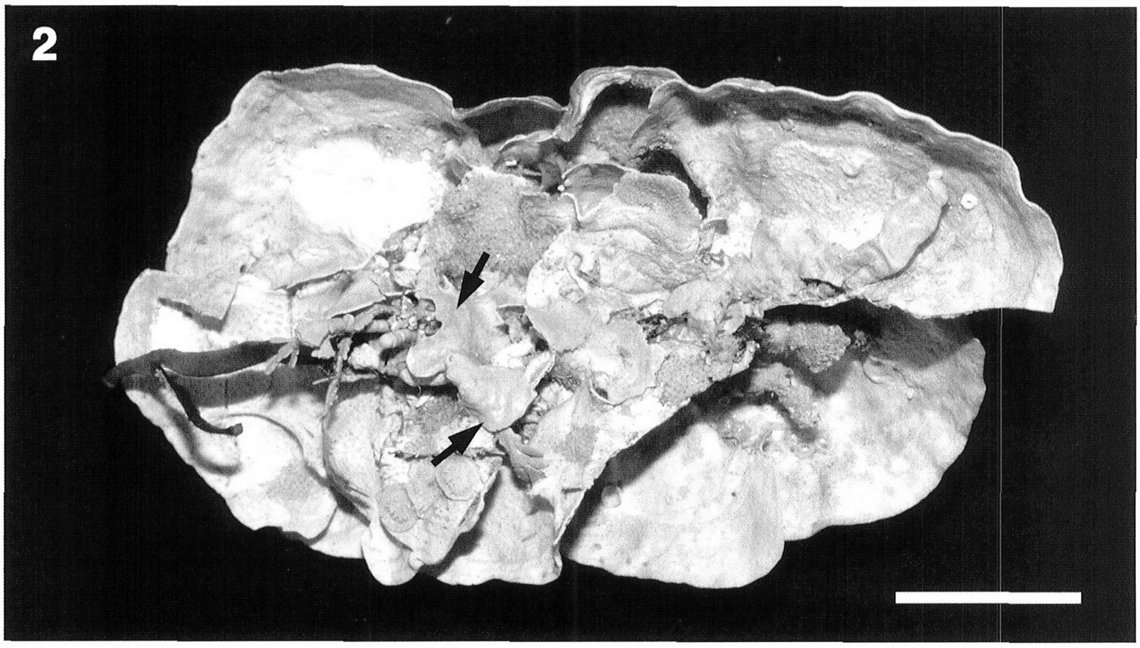

Figs 1, 2. *Synarthrophyton chejuensis*, holotype (SNU 98-CMP407). Scale bars = 1 cm.

Fig. 1. Dorsal view, showing habit and superficial lobes (arrows).

Fig. 2. Ventral view of holotype on *Marginisporum crassissimum*, showing complete envelopment of the host (arrows).

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Figs 3–8. Growth forms of *Synarthrophyton chejuensis*. Scale bars = 1 cm, except Fig. 6 (3 mm).

Fig. 3. Leafy plants growing on the geniculate coralline alga *Marginisporum crassissimum* (isotype: SNU 98-CMP408) with groups of tetrasporangial conceptacles (arrows).

Fig. 4. Discoid and encrusting plants on the red alga *Gelidium amansii* (SNU 98-EGJ201).

Fig. 5. Encrusting plant completely enveloping the thallus of the red alga *Chondrus ocellatus* (SNU 98-EGJ202).

Fig. 6. Encrusting plants overgrowing each other on a shell (SNU 99-CSS001).

Fig. 7. Encrusting female plants on a sponge with geniculate coralline alga (SNU 98-CMP409).

Fig. 8. Male plants on the geniculate coralline alga *Amphiroa anceps* (SNU 99-CEY002).

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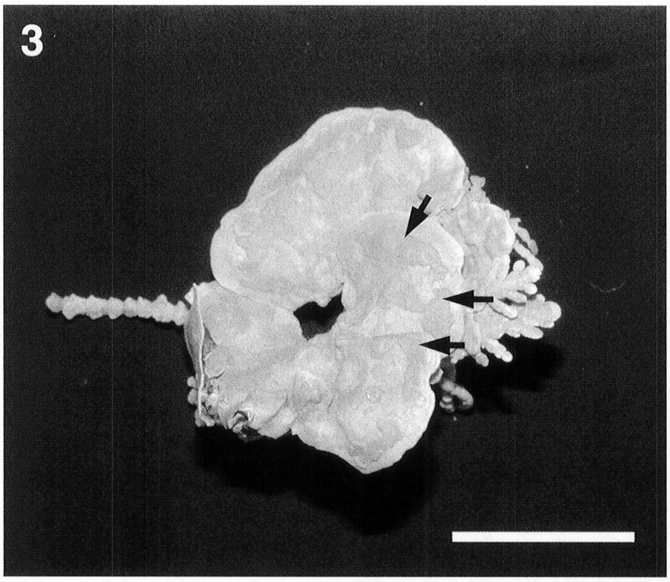
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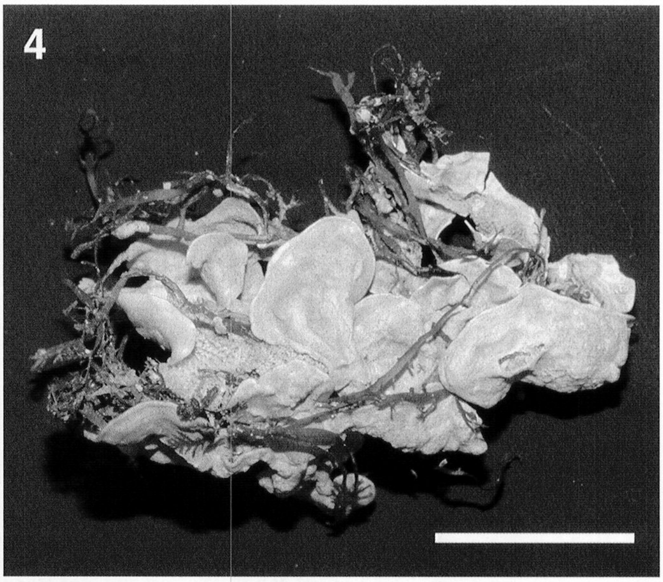
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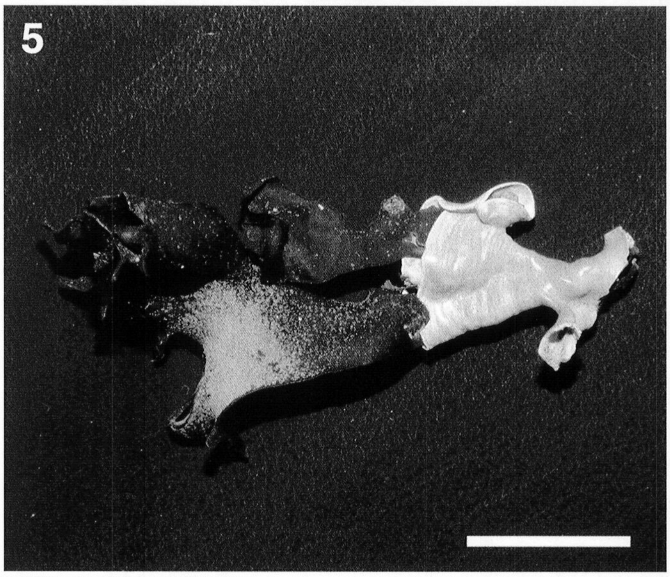
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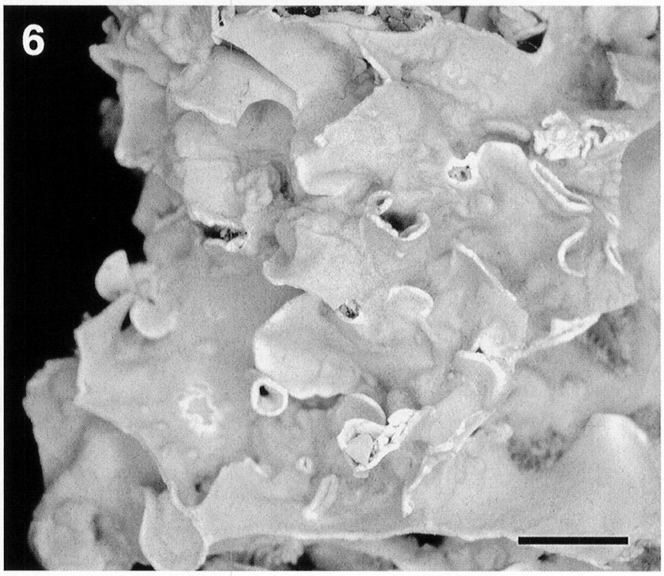
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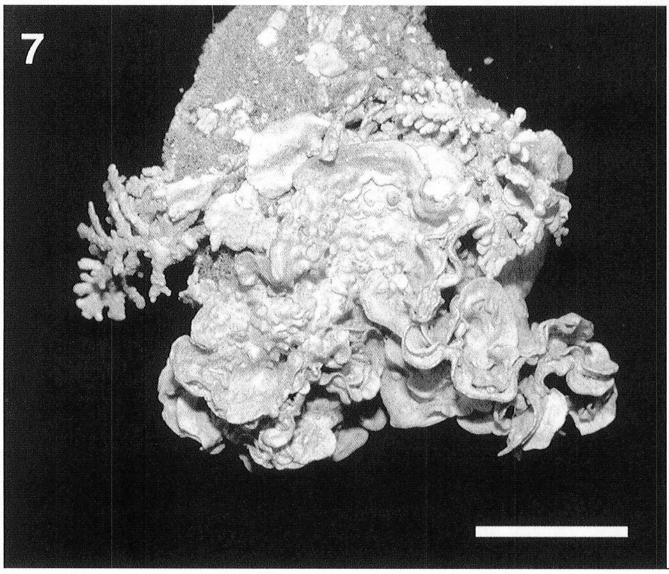
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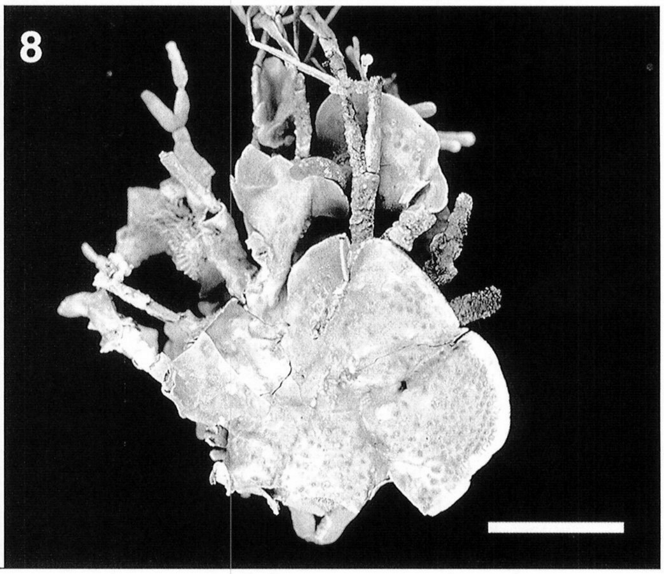
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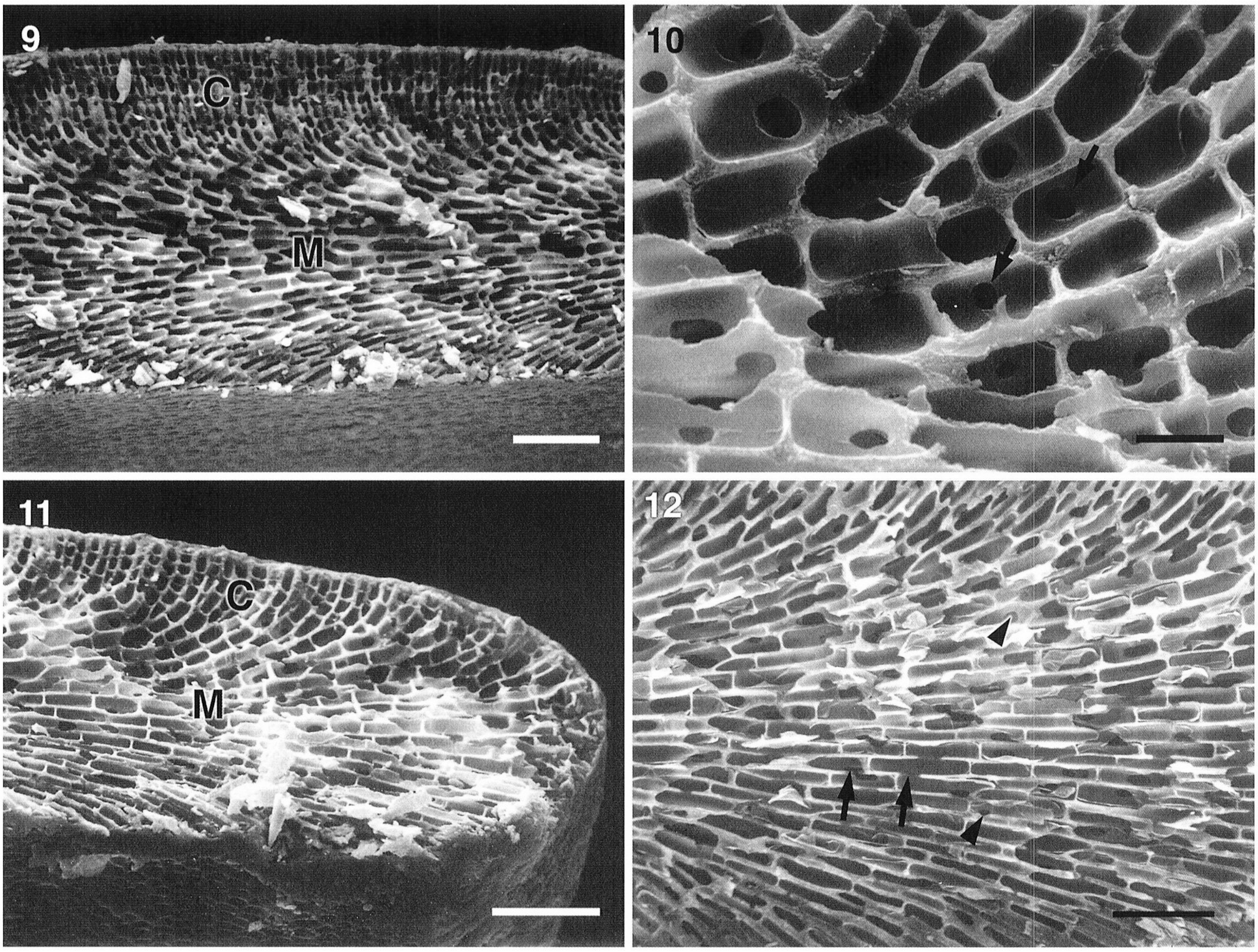

Figs 9–12. Vegetative anatomy of *S. chejuensis* (SNU 98-CMP407), SEM. Scale bars = 50 μm, except Fig. 10 (10 μm).
Fig. 9. Vertical fracture of thallus, showing cortical filament (C) and plumose medullary filaments (M).
Fig. 10. Vertical fracture of thallus, showing only small cell fusions (arrows).
Fig. 11. Vertical fracture of the margin with noncoaxial medullary filaments (M) and a thin layer of cortical filaments (C).
Fig. 12. Vertical fracture of thallus showing medullary filaments with both small cell fusions (arrowheads) and large cell fusions (arrows).

OBSERVATIONS

Synarthrophyton chejuensis J.H. Kim, H. Chung, D.S. Choi & I.K. Lee, *sp. nov.*

Figs 1–44, Table 1

Thallus foliosus, lamelliformis, irregulariter orbiculatus; tectum conceptaculi maturi tetra/bisporangialis, ad instar tumuli ad complanus paginis; cellulae affines fossulis pororum conceptaculorum tetra/bisporangialium similes magnitudine formaque ceteris tecti cellulis in pororum patella; cellulae rosulantes similes ambientibus tecti cellulis; thalli gametophytici monoecii vel dioecii; conceptacula tetra/bisporangialia confluentia se non in thallo infodiunt, sed senescentia exuta saepe in superficie craters non profundos relinquunt.

Thallus leafy, lamelliform, irregularly roundish in shape; roof of mature tetra/bisporangial conceptacles, moundlike to flush with the surface; cells bordering the tetra/bisporangial conceptacle pore canal similar in size and shape to the other roof cells within the pore plate; rosette cells similar to surrounding roof cells; gametophytic thalli monoecious to dioecious; tetra/bisporangial conceptacles confluent, not becoming buried in the thallus, but shed on senescence, often leaving shallow craters on the surface.

MISAPPLIED NAMES: *Lithothamnion cystocarpideum auct. non.* Foslie: Masaki (1968, p. 11, pls. 5, 6, 43, 44 as *Lithothamnium cystocarpideum*); Park (1977, p. 62, pl. 1, figs 6, 7, pl. 5, figs 1–6 as *Lithothamnium cystocarpideum*); Lee & Kang (1986, p. 320 as *Lithothamnion cystocarpioideum. Mesophyllum cystocarpideum* (Foslie) Adey: Park (1980, p. 4, pl. I-1, fig. 2A–E).

HOLOTYPE: **Korea.** South-western coast of Cheju Island, Moseulpo, 10–15 m deep, on *Marginisporum crassissimum* (Yendo) Ganesan, 18.v.1998, *J.H. Kim & H. Chung*, SNU 98-CMP407 (Figs 1, 2).

ISOTYPE: Same locality, 10–15 m deep, on *M. crassissimum*, SNU 98-CMP408 (Fig. 3).

ETYMOLOGY: The specific epithet *chejuensis* refers to the place where the species was first discovered: Cheju Island, on the southern coast of Korea.

REPRESENTATIVE SPECIMENS EXAMINED: **Korea.** Cheju Island, Saesum, 10–15 m deep, on rock, *Amphiroa anceps* (Lamarck) Decaisne, *Cladophora japonica* Yamada and *M. crassissimum* (*J.H. Kim*, 20 July 1998, SNU 98-CSS428); Cheju Island, Saesum, 11 m deep, on abalone shells and *M. crassissimum* (*J.H. Kim*, 11 February 1999, SNU 99-CSS001); Cheju Island, Eoyoung, 8 m deep, on *A. anceps* (*J.H. Kim*, 11 February 1999, SNU 99-CEY002); south-eastern coast of Korea, Gijang, 5–10 m deep, on *Alatocladia modesta* (Yendo) Johansen, *Chondrus ocellatus* Holmes, *Corallina pilulifera* Pos-

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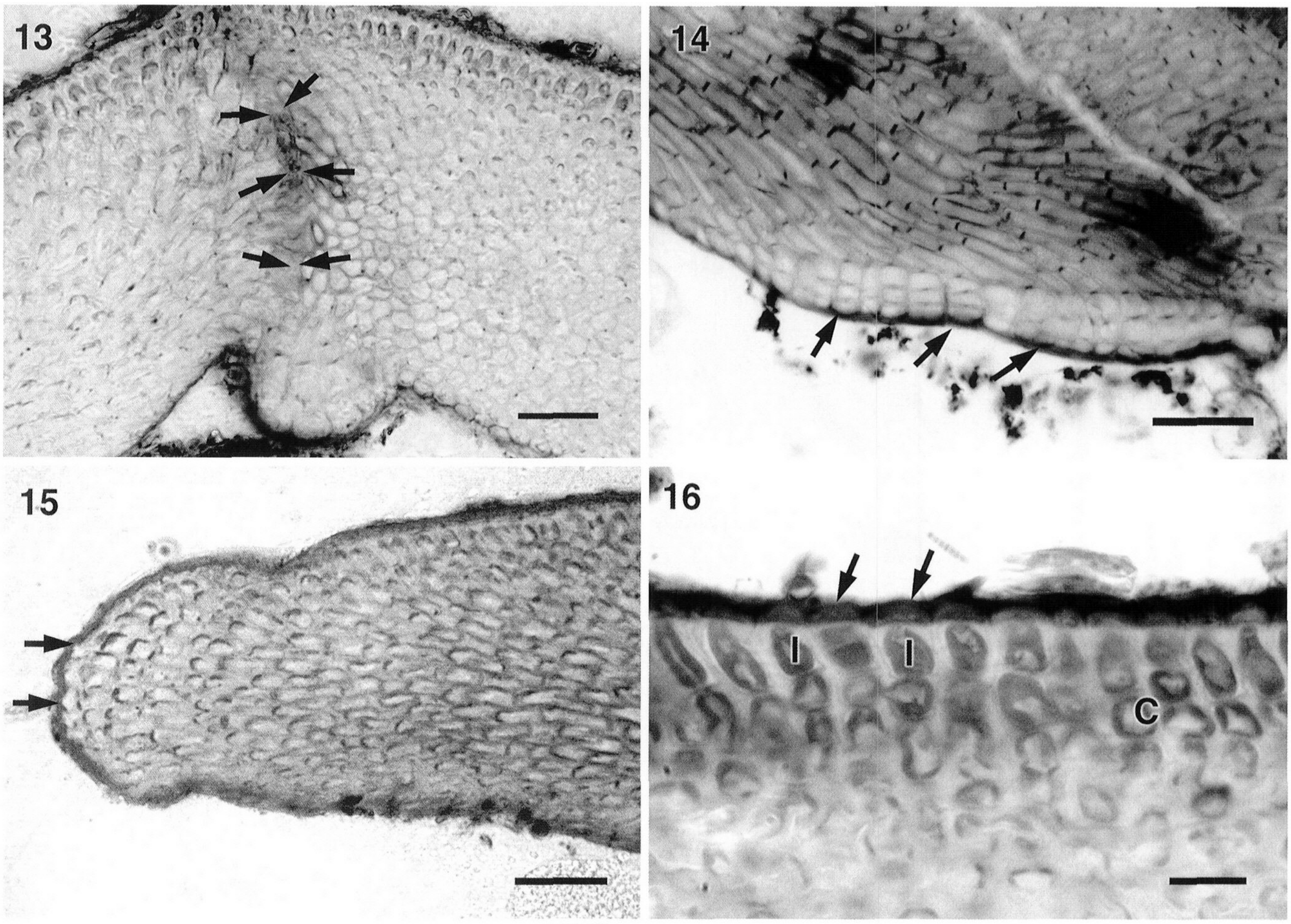

Figs 13–16. Vegetative anatomy of *Synarthrophyton chejuensis* (SNU 98-CMP407), light microscopy (LM). Scale bars = 10 μm (Fig. 16), 20 μm (Fig. 14), 25 μm (Fig. 13) or 50 μm (Fig. 15).
Fig. 13. Vertical section of fusion (arrows) of two thalli.
Fig. 14. Vertical section of thallus showing secondary thickening (arrows).
Fig. 15. Vertical section of thallus at margin, showing terminal marginal initials (arrows).
Fig. 16. Vertical section of upper thallus showing cortical filaments (C), subepithallial initials (I) and epithallial cells (arrows).

tels & Ruprecht and *Gelidium amansii* (Lamouroux) Lamouroux (*J.H. Kim*, 9 June 1998, SNU 98-EGJ201-204); south-eastern coast of Korea, Gijang, 5–10 m deep, on *G. amansii* (*J.H. Kim*, 24 February 1999, SNU 99-EGJ001).

HABITAT AND PHENOLOGY: *Synarthrophyton chejuensis* is most abundant along the south coast of Korea at sites exposed to moderate wave action. Here, it forms conspicuous reddish purple to pinkish red (in the water) leafy thalli that grow on geniculate coralline algae, other algae or rocks and shells, between 5 and 15 m deep. Reproductive materials were found from February to June but there are no collections in other months. At sites along Cheju Island, the alga was usually attached to *Amphiroa anceps*, *C. pilulifera* and *M. crassissimum*, whereas at sites off the south-eastern coast of Korea it was often epiphytic on *Alatocladia modesta* or *G. amansii*.

DISTRIBUTION: **Korea.** Cheju Island, southern and eastern coast of Korea. **Japan.** Honshu, Sikoku and Kyushu (Yoshida 1998, as *L. cystocarpideum*).

HABIT AND VEGETATIVE STRUCTURE: The plants are nongeniculate, thin, foliose and have more or less proliferously lobate or branched lamellae, which spread out from or surround the axes of the host (Figs 1–5, 7, 8). Thalli are up to 30 mm long and 50 mm broad, but the nature of the substrate may limit the extent to which the thallus can develop (Hamel & Lemoine 1953, p. 77). The plants are attached primarily through envelopment of host axes, with the epiphytic lamellae commonly becoming fused with another lobe of the same plant (Figs 6, 13). Where the epiphyte more or less completely surrounds the host axis, envelopment and fusion are extensive, and the ventral surface of the thallus becomes largely or entirely obscured (Fig. 5). In more expanded spreading plants, envelopment and fusion are localized, and both the dorsal and ventral surfaces of lamellae remain clearly visible (Fig. 2). Lobes and branches may develop by differential growth along the margin or superficially from either surface of the lamellae (Figs 1, 6). They may expand horizontally or curl and fuse along apposite margins. They may also grow by abutting, fusing with or overgrowing other lobes or branches (Figs 1, 6, 7). The overall form and appearance of a thallus is determined by the extent to which each of these types of development has occurred.

The thallus is monomerous (Figs 9, 17). The medullary region is plumose (Figs 9, 12), and measures 75–170 μm thick, which is usually more than 85% of the mature thallus thickness. Cells of medullary filaments (Figs 10–13) are elon-

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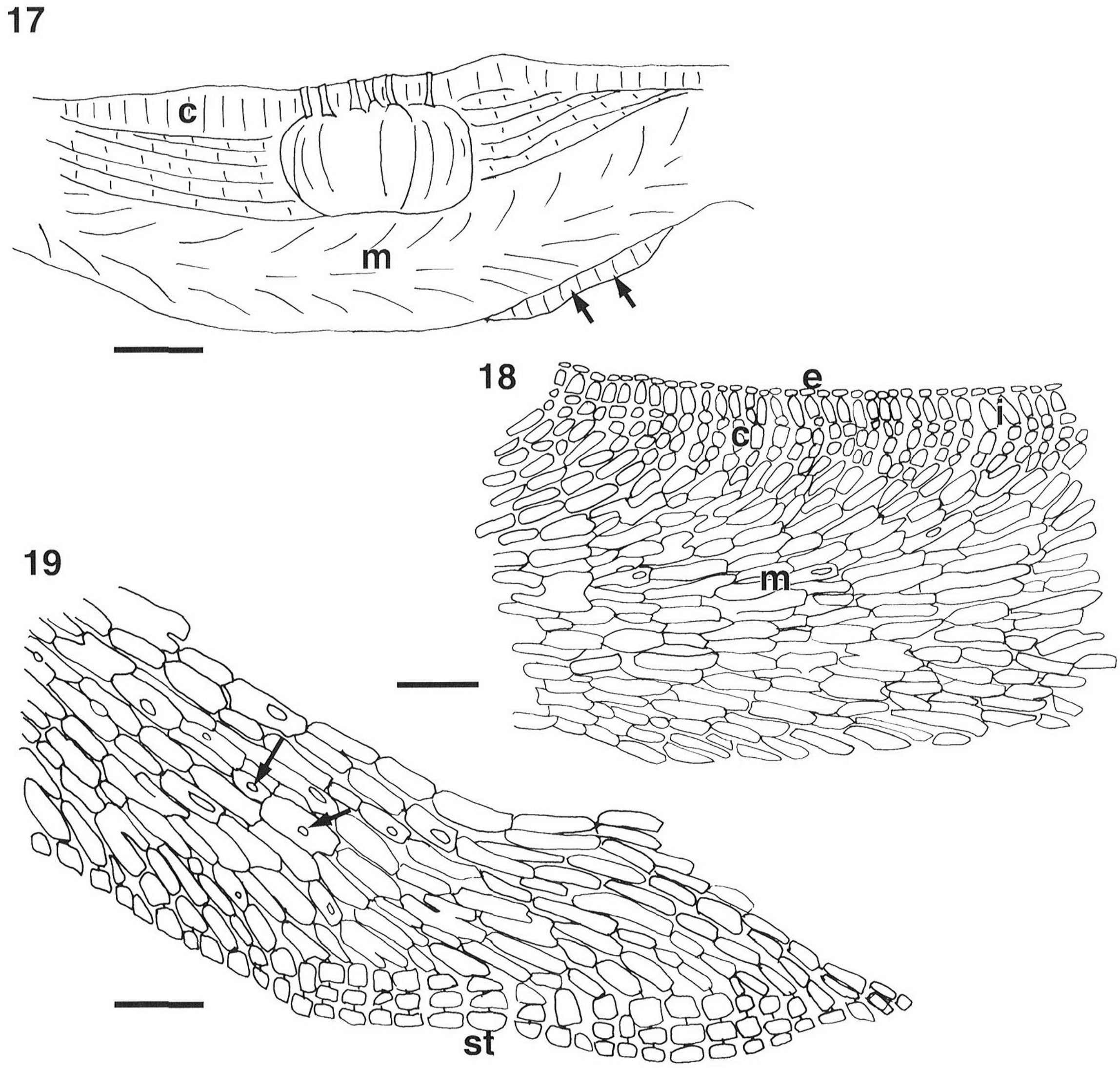

Figs 17–19. Drawings of vertical sections of thallus of *Synarthrophyton chejuensis* (SNU 99-EGJ201). Scale bars = 20 μm (Fig. 19), 30 μm (Fig. 18) or 200 μm (Fig. 17).

Fig. 17. Diagram showing medullary (m) and cortical (c) filaments, secondary thickening (arrows) and a tetrasporangial conceptacle.

Fig. 18. Vertical section showing epithallial cells (e), subepithallial initials (i) and cortical (c) and medullary (m) filaments with cell fusions.

Fig. 19. Partial section showing ventral secondary thickening (st) and medullary filaments with cell fusions (arrows).

gate, 10–28 μm in length and 4–8 μm in diameter. Small and large cell fusions commonly occur in both anticlinal and periclinal cell walls (Figs 10, 12, 14, 18), but secondary pit connections have not been seen. Ventrally situated medullary filaments are oriented at a shallow angle towards the substratum. They terminate in elongate or epithallial cells with secondary thickening at the ventral surface (Figs 14, 19). Secondary thickening begins when inactive vegetative initials on the ventral surface react to produce rows of filaments with uniformly shaped cells shorter than those within the rest of the thallus (Figs 14, 19). Ventral secondary thickening also occurs in *S. patena* (J.D. Hooker & W.H. Harvey) Townsend (Harvey *et al.* 1994, figs 12, 13), the type species for the genus *Synarthrophyton*. In plants of *S. chejuensis*, secondary thickening is less developed than in *S. patena*. Medullary filaments terminate at the margin in primary meristematic cells (Fig. 15). The cortical region is 13–20 μm thick and usually occupies less than 15% of the thallus thickness (Figs 9, 11, 16). Cells of cortical filaments are square to rectangular, and measure 7–13 μm in length and 4–7 μm in diameter. Cell fusions are common and vary from narrow fusions to those eliminating most of the wall between adjoining cells. Trichocytes have not been seen. Subepithallial initials are square to elongate and may be similar to or longer than the cells subtending them (Figs 16, 18). They measure 5–15 μm in length and 5–6 μm in diameter. Epithallial cells occur singly, are flattened and more or less rectangular, but are not flared (Figs 16, 18). They measure 5–8 μm in length and 4–8 μm in diameter.

REPRODUCTION: Gametangial plants are monoecious to dioecious (Fig. 33). Male conceptacles are low cones with elliptical chambers measuring 275–425 μm in diameter and 65–80 μm in height, and with a roof 50–65 μm in thickness (Figs 20, 21). The roof is formed from filaments peripheral to the fertile area. During the early stages of male conceptacle development, filaments destined to produce spermatangial

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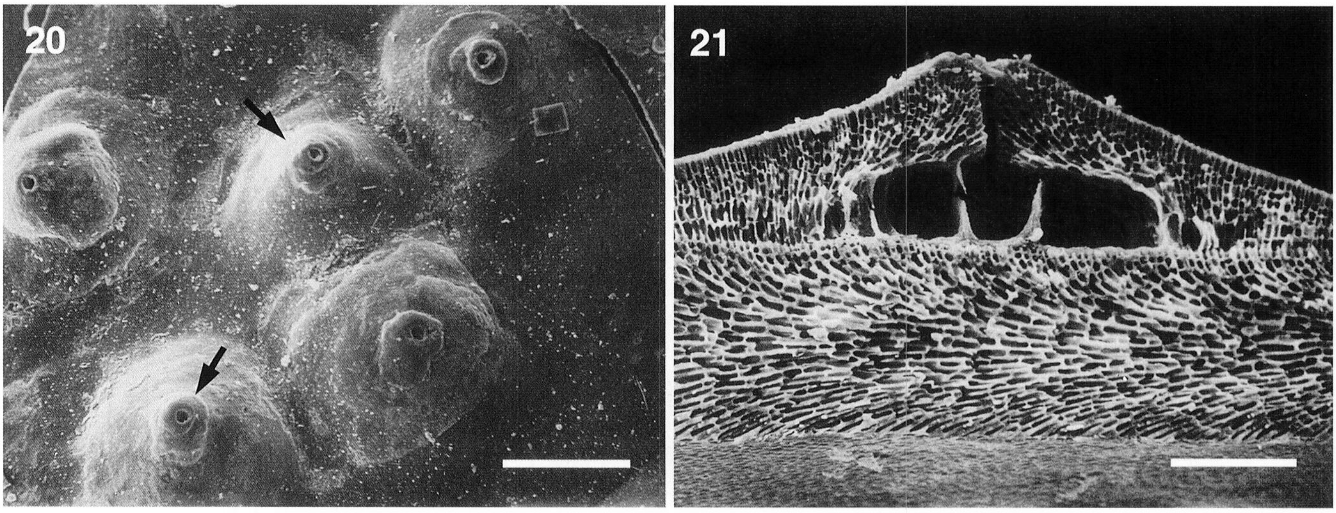
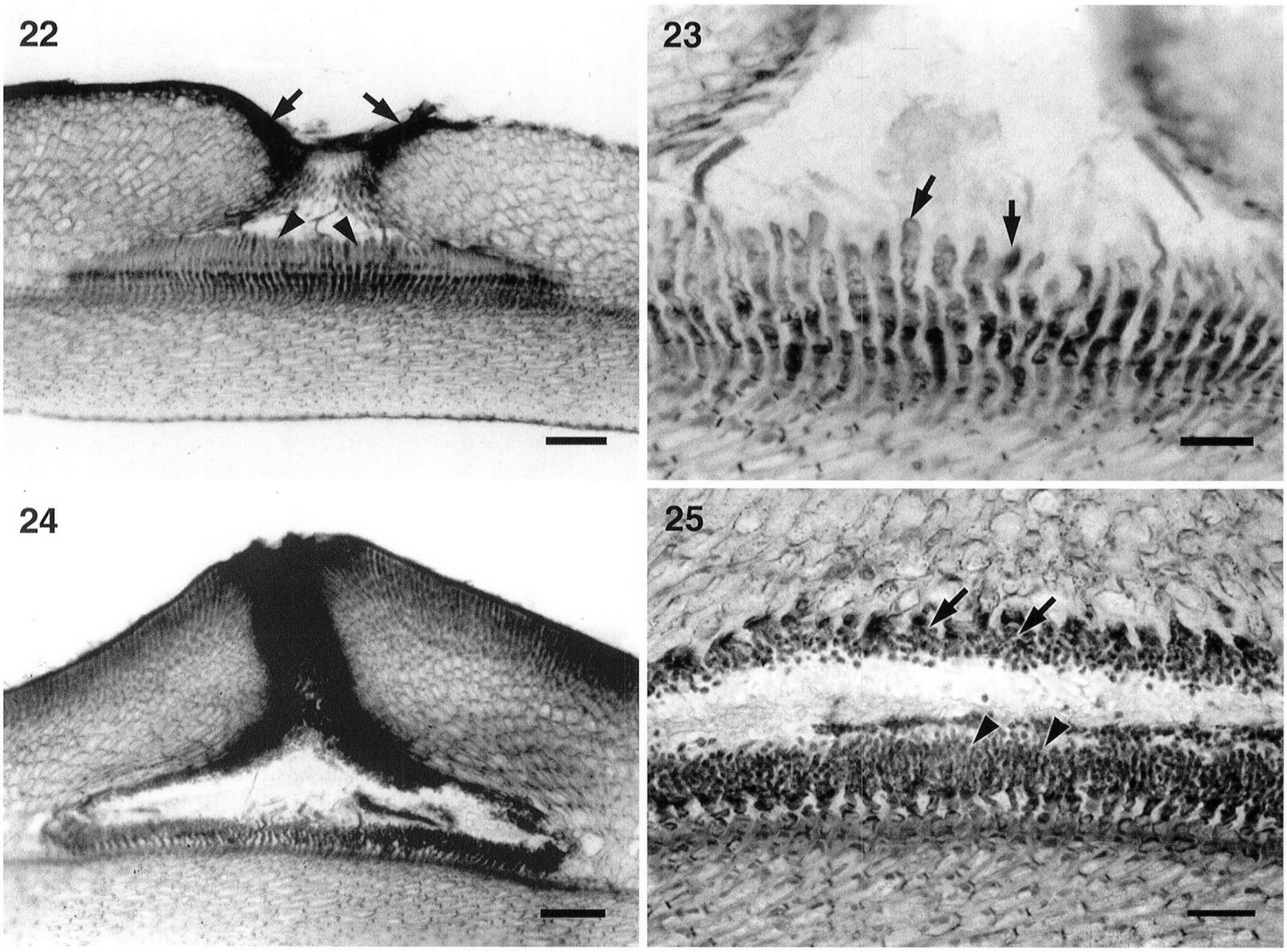


Figs 20, 21. Male gametophytic thallus of *Synarthrophyton chejuensis* (SNU 99-CEY002), SEM. Scale bars = 100 μm (Fig. 21) or 500 μm (Fig. 20).

Fig. 20. Surface aspect of spermatangial conceptacles (arrows).

Fig. 21. Vertical fracture of a spermatangial conceptacle.



Figs 22–25. Vertical sections of male conceptacles of *Synarthrophyton chejuensis* (SNU 99-CEY002), LM. Scale bars = 20 μm (Figs 23, 25) or 50 μm (Figs 22, 24).

Fig. 22. Early stage of development showing elongate protective cells (arrowheads) and the developing conceptacle roof (arrows).

Fig. 23. Portion of the central region of conceptacle in Fig. 22 showing protective cells resembling carpogonia (arrows).

Fig. 24. Mature spermatangial conceptacle with dendroid spermatangial branches on the chamber floor and simple spermatangial branches on the chamber roof.

Fig. 25. Spermatangial systems from the roof (simple, arrows) and floor (dendroid, arrowheads) of a mature conceptacle.

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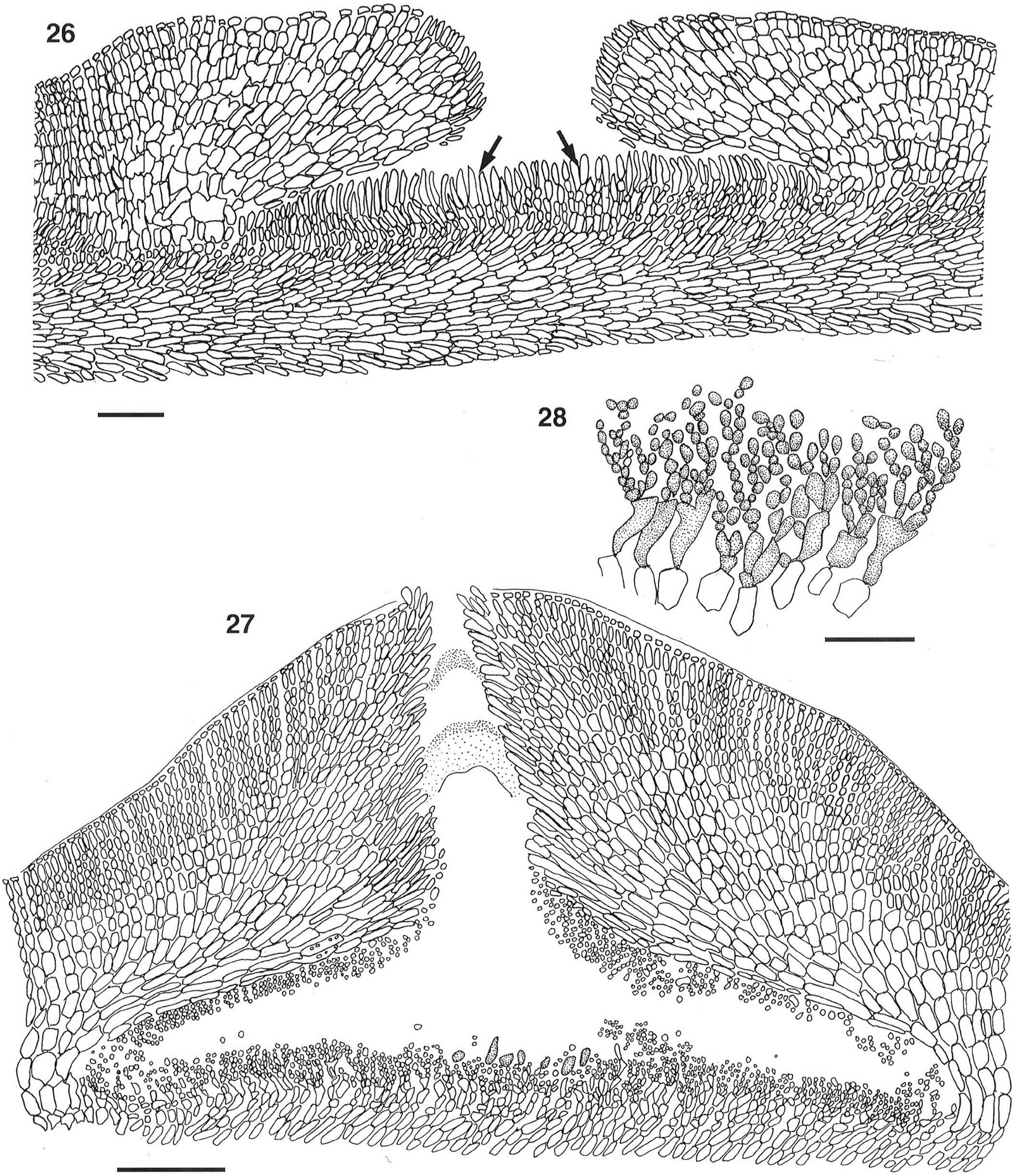

Figs 26–28. Drawings of male conceptacles of *Synarthrophyton chejuensis* (SNU 99-CEY002). Scale bars = 10 μm (Fig. 28) or 50 μm (Figs 26, 27).

Fig. 26. Early stage of development showing elongate protective cells (arrows).

Fig. 27. Mature spermatangial conceptacle with dendroid spermatangial branches on the chamber floor and simple spermatangial branches on the chamber roof.

Fig. 28. Dendroid spermatangial branches from the chamber floor.

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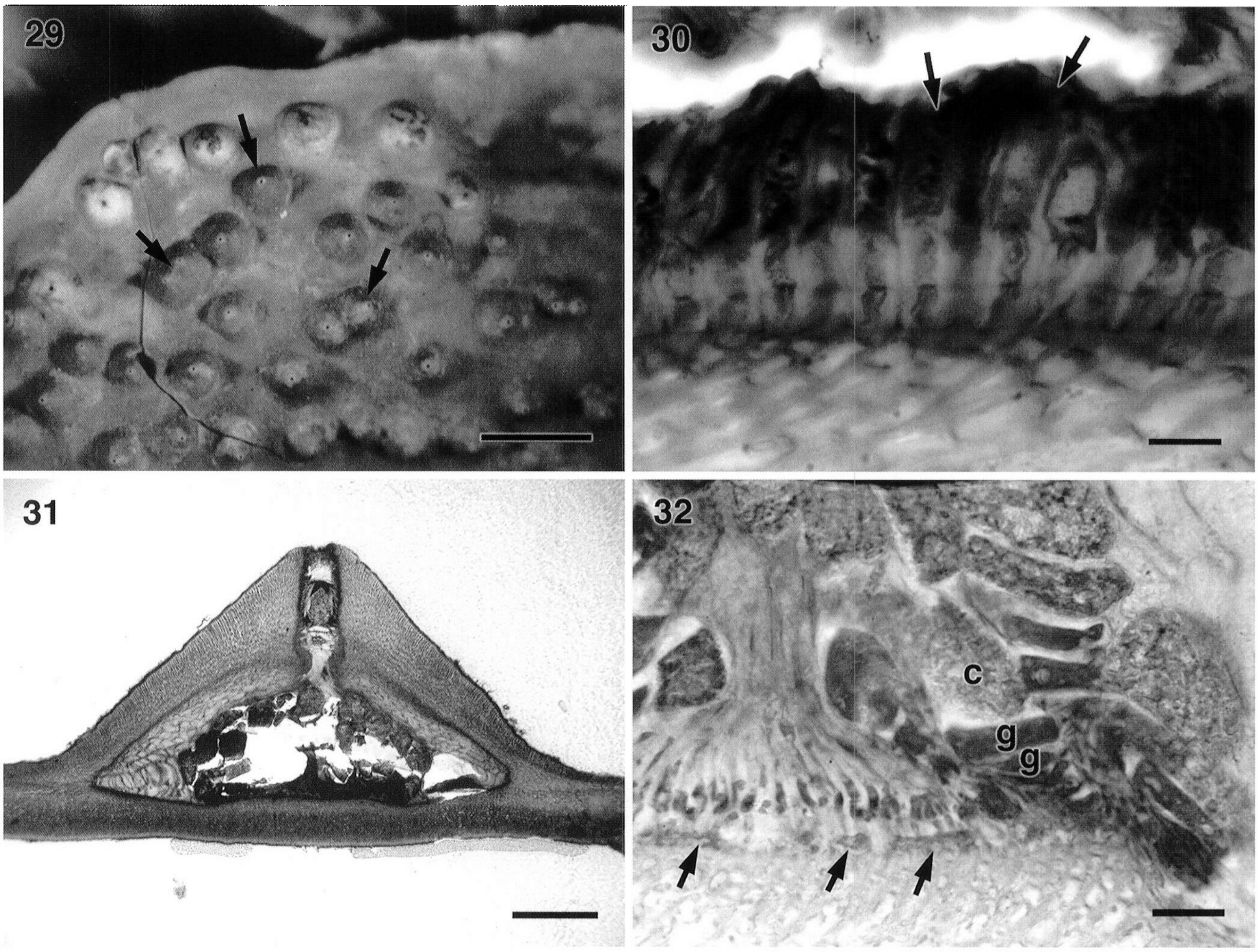

Figs 29–32. Female conceptacles of *Synarthrophyton chejuensis* (SNU 98-CMP409). Scale bars = 10 μm (Fig. 30), 20 μm (Fig. 32), 100 μm (Fig. 31) or 2 mm (Fig. 29).

Fig. 29. Surface aspect of female conceptacles (arrows).

Fig. 30. Vertical section of carpogonial conceptacle to show carpogonial branches (arrows), LM.

Fig. 31. Vertical section of carposporangial conceptacle showing shape, LM.

Fig. 32. Vertical section of carposporangial conceptacle showing several parts of fusion cell (arrows) and gonimoblast filaments (g), each terminating in a carposporangium (c), LM.

branches on the conceptacle chamber floor terminate in elongate cells resembling young carpogonia (Figs 22, 26). These cells are sterile and overlay subterminal initials involved in spermatangial branch formation. Lebednik (1978) termed them 'protective cells' (Fig. 23) and they are reported in *Mesophyllum* Lemoine (Lebednik 1978; Woelkerling & Harvey 1992) and *Synarthrophyton* (Harvey *et al.* 1994; Keats & Chamberlain 1997; Keats & Maneveldt 1997). The subterminal spermatangial initials may repeatedly divide to produce dendroid spermatangial branches on the floor of the conceptacle chamber (Figs 24, 25, 27, 28). Spermatangial branches also develop on the conceptacle chamber roof (Figs 25, 27). However, protective cells have not been observed, and it is unclear whether spermatangial branches develop from distinct initials or are produced adventitiously from cells of roof filaments.

Carpogonial conceptacle chambers are flask-shaped and measure 400–650 μm in internal diameter and 105–250 μm in height, with the roof about 150–210 μm in thickness. Carpogonial branches develop across the floor of the conceptacle and comprise a supporting cell and a hypogynous cell bearing a carpogonium with a trichogyne and a sterile cell (Fig. 30). After presumed karyogamy, the carposporophyte develops in the carpogonial conceptacle.

Carposporangial conceptacles are sharply raised cones and measure about 500–980 μm in external diameter (Figs 29, 30). Their chambers are elliptical to flask-shaped and measure 450–660 μm in diameter, 210–300 μm in height and have a roof of 120–200 μm in thickness (Figs 31, 34). The pore canal is lined with papillae. Gonimoblast filaments are often difficult to detect (Fig. 32), but are located at the surface and margin of a fusion cell that is discoid and appears to be discontinuous. These filaments comprise up to six cells, including a terminal carposporangium (Figs 32, 34).

Tetra- or bisporangial conceptacles are slightly domed or flush with the surrounding surface (Figs 36, 37, 43); most are

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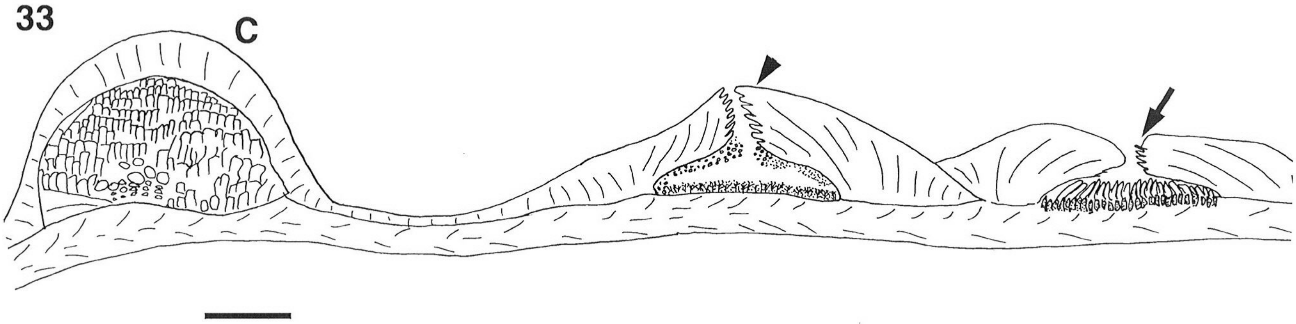

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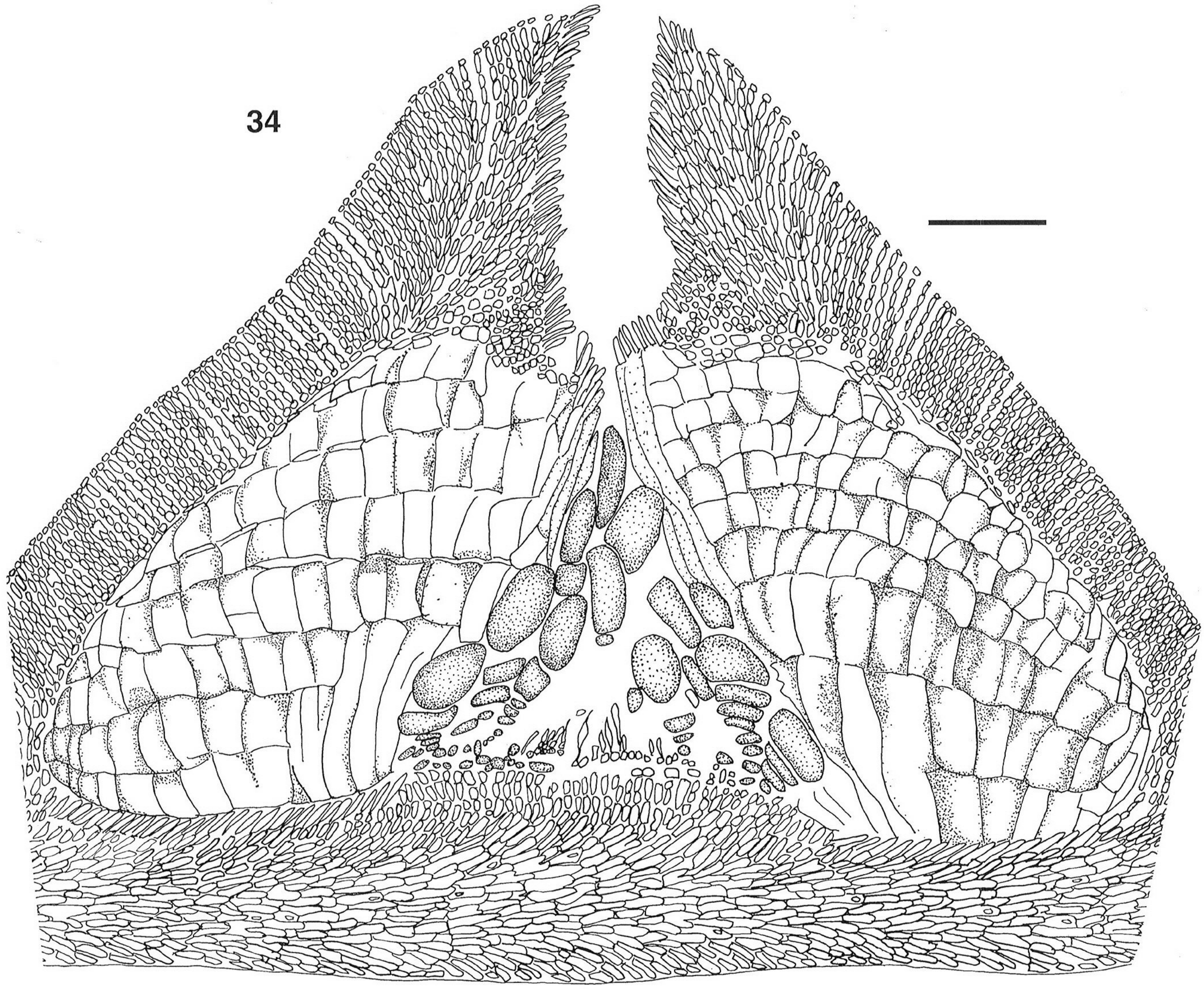

Figs 33, 34. Drawings of vertical sections of thallus of *Synarthrophyton chejuensis* (SNU 98-CMP409). Scale bars = 50 μm (Fig. 34) or 200 μm (Fig. 33).

Fig. 33. Diagram of the monoecious thallus showing carposporangial conceptacle (C), early stage (arrow) and mature spermatangial conceptacles (arrowhead).

Fig. 34. Vertical section of carposporangial conceptacle showing shape, indistinct fusion cell, and gonimoblast filaments, each terminating in a carposporangium.

fused and they measure up to 780 μm in diameter. They occupy most of the surface of a thallus except the marginal surface. Pore plates have a diameter of approximately 230 μm and contain up to 30 pores that are conspicuous due to a small rim (Fig. 37). Each pore is surrounded by a rosette of seven or eight cells that are flush with the cells of the surrounding roof surface. Chambers are elliptical, often relatively shallow and wide (Figs 39, 40). They measure 210–340 μm in di-

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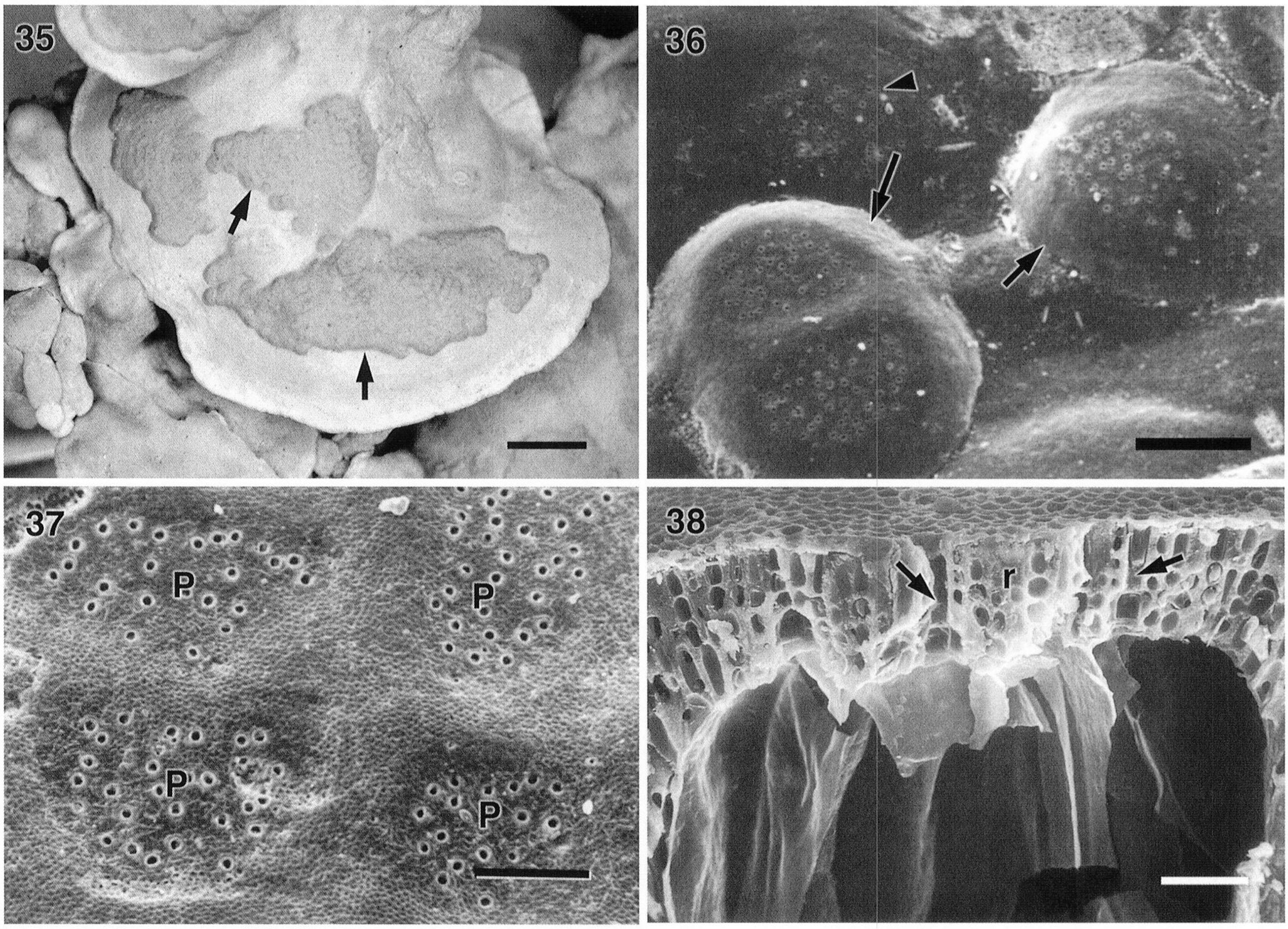

Figs 35–38. Discoid tetrasporophyte and SEMs of tetrasporangial conceptacles of *Synarthrophyton chejuensis* (SNU 99-EGJ201). Scale bars = 25 μm (Fig. 38), 100 μm (Fig. 37), 250 μm (Fig. 36) or 2 mm (Fig. 35).
Fig. 35. Confluent tetrasporangial conceptacles (arrows) on a discoid thallus.
Fig. 36. Conceptacles showing roofs flush with surrounding surface (arrowhead) and protruding from surface (arrows), SEM.
Fig. 37. Conceptacles showing pore plates (P) with pores (darker dots), SEM.
Fig. 38. Vertical fracture through pore plate showing pore canal (arrows) and roof cells (r), SEM.

ameter and 75–125 μm in height, with the roof four to five cells thick at the pore plate. Pore plugs are present and block the pores in mature conceptacles. In a vertical section, the filaments lining the pore canal do not differ from those that make up the rest of the pore plate (Figs 38, 42, 44). Tetra- and bisporangia measure 50–110 μm in height, and have been found in different plants (Figs 40, 41). Tetra- or bisporangial conceptacle initiation has not been seen. Old conceptacles may be shed on senescence; buried conceptacles have not been seen in the thallus.

Mesophyllum cystocarpideum (Foslie) Adey (1970, p. 23)

Figs 45–62

BASIONYM: *Lithothamnion cystocarpideum* Foslie (1906, p. 7).

HOLOTYPE: **Chatham Island.** Epiphytic on *Cheilosporum wardii* (Harvey) De Toni, *Maltby* 39, TRH! (Figs 45–48).

The following account is based only on a study of the type collection.

HABIT AND VEGETATIVE STRUCTURE: Plants are nongeniculate, thin, foliose, have more or less proliferously lobate or branched lamellae and are folded at the margin or surround the axes of the host (Figs 46, 47). The surface is mainly smooth but sometimes becomes warty (Fig. 46). The thallus is brownish pink and somewhat glossy with a surface covered by large sporangial conceptacles that have a prominent raised rim and a sunken pore plate (Fig. 46). Thalli are up to 10 mm long and 13 mm broad. The plants are attached primarily through envelopment of host axes, the epiphytic lamellae then commonly becoming fused with one another. Where the epiphyte more or less completely surrounds the host axis, envelopment and fusion are extensive, and the ventral surface of the thallus becomes largely or entirely obscured (Figs 47, 51). In more expanded, spreading plants, envelopment and fusion are localized, and both the dorsal and ventral surfaces of lamellae remain clearly visible (Fig. 48). Lobes and branches may develop by differential growth along the margin or superficially from either surface of the lamellae.

The thallus is monomerous (Figs 49, 52), measuring 210–270 μm in thickness. The medullary region is coaxial (Figs 50, 52, 53), and measures 190–260 μm in thickness, which

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Table 1. A comparison of recently documented *Synarthrophyton* species based on selected characters.

Character	*S. chejuensis* (this study)	*S. patena*[1]	*S. schielianum*[2]	*S. schmitzii*[3]	*S. eckloniae*[4]	*S. magellanicum*[4]	*S. robbenense*[5]	*S. munimentum*[5]
Morphology	leafy	encrusting to leafy	leafy, with struts	encrusting to leafy	encrusting, smooth	encrusting, smooth to layered, to leafy	encrusting, warty	encrusting, smooth to warty
Protuberances	absent	present or absent	present	present	absent	absent	narrow, fused into scroll patterns	rare, thin and narrow when present
Struts	absent	absent	present	absent	absent	absent	absent	absent
Substrata	sometimes epilithic, mainly epiphytic	sometimes epilithic, mainly epiphytic	rock, algae, mainly animal	epilithic, epizoic	epiphytic on stipes of *Ecklonia maxima* (Osbeck) Papenfuss	rock and shells	subtidal rock and shells	subtidal rock, shell and kelp holdfasts
Epithallial cells on ventral surface	present or absent	present	absent	no data	absent	present or absent	absent	absent
Tetra- and bisporangial conceptacle								
Form	flush with the surface or moundlike	moundlike, more or less convex	with a peripheral rim and central, depressed pore plate	no data	flush with the surface or sunken below it	moundlike with a flattened pore plate	with a peripheral rim and central, depressed pore plate	volcano-shaped with a peripheral rim and central, depressed pore plate
Cells of filaments in conceptacle rim	same as cells of other pore plate filaments	same as cells of other pore plate filaments	more elongate than cells of other pore plate filaments	no data	same as cells of other pore plate filaments	same as cells of other pore plate filaments	more elongate than cells of other pore plate filaments	more or less same as cells of other pore plate filaments
Cell shape in conceptacle roof filaments	rectangular to elongate	more or less isodiametric or broader than long	elongate in peripheral filaments; elongate or isodiametric in pore plate filaments	no data	elongate	elongate	rectangular to elongate	rectangular to elongate
External diameter	up to 780 μm	750–1300 μm	no data	no data	up to 600 μm	270–620 μm	185–300 μm	475–900 μm
Chamber diameter	210–340 μm	260–560 μm	460–600 μm	370–550 μm	*c.* 300 μm	200–325 μm	140–220 μm	350–450 μm
Thickness of conceptacle roof	25–40 μm	18–45(–68) μm	no data	no data	40–78 μm	20–50 μm	12–25 μm	41–55 μm
Number of cells in conceptacle roof filaments	4–5	3–8	no data	no data	5–7	4–6	2–3	5–7
Rosette cell position with respect to surrounding roof	flush	no data	no data	no data	flush	flush	tilted inward but not sunken	sunken

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Table 1. Continued.

Character	*S. chejuensis* (this study)	*S. patena*[1]	*S. schielianum*[2]	*S. schmitzii*[3]	*S. eckloniae*[4]	*S. magellanicum*[4]	*S. robbenense*[5]	*S. munimentum*[5]
Epithallial cells on pore plate filaments	present	present	absent	no data	present	present	present	present
Initials of conceptacle roof filaments	longer than broad	broader than long	longer than broad	no data	longer than broad	longer than broad	commonly somewhat enlarged	variable but not enlarged
Conceptacle fusion	prominent	rare	rare	no data	rare	absent	absent	absent
Gametangial thalli	monoecious or dioecious	dioecious	?dioecious	no data	monoecious	monoecious or dioecious	dioecious	monoecious
Shape of hypogynous cells of carpogonial filaments	squarish	more or less globular or ovoid; not markedly elongate	cylindrical and more or less elongate	no data	elongate	elongate	rectangular to elongate	squarish to twice as long as wide
Cell shape in roof filaments of male conceptacles	isodiametric to elongate	mostly more or less isodiametric	commonly narrow and elongate	no data	narrow and elongate	narrow and elongate	commonly narrow and elongate	commonly narrow and elongate
Shape of terminal cells of pore canal filaments of male conceptacles	cylindrical or attenuate	cylindrical or attenuate; not inflated and balloonlike	often inflated and more or less balloonlike	no data	cylindrical	cylindrical	elongate, not inflated	elongate, not inflated
Occurrence of inflated cells among spermatangial systems	absent	absent	present	no data	absent	absent	absent	absent

[1] May & Woelkerling (1988), Harvey *et al.* (1994).
[2] Woelkerling & Foster (1989).
[3] Mendoza *et al.* (1996).
[4] Keats & Chamberlain (1997).
[5] Keats & Maneveldt (1997).

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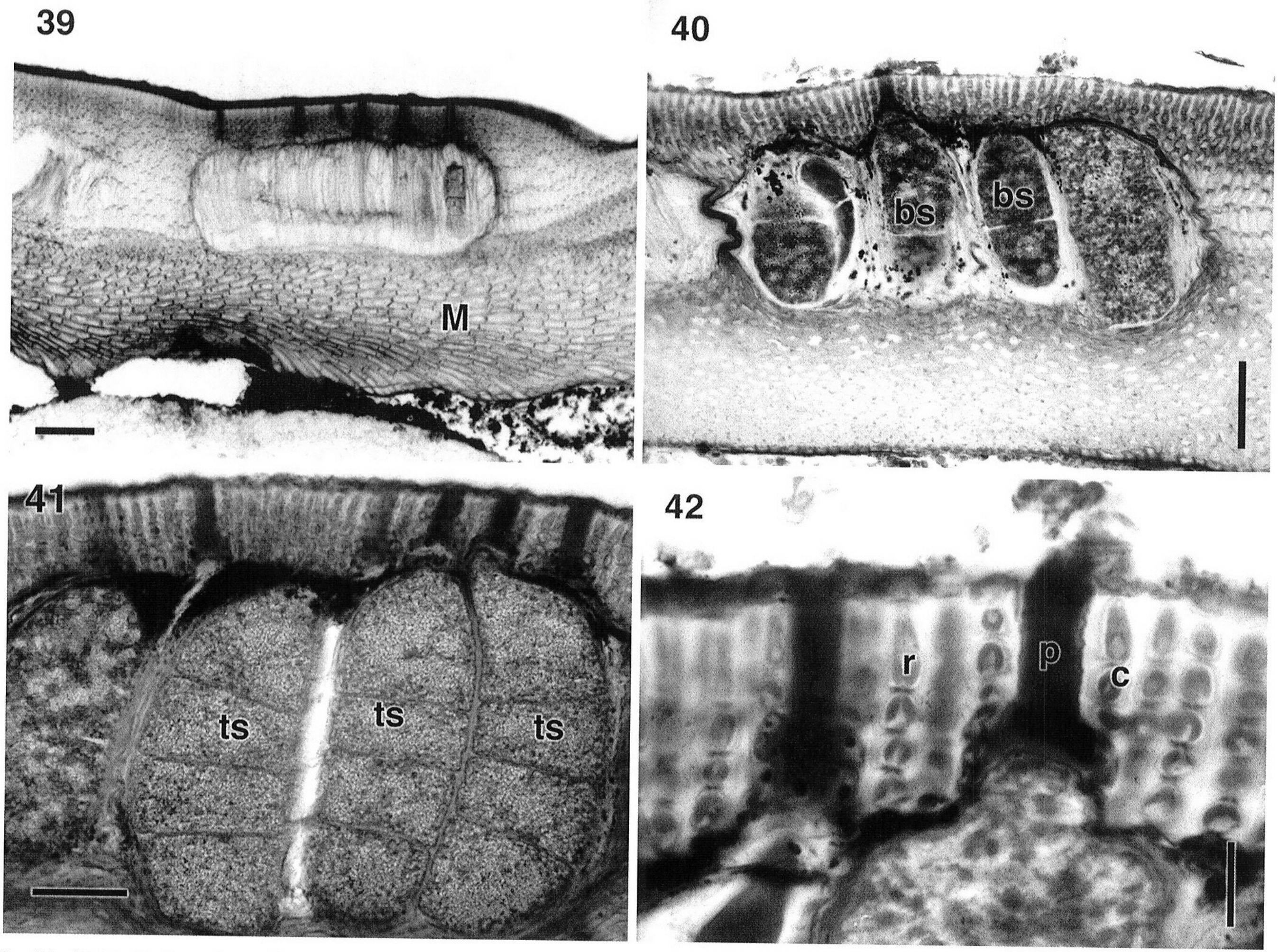

Figs 39–42. Vertical sections of tetrasporophyte and bisporophyte of *Synarthrophyton chejuensis*, LM. Scale bars = 10 μm (Fig. 42), 30 μm (Fig. 41) or 50 μm (Figs 39, 40).
Fig. 39. Tetrasporophyte with elliptical conceptacle and plumose medullary filaments (M) (SNU 98-CMP407).
Fig. 40. Bisporangial conceptacle with bisporangia (bs).
Fig. 41. Tetrasporangial conceptacle with tetrasporangia (ts).
Fig. 42. Detail of pore plate with pore plug (p), roof cells (r) and canal cells (c).

usually is more than 95% of the mature thallus thickness. The cells of medullary filaments are elongate (Figs 50, 53), 15–48 μm in length and 5–13 μm in diameter. Cell fusions commonly occur in both anticlinal and periclinal cell walls (Figs 49, 50), but secondary pit connections have not been seen. Medullary filaments terminate at the margin in primary meristematic cells. Ventrally situated medullary filaments are oriented towards the substratum at a shallow angle. They terminate in elongate cells or flattened epithallial cells (Fig. 55). The cortical region is up to four cells thick and usually occupies less than 5% of the thallus thickness (Fig. 50). Cells of cortical filaments are square to elongate and measure 10–15 μm in length and 5–10 μm in diameter. Cell fusions are common, mainly narrow and occupy less than 20% of adjoining walls. Trichocytes are fairly common on both surfaces (Fig. 56). Subepithallial initials are square to elongate, and may when actively dividing be similar to or longer than the subtending cells, but may be shorter following cell division (Fig. 50). They are 15–18 μm in length and 7–10 μm in diameter. Epithallial cells, 7–10 μm in length and 5–10 μm in diameter, occur singly except when actively shedding and have rounded and more or less flattened distal walls (Fig. 54).

REPRODUCTION: Tetrasporangial conceptacles are predominantly raised or flush with the surrounding surface with a prominent rim and a deeply depressed pore plate (Figs 57–59). They are distributed over the dorsal surface and ventral margin of the thallus surface (Figs 46, 48). Conceptacle chambers are elliptical to globular in shape and measure 200–510 μm in diameter and 150–290 μm in height (Figs 59, 60). Pore plates are approximately 100 μm in diameter, with up to 20 pores that are very close to each other (Fig. 58). Most pore plates are oblique to the thallus surface. Each pore is surrounded by a rosette of seven or eight cells that are smaller than the epithallial cells of the surrounding roof, and are sunken below the pore (Figs 60–62). The rosette cells are often obscured by pore plugs. Pores are blocked by pore plugs, as are mature conceptacles. The filaments lining the pore canal

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Table 2. Features collectively used separate *Synarthrophyton* from other genera of Corallinales (Townsend 1979; May & Woelkerling 1988; Woelkering 1988; Harvey *et al.* 1994; Keats & Chamberlain 1997; Keats & Maneveldt 1997).

1. Thallus nongeniculate
2. Thallus not arborescent in growth form
3. Internal construction monomerous
4. Haustoria absent
5. Cell fusion present
6. Secondary pit connections absent
7. Outermost walls of terminal epithallial cells rounded or flattened but not flared
8. Actively dividing vegetative initials as long as or longer than their immediate inward derivatives
9. Tetrasporangia bearing apical plugs and borne within multiporate conceptacles
10. Male conceptacle roofs formed centripetally from groups of peripheral filaments
11. Spermatangial initials overlain by a layer of protective cells
12. Dendroid, or both dendroid and simple spermatangial systems present
13. Gonimoblast filaments borne at the conceptacle periphery

are smaller and narrower than the cells that make up the rest of the pore plate (Figs 61, 62). The filament cells within the conceptacle rim are longer than the pore plate cells, but are similar in size and shape to the cells surrounding vegetative filaments (Fig. 61). Tetrasporangial conceptacle initiation and bisporangial conceptacles have not been seen. Old conceptacles may be shed on senescence; buried conceptacles have not been seen in the thallus.

REMARKS: The type specimen of *M. cystocarpideum* is not conspecific with *S. chejuensis*. *Mesophyllum cystocarpideum* can be distinguished by many characters: the base of strongly coaxial medullary region, sunken pore plates, sunken rosette cells surrounding the tetrasporangial pore, a roof of one to two cells in thickness, a more or less weakly developed cortex and the formation of tetrasporangial conceptacles at the margin of the thallus. According to the key developed by Printz (1929, p. 54), *M. cystocarpideum* (as *L. cystocarpideum*) is characterized by convex or hemispherical tetrasporangial conceptacles with a deep central depression. Masaki (1968) reported that the tetrasporangial conceptacles distinguish this alga from *L. conchatum* Setchell & Foslie [as *Polyporolithon conchatum* (Setchell & Foslie) L.R. Mason] and from *S. patena* [as *P. patena* (Hooker F. & Harvey) L.R. Mason]. However, it appears that Masaki rarely observed the tetrasporangial conceptacles with sunken pore plates. Most photographs and illustrations in Masaki (1968) correspond to *S. chejuensis*. The following characteristics are shared by Korean plants and Japanese plants described in Masaki (1968): the medullary region is plumose (Figs 9, 12; Masaki 1968, pl. 6, figs 3–9, pl. 43, figs 1, 3, pl. 44, fig. 4), the epithallium is composed of one layer of cells, which are subrectangular; gametangial plants are monoecious (Fig. 33; Masaki 1968, pl. 6, fig. 9); the carposporangial conceptacle is conical and carpospores arise from the whole surface of conceptacle floor, and the fusion-cell is discontinuous in section (Figs 29, 31, 32; Masaki 1968, pl. 6, fig. 8, pl. 43, fig. 2, pl. 44, figs 1, 2); the spermatangial conceptacles are subconical, produced on dendroid systems of filaments (Figs 20, 25; Masaki 1968, pl. 6, fig. 2, pl. 44, figs 3, 4); tetra- and bisporangial conceptacles do not have a sunken pore plate, but are slightly domed or flush with the surrounding surface (Figs 36, 37; Masaki 1968, pl. 6, figs 1, 2, pl. 43, fig. 1) and gathered in groups in nemathecial elevations of the thallus surface; in sectional view, two or three conceptacles are sometimes confluent (Figs 35, 43; Masaki 1968, pl. 6, fig. 1). Since the report by Masaki (1968), this species has been described as *Lithothamnium cystocarpideum* in Korea and Japan (Park 1977; Lee & Kang 1986 as *Lithothamnion cystocarpioideum;* Yoshida 1998).

Adey (1970, p. 23) moved *L. cystocarpideum* Foslie to the genus *Mesophyllum* based on its coaxial medullary filaments. However, the presence or absence of a coaxial core of filaments no longer constitutes a reliable basis on which to distinguish genera within the Melobesioideae (Woelkerling & Harvey 1993). Plants of *Synarthrophyton,* although predominantly noncoaxial, may produce localized coaxial areas (May & Woelkerling 1988). Conversely, plants of *Mesophyllum* can produce large areas of noncoaxial filaments (Woelkerling & Harvey 1993).

Lebednik (1978) and Woelkerling & Harvey (1992, 1993) provided further information about using spermatangial characters to distinguish genera within the Melobesioideae. Townsend (1979, fig. 8) reported that male conceptacles of *Synarthrophyton* have dendroid spermatangial branches on the conceptacle floor and simple or dendroid spermatangial branches on the conceptacle roof. The only character distinguishing *Mesophyllum* from *Synarthrophyton* is the absence of dendroid spermatangial systems in *Mesophyllum* (Woelkerling & Harvey 1993). The extent to which characters associated with male conceptacles can be successfully used to help distinguish genera within the Melobesioideae requires further study. Data are lacking for the type species of some genera and uncertainty surrounds the published data that describe the type species of others (Woelkerling & Harvey 1992, 1993). However, the available data relating to characters associated with male conceptacles are increasing. These characters can play an important role in the distinction of some genera within the subfamily (Chamberlain 1992; Woelkerling & Harvey 1992; Chamberlain & Irvine 1994). Unfortunately, spermatangial conceptacles are not found in the type specimen of *M. cystocarpideum.* The absence of a spermatangial system in the type specimen means that further studies of field material from the type locality are needed in order to make clear the taxonomic position of the species. This species has not been recorded in Korea.

DISCUSSION

The genus *Synarthrophyton* was proposed by Townsend (1979) and has been reassessed several times (May & Woelkerling 1988; Woelkerling 1988; Harvey *et al.* 1994; Keats & Chamberlain 1997; Keats & Maneveldt 1997). Currently, *Synarthrophyton* can be distinguished from other genera of the Corallinaceae on the basis of a combination of 13 characters (Table 2). *Synarthrophyton chejuensis* conforms to *Synarthrophyton* on the basis that it has all of the generic characters. Keats & Maneveldt (1997) tabulated the differences between six species of *Synarthrophyton.* In the present study, their table has been adapted and we have added data on *S. schmitzii* (Hariot) Mendoza, Molina & Ventura (Mendoza *et al.* 1996)

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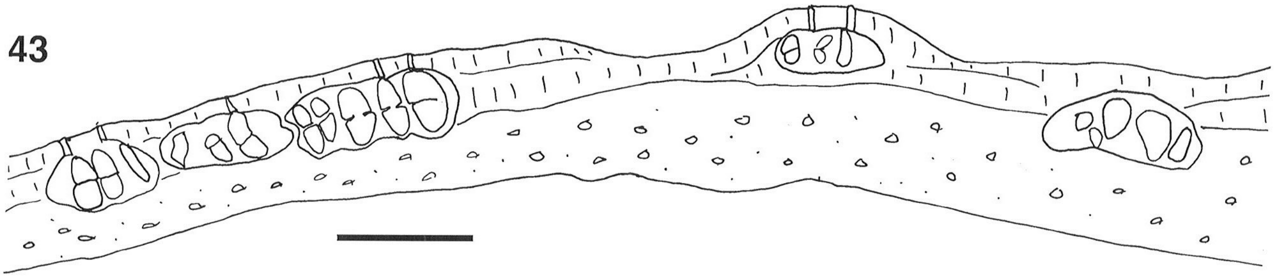

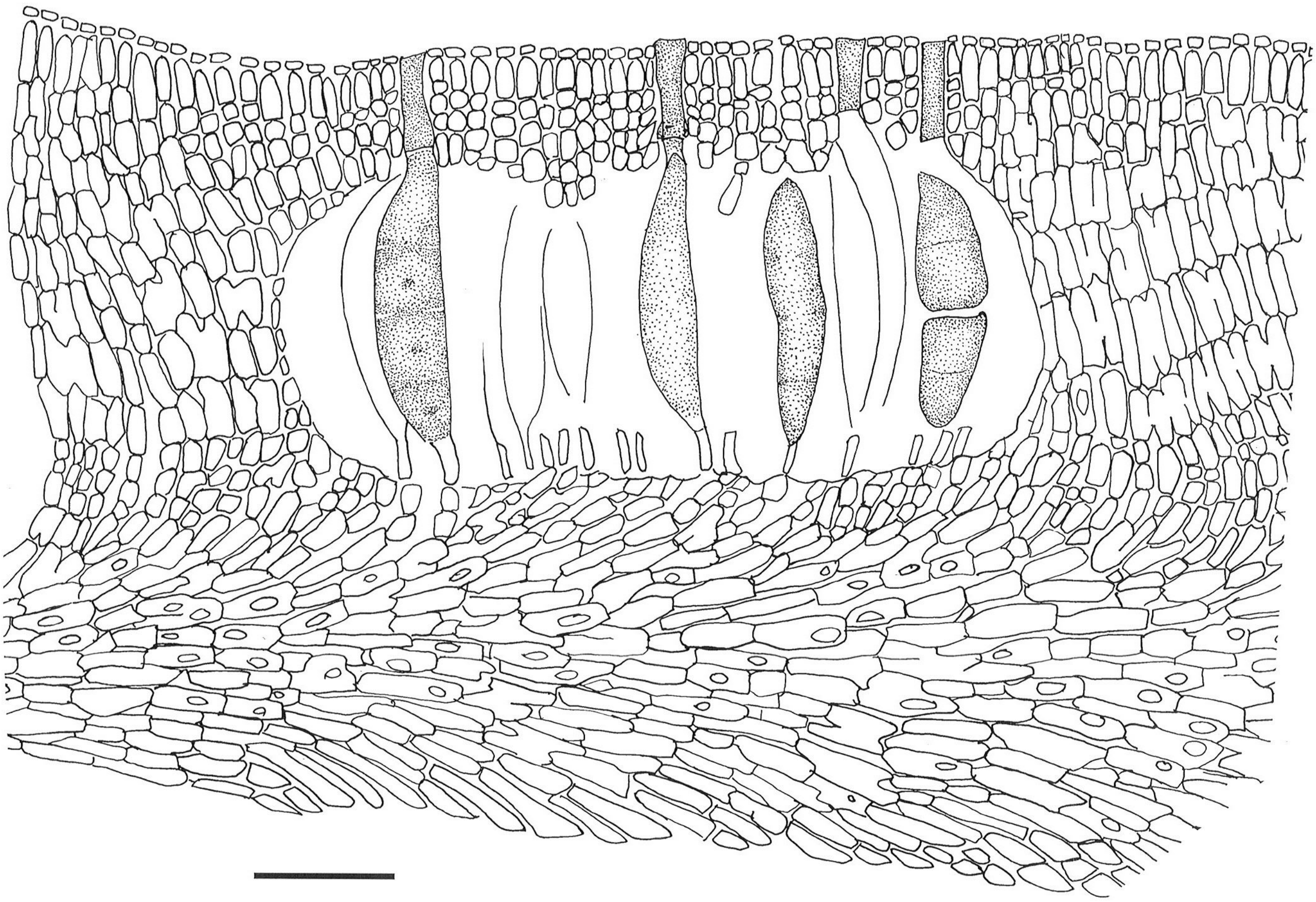

Figs 43, 44. Drawings of bisporangial and tetrasporangial conceptacles of *Synarthrophyton chejuensis*. Scale bars = 50 μm (Fig. 44) or 200 μm (Fig. 43).

Fig. 43. Diagram of bisporangial thallus (SNU 99-CSS001).

Fig. 44. Mature tetrasporangial conceptacle showing tetrasporangia, roof structure and pore plate (SNU 98-CMP407).

to show the differences between seven species and the new species in this genus (Table 1). We regard this new species to be characterized by the following features: (1) struts absent; (2) tetra- and bisporangial conceptacles moundlike or flush with the surrounding surface; (3) tetra- and bisporangial conceptacle roofs four to five cells thick; (4) tetra- and bisporangial conceptacle fusion prominent; (5) cells bordering the tetra- and bisporangial conceptacle pore canal similar in size and shape to the other roof cells within the pore plate; (6) cell shape in roof filaments of male conceptacles isodiametric to elongate; and (7) inflated cells among spermatangial systems absent.

The spermatangial systems on the floor of *S. chejuensis* are bushy and somewhat dendroid (Figs 25, 28), differing from the simple systems seen in the *Mesophyllum* type species, *M. lichenoides* (Ellis) Lemoine (Woelkerling & Irvine 1986, fig. 27). However, they also differ from the strongly dendroid systems seen in *S. patena* (May & Woelkerling 1988, figs 35–38), the type species of *Synarthrophyton*. *Synarthrophyton* has an interspecific gradation of branch complexity in the sper-

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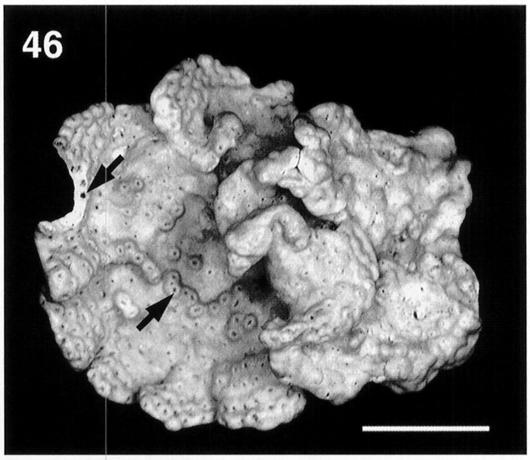
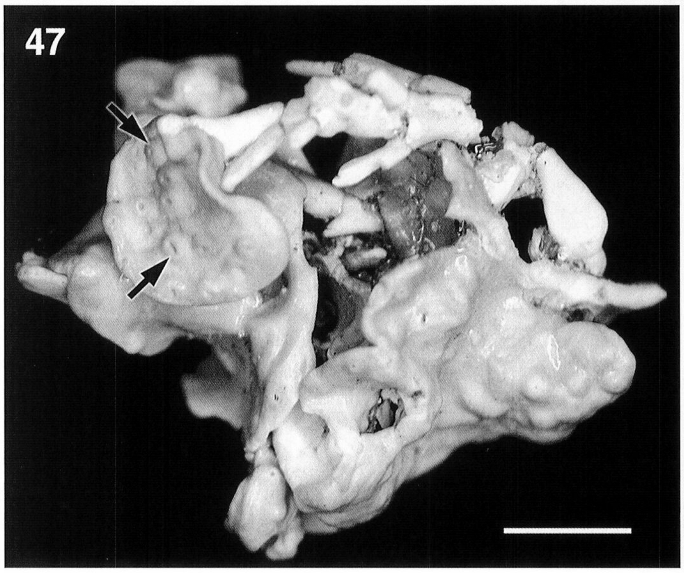
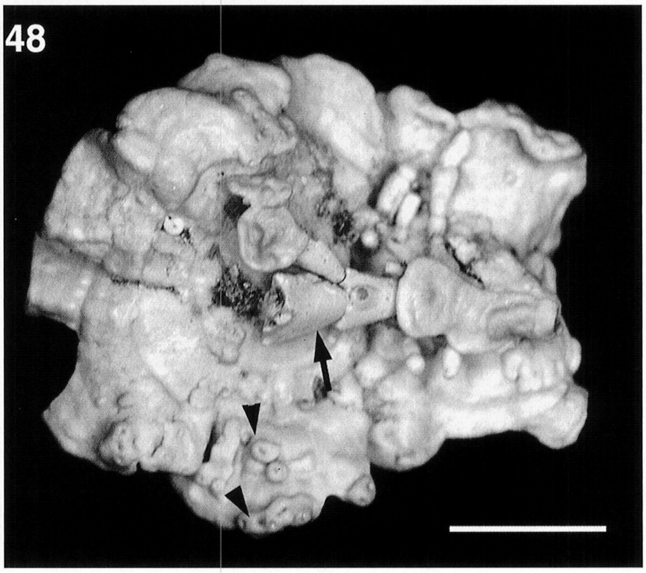






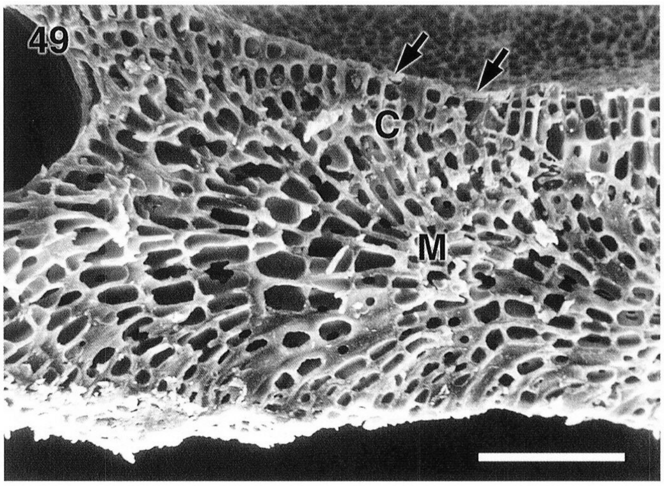
Figs 45–48. Holotype of *Mesphyllum cystocarpideum* (as *Lithothamnion cystocarpideum*) (TRH). Scale bars = 2 mm (Fig. 47), 3 mm (Fig. 45) or 4 mm (Figs 46, 48).

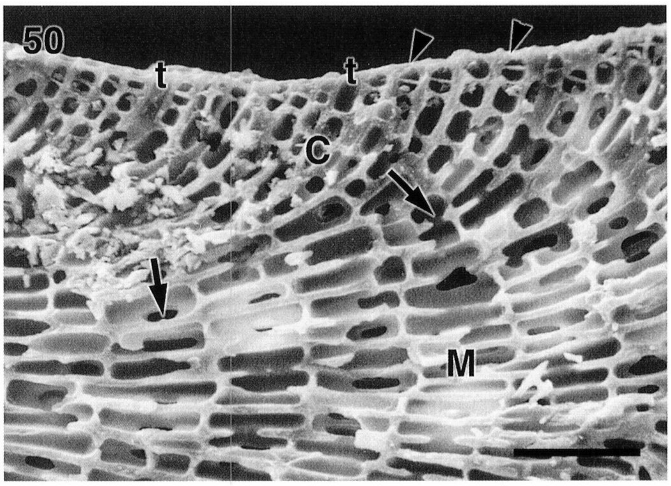
Fig. 45. The specimens and labels that constitute the holotype.

Fig. 46. Dorsal surface of larger specimen with tetrasporangial conceptacles (arrows).

Fig. 47. Smaller specimen showing small thalli on geniculate coralline alga with tetrasporangial conceptacles (arrows).

Fig. 48. Ventral surface of larger specimen completely enveloping genicula of *Cheilosporum wardii* (arrows) with tetrasporangial conceptacles (arrowheads).





Figs 49, 50. Vegetative anatomy of *Mesophyllum cystocarpideum* (TRH), SEM. Scale bars = 50 μm (Fig. 50) or 100 μm (Fig. 49).

Fig. 49. Vertical fracture of monomerous thallus showing medullary filaments (M), cortical filaments (C) and epithallial cells (arrows).

Fig. 50. Vertical fracture of thallus showing distinct coaxial medullary filaments (M) with cell fusions (arrows), thin cortical layer (C), trichocytes (t) and epithallial cells (arrowheads).

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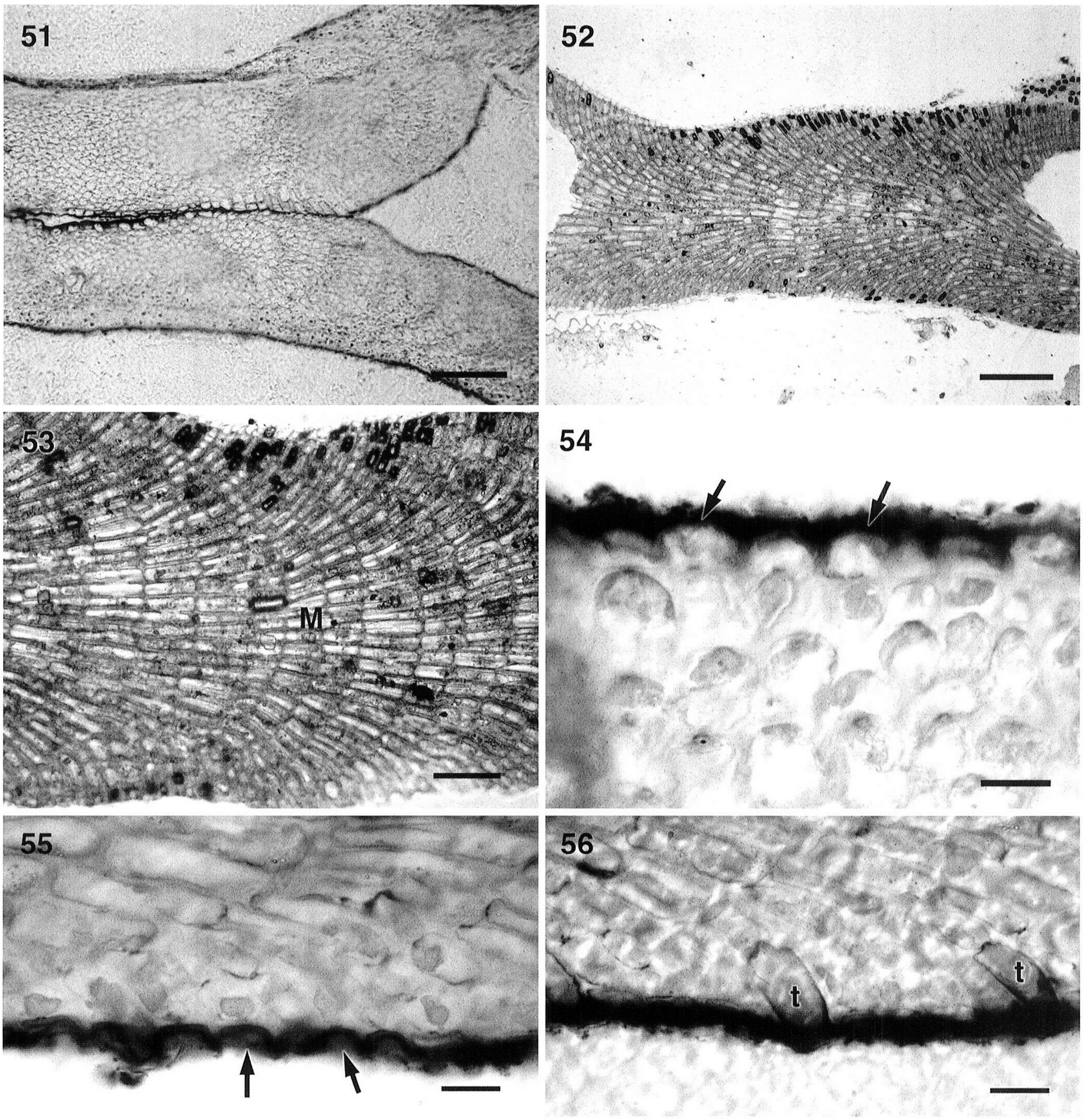

Figs 51–56. Vertical sections of holotype of *Mesophyllum cystocarpideum* (TRH), LM. Scale bars = 10 μm (Figs 54–56), 50 μm (Fig. 53) or 100 μm (Figs 51, 52).

Fig. 51. Fusion of ventral surface of thallus enveloping holdfast.

Fig. 52. Thallus (slide no. 1191).

Fig. 53. Thallus (slide no. 1191) showing coaxial medullary filaments (M).

Fig. 54. Partial section showing epithallial cells with rounded and more or less flattened distal walls (arrows).

Fig. 55. Partial section showing ventral epithallial cells (arrows).

Fig. 56. Ventral surface showing trichocytes (t).

matangial systems. The spermatangial systems of *S. chejuensis* are less branched than those of *S. patena,* and hold an intermediate position among the eight species in this genus. The degree of elaboration in the spermatangial systems in *S. chejuensis* is similar to *S. robbenense* Keats & Maneveldt, *S. munimentum* Keats & Maneveldt and *S. magellanicum* (Foslie) Keats & Chamberlain, as shown in the diagram drawn by Keats & Maneveldt (1997, fig. 54). Intraspecific variation of branch complexity in spermatangial systems may appear in populations of *S. patena.* The type specimen of *S. patena* has

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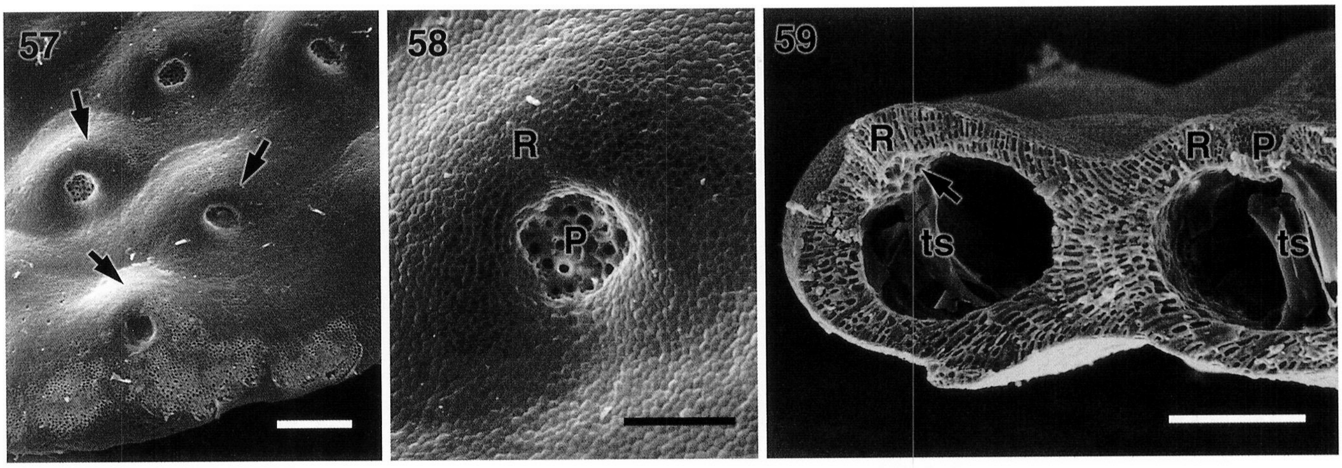


Figs 57–59. Tetrasporophyte of *Mesophyllum cystocarpideum* (TRH), SEM. Scale bars = 100 μm (Fig. 58), 200 μm (Fig. 59) or 250 μm (Fig. 57).

Fig. 57. Surface aspect of tetrasporangial conceptacles (arrows).

Fig. 58. Detail of sporangial conceptacle showing raised rim (R) and sunken pore plates (P).

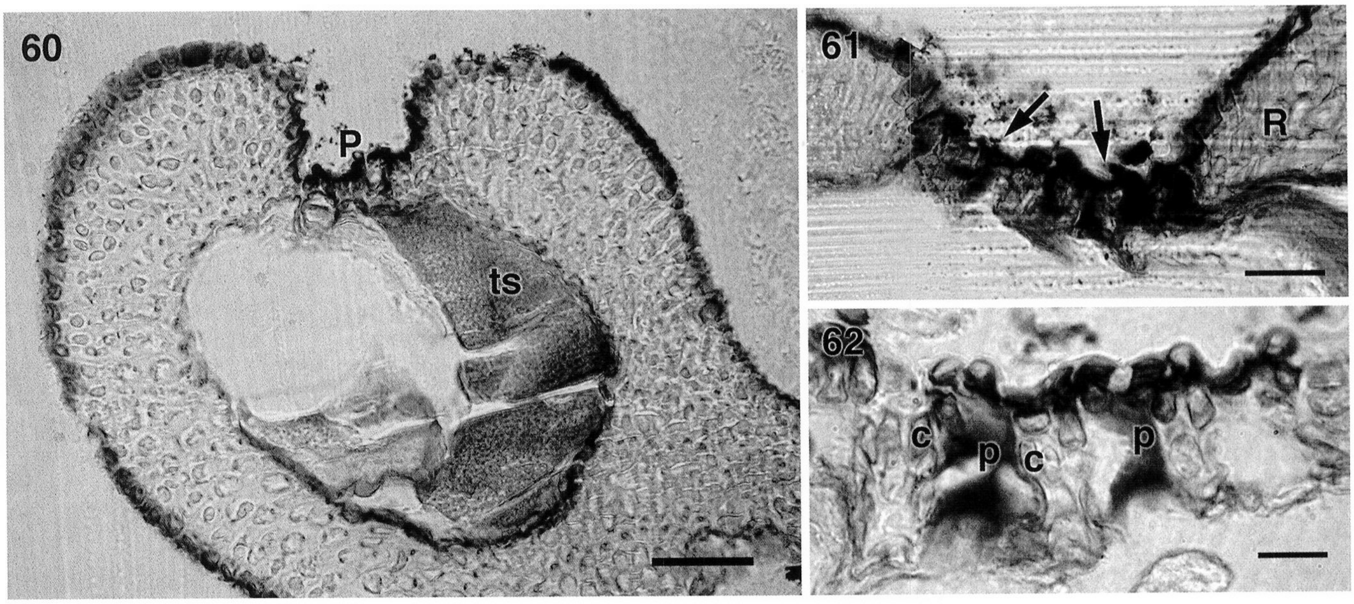
Fig. 59. Vertical fracture through sporangial conceptacle at thallus margin, showing rim (R), sunken pore plate (P), pore (arrow) and remains of tetrasporangium (ts).

strongly dendroid systems (May & Woelkerling 1988, figs 35, 36), whereas Australian plants have been shown to be more weakly branched (Harvey *et al.* 1994, fig. 24).

Since its description by Townsend (1979), *Synarthrophyton* had been thought to be restricted to the southern hemisphere with seven known species (May & Woelkerling 1988; Woelkerling & Foster 1989; Mendoza *et al.* 1996; Keats & Chamberlain 1997; Keats & Maneveldt 1997). Of these, *S. robbenense, S. munimentum, S. eckloniae* (Foslie) Keats & Chamberlain, *S. patena* and *S. magellanicum* occur in southern Africa and Australia. The remaining species, *S. schielianum* Woelkerling & Foster, is restricted to the Chatham Islands, New Zealand, and *S. schmitzii* occurs in Argentina and Antarctica. However, *S. chejuensis,* the eighth species has been recorded in Korea as *S. cystocarpideum* (Lee & Kang 2001, as *S. cystocarpedium*) and in Japan as *L. cystocarpideum* (Masaki 1968 as *Lithothamnium cystocarpideum*; Yoshida 1998). *Synarthrophyton chejuensis* is very common in Korea. Therefore, the genus *Synarthrophyton* inhabits the northern hemisphere in addition to the southern hemisphere.

ACKNOWLEDGEMENTS

We are most grateful to Sigurd M. Såstad (TRH) for locating and lending us the types of *Lithothamnion cystocarpideum.*



Figs 60–62. Vertical sections of tetrasporangial conceptacle (TRH), LM. Scale bars = 10 μm (Fig. 62), 30 μm (Fig. 61) or 50 μm (Fig. 60).

Fig. 60. Tetrasporangial conceptacle at margin, showing sunken pore plate (P) and tetrasporangium (ts).

Fig. 61. Details of conceptacle pore plate (arrows) and raised rim (R).

Fig. 62. Detail of conceptacle pore plate, showing pore canal with pore plug (p) and pore canal cells (c).

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