

New Red Algae of *Martensia* (Delesseriaceae), *M. palmata* sp. nov. and *M. projecta* sp. nov. from Jeju Island, Korea

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Two new species of *Martensia* (Delesseriaceae, Rhodophyta) are described from Jeju Island, Korea. *Martensia palmata* sp. nov. is characterized by the following traits: more or less linearly elongated lobes arising from the distal margin of the flabellate membranous section; intact latticework with coarse and loose mesh; numerous spine-like projections on the leading margin of the latticework; tetrasporangia produced in sori along the entire blade; spermatangia borne in sori on the membranous section and the longitudinal lamellae of the latticework; and cystocarps borne on the margins of the membranous section. *Martensia projecta* sp. nov. has the following characteristics: subdichotomously furcated blades, with terminal segments slightly attenuated toward the apex; blades with uneven surfaces; basal parts with a multi-layered parenchymatous construction; small and poorly-defined latticework; tetrasporangia and spermatangia produced in sori on the membranous section; and cystocarps borne on the marginal surfaces of the blades. The existence of *M. projecta* sp. nov. supports the proposal that the genus *Opephyllum* Schmitz in Schmitz et Hauptfleisch should be assigned to the genus *Martensia*.

Key Words: Delesseriaceae, *Martensia*, *Martensia palmata*, *Martensia projecta*, *Opephyllum*, red algae

INTRODUCTION

The genus *Martensia* Hering (1841) is defined as: having thalli that are composed of membranous section and have a latticework organization; lacking macroscopic and microscopic nerves or veins; and having reproductive structures that are formed on the latticework (Harvey 1847-1849; J. Agardh 1863; De Toni 1900; Kylin 1956; Millar 1990; Wynne 1996). Svedelius (1908) investigated the comparative morphology of thallus and the process of latticework formation in *Martensia*, as well as the reproductive structures in this genus. Subsequently, the organization of the latticework was considered one of the diagnostic characters of the genus. Recently, *Opephyllum martensii* Schmitz in Schmitz et Hauptfleisch (1897), a monotypic species of the genus *Opephyllum* that lacks the latticework organization, was assigned to the genus *Martensia* as *M. martensii* (Lin et al. 2001). Consequently, the latticework organization may no longer be a diagnostic characteristic of this genus. Moreover, it is not reasonable to assume that the latticework is the only region in which reproductive

structures are formed (Millar 1990; Lin et al. 2001; Lin et al. 2004; Lee 2004). *Martensia flabelliformis* Harvey ex J. Agardh (1863) was removed from the genus *Martensia* and was recombined to the genus *Neomartensia* as *N. flabelliformis* because the vegetative cells are not regularly stacked in anticlinal lines and the carposporangia are formed in short chains (Yoshida and Mikami 1996). However, in some species of *Martensia*, the vegetative cells are somewhat variably arranged (Lee 2004). Two of the previously described species of *Martensia*, *M. beccariana* Zanardini and *M. gigas* Harvey, have been excluded from this genus (De Toni 1900). Also, two species, *M. denticulata* Harvey and *M. pavonia* J. Agardh, and a species, *M. speciosa* Zanardini, have been synonymous with *M. fragilis* Harvey and *M. australis* Harvey, respectively (Millar 1990). Consequently, eight species of *Martensia* are currently recognized: *M. australis* Harvey (1855), *M. bibarii* Y. Lee (2004), *M. elegans* Hering (1841), *M. formosana* Lin, Hommersand et Fredericq (2004), *M. fragilis* Harvey (1854), *M. indica* Krishnamurthy et Thomas (1977), *M. jejuensis* Y. Lee (2004), and *M. lewisiae* Lin, Hommersand et Fredericq (2004).

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MATERIAL AND METHODS

Plants were collected from the subtidal region off Jeju Island, Korea, by SCUBA diving. Collected specimens were kept in seawater during transport to the laboratory because they tend to die quickly and discolor when exposed to air. Samples were immediately fixed in 5% formalin/seawater for 3-5 days. Most of the fixed samples were used to make dried herbarium specimens. Thalli were sectioned using a bench-top freezing microtome (MFS no.222; Nippon Optical Works, Tolyo, Japan). The sections and pieces of specimens were mounted on microscopic glass slides in 50% corn syrup solution. Olympus microscopes (BX50F(3, BX50F4; Olympus Optical Co., LTD, Japan) with photographic apparatus (Olympus PM(C35DX, PM(P20, PM(20; Olympus Optical Co., LTD, Japan) were used to observe the thalli. The length and width of vegetative cells were measured on the surface view. The thickness of the vegetative cells was measured on transverse or longitudinal sections. Images of wet-preserved or pressed specimens were captured using a camera (Nikon F2; Nikon, Tokyo, Japan) mounted on a photo-stand. All examined specimens were deposited in the Herbarium of the Department of Life Science, Cheju National University, Korea (CNU).

OBSERVATIONS

Martensia palmata Lee sp. nov.

Diagnosis: Thalli membranacei, flabellate, unis versus aliquot laminis constati, erythrini purpurascetes, 5-7 cm alti. Laminae palmatae, partibus membranaceis proxime et reticules remote constatae, rhizoideis affixae. Partes membranaceae flabellatae, in margine distali aliquot lobis, in marginibus lateralibus projecturis spiniformibus, 2-4-stratae. Lobi ad 5 cm longitudine prolati, lineares vel versus apicem leviter angustati, reticulum in margine distali ferentes. Cellulae parti membranaceae aspectu paginali 5-8-angulae angulis obtusis, 25-70 μm longae, 20-45 μm latae, 10-35 μm crassae. Reticulum in distali margine loborum factum, flabelliforme, maculis grossis, raro latitudinem marginis apicalis loborum excedens, margine principiti angusto projecturans spiniformes ferenti, plerumque formam intactam ipsius retinens. Gametophyta et tetrasporophyta isomorphus. Gametophyta dioecia et isomorphus. Cystocarpia ad marginibus parties membranaceae plerumque et reticulo rare facta, globosa, 1-1.3

mm diametro, ostiolo ad apice. Carposporae pyriformes, 100-130 μm longae, 45-55 μm diametro. Sori spermatangiorum in parte membranacea et lamellis longitudinalibus facti, diverse discoidei, dilute colorati. Spermatangia ovoidea, 2-3 μm diametro. Tetrasporangia in parte membranacea et lamellis longitudinalibus reticuli nata, globosa vel subglobosa, divisio tetraedrice, 80-100 μm diametro.

The thalli of this species are membranous, flabellate, composed of one or several blades, purplish red, and ca. 5-7 cm high. The blades are palmate, composed proximally of membranous sections and distally of latticework, and are attached by rhizoids. The membranous sections are flabellate, with several lobes on the distal margin and spine-like projections on the lateral margins, and comprise two to four cell layers. The lobes are elongate, up to 5 cm in length, linear or slightly narrowed to the tip, finger-like, and support a latticework on the distal margin. Cells of the membranous section are pentagonal to octagonal with obtuse corners in the surface view, 25-70 μm long, 20-45 μm wide, and 10-35 μm thick. A latticework is formed on the distal margins of the lobes, flabellate, coarse-meshed, rarely exceeding the width of the apical margins of the lobes, and with narrow leading margins bearing spine-like projections; this latticework generally retains its intact form. The gametophytes and tetrasporophytes are isomorphic. The gametophytes are dioecious and isomorphic. Cystocarps are usually formed on the edges of the membranous section and are sparse on the latticework; they are globose, 1-1.3 mm in diameter, and have an ostiole on the top. Carpospores are pyriform, 100-130 μm long, and 45-55 μm in diameter. Spermatangial sori are formed on the membranous section and the longitudinal lamellae of the latticework and are variously discoid in shape and faintly colored. Spermatangia are ovoid and 2-3 μm in diameter. Tetrasporangia are borne on the membranous section and the longitudinal lamellae of the latticework; they are globose or subglobose, 80-100 μm in diameter, and tetrahedrally divided.

Korean name: Jomagsonbidanmangsa

Holotype: The Herbarium of Cheju National University (CNU Herbarium Y. Lee, LYP-1670 Moonseom, Jeju Island 2001-06-21. ♀).

Type locality: The subtidal region (4-6 m deep) off the northern slope of Moonseom, Jeju Island, Korea.

Vegetative morphology: Thalli are epilithic or

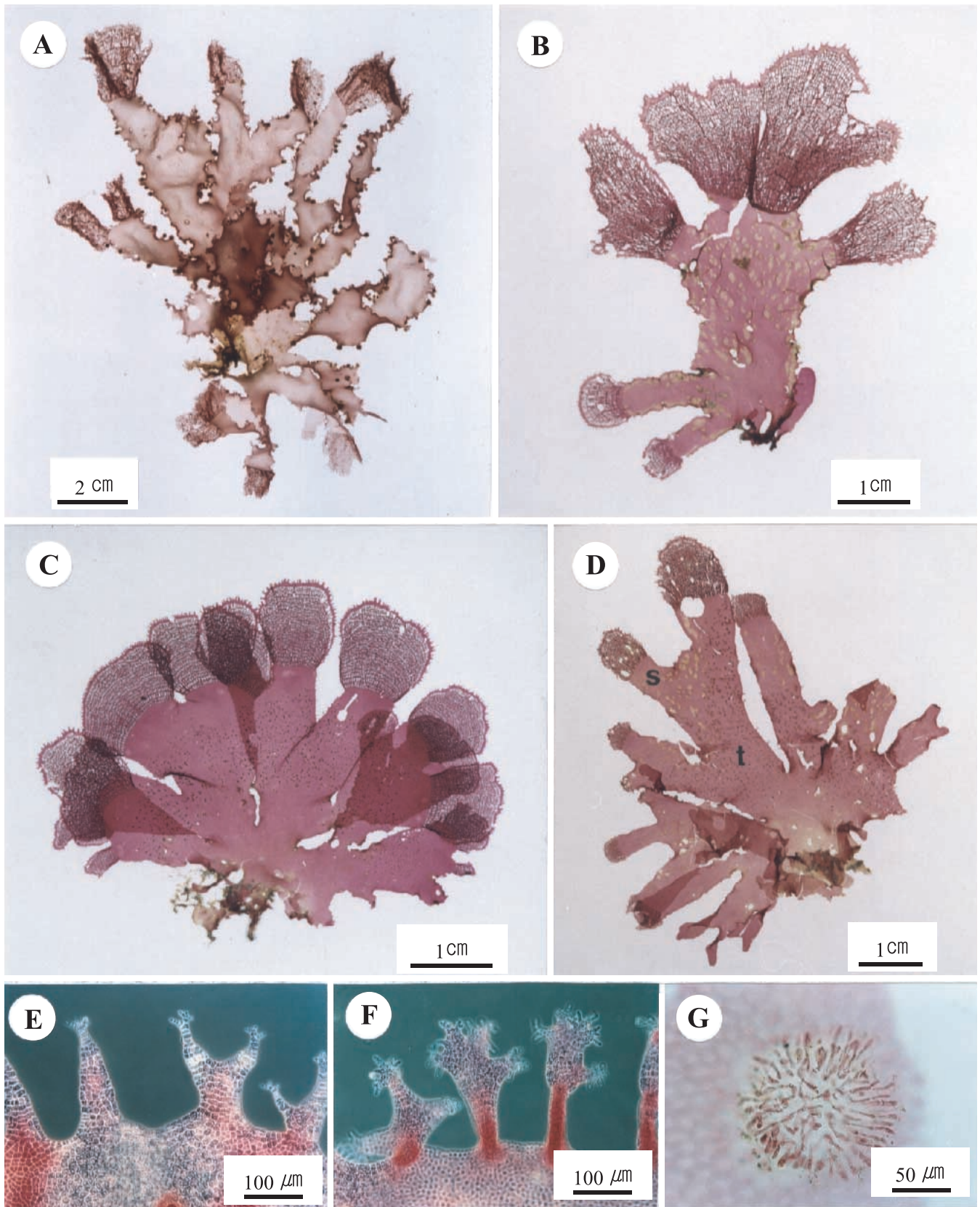


Fig. 1. *Martensia palmata* sp. nov. A. Holotype in liquid preserved condition (LYP-1670). B. Male thallus (LYP-1671). Note the small faintly colored spots (spermatangial sori) on membranous section. C. Tetrasporangial thallus (LYP-1671). Note the black spots (tetrasporangial sori) on membranous section. D. Mixed phase with spermatangial sori (s) and tetrasporangial sori (t) LYP-1673). E. F. Projections on the leading margin. G. Hapteron on the blade.

epiphytic on other algae, bright red, and composed of one to several blades that are ca. 5-7 cm tall. The thallus is composed of membranous sections and latticework on the distal margins of the lobes of the membranous section, attached by rhizoids arising from the lowermost portion (Fig. 1A-D). Occasionally, several discoid haters are formed in the lower regions of the membranous section and become attached to the overlapping blades (Fig. 1G). Typically, the membranous sections are initially flabellate with marginally diffused growth, later giving rise to lobes from the distal margins, resulting in a palmate outline with short spine-like projections at the lateral margins; these sections comprise two to four cell layers and are 50-120 μm thick. The membranous section becomes gradually thicker and more layered proximally. The margins of the female thalli are more undulate and give rise to many projections, while those of male and tetrasporangial thalli are only slightly undulate and give rise to fewer projections. The membranous section of the tetrasporangial thalli comprises either one or two layers and is 40-50 μm thick (Fig. 2H). Cortical cells of the membranous section are five- to eight-angled with obtuse corners in the surface view, and oblong to ellipsoid in transverse sections, 25-70 μm long, 20-45 μm wide, and 10-35 μm thick (Fig. 2C, F-H). In general, the vegetative cells are regularly stacked in anticlinal lines (Fig. 2G). Chloroplasts are very small, discoid, ca. 1.5 μm in diameter, and congregate along the inside of the exterior wall of the cortical cells. The lobes on the distal margins of the membranous section are elongated, more or less attenuated or rarely somewhat expanded toward the apex, and show fingerlike projections up to 5 cm long. Occasionally, some lobes are subdichotomously branched. The lobes form the latticework on the distal margin early in their development and elongate continuously after the completion of the latticework. The growth of these lobes may be more active than that of the latticework.

The cells of the distal margin of the blade elongate and undergo transverse divisions several times to produce a series of short columns with hemispherical terminal cells and several discoid intercalary cells. The apical cells of the columns develop into a leading margin through various divisions and connect to those of the neighboring columns (Fig. 2A, B). The latticework, which retains its form, comprises somewhat coarse mesh with a narrow leading margin. Spine-like projections, which are conical to spatulate, and are about 150-250 μm long, arise from the leading margin of the latticework (Fig. 1E, F).

Occasionally, these projections grow up to 2-3 mm long and are furcated two or three times. All projections give rise to additional short spine-like projections radially on the apex (Fig. 1E, F). However, these projections do not develop into small bladelets, as do those of *M. fragilis* and *M. jejuensis* (Millar 1990, fig. 53F; Lee 2004, figs 2, 6). The longitudinal lamellae of the latticework are derived from the intercalary cells of the column and are belt-shaped due to a combination of transverse, periclinal, and anticlinal divisions of the intercalary cells. The faces of the longitudinal lamellae are perpendicular to the surface of the blade and have two cell layers, and they are about 400 μm wide (Fig. 2D). Cross-connecting strands are formed as spine-like projections at right angles on both marginal surfaces of the longitudinal lamella, varying in form from linear to membranous; they are elongated and adhere to the marginal region of neighboring longitudinal lamellae. Additional projections arise at right angles from the center regions of cross-connecting strands (Fig. 2E). The cross-connecting strands of the latticework tend to be formed in double lines at intervals along the longitudinal lamellae. Such double lines appear as dark-colored, bold lines within the latticework (Fig. 2I).

Reproductive morphology: The tetrasporophyte is isomorphic with the gametophyte (Fig. 1A-D). Male and female gametangial thalli are also morphologically similar (Fig. 1A, B). The margins of the membranous section of the female thalli are somewhat undulate and have more projections than those of male or tetrasporangial thalli. Cystocarps are formed along the margins of the membranous section and even on the edges of the openings when the membranous section is perforated. They are globose with a non-protruding ostiole, have a thick pericarp (ca. 200 μm), and are 1-1.3 mm in diameter (Figs. 1A, 3D). On the other hand, cystocarps are rarely found on the latticework. The carposporophytes are filamentous and branch trichotomously; they are subspherical and are composed of pellucid and fusiform cells, bearing two carpospores in chains on every branch tip (Fig. 3F, H). The intercalary carpospores appear to mature and become pyriform after the terminal ones are shed (Fig. 3F). The carpospores are pyriform, dark red, 100-130 μm long, and 45-55 μm in diameter (Fig. 3E). Spermatangia are borne in sori resembling small, ellipsoid, faintly colored spots on the surface of the membranous section and the longitudinal lamellae of the latticework (Fig. 3A-C). The part of the membranous section producing spermatangia has three

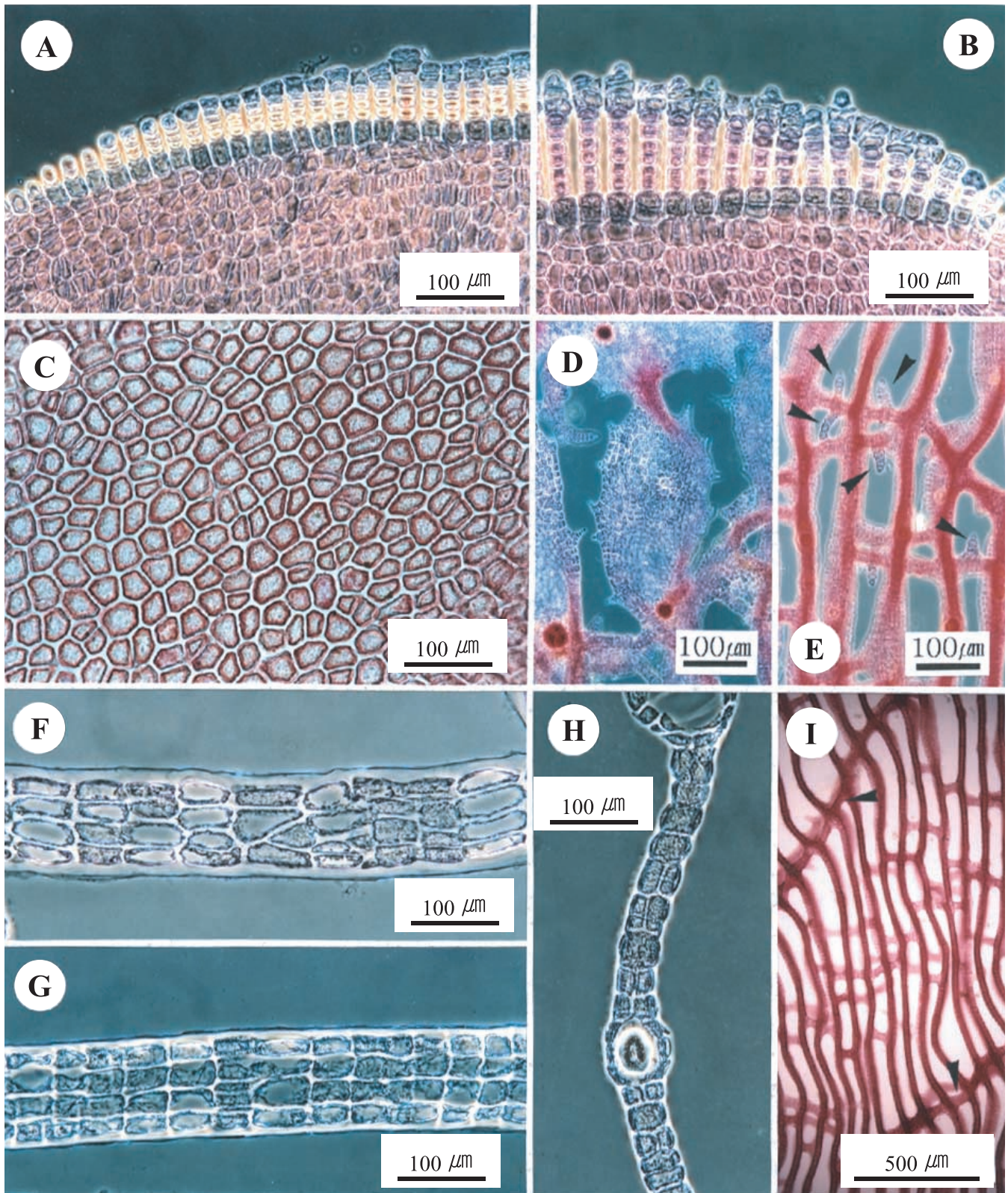


Fig. 2. *Martensia palmata* sp. nov. A. B. Early stages of laticework development. C. Cortical cells of membranous section in surface view. D. Longitudinal lamella of laticework with many projections on the margins. E. Adventitious projections (arrow heads) from the cross-connecting strands of laticework. F. G. H. Transverse sections of membranous section. I. Part of laticework with double lines of cross-connecting strands (arrow heads).

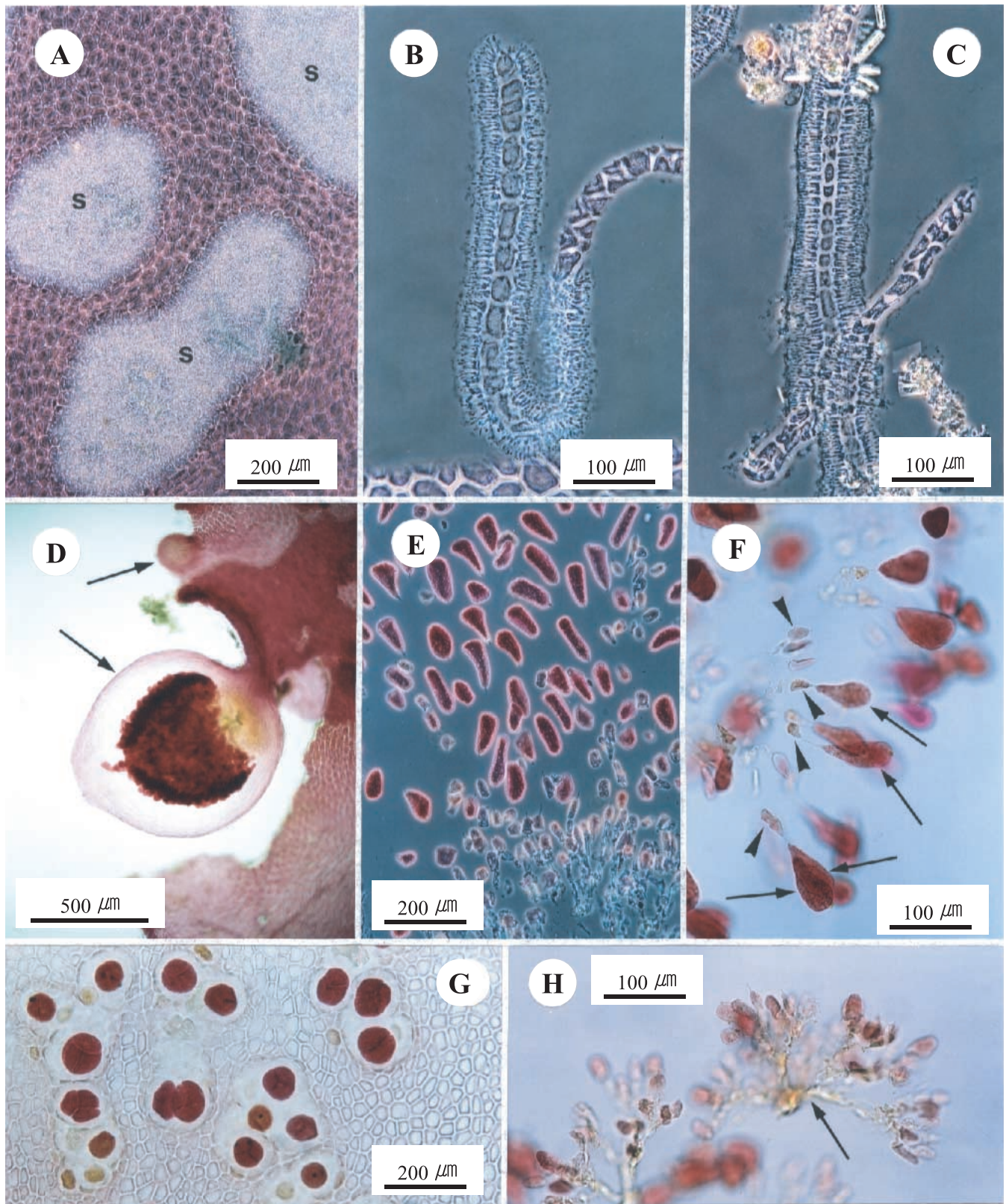


Fig. 3. *Martensia palmata* sp. nov. A. Surface view of spermatangial sori. B. Transverse section of membranous section with spermatangial sori. C. Transverse section of longitudinal lamella with spermatangial sori. D. Cystocarps (arrows) on margins of membranous section. E. Carpospores. F. Terminal carpospores (arrows) and intercalary carpospores (arrow heads). G. Surface view of tetrasporangial sori on the membranous section. H. Carposporophyte (arrow).

cell layers, consisting of two cortical and one medullary cell layer. The cortical cells undergo cell divisions to become several small spermatangial mother cells. Consequently, a large medullary cell in the middle of the membranous section produces several spermatangial mother cells on both surfaces. The spermatangial mother cells are conical, outwardly mucronate, bear a spermatangium on each mucronate tip, and are 8-17 μm long and 3-5 μm in diameter (Fig. 3B, C). Spermatangia attached to the tip of spermatangial mother cells are ellipsoid to ovoid, colorless, and 2-3 μm in diameter. Indusia of the spermatangial sori are absent. Tetrasporangia are borne in sori resembling small round spots on the membranous section, as well as on the longitudinal lamellae and the leading margins of the latticework (Figs. 1C, D, 3G). Tetrasporangial sori have envelopes on both surfaces, which are single cell-layered and inflated outward in the transverse section (Fig. 2H). The cells of the envelope of tetrasporangial sori are irregularly shaped in the surface view and linear in the transverse section.

Plants of *M. palmata* sp. nov. grow solitarily without forming populations. They are usually epiphytic on *Acanthopeltis longiramulosa* Lee et Kim and *Lomentaria catenata* Harvey, which grow in the lower tidal to the subtidal regions of Moonseom and Seobseom. In Hwasoon on Jeju Island, the plants usually grow on rocks on sandy substrates at depths of about 18 m. They grow from March to August and reproduce between May and June.

Specimens examined: LYP-1627 (Hwasoon, Jeju Island 2005-05-25. \oplus coll. by Y. Ko. 2005-55); LYP-1669 (Moonseom, Jeju Island 2002-07-31. coll. by B. Kim. \ominus , \uparrow , \oplus); LYP-1670 (Moonseom, Jeju Island 2001-06-21. \ominus , \uparrow , \oplus); LYP-1671 (Seobseom, Jeju Island 2002-06-09. \oplus . coll. by B. Kim); LYP-1673 (Seobseom, Jeju Island 2002-03-24. \uparrow , \oplus . coll. by B. Kim); LYP-1911 (Moonseom, Jeju Island 2002-08-04. coll. by B. Kim); LYP-1924 (Seobseom, Jeju Island 2005-06-12. 2005-112); LYP-1942 (Seobseom, Jeju Island 2004-05-16. \uparrow , \oplus . 2004-321); LYP-1968 (Moonseom, Jeju Island 2005-06-11. \ominus , \uparrow , \oplus . coll. by Y. Ko. 2005-83); LYP-1970 (Seobseom, Jeju Island 2004-05-14. 2004-324); LYP-1971 (Seobseom, Jeju Island 2004-05-14. 2004-323).

Remarks: *Martensia palmata* sp. nov. is very distinct from *M. lewisiae* Lin, Hommersand et Fredericq (2004) and *M. martensii* Lin, Fredericq et Liao (2001) because the latticework of the latter species is lacking or sparse on the blades of the thalli. *Martensia palmata* sp. nov. is also

easily distinguished from *M. bibarii* Lee (2004), which has ribbon-shaped blades and pilus tufts instead of the latticework. *Martensia palmata* sp. nov. is more or less related to *M. australis* Harvey (1855), *M. elegans* Hering (1841), *M. formosana* Lin, Hommersand et Fredericq (2004), *M. fragilis* (Harvey 1854), *M. indica* Krishnamurthy et Thomas (1977), and *M. jejuensis* (Lee 2004) in terms of the flabellate blades of the thalli. However, *M. palmata* sp. nov. is easily distinguished from *M. australis*, *M. elegans*, and *M. formosana* because the thallus blades do not branch in these species (Harvey 1858; Svedelius 1908; Millar 1990; Lin et al. 2004). *Martensia palmata* sp. nov. is also distinguished from *M. jejuensis* by the stipe-like structures, which are derived from the upper portion of the longitudinal lamellae of the latticework and carry the second-order bladelets laterally and terminally (Lee 2004). *Martensia palmata* sp. nov. is distinct from *M. indica*, which has stipes on the thalli (Krishnamurthy and Thomas 1977). *Martensia palmata* sp. nov. is also related to *M. fragilis* in terms of the branched blades. However, the branches of *M. palmata* sp. nov. are formed by the elongation of the lobes on basal flabellate blades, while those in *M. fragilis* are formed by the divergence of the blades. Consequently, the branches of *M. fragilis* are somewhat regularly dichotomous and expand into cuniate or broadly triangular segments, while those in *M. palmata* sp. nov. are rather irregular in branching mode and length and have obtuse or round angles (Harvey 1860; Svedelius 1908). *Martensia palmata* sp. nov. shares some characteristics with *M. lewisiae* in terms of the cystocarps formed on the blade margins (Lin et al. 2004).

A specimen of *M. palmata* sp. nov. bearing both spermatangial and tetrasporangial sori on the same thallus was found (Fig. 1D). The spermatangial sori were formed in the distal region of the blade, whereas the tetrasporangial sori were found in the proximal region (Fig. 1D). Also, the tetrasporangial sori aggregated in the basal region of the latticework, while the spermatangial sori aggregated in the upper region. This mixed phase of *M. palmata* sp. nov. raises some interesting questions. Do thalli bearing tetrasporangial sori distally and spermatangial sori proximally occur in nature? Are the spermatangial sori assembled laterally on one side and tetrasporangial sori on the other side of the membranous section? Why are the spermatangial sori not intermingled with the tetrasporangial sori? Do thalli bearing both cystocarps and tetrasporangial sori occur in nature? Given these unanswered questions, further

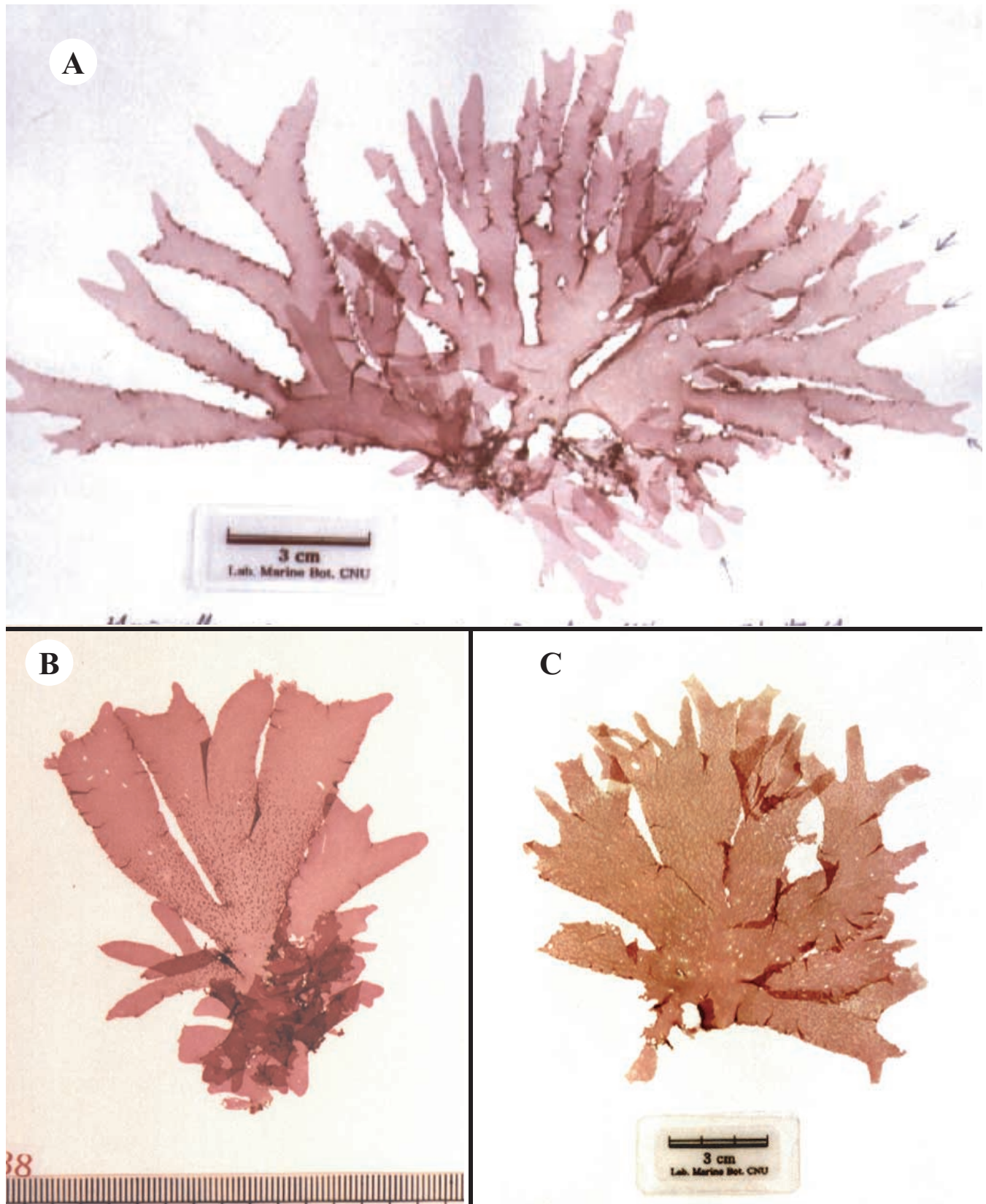


Fig. 4. *Martensia projecta* sp. nov. A. Holotype (LYP-1959, Female gametophyte). Note the arrows indicate the latticework. B. Tetrasporangial plant (LYP-1938). C. Male gametophyte (LYP-1933).

studies on the phenology and life history of *M. palmata* sp. nov. will be of great interests.

***Martensia projecta* Lee sp. nov.**

Diagnosis: *Thalli epilithici, rosei, aliquot laminis constati, substrato parte ima affixi, 10-15 cm alti. Haptera cellulosis filamentosis constata, quae contortae et intricatae irregulariter. Laminae flabellatae, ramificantes subdichotome ad angulos obtusos, ramis plus minusve attenuates versus apicem, plerumque paginis aspris vel projecturis verruciformibus in superficiebus ambabus parties mediae, projecturis spiniformibus in margine, 1-4-stratae, 60-150 μm crassae. Cellulae corticales 4-7-angulae angulis obtusis aspectu paginali, ellipsoideae vel oblongae, 25-40 μm longae, 15-30 μm diametro, 20-30 μm crassae. Reticulum rarum, infirmissimum, parte apicali segmentiorum evolutum, 2-4 mm latum. Gametophyta et tetrasporophyta isomorphus. Gametophyta dioecia et isomorphus. Cystocarpia superficialis parties membranacea facta, globosa, ostiolo protuberanti raviter, 1.4-1.6 mm diametro. Carposporae pyriformes, 100-150 μm longae, 60-80 μm diametro. Sori spermatangiorum ellipsoidei irregulariter superficialis parties membranacea, decolorati, indusio communi. Spermatangia ellipsoidea, ca. 5 μm longa, ca. 3 μm diametro. Tetrasporangia parte membranacea facta, aliquot involucro communi, globosa, tetraedrice divisa, 100-120 μm diametro.*

The thalli of this species are epilithic, pale red, composed of few blades, attached to the substratum by the lowermost part, and 10-15 cm high. The holdfasts of the thalli are composed of filamentous cells, which are contorted and irregularly entangled. The blades are flabellate, branching subdichotomously at obtuse angles, with branches more or less attenuated toward the apex, usually with uneven surfaces or wart-like projections on both surfaces of the middle region, with spine-like projections on the margin, one- to four-cell-layered, and 60-150 μm thick. Cortical cells are tetragonal to heptangular, with obtuse corners in the surface view, ellipsoid to oblong, 25-40 μm long, 15-30 μm in diameter, and 20-30 μm thick. Latticework is rare, and when present, it is very poorly developed in the apical region of the segments and is 2-4 mm wide. Gametangial and tetrasporangial thalli are isomorphic, and gametangial thalli are dioecious. Cystocarps are formed on the marginal surfaces of the membranous section; they are globose, 1.4-1.6 mm in diameter, with a slightly swollen ostiole. Carpospores are pyriform, 100-150 μm long and 60-80 μm in diameter. Spermatangial sori are irregularly

ellipsoid on the surface of the membranous section, faintly colored, and have a common indusium. Spermatangia are ellipsoid, about 5 μm long and 3 μm in diameter. Tetrasporangia are formed on the membranous section, several in a common envelope; they are globose, 100-120 μm in diameter, and tetrahedrally divided.

Korean name: Dotolbidanmangsa.

Holotype: The Herbarium of Cheju National University (CNU Herbarium Y. Lee, LYP-1959 Seobseom 2002-03-24. ♀. coll. by B. Kim).

Type locality: The subtidal region (4-6 m deep) off the northern slope of Seobseom, Jeju Island, Korea.

Vegetative morphology: Thalli are bright red, epilithic or epiphytic on other algae, composed of several blades, and grow 10-15 cm tall (Fig. 4A-C). The holdfasts of the thalli are multilayered, composed of filamentous cells, and up to 200 μm thick (Fig. 5H). The filamentous cells of the holdfasts are derived from the lowermost cells of the blade; they are slightly contorted and conglutinated together. The blades of the thallus are membranous with uneven surfaces, flabellate, furcate or subdichotomously branching, comprise one to four cell layers, increasing in cell layers and thickness toward the base, with spine-like projections on the margins, and 60-150 μm thick (Fig. 5B, C, E, F, G, I). The blade segments are band-shaped and gradually widen upward, whereas the terminal segments are short and conical. The blades of female gametangial thalli have fairly undulate margins and are furcated more than those of male or tetrasporangial thalli. In some blades, numerous wart-like projections are formed on the surfaces of the center portion (Fig. 5A, D, G). Some cortical cells protrude outward to form the beginnings of projections (Fig. 5G). The cortical cells of the blade are ellipsoid, with one or two acute corners, or polygonal with obtuse corners in the surface view and ellipsoid to oblong in the transverse section; they are 25-40 μm long, 15-30 μm in diameter, and 20-30 μm thick (Fig. 5C, E, F, I, J). The cortical cells in the upper portion of the blade show wrinkles on both radial walls and are irregularly shaped in the transverse section (Fig. 5C, F). The medullary cells are similar in shape to the cortical cells except that they lack chloroplasts. The vegetative cells are coarsely stacked in anticlinal lines (Fig. 5E). The lower part of the blade has a parenchymatous organization and an irregular arrangement of cells (Fig. 5H, I).

The latticework of *M. projecta* sp. nov. is seldom

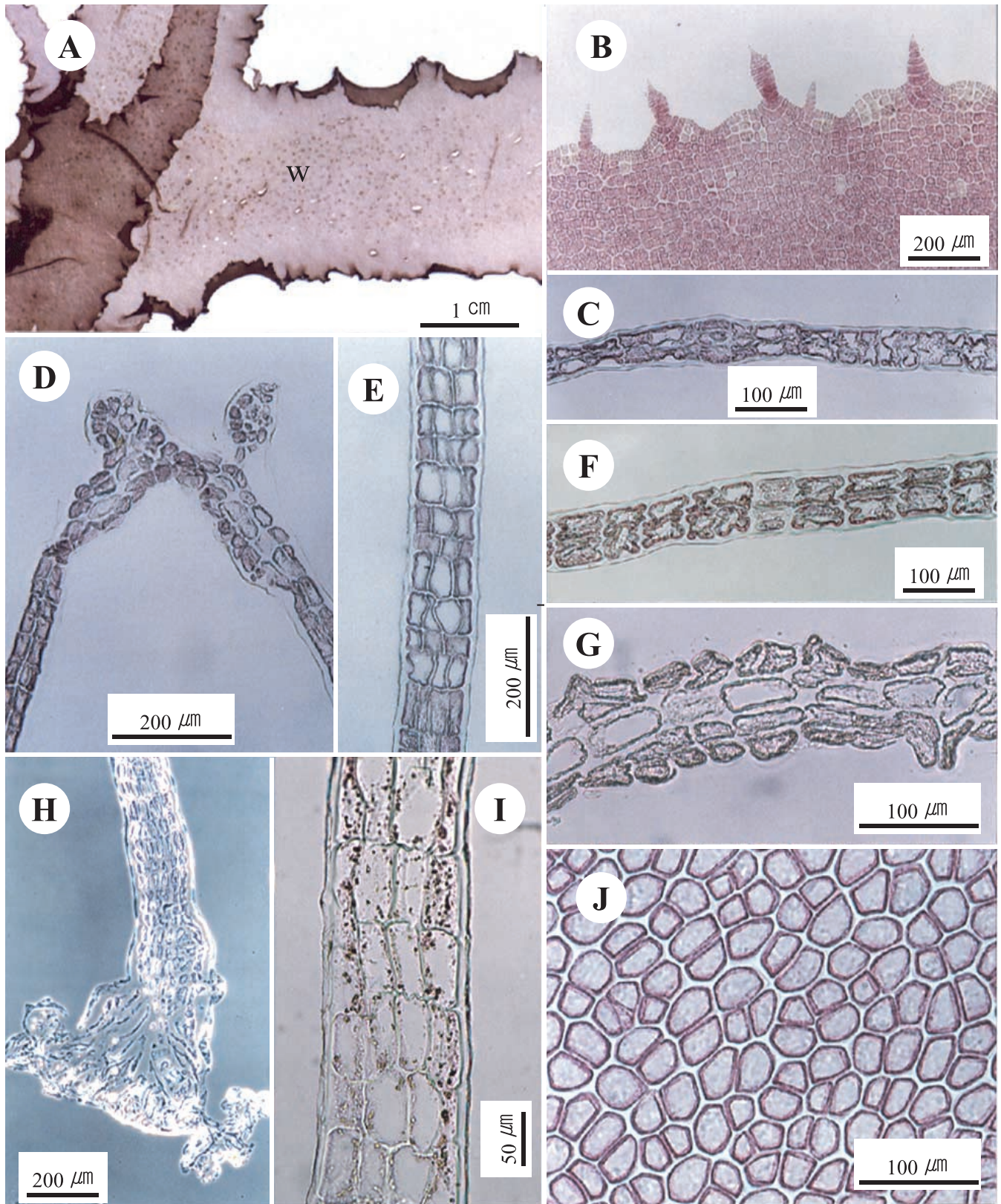


Fig. 5. *Martensia projecta* sp. nov. A. Wart-like projections (w) on the surface of segments. B. Spine-like projections on the margin of blade. C. F. Transverse section of the upper part of blade. D. G. Transverse section of the blade bearing wart-like projections. E. Transverse section of the middle part of blade. H. Radial section of holdfast. I. Transverse section of the lower part of blade. J. Cortical cells in surface view.

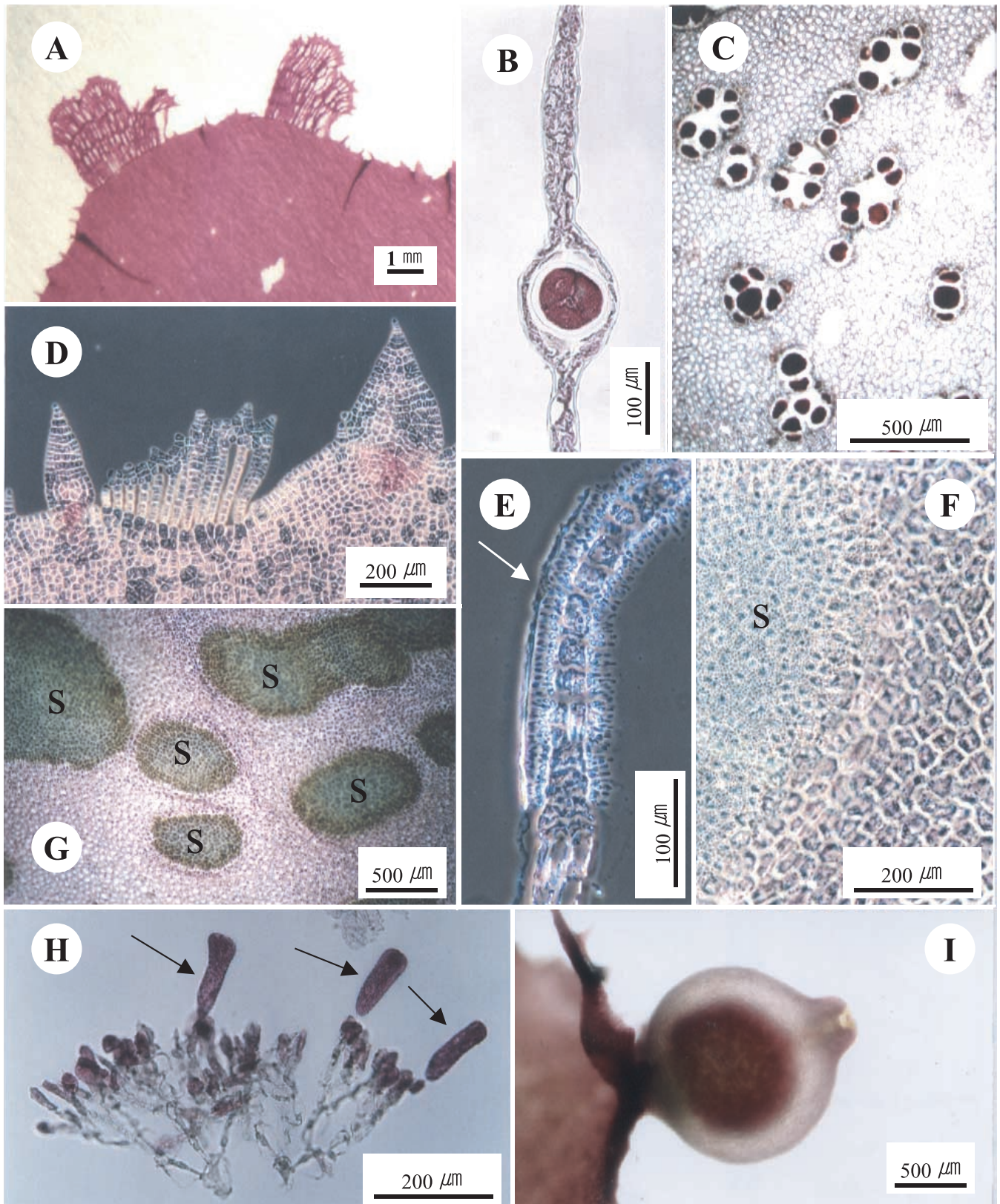


Fig. 6. *Martensia projecta* sp. nov. A. Latticeworks. B. Transverse section of blade bearing a tetrasporangium. C. Surface view of tetrasporangial sori. D. Latticework formed between the spine-like projections. E. Transverse section of spermatangial sorus with an indusium (arrow). F. Surface view of a part of spermatangial sorus (s). G. Spermatangial sori (s) in surface view. H. Part of gonimoblast filaments bearing carposporangia (arrows). I. Cystocarp.

observed; when it is present, it is small, formed on the distal margin of a segment, and is less than 5 mm in size (Fig. 6A, D). The production of latticework is unpredictable, as the organization of the latticework occurs between spine-like projections on the margin (Fig. 6A, D). No tetrasporangia, spermatangia, or cystocarps are formed on the latticework.

Reproductive morphology: Gametophytes and tetrasporophytes of *M. projecta* sp. nov. are generally isomorphic, although female gametangial thalli are somewhat more branched with more undulate margins than male gametangial or tetrasporangial thalli (Fig. 4A-C). Cystocarps are borne near the edges of the segment; they are globose, 1.4-1.6 mm in diameter, with a slightly protruding ostiole and a multilayered pericarp (Fig. 6I). Gonimoblasts arise from a large fusion cell, branching trichotomously and forming a subglobose tuft, and bear carpospores terminally (Fig. 6H). Carpospores are pyriform, 100-150 μm long, and 60-80 μm in diameter. Spermatangial sori are formed on the surfaces of the blades, resembling irregularly round, faintly colored spots, and have indusia (Fig. 6E-G). The part producing spermatangial sori has three cell layers, i.e., two cortices on both sides and a central medulla. The cortical cells undergo divisions several times and become the spermatangial mother cells on both sides of the medullary cells. The spermatangial mother cells are conical, bear a spermatangium on the acute apex, and are ca. 10 μm long and ca. 5 μm in diameter. Spermatangia attached to the spermatangial mother cells are ellipsoid, colorless, ca. 5 μm long, and ca. 3 μm in diameter. Tetrasporangia are borne on the membranous section of the blade, appearing as somewhat round sori in a common envelope, globose with tetrahedral divisions, and 100-120 μm in diameter (Fig. 6B, C). The envelope of tetrasporangial sori is mono-layered and outwardly biconvex (Fig. 6B).

Martensia projecta sp. nov. is usually epiphytic on other algae growing at depths of 15 m near Seobseom and Moonseom from March to July. In May, *M. projecta* sp. nov. in Hwasoon, Jeju Island, grows on rocks in sandy substrates at depths of approximately 18 m.

Other specimens examined: LYP-1619 (Munseom, Jeju Island 2002-07-31); LYP-1918 (Munseom, Jeju Island 2005-06-11. ♂ coll. by Y. Ko, 2005-84); LYP-1933 (Seobseom, Jeju Island 2004-04-10. ♂ ♀ coll. by M. Kim, 2004-239); LYP-1938 (Seobseom, Jeju Island 2004-05-14. ♂ ♀ coll. 2004-322); LYP-1948 (Hwasoon, Jeju Island 2005-05-25. ♀ ⊕ coll. by Y. Ko. 2005-62); LYP-1959 (Seobseom,

Jeju Island 2002-03-24. ♀ coll. by B. Kim. 2005-46).

Remarks: Segments of blades of *M. projecta* sp. nov. are usually long, broadened upward, and subdichotomous, although terminal blades are short and attenuate upward. The terminal segments of the blades may be lobed or forked. The upper parts of some segments of the blade have somewhat rough surfaces, i.e., the cortical cells line up unevenly in transverse sections while the basal part is multilayered and show a parenchymatous organization of the cells (Fig. 5C, F, H, I). A similar structure of the basal part of the blade is observed only in thalli of *M. projecta* sp. nov.; this structure may become the stipe-like structure of the thallus. The wart-like projections on the surface of the blade are novel in character, and are not expected of the previously described species. These projections are not always formed on the surface of all blades of the thallus, and seem to occur on non-reproductive surfaces of mature blades. Consequently, it is difficult to rely on this feature as a diagnostic characteristic of *M. projecta* sp. nov. The spermatangial sori bearing an indusium are the only character unique to *M. projecta* sp. nov. of the species described to date. The indusium may be composed of the outer walls of the cortical cells because their shapes in the surface view are reflected in the indusium. Consequently, the process of producing spermatangia in the mucronate tips of the spermatangial mother cells from the division of the cortical cells occurs on the inside of the outer wall of the cortical cells. Occasionally, neither an indusium nor the stub of an indusium was observed in certain spermatangial sori, even on the same blade. Thus, the indusium may be easily lost during early spermatangial formation. The latticework of *M. projecta* sp. nov. was not only very rare, but also very poorly developed and difficult to locate without careful observation (Fig. 6A, D). Arrows on the herbarium sheets indicate latticework on the apex of the segments of the blades (Fig. 4A). In *M. projecta* sp. nov., the spine-like projections dominate the entire margin of the blade. Consequently, only the marginal cells between the projections can develop into the longitudinal lamellae of the latticework, and the latticework has difficulty expanding beyond the projections because the cells forming these projections are not arranged in series as they are in the marginal lamellae.

Martensia projecta sp. nov. is related to *M. fragilis*, *M. indica* and *M. palmata* sp. nov. in terms of having a thallus with branching blades. However, *M. projecta* sp.

nov. can easily be distinguished from the latter species because of its inconspicuous latticework, although the branching patterns are also different. *Martensia projecta* sp. nov. is somewhat related to *M. lewisiae* in terms of the weak latticework and the vegetative cells with wrinkles in the radial wall (Lin et al. 2004). However, *M. projecta* sp. nov. is easily distinguished from *M. lewisiae* by its branching, multi-layered blades.

DISCUSSION

Svedelius (1908) investigated the latticework organization and reproductive development in several species of *Martensia*. The criteria used for separating the species of *Martensia* are combinations of the following characters: shape of the blades, i.e., whether they are flabellate, ribbon-shaped, lobed, branching, or unbranching; presence or absence of a stipe; presence or absence of latticework; state of the latticework, i.e., whether it is intact, partially fragmented, or transformed to pilus tufts, and whether it is larger or smaller than the membranous section; whether the leading margin of the latticework has developed second-order bladelets. The characteristics of the latticework are consistent and species-specific in *Martensia*. The blades of *M. elegans*, *M. australis*, *M. formosana*, and *M. jejuensis* are flabellate and unbranched (Harvey 1847-1849, 1858; Svedelius 1908; Millar 1990; Lin et al. 2004; Lee 2004). The blades of *M. fragilis* and *M. indica* are usually flabellate and dichotomously branched (Svedelius 1908; Harvey 1860; Krishnamurthy and Thomas 1977; Millar 1990). *Martensia indica* has a stipe on the thallus (Krishnamurthy and Thomas 1977). *Martensia palmata* sp. nov. has the flabellate blades that are lobed and branched. The blades of *M. bibarii* are ribbon-shaped and lobed (Lee 2004). The latticework is larger than the membranous section in *M. australis*, *M. fragilis*, and *M. formosana* (Harvey 1858, 1860; Kützing 1869; Svedelius 1908; Millar 1990; Yoshida and Mikami 1996; Lin et al. 2004). The latticework is rare and substantially smaller than the membranous section in *M. lewisiae* and *M. projecta* sp. nov. (Lin et al. 2004). The latticework is absent in *M. martensii* (Lin et al. 2001). The latticework is usually intact in *M. australis*, *M. elegans*, *M. fragilis*, *M. indica*, *M. formosana*, and *M. palmata* sp. nov. (Harvey 1858, 1860; Kützing 1869; Svedelius 1908; Krishnamurthy and Thomas 1977; Millar 1990; Yoshida and Mikami 1996; Lin et al. 2004). The latticework is partially fragmented, and some of the longitudinal lamellae of the latticework develop into stipes in *M.*

jejuensis (Lee 2004). The longitudinal lamellae are elongate and become fine hair-like filaments after the complete fragmentation of the leading margin and cross-connecting strands in *M. bibarii* (Lee 2004). The second-order bladelets develop on the leading margin of the latticework in *M. fragilis*, *M. indica*, and *M. jejuensis* (Børgesen 1919, as *M. pavonia*; Krishnamurthy and Thomas 1977; Millar 1990). Millar (1990) described the second-order bladelets on the leading margin of the latticework in *M. pavonia* as 'the alternation of membranous section and latticework organization' (see Kützing 1869; Svedelius 1908; Børgesen 1919; Taylor 1960; Littler et al. 1989).

Lin et al. (2004) proposed that the orientation of cross-connecting strands, whether unidirectional or bidirectional, may provide a useful taxonomic characteristic, although its taxonomic significance is unclear at this time. A unidirectional orientation of cross-connecting strands is typical in latticework with coarse and loose mesh, such as in *M. elegans* (specimens at hand), *M. jejuensis* (Lee 2004), *M. bibarii* (Lee 2004), and *M. lewisiae* (Lin et al. 2004). A bidirectional orientation of cross-connecting strands is more common in latticework with fine mesh because it subdivides the mesh as observed in *M. australis* and *M. fragilis* (Svedelius 1908; Børgesen 1919, as *M. pavonia*). However, in *M. palmata* sp. nov., a bidirectional orientation of cross-connecting strands is somewhat common in the upper portion of the latticework, while a unidirectional orientation is exclusive in the lower portion of the latticework (Fig. 2E, I).

The blades of *Martensia* show a fairly regular latticework organization on the distal margin of the membranous section, whereas those of *Opephyllum* lack the latticework, but are abundantly perforated by small rounded holes (Wynne 1983, 1996; Kylin 1956; Millar 1990; Lin et al. 2001). The latticework of *Martensia* was once regarded as the region in which reproductive structures were produced (Svedelius 1908; Fritsch 1945; Kylin 1956). It was later determined that the formation of reproductive structures is not restricted to within the latticework, but also occurs on the surface or margins of membranous sections in *M. fragilis*, *M. lewisiae*, *M. jejuensis*, and *M. bibarii* (Millar 1990; Lin et al. 2004; Lee 2004). Lin et al. (2001) concluded that *Opephyllum Schmitz in Schmitz et Hauptfleisch* is congeneric with *Martensia* Hering on the basis of morphological observations and sequence analysis of the chloroplast-encoded *rbcL* and the nuclear-encoded large subunit

ribosomal DNA gene (LSU rDNA). Consequently, it is no longer useful to characterize the genus *Martensia* based on whether the latticework organization is present or absent. In *M. projecta* sp. nov., spine-like projections arise along the entire margin of the blade, while small latticework is organized very rarely between the spine-like projections on the margin. Lin *et al.* (2001) suggested that in *M. martensii*, the retention of the juvenile body features in adults may be an example of phaedomorphosis. In the thalli of *M. elegans*, *M. australis*, and *M. fragilis*, several small, and probably juvenile, blades with latticework are always intermingled with adult blades bearing reproductive structures. In these species, the latticework organization may be activated in the early stages of blade development. In *M. lewisiae* and *M. projecta*, the thallus also consists of juvenile and adult blades, of which only a few adult blades support a weak latticework. In the case of the latter species, the latticework organization may be poorly activated in the adult stage of blade development. Perhaps the activation of latticework organization is arrested or the genetic information for latticework organization is absent in *M. martensii*.

The longitudinal lamellae of the latticework are membranous, bi-layered, long, belt-shaped, usually with smooth margins, and equal in width along the whole length. The faces of the longitudinal lamellae in the latticework are perpendicular to the membranous section of the blade and the leading margin of the latticework. The longitudinal lamellae of the latticework in *M. palmata* have dentate margins (Fig. 2D). In *M. jejuensis*, the longitudinal lamellae of the latticework are transformed into stipe-like structures with lateral blades when they become partially free after the leading margin and cross-connecting strands are fragmented (Lee 2004). On the other hand, in *M. bibarii*, the longitudinal lamellae of the latticework are elongated continuously while retaining their original state (belt-form) when the leading margin and the cross-connecting strands of the latticework are fragmented (Lee 2004). In some *Martensia* species (specimens at hand), numerous bladelets arise on the longitudinal lamellae constructing the latticework. Consequently, the morphology of the longitudinal lamellae of the latticework may provide a useful taxonomic character.

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