The genus *Martensia* Hering (Delesseriaceae, Rhodophyta) with *M. albida* sp. nov. and *M. flammifolia* sp. nov. on Jeju Island, Korea

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The genus *Martensia* (Delesseriaceae, Rhodophyta) is characterized by thalli composed of one to several blades that consist of proximal membranous sections and distal latticework. Nerves or veins are absent in the membranous sections. The life cycle of *Martensia* is accomplished by isomorphic alternation of generations. The gametophytes of *Martensia* are dioecious, and the male and female gametangial plants are morphologically similar. The type species of *Martensia* is *M. elegans* Hering. In this study, nine species were confirmed to occur in the subtidal regions of Jeju Island, Korea: *M. albida* sp. nov., *M. australis* Harvey, *M. bibarii* Y. Lee, *M. elegans* Hering, *M. flammifolia* sp. nov., *M. fragilis* Harvey, *M. jejuensis* Y. Lee, *M. palmata* Y. Lee, and *M. projecta* Y. Lee. Three of these, *M. australis*, *M. fragilis*, and *M. elegans*, are new records in the flora of Korea. The results of molecular analyses of the internal transcribed spacer (ITS) 1 region in the nrDNA showed that *M. elegans* is identical to *M. australis*, and *M. fragilis* coincides with *M. bibarii*. It may be a less effective tool for the species discrimination in *Martensia*.

**Key Words:** Delesseriaceae, *Martensia*, *M. albida*, *M. australis*, *M. elegans*, *M. fragilis*, *M. flammifolia*

INTRODUCTION

The genus *Martensia* (Delesseriaceae, Rhodophyta) was established on the basis of *M. elegans* Hering (1841) from Port Natal, South Africa, and is characterized by the blades consisting of membranous parts and latticework, the absence of microscopic veins or nerves on the membranous parts, and reproductive structures that are generally formed on the latticework. The monographic study of *Martensia* by Svedelius (1908) describes the genus in detail. Svedelius (1908) investigated the process of latticework formation, the structure of the latticework, and the reproductive structures. The tribe *Martensiae* Wynne (2001) comprises three genera: *Neomartensia* Yoshida et Mikami and *Opephyllum Schmitz in Schmitz et Hauptfleisch*, and *Martensia* Hering, and is characterized by thalli with marginal growth, without nerves or veins, and with reticulate organization (Wynne 2001; Lin et al. 2001b). Papenfuss (1950) clarified the nomenclature of *Martensia* Hering (*nom. cons.*), although it was replaced at one time by the generic names *Hemitrema* Brown (*in Endlicher* 1843), *Mesotrema* J. Agardh (1854), and *Capraella* De Toni (1936).

Since the classification by Hering (1841), the genus referred to as *Martensia* includes the following 16 species: *M. beccariana* Zanardini (1878), *M. denticulata* Harvey (1855), *M. flabelliformis* Harvey *ex* J. Agardh (1863), *M. gigas* Harvey (1863), and *M. speciosa* Zanardini (1874) from the South Pacific; *M. australis* Harvey (1855), *M. elegans* Hering (*M. fragilis* Harvey, *M. jejuensis* Y. Lee, *M. palmata* Y. Lee, and *M. projecta* Y. Lee. Three of these, *M. australis*, *M. fragilis*, and *M. elegans*, are new records in the flora of Korea. The results of molecular analyses of the internal transcribed spacer (ITS) 1 region in the nrDNA showed that *M. elegans* is identical to *M. australis*, and *M. fragilis* coincides with *M. bibarii*. It may be a less effective tool for the species discrimination in *Martensia*.

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collections of these three species were identical in all respects. Yoshida and Mikami (1996) established the new genus Neomartensia on the basis of M. flabelliformis, which forms caposporangia in short chains and has vegetative cells that are irregularly arranged. However, the genus Neomartensia was not widely accepted (Lin et al. 2004). On the other hand, Lin et al. (2001b) transferred Opephyllum martensii Schmitz in Schmitz et Hauptfleisch (1897), which is the type species of the genus Opephyllum, to the genus Martensia on the basis of comparative molecular analyses of both chloroplast-encoded rbcL and nuclear large-subunit ribosomal DNA (LSU rDNA). Consequently, eleven species of Martensia are currently recognized.

In Korea, Chyung and Park (1955) reported Martensia denticulata Harvey at the Meeting of the Korean Society of Biology in 1954 and gave it the Korean name ‘Maltensi’. Latter, M. denticulata was reported from the southern coast of Korea and Jeju Island (Rho 1958; Kang 1960; Kang 1966; Noda 1966; Lee 1976; Koh 1990; Lee et al. 1990; Lee and Koh 1991; Park et al. 1994). Kang (1962) changed the Korean name for Martensia denticulata to ‘Bidanmangsa’ and this name is currently used. Recently, four new species of Martensia, i.e., M. jejuensis Y. Lee, M. bibarrii Y. Lee, M. palmata Y. Lee, and M. projecta Y. Lee, have been described from Jeju Island, Korea (Lee 2004; Lee 2005). This paper provides a diagnostic key for the nine species of Martensia that occur on Jeju Island.

MATERIAL AND METHODS

Plants were collected in the subtidal region of Jeju Island, Korea, between 2000 and 2004. All plants had subtidal habitats and were therefore collected by scuba diving. The samples were kept in seawater during transport to the laboratory because they die easily and discolor when exposed to air. The collected samples were immediately fixed in 5% formalin/seawater for 3-5 days. Most of the fixed samples were prepared as dried herbarium specimens. Sections of thalli were cut using a bench-top freezing microtome (MFS no. 222; Nippon Optical Works, Tokyo, Japan). Sections and parts of specimens were mounted on glass slides in 50% corn syrup solution. Olympus research 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 breadth of the vegetative cells was measured from the surface view. The thickness of the vegetative cells was measured from transverse or longitudinal sections. The images of wet- or pressed specimens were captured using a camera (Nikon F2; Nikon, Tokyo, Japan) mounted on a photo-stand. All collections examined were deposited in the Herbarium of the Department of Life Science, Cheju National University, Korea.

Pieces of thalli from the dried herbarium sheets were used for molecular analyses. The samples were frozen in liquid nitrogen and stored at -70°C until DNA isolation. Total DNA was extracted using the SV Genomic DNA Purification System (Promega, USA), according to the manufacturer’s instructions. The sequence boundaries of internal transcribed spacer (ITS) 1 regions were determined by comparing them to published sequences of various algae (Saunders et al. 1996; Freshwater et al. 1999). The sequences were aligned using the program Clustal W (Thompson et al. 1994) and then adjusted manually to align several conserved regions. Sites with missing data or gaps were excluded from all analyses. Sequence divergence among the taxa was calculated using the program DNADIST in PHYLIP 3.572 (Felsenstein 1993), and the numbers of nucleotide substitutions were estimated using Kimura’s two-parameter method (Kimura 1980). A transition/transversion ratio of 2.0 was used. A bootstrap analysis of these data was done using 1000 resampled datasets, generated using the SEQBOOT program (Felsenstein 1993), before calculating the distance matrices and neighbor-joining trees. The resulting matrices were subsequently subjected to maximum parsimony analysis using the program DNAPARS (Felsenstein 1993). The program CONSENS in PHYLIP was then used to construct a strict consensus tree.

RESULTS AND DISCUSSION

Martensia Hering 1841: 92, nom. cons.


Capraella De Toni 1936.

Type species: M. elegans Hering 1841: 92.
**Korean name:** Bidanmangsa (비단망사).

Hering (1841) circumscribed the genus *Martensia* as 'Frons plana, areolata, avenia, margine fenestra; fructus duplex; sphœrospermia longitudinaliter in reticulo simplici serie disposita; capsule sphœricæ, reticulo affixe, sporidia subglobosa foventes.' It is estimated from the above description that the thallus of *Martensia* consists of a membranous section and latticework organization and produces tetrasporangia and cystocarps on the latticework. Also, we assume that the gametophyte and tetrasporophyte of *Martensia* are isomorphic. More recently, the genus *Martensia* has been circumscribed by the blades of the thallus partitioned into distal latticework and proximal membranous section, growth by means of marginal rows of obliquely dividing apical cells, macro- and microscopic veins lacking, tetrasporangia borne on both membranous section and latticework, and cystocarps borne on latticework (Wynne 1983, Millar 1990). Yoshida and Mikami (1996) established the genus *Neomartensia* on the basis of *M. flabelliformis* Harvey ex J. Agardh (1863), which has carposporangia in short chains and vegetative cells that are variable in size and irregularly arranged. Consequently, vegetative cells that are regularly stacked in anticlinal lines and terminally-borne carposporangia also characterize the genus *Martensia*. Lin et al. (2004) ascribed *Opophyllum martensii* Schmitz in Schmitz et Hauptfleisch (1897) to *Martensia* on the basis of the results of comparative molecular analyses of both chloroplast-encoded *rbcL* and LSU rDNA. Thus, the latticework organization and cystocarps borne within the latticework are no longer taxonomic characters of *Martensia* because *O. martensii* has a thallus that is perforated, but lacking the latticework organization. The latticework of *M. bibarii* and *M. projecta* may not be involved in the production of reproductive structures (Lee 2004; Lee 2005).

**Vegetative morphology**

**Thalli:** The thalli of *Martensia* grow solitarily or in fairly broad populations on rocks and shells, or they are epiphytic on other algae near sand substratum in 5–20 m deep subtidal regions. The thalli are white, purplish-blue, or yellowish-brown with fluorescence and have a peculiar odor in live specimens. In *M. elegans*, *M. australis*, *M. formosana*, *M. fragilis*, *M. palmata*, and *M. projecta*, the thalli have a bunch of several blades and grow in clusters, whereas those of *M. lewisiae* and *M. albida* sp. nov. are caespitose. The thalli of *M. jejuensis* and *M. bibarii* grow close to each other and appear in tufts on a host thallus. In *M. albida*, *M. australis*, *M. elegans*, *M. formosana*, *M. fragilis*, and *M. lewisiae*, the thalli consist of several blades that arise from the lower prostrating parts (Millar 1990; Lin et al. 2004). However, the thalli of *M. australis* from Australia each consist of a single blade (Millar 1990, fig. 52A). In *M. palmata* and *M. projecta*, the thalli consist of several blades, but are easily segregated into each blade because they may have no prostrating blade. The thalli of *M. flammifolia* sp. nov. consist of a single blade each, although they grow in clusters as bunches of blades. The thalli of *Martensia* generally have no stipes or stipe-like structures between the membranous sections and the holdfasts. However, in *M. indica*, *M. australis*, and *Neomartensia flabelliformis*, the thalli have stipes (Krishnamurthy and Thomas 1977; Kützing 1869; Yoshida and Mikami 1996; Womersley 2003: fig. 42E). Some specimens of *M. bibarii* also had a stipe-like structure (Fig. 6A). The thalli may lose their color and fluorescence when they are fixed in 5% formalin/seawater and become very soft and weak.

The thalli of *Martensia* are attached to the substratum by the holdfasts. The holdfasts of the thallus are formed in bundles of short rhizoids or haptera of short filamentous cells. The rhizoids are formed on thalli growing on rocks or shells and are long, filamentous, multiseriate, and simple or branched. The rhizoidal filaments develop from the lowermost cells of the blade and are simple and monosiphonous at the beginning of development. Subsequently, the rhizoidal filaments elongate and become polysiphonous with or without branches (Fig. 2C). The haptera are short, thick, unbranched, and arise on the thalli of species that are epiphytic on other algal thalli. The haptera are composed of several filamentous cells, which coaglutinate together (Fig. 11F). In most thalli of *Martensia*, several discoid haptera are formed on various surfaces of the blades and result in the tight adhesion of the overlapping parts of the blades (Lee 2005, fig. 1G).

**Blades:** The blades of the thallus in *Martensia* usually are like cellophane when alive and become more or less softened when fixed in 5% formalin/seawater. The blades are partitioned into two sections: the proximal membranous section and the distal latticework organization; they are flabellate, with or without branches, ribbon-shaped, and without macroscopic and microscopic ribs or veins. The latticework is absent on the blades of *M. martensii* and *M. flammifolia* (Fig. 9A; Lin et al. 2001b). However, in the blades of *M. pavonia*, the membranous sections alternate with the latticework organization at
least twice (Taylor 1960; Littler et al. 1989; Millar 1990). In *M. puvonia*, there is no distinction between the second-order membranous sections and the leading margins of the first-order latticework. It means here that the second-order bladelet is the miniature of the primary blades. In *M. fragilis*, *M. indica*, and *M. jejuensis*, the second-order bladelets are derived from spatulate projections with short stalks, and are differentiated from the leading margins of the first-order latticework (Fig. 10B-D; Krishnamurthy and Thomas 1977; Millar 1990; Lee 2004). The blades in *M. bibarii* are band-shaped and laterally give rise to several lobes with latticework (Lee 2004). The blades are prostrate, overlapping decumbent, lobed, and give rise to several lobes with latticework (Fig. 10B-D; Krishnamurthy and Thomas 1977; Millar 1990; Lee 2004). The blades in *M. bibarii* are band-shaped and laterally give rise to several lobes with latticework (Lee 2004). The blades are prostrate, overlapping decumbent, lobed, and have a highly irregular outline in *M. lewisiæ* and *M. albida* (Fig. 2A; Lin et al. 2004). In *M. indica*, the blades have a stipe between the membranous section and the holdfast (Krishnamurthy and Thomas 1977). However, in *M. jejuensis*, the free upper part of the longitudinal lamellae of the latticework is somewhat thickened and shows a stipe-like feature with several bladelets terminally and laterally (Lee 2004). In *M. australis*, *M. elegans*, *M. formosana*, *M. jejuensis*, and *M. martensiæ*, the blades are fan-shaped, without branching, although at times they split deeply (Harvey 1858; Kützing 1869; Millar 1990; Lin et al. 2001b; Lin et al. 2004; Lee 2004). The blades in *M. fragilis* and *M. indica* branch dichotomously or subdichotomously and comprise somewhat linear to broadly cuneate segments (Harvey 1860, as *M. denticulata*; Svedelius 1908; Krishnamurthy and Thomas 1977; Millar 1990). The blades in *M. projecta* branch subdichotomously.

**Membranous sections:** The membranous sections of the blades in *Martensia* are lamellate and lack wrinkles or macro- and microscopic veins. These usually have even and glossy surfaces, comprise one to several cell layers, and have entire or dentate and slightly undulate margins. The membranous section increases in cell layers and thickness toward the base. However, the membranous sections in *M. martensiæ*, *M. lewisiæ*, and *M. flammi-folia* are entirely monostromatic, except in the region of the holdfast and reproductive structures (Fig. 9F; Lin et al. 2001b; Lin et al. 2004). Rarely, the membranous sections of the blades in *M. projecta* have uneven surfaces with occasional small wart-like projections (Lee 2005). The membranous sections in *M. australis*, *M. elegans*, *M. formosana*, and *M. martensiæ* are fan-shaped without branching (Harvey 1849; Harvey 1858; Kützing 1869; Millar 1990; Lin et al. 2001b; Lin et al. 2004). In *M. jejuensis*, the membranous sections of the first-order blade are usually obtriangular, without branching (Lee 2004). The membranous sections in *M. palmata* are flabellate, with branching or lobes (Lee 2005). In *M. fragilis*, *M. indica*, and *M. projecta*, the membranous sections are linear, with dichotomous or subdichotomous branches (Fig. 10A; Harvey 1860, as *M. denticulata*; Svedelius 1908; Kützing 1869; Krishnamurthy and Thomas 1977; Lee 2005). In *M. lewisiæ* and *M. albida*, the membranous sections are ribbon-shaped, decumbent, undulate, and lobed upward (Fig. 2A; Lin et al. 2004). In *M. bibarii*, the membranous sections are rather long, twisted and erect, branched, and are lobed laterally (Lee 2004). Consequently, the morphology of the membranous section may be one of the characters for the discrimination of *Martensia* species. Agardh J. (1863) used the morphological characters of the membranous sections to distinguish species of *Martensia*.

In *M. elegans*, *M. australis*, *M. lewisiæ*, *M. formosana*, *M. fragilis*, *M. flammi-folia*, *M. martensiæ*, and *M. albida*, the membranous sections have entire margins (Kützing 1869; Millar 1990; Lin et al. 2001b; Lin et al. 2004). In *M. fragilis*, *M. jejuensis*, *M. bibarii*, *M. palmata*, and *M. projecta*, the margins of the membranous section of the blade are more or less undulate and have numerous projections (Fig. 3; Harvey 1860, as *M. denticulata*; Svedelius 1908; Lee 2004, Lee 2005). Moreover, the female thalli of *M. palmata* and *M. projecta* have more projections than the male or tetrasporangial thalli (Lee 2005). The projections are spinelike, conical, or spatulate. The spinelike and conical projections have an acute apex; this apex is simple or short projections protrude radially. The spathulate projections of the membranous section have a stalk and develop into bladelets in *M. jejuensis* (Lee 2004). However, in *M. palmata*, the spathulate projections have short projections on the distal margins and do not develop into bladelets (Lee 2005).

**Vegetative cells:** The vegetative cells are rather flat, usually pentagonal to heptagonal with rather obtuse corners in the surface view, ellipsoid to oblong in the transverse section, and have several pit-connections with neighboring cells. The vegetative cells are generally stacked in anticlinal lines, although they are arranged somewhat irregularly in the stalks, stipe-like structures, and holdfasts (Yoshida and Mikami 1996; Lee 2004). The radial walls of the vegetative cells in *M. lewisiæ* and *M. palmata* are wrinkled and show irregularly lobed shapes in the transverse section (Lin et al. 2004; Lee 2005). The vegetative cells in the marginal region of the blades in *M. flammi-folia* include one to three glossy granules near the cell walls (Fig. 9C). In transverse sections, the vegetative
cells in blades consisting of more than three layers are distinguished into central medullary cells flanked by cortical cells. The cortical cells are generally thinner than the medullary cells and contain chloroplasts. However, the medullary cells in *M. albida* also contain numerous chloroplasts.

**Latticework:** When the latticework begins to form, the marginal cells in the distal region of the membranous section elongate, undergo transverse divisions, and become a series of cell-columns. The cell-columns are composed of an apical cell and several intercalary cells. The intercalary cells continue elongation and transverse division, which results in elongation of the columns. The apical cells are hemispherical and undergo various divisions. The daughter cells from the apical cell divisions contact the cells derived from the apical cells of the neighboring columns and result in the initiation of the leading margin of the latticework. At the stage of the leading margin formation, the intercalary cells undergo transversal and radial divisions and result in the initiation of the longitudinal lamellae of the latticework. The longitudinal lamellae are belt-shaped, two cell layers thick, and elongated at a uniform width; their planes are established perpendicularly to the planes of the membranous sections and the leading margins. In *M. jejuensis*, the distal parts of the longitudinal lamellae of the latticework, which are free because of the fragmentation of the leading margins and cross-connecting strands, are slightly widened and dentate. Occasionally, the longitudinal lamellae of the latticework in *M. fragilis* gradually widen upward and are up to 5 mm wide, with dentate margins. Spinelike projections that become cross-connecting strands arise in the marginal region along the entire longitudinal lamellae. These spinelike projections develop perpendicularly to the plane of the longitudinal lamellae, contact the surface of the neighboring longitudinal lamellae, and result in the cross-connecting strands of the latticework. Thus, the mesh of the latticework is formed by the series of processes described above. The cross-connecting strands are variable in shape, and include linear, filamentous, and laminate strands. Generally, the cross-connecting strands arise in both marginal regions of the longitudinal lamellae and arrange in double lines (Svedelius 1908; Lee 2004; Lee 2005). Occasionally, in some species, additional cross-connecting strands are formed from the center of the cross-connecting strands. Lin et al. (2004) suggested that it may be of taxonomic significance whether the formation of additional cross-connecting strands is present (‘bidirectional orientation’) or absent (‘unidirectional orientation’). The formation of cross-connecting strands is bidirectional in *M. pavonia, M. formosana*, and *M. palmata* and unidirectional in *M. lewisiae, M. bibarii, M. projecta*, and *M. albida* (Børgesen 1919; Lin et al. 2004; Lee 2004; Lee 2005).

The leading margins of the latticework are ribbon-shaped, two cell layers thick, with somewhat uneven outer edges, and run parallel to the planes of the membranous sections. The leading margins of the latticework in *M. elegans* and *M. albida* are rather narrow and the outer edges are smooth (Figs 2H, 2I, 7C; Millar 1990). In *M. australis, M. lewisiae*, and *M. formosana*, the leading margins of the latticework are dentate (Millar 1990; Lin et al. 2004). The leading margins of the latticework in *M. palmata* and *M. jejuensis* form spinelike or spatulate projections along the outer edges (Lee 2004; Lee 2005). All projections give rise to additional short spinelike projections radially on the apex in *M. palmata* whereas the spatulate projections develop into bladelets in *M. jejuensis* (Lee 2004; Lee 2005). In *M. fragilis* the latticework forms several lobes from the outer edges of the leading margins; these lobes develop into bladelets (Fig. 10A(D; Harvey 1860, as *M. denticulata*; Millar 1990). Several bladelets are formed along the outer edges of the leading margins of the latticework in *M. indica* (Krishnamurthy and Thomas 1977). However, it is not clear whether these bladelets in *M. indica* are derived from spatulate projections or lobes. In the thalli of *M. pavonia*, the leading margins of the latticework are fairly wide and form the latticework on the outer edges of the leading margins (Taylor 1960). Millar (1990) described this character as ‘alternation of membranous and reticulate parts’ and this second-order latticework is not formed on the distal margins of spatulate projections or lobes, but directly along the outer edges of the leading margins.

The latticework in *Martensia* seems to continue to growth until reproductive structures are produced. In *M. australis* and *M. fragilis*, the mature latticework is usually ellipsoid and concave at the center. This may be because the longitudinal lamellae elongate more actively than the leading margins expand in the latticework. The latticework retains its intact form in *M. fragilis, M. australis, M. elegans, M. indica*, and *M. formosana* (Harvey 1849; Harvey 1858; Harvey 1860, as *M. denticulata*; Kützing 1869; Svedelius 1908; Krishnamurthy and Thomas 1977; Millar 1990; Lin et al. 2004). In *M. australis* and *M. formosana*, the latticework is rather compact, with small mesh, because the original mesh of the latticework is subdivided by the additional cross-connecting strands.
ticework in (Svedelius 1908; Millar 1990; Lin et al. 2004). The lattice-
work of *M. australis* is occasionally lacerated longitudi-
nally by environmental factors (Harvey 1858). The lat-
ticework in *M. fragilis* and *M. jejuensis* is compact at the
lower part and becomes gradually looser distally (Lee
2004). In *M. jejuensis*, the cross-connecting strands in the
distal region of the longitudinal lamellae, as well as the
leading margins of the latticework, are fragmented.
Subsequently, the distal parts of the longitudinal lamel-
lae become free and develop into stipe-like structures
bearing terminal and lateral blades (Lee 2004). In *M. bibarii*, the leading margins and cross-connecting strands
of the latticework are poorly developed and easily frag-
mented; the pilose tufts of the longitudinal lamellae take
the place of latticework on the blades (Lee 2004). Consequently, the morphology and development of the
latticework are variable among species of *Martensia*.

The latticework is generally formed on the distal mar-
gin of the membranous section of the blade. The apical
growth of the blade may be arrested by forming the lat-
ticework on the distal margin because the blades grow
by means of the marginal rows of obliquely dividing
cells (Wynne 2001; Millar 1990; Lin et al. 2004). This
hypothesis is supported by the fact that the membranous
sections are fan-shaped in *M. elegans*, *M. australis*, *M. for-
mosana*, and *M. jejuensis* (Harvey 1849; Harvey 1858;
Millar 1990; Lin et al. 2004; Lee 2004). Moreover, the lat-
ticework in *M. bibarii* is formed on the sub-apical mar-
gins of the lateral lobes and results in the triangular or
lanceolate shape of the membranous section (Lee 2004).
The latticework in *M. lewisiae* and *M. projecta* is very rare
and weakly developed when the thalli are mature (Lin et al.
2004; Lee 2005). Moreover, the latticework in *M. pro-
jecta* is formed between the spinelike projections that are
formed along the entire margins of the blade (Lee 2005).
The segments of the blades in *M. fragilis* also elongate lin-
early and then form a latticework terminally (Harvey
1860, as *M. denticulata*; Svedelius 1908). In *M. palmata*, the
lobes of the blades in mature thalli are usually long,
whereas every lobe in immature thalli is very short and
bears a conspicuous latticework (Lee 2005). It is not clear
whether the membranous section continues to grow,
even though the latticework is formed completely in *M.
palmata*. If this is the case, then it is not so clear why the
membranous section does not expand into a flabellate
shape, but rather, elongates linearly. In *M. lewisiae* and
*M. projecta*, the latticework organization may be poorly
activated in the adult stage of blade development. In *M.
martensii* and *M. flammifolia*, the latticework is not formed
at all. Perhaps the activation of latticework organization
is arrested or the genetic information for latticework
organization is absent in *M. martensii* and *M. flammifolia*
(Lin et al. 2001b).

**Chloroplasts:** The cortical cells contain a lamella just
inside the cell walls and numerous discoid granules in
the surface view. The lamellae are reddish, but their con-
tours are not defined. In the transverse section, the
lamellae are parietal only in the cortical cells, but they
are absent in the medullary cells. The granules are dis-
coid to linear, gray, generally scattered or aggregated in
the cells, and present in both the cortical and medullary
cells. It is difficult to confirm to presence of chloroplasts
without ultrastructural examinations of the cells.
However, the granules in the vegetative cells of *Martensia
diandra* are confirmed to be chloroplasts on the basis of their reddish color and parietal arrangement. Consequently, the granules in the vegetative cells are
recognized as the chloroplasts of *Martensia*. The chloro-
plasts found in the vegetative cells of most *Martensia*
species are discoid, round or ellipsoid, and 1-2 µm in
diameter (Fig. 8A). The chloroplasts of *M. flammifolia* are
discoid to ellipsoid, 3-8 µm in diameter, and comparatively larger than those of other *Martensia* species (Fig.
9D). It is not known whether *M. martensii* has the same
chloroplasts as *M. elegans* or *M. flammifolia*.

**Reproductive morphology**

The gametophytes and tetrasporophytes of *Martensia*
species are isomorphic, and the male and female
gametangial plants are also morphologically similar.
Historically, the latticework was considered the only
region in which reproductive structures were produced
(Harvey 1860; Kützing 1869; Svedelius 1908; Yoshida and
Mikami 1996). In *M. australis*, *M. elegans*, *M. formosana*, *M.
fragilis*, and *M. indica*, it was assumed that the reproduc-
tive structures were produced only in the latticework
(Harvey 1849; Harvey 1858; Kützing 1869; Svedelius 1908;
Krishnamurthy and Thomas 1977; Millar 1990). However,
Millar (1990) reported that tetrasporangia were produced on the membranous section of the blade
in *M. fragilis*. Also, in *M. australis*, *M. jejuensis*, *M. lewisiae*,
and *M. palmata*, the reproductive structures are borne on
the membranous sections, as well as in the latticework
(Lin et al. 2004; Lee 2004; Lee 2005). In contrast, the repro-
ductive structures are borne exclusively on the membra-
nous sections of the blade in *M. bibarii* and *M. projecta*
(Lee 2004; Lee 2005). By necessity, the reproductive
structures of *M. martensii* and *M. flammifolia* are borne
only on the membranous section because the latticework is absent in these species (Lin et al. 2001b).

**Spermatangia:** Spermatangia are borne in sori resembling small, ellipsoid, and faintly colored spots. The part of the membranous section producing spermatangia has three cell layers, consisting of two cortical and one medullary layer. Either one of the cells in the part producing spermatangia divides periclinally and results in three cell layers when the spermatangia are produced in the two-cell-layered membranous sections or the longitudinal lamellae of latticework. The cortical cells of the both layers undergo 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, and bear a spermatangium on each mucronate tip (Svedelius 1908; Yoshida and Mikami 1996; Lee 2005). However, one or two spermatangia are borne on the tip of the spermatangial mother cells in *M. lewisiae* and *M. formosana* (Lin et al. 2004). Spermatangia attached to the tip of spermatangial mother cells are ellipsoid to ovoid, colorless, and 2-3 µm in diameter (Lee 2005). A specimen of *M. palmata* bearing both spermatangial and tetrasporangial sori on the same thallus was found; the spermatangial sori were formed in the distal region, whereas the tetrasporangial sori were found in the middle region. Tetrasporangia are not species specific and no useful morphological features are related to the species examined. In particular, *Opephyllum beaucae* it lacks latticework, is more closely related to *M. australis, M. elegans, M. formosana,* and *M. fragilis* (Harvey 1849; Harvey 1858; Kützing 1869; Svedelius 1908; Millar 1990; Lin et al. 2004). The cystocarps are formed both on the blades and latticework in *M. palmata* (Lee 2005). The cystocarps in *M. martensii* are scattered across the blades as well as along the thallus margins, whereas those in *M. projecta* are borne along the margins of the blades (Lin et al. 2001b; Lee 2005). A specimen of *M. projecta* bearing both cystocarps and tetrasporangial sori on the same thallus was also found; the cystocarps were formed along the marginal region, whereas the tetrasporangial sori were found in the middle region of the blade.

**Tetrasporangia:** The tetrasporangia of *Martensia* are globose and tetrahedrally divided. The tetrasporangia are borne solitarily in the early stages of tetrasporangial formation. Subsequently, new sporangia are borne near those formed earlier and result in small roundish sori with a common envelope that is biconvex and one cell layer thick, with thinner discoid cells. The tetrasporangia are borne on the membranous sections as well as on the latticework in *M. albida, M. fragilis, M. formosana, M. lewisiae,* and *M. jejuensis* (Millar 1990; Lin et al. 2004; Lee 2004). In *M. bibarii* and *M. projecta,* the tetrasporangia are produced only on the membranous sections. *Martensia martensii* and *M. flammifolia,* which lack the latticework, also produce tetrasporangia on the membranous sections (Lin et al. 2001b). Consequently, the size and location of the tetrasporangia are not species specific and no useful for the circumscription of species in the genus *Martensia.*

**Molecular analyses**

The length of the ITS1 sequence in the *nrDNA* of all species examined was 303 bp. The GC content of the ITS1 sequence in the *Martensia* species examined ranged from 58.42 to 61.06%. The GC content of the ITS1 sequence was highest in *M. australis* and *M. elegans,* at 61.06%, and lowest in *M. palmata,* at 58.42%. The GC content of the ITS1 sequence in *M. fragilis* and *M. bibarii* was 60.40%, and that in *M. projecta* and *M. flammifolia* was 60.07%. The GC content of the ITS1 sequence in *M. jejuensis* and *M. albida* was 59.74% and 59.08%, respectively. The distance index for each species was calculated using the ITS1 sequence and the *nrDNA,* and the species relationships were illustrated as a phylogenetic tree (Fig. 1). According to the results of these molecular analyses, *M. flammifolia,* which may be a member of the genus *Opephyllum* beaucae it lacks latticework, is more closely related to *M. fragilis* and *M. bibarii* than to *M. australis*
and *M. jejuensis*. *Martensia australis* and *M. elegans* are conspecific because the GC contents and ITS1 sequences of both species were identical. The results for *M. fragilis* and *M. bibarii* were similar. Seven species, form a central cluster of *Martensia* species with similarity indices < 0.01: *M. elegans*, *M. australis*, *M. flammifolia*, *M. projecta*, *M. fragilis*, *M. bibarii*, and *M. jejuensis*. Based on molecular analyses, *M. fragilis* and *M. bibarii*, and *M. australis* and *M. elegans* are conspecific. Therefore, it is very unclear whether the morphological characteristics or molecular analyses are more reliable for identifying *Martensia* species. In addition, it is doubtful whether the molecular analysis of the ITS1 sequence in the *nr*DNA is useful for generic discrimination within the tribe Martensieae.

**Key to the species of Martensia in Jeju, korea**

1. Blades flabellate ---------------------------------------------------------------2
2. Membranous sections generally branch ------------------------------------------3
3. Second-order bladelets arising on the leading margins of latticework ----------*M. fragilis*
4. Second-order bladelets absent on the leading margins of latticework ----------*M. palmata*
5. Latticework developed lately and feeble ------------------------------------------*M. albida* sp. nov.
6. Latticework partially fragmented and second-order bladelets present --------*M. elegans*
7. Latticework becoming pilose tufts ---------------------------------------------*M. bibarii*
8. Blades without openings, with undulate margins bearing numerous projections ---*M. projecta*
9. Blades heavily perforated, with even and smooth margins ------------------*M. flammifolia* sp. nov.

**Martensia albida** sp. nov.

**Diagnosis:** Thalli epilithici, caespitosi, teges parvas formantes, laminis prostrates et erectis constatis, candidi vel albi-dii, 4-8 cm alti. Rhizoida filamentosa, multicellulara, marginibus basaliibus exorientia. Laminae erectae, elongatae laterali-ter, valde undulatae et implexae, marginibus integeribus, lobos flabellatos margine dorsali efferentes, 2-4-stratae, 100-180 \( \mu \text{m} \) crassae. Cellulae corticales planae, aspectu pagina di 5-7-angulæ angulis obtusis, 40-80 \( \mu \text{m} \) longe, 30-50 \( \mu \text{m} \) latae 5(15) \( \mu \text{m} \) crassæ. Cellulae medullales oblongæ, aliquot pit-connexionibus, 15-35 \( \mu \text{m} \) crassæ. Cellulae vegetativaë laminae generatim per lineas perpendicularis versus paginam laminae cumulatae. Reticula imbicella nuper secus margines supremos laminae facta, rara. Principites margines angusti, cum vel sine prominentiis pusillis, 100-120 \( \mu \text{m} \) lati. Tetrasporangia in lamina portata, in parvos circulares so ros involucro communi, globosas, tetraedrice divisa, 110-130 \( \mu \text{m} \) diametro. Structurae reproductiove ceterae ignotae.

Thalli are epilithic, caespitose, form small mats, composed of prostrate and erect blades, white or milky white, and are 4-8 cm high. Rhizoids are filamentous, multicellular, and arise from the basal margins of the blades. Blades are erect, laterally elongated, strongly undulated and tangled, with entire margins, give rise to flabellate lobes from the dorsal margin, comprise three to six cell layers, and are 100-180 \( \mu \text{m} \) thick. Cortical cells are flat, pentagonal to heptagonal with obtuse corners in the surface view, 40-80 \( \mu \text{m} \) long, 30-50 \( \mu \text{m} \) wide, and 5-15 \( \mu \text{m} \) thick. Medullary cells are oblong, with several pit-connections, and 15-35 \( \mu \text{m} \) thick. The vegetative cells of the blade are generally stacked in anticlinal lines. Weak latticeworks are formed late on the uppermost margins of the blade and they are rare. Leading margins are narrow, with or without small projections, and 100-120 \( \mu \text{m} \) wide. Tetrasporangia are borne on the blade in small round sori with a common envelope; they are globose, tetrahe- drally divided, and 110-130 \( \mu \text{m} \) in diameter. Other repro-
ductive structures are unknown.

**Korean Name:** Myeongjubidanmangsa (명주비단망사)

**Holotype:** LYP-1547 Hamdeog, Jeju Island 2002-05-23, ⊕, Y. Lee; The Herbarium of Cheju National University.

**Type Locality:** The subtidal region at 5-8 m depths off the coast of Hamdeog, Jeju Island, Korea.

**Etymology:** The specific epithet ‘albida’ indicates that plants of this species appear white under water.

**Vegetative morphology:** The thalli are pure white or milky white under water but turn to grayish white or greenish white when exposed in air or fixed in formaline/seawater (5%), or dull red when dried on herbarium sheets, whereas the latticework of fully grown specimens is red or brownish red irrespective of the conditions (Fig. 2A, B). The thalli consist of the prostrating blade and several lobes and are 4-8 cm high. The prostrating blades are contorted, tangled, and give rise to rhizoids and lobes from the ventral and dorsal margins, respectively. The rhizoids arise in bundles from the base of the blade. Two types of rhizoid, monosiphonous and polysiphonous, are mixed in the bundle, and the polysiphonous type is generally longer than the monosiphonous type (Fig. 2C). The lobes on the dorsal margins of the prostrating blades develop into flabellate blades that often form a latticework along the distal margin. The lobes are simple or seldom branched, often diverged, with entire margins, 100-180 µm thick, and gradually thicker downwards. The cells of the membranous section are rather flat, pentagonal to heptagonal with obtuse corners in the surface view, oblong to ellipsoid in the transverse section, have several pit-connections with neighboring cells, and are stacked in anticlinal lines (Fig. 2E, F). The cortical cell walls are very thick and glossy in the region facing the surface of the blade (Fig. 2E). Chloroplasts are distributed near the cell walls of all vegetative cells and are small, discoid or ellipsoid, and ca. 2 µm in diameter. The latticeworks are formed along the distal margins of the lobes, develop late, with a narrow leading margin, and are rather feeble because the cross-connecting strands are arranged in a unidirectional orientation (Fig. 2H). In a thallus (LYP-1549, on the slide glass), double latticeworks are observed, of which the second-order latticework develops directly along the narrow leading margin without forming such subsidiary structures as spatulate projections, lobes, or partial expansion of the leading margin (Fig. 2I).

**Reproductive morphology:** Tetrasporangia are borne in small roundish sori on the longitudinal lamellae of the latticework and the membranous section of the blade; they are globose with tetrahedral divisions and 110-130 µm in diameter (Fig. 2D, G). The envelope of the tetrasporangial sori comprises two cell layers. The tetrasporangial sori are borne on the membranous section of the blade lacking the latticework. However, the tetrasporangia are borne on both the longitudinal lamellae of the latticework and the membranous section or only on the longitudinal lamellae when the blade has a fully grown latticework. Consequently, it seems that the longitudinal lamellae of the latticework in *M. albida* are dominant over the membranous section in the production of tetrasporangia.

**Habitats:** Plants of *M. albida* may grow along the entire coast of Jeju Island. This species grows luxuriantly from April to June and is found in August, September, and January, albeit rarely. However, it is difficult to determine whether this species is perennial because plants found in the spring disappear from those locations in the fall of the same year.

**Specimens examined:** LYP-1393 (Sinchon, Jeju Island 2000-04-22); LYP-1394 (Jongdal, Jeju Island 2000-09-03); LYP-1395 (Jongdal, Jeju Island 2000-12-07); LYP-1396 (Jongdal, Jeju Island 2000-12-19, analysis); LYP-1397 (Jongdal, Jeju Island 2001-01-11); LYP-1398 (Jongdal, Jeju Island 2001-04-07); LYP-1400 (Hyeongjesom, Jeju Island 2001-06-22); LYP-1545 (Hamdeog, Jeju Island 2002-05-11); LYP-1546 (Hamdeog, Jeju Island 2002-05-11); LYP-1547 (Hamdeog, Jeju Island 2002-05-23, ⊕, analysis); LYP-1548 (Hamdeog, Jeju Island 2002-06-19); LYP-1549 (Haye, Jeju Island 2002-08-22); LYP-1585 (Hamdeog, Jeju Island 2002-05-11); LYP-1677 (Hamdeog, Jeju Island 2003-06-05); LYP-1678 (Hamdeog, Jeju Island 2003-07-04, ⊕, 2003-203); LYP-1930 (Sinchon, Jeju Island 2001-04-07); LYP-1947 (Hamdeog, Jeju Island 2002-05-11); LYP-1952 (Jongdal, Jeju Island 2003-06-15, 2003-207); LYP-1962 (Jongdal, Jeju Island 2003-04-24, coll. B. Kim R-283).

**Remarks:** Thalli of *M. albida* grow on rocks in 5-8-m-deep subtidal regions. They are caepitose, form small populations, and are easily perceptible in the field because of their peculiar bright white color. This thallus habit is easily distinguished from other species, such as *M. australis, M. fragilis, M. elegans*, and *M. palmata* because thalli of these other species are clustered in bunches of blades. The thallus habit of *M. albida* is quite similar to that of *M. lewisiae*, although the two species are easily distinguished by the color of the thallus (Lin et al. 2004). The color of the plants may be unique among the described species of the genus *Martensia*. Reddish lamel-
lae inside the cortical cells wall are not perceptible. It is of interest to determine whether lamellae are absent or simply no visible because they lack color.

The latticework of \textit{M. albida} is developed late compared to the membranous section and is very feeble, as in \textit{M. lewisiae} and \textit{M. projecta} (Lin et al. 2004; Lee 2005).

However, in \textit{M. albida} the tetrasporangial sori are borne on the longitudinal lamellae of the latticework more dominantly than on the membranous sections, whereas those of \textit{M. lewisiae} are rarely borne on the latticework (Lin et al. 2004). The tetrasporangial sori in \textit{M. projecta} are absent on the latticework (Lee 2005). The double lattice-
work in *M. albida* is also unique in the genus *Martensia*, although it occurs rarely. *Martensia albida* is related to *M. pavonia* in having a second-order latticework that is directly formed along the leading margins of the first-order latticework (Taylor 1960; Littler et al. 1989). However, the membranous sections between the first- and second-order latticeworks in *M. pavonia* are partially or entirely expanded; these membranous sections do not resemble the leading margins of the latticework. The leading margins of the latticework in *M. albida* are narrow and have the same width across the whole length, even in the parts forming the second-order latticework. The second-order latticeworks are generally formed on the distal margins of the spatulate projections or lobes, which are developed along the outer edges of the leading margins of the first-order latticework in *M. fragilis* and *M. jejuensis*.

**Martensia australis** Harvey 1855: 537.


**Korean Name:** 호주비단망사


**Type Locality:** King George Sound, Western Australia (Harvey 1855: 537).

**Distribution:** Korea, Australia, Philippines, Japan.

**Vegetative morphology:** Thalli are epilithic, grow solitarily in a bunch of several blades, deep purplish blue, irradiant, and up to 25 cm high (Fig. 3A, B, C). The blades are compartmented into the membranous sections proximally and the latticework distally. The membranous sections are flabellate to almost circular, or obovate to broadly clavate, seldom branch, comprise 4-11 cell layers, and are 100-300 µm thick (Fig. 4H, I). The cortical cells of the membranous sections are flat, 5-7-angled with obtuse corners in the surface view, oblong to ellipsoid with somewhat protruding corners in transverse sections, 30-60 µm long, 25-45 µm wide, and 25-40 µm thick (Fig. 4B, H, I). The medullary cells are similar to the cortical cells. Generally, the vegetative cells in the membranous sections are stacked in antical lines (Fig. 4H, I). Chloroplasts are disposed parietally, small, discoid, and ca. 2 µm in diameter. The latticework is formed early in the development of the blade and is usually longer and wider than the membranous sections, flabellate to ellipsoid, compacted with small mesh, and retains the entire form. Usually, the full-grown latticeworks are more or less concave in the middle because the growth of the longitudinal lamellae continues over the expansion of the leading margins (Fig. 3B). The leading margins are narrow, with dentate or smooth outer edges, and about 2 mm wide (Fig. 3D). Spatulate projections or second-order bladelets are rarely formed on the outer edges of the leading margins. The longitudinal lamellae of the latticeworks are two cell layers thick, of even width along the entire length, and ca. 2 mm wide (Fig. 3E). The longitudinal lamellae generally have smooth margins, although they have spinelike projections on the margins in older latticeworks. The cross-connecting strands are bidirectional, fairly actively formed, subdivide the original mesh, and are linear to laminate (Fig. 4A). The latticework of *M. australis* is very compact with small mesh, has a somewhat heavy texture, and is distinct from those of the other described species of *Martensia* (Fig. 3D).

**Reproductive morphology:** Cystocarps are formed on the longitudinal lamellae of the latticeworks and are globose, with a slightly protruding ostiole, and 1.3-1.8 mm in diameter. The gonimoblasts are composed of ellipsoid cells, branch dichotomously and three-dimensionally, and produce carposporangia terminally (Fig. 4G). Generally, two carposporangia are borne on the tip of the gonimoblasts; the terminal carposporangium is comparatively larger and mature, whereas the intercalary carposporangium is immature and hemispherical to cylindrical with a concave base. The carposporangia are deep red, pyriform, 100-120 µm long, and 50-60 µm wide (Fig. 4D). The spermatangial sori are borne on both surfaces of the longitudinal lamellae of the latticework, variously discoid in the surface view, and faintly colored (Fig. 3F). Spermatangial mother cells are ovoid, bear a spermatangium on the mucronate tip, 7-10 µm long, and ca. 5
µm in diameter (Fig. 4F). Spermatangia are ellipsoid, 5-6 µm long, and 3-4 µm in diameter. Tetrasporangia are borne in small sori, globose with tetrahedral divisions, and 100-110 µm in diameter. The tetrasporangial sori are variously roundish, with a cell-layered envelop, biconvex, and usually borne on the longitudinal lamellae and seldom on the membranous sections.

**Habitats:** Thalli grow solitarily on rocks or shells in

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**Fig. 3.** *Martensia australis* Harvey. A. Thallus (LYP-1551). B. Thallus (LYP-1932) in liquid preserved condition. C. Thallus (LYP-1559) with cystocarps in liquid preserved condition. D. Latticework. E. Longitudinal lamellae bearing tetrasporangial sori (black dots). F. Spermatangial sori in surface view.
Fig. 4. *Martensia australis* Harvey. A. Bidirectional cross-connecting strands in latticework. B. Cortical cells in surface view. C. Tetrasporangia in surface view. D. Carposporangia. E. Transverse section of longitudinal lamellae bearing tetrasporangial sori. F. Transverse section of longitudinal lamellae bearing spermatangial sori. G. Carposporophyte. H. Transverse section of the middle part of blade. I. Transverse section of the lower part of blade.
the 5-8-m-deep subtidal region along the northern coasts of Jeju Island. The thalli appear from February to July on Jeju Island; the tetrasporangial and female cystocarpic plants are found from April to July, whereas the male gametangial plants are only found in April. Cystocarpic plants are more dominant in July than tetrasporangial

Specimens examined: Lectotype in TCD Herb. Harvey Aust. Alg. Exsic. 111-B, KGS; LYP-700 (Tabdong, Jeju Island 1951, Gimnyeong, Jeju Island 2003-06-16, coll. B. Kim); LYP-1555 (Hamdeog, Jeju Island 2002-04-11, , , ); LYP-1556 (Hamdeog, Jeju Island 2002-04-27, , , ); LYP-1557 (Hamdeog, Jeju Island 2002-05-16, , , , analysis); LYP-1558 (Hamdeog, Jeju Island 2002-05-11, , , , , coll. B. Kim, analysis); LYP-1559 (Hamdeog, Jeju Island 2002-05-23, , , ); LYP-1560 (Hamdeog, Jeju Island 2002-06-19, , , ); LYP-1563 (Hado, Jeju Island 1984-04-14, coll. J. Yoon); LYP-1920 (Hansoo, Jeju Island 2003-06-05, , , analysis); LYP-1936 (Woljeong, Jeju Island 2003-04-16, , , Coll. S. Cho); LYP-1937 (Biyangdo, Jeju Island 2003-04-25, , , 2004-298, analysis ?); LYP-1939 (Hamdeog, Jeju Island 2003-06-05, , , , analysis); LYP-1951 (Gimnyeong, Jeju Island 2003-06-16, , , coll. B. Kim); LYP-1954 (Hamdeog, Jeju Island 2003-06-17, , , coll. MBC H. Kang); LYP-1960 (Hengwon, Jeju Island 1988-05-29, coll. K.C.H.); LYP-1965 (Hamdeog, Jeju Island 2003-07-04, , , ).

**Martensia gigas** Harvey: Specimens from King George Sound, Western Australia, in TCD Herb. Harvey (see Womersley 2003: 98).

**Remarks:** The examined plants agreed well with the lectotype of *M. australis* deposited in the Herbarium of Trinity College, Dublin, Ireland (TCD, Harvey 1858). The latticework of *M. australis* is a characteristic deep brownish red, generally ellipsoid, concave in the center, compacted with small mesh, retains its intact form, and feels like velvet. The leading margins of the latticework in *M. australis* are rather narrow, with dentate outer edges, and rarely with spatulate projections that become second-order bladelets. The thalli of *M. australis* are morphologically similar to those of *M. fragilis*. However, in *M. fragilis*, the mesh of the latticework becomes gradually larger distally, and the second-order bladelets are numerous on the leading margins of the latticework. Millar (1990) recognized the flabellate membranous sec-


Figs 5, 6.

**Martensia bibarii** Y. Lee 2004: 258.

**Korean Name:** 비바리비단망사

**Holotype:** CNU (LYP-1594, Cheju National University, Jeju. Herb. Y. Lee).

**Type Locality:** Subtidal regions at 68 m depths off Jongdal, Jeju Island, Korea, 2000-07-07 (Lee 2004: 258).

**Distribution:** Korea.

**Vegetative morphology:** Thalli are epiphytic, ribbon-like with short lateral lobes and branches, purplish red or purplish blue, fluorescent, and up to 25 cm high (Fig. 5A, B, C). Thalli grow solitarily or in groups on a host and form large populations in subtidal regions. The blades are membranous and give rise to numerous lobes along both margins; they are undulate, convoluted, branch rarely, with partially uneven width and thickness, sometimes partially transform into stipe-like structures, and three to five cell layers thick (Fig. 6A). The lobes are generally short, without a stalk, without a constriction at the base, and with a terminal or subterminal latticework. Occasionally, the lobes elongate linearly and have lateral and terminal lobes as branches. The cortical cells are tetragonal to octagonal in the surface view, oblong to triangular in transverse sections of the blade, 30-55 µm long, 25-35 µm wide, and 15-20 µm thick. The medullary
cells are globose to ellipsoid in transverse sections of the blade, 50-75 µm long and 20-40 µm thick. The cells of the blades are arranged rather irregularly, whereas those of the lobes show the arrangement of regularly stacked sets in anticlinal lines. Chloroplasts are very small, compacted in the cortical cells, discoid, and up to 2 µm in diameter. The latticework is formed early in the development of the lobes, quite pliable, and transforms into pilose tufts; it is weak, organized with loose and coarse mesh, with narrow leading margins, and has few cross-connecting strands (Fig. 6B). The pilose tufts are derived from the free longitudinal lamellae of the latticework caused by fragmentation of the leading margins and cross-connecting strands. The free longitudinal lamellae expand slightly and are up to 1 mm wide.

Reproductive morphology: Tetrasporangia are formed in the middle region of the membranous sections, the latticework, and the lower region of the pilose tufts; they are borne in small round sori and are globose, with tetrahedral divisions, and 65-95 µm in diameter. No tetrasporangia are formed on the membranous section of the lobes.

Habitats: The plants of *M. bibarii* are epiphytic on the thalli of *Gelidium amansii* (Lamouroux) Lamouroux, *Pterocladia capillacea* (Gmelin) Santelices et Hommersand, and *Lomentaria catenata* Harvey, among other species, and generally grow luxuriantly and form rather broad populations from May to July. The plants are found from December to July, whereas they do not occur from August to November. Plants bearing tetrasporangia are found only in July and September. The host plants grow in populations in lower tidal to subtidal regions or in large rock pools. However, plants of *M. bibarii* are epiphytic only on thalli of hosts growing in subtidal regions.

Specimens examined: Holotype (LYP-1594, Jongdal, Jeju Island 2000-12-07, @); Syntype (LYP-1654, Jongdal, Jeju Island 2000-12-07, @, analysis); LYP-1584 (Jongdal, Jeju Island 2000-06-29, analysis); LYP-1597 (Jongdal, Jeju Island 2001-02-11, analysis); LYP-1598 (Jongdal, Jeju Island 2000-03-25, analysis); LYP-1603 (Jongdal, Jeju Island 2000-08-03, @, syntype, analysis); LYP-1604 (Seogeondo, Jeju Island 2001-06-24); LYP-1605 (Boogchon, Jeju Island 2001-07-05, @); LYP-1606 (Haye, Jeju Island 2001-12-20, @, coll. B. Kim, analysis); LYP-1608 (Guideog, Jeju Island 2002-06-23, coll. M. Kim); LYP-1610 (Jongdal, Jeju Island 2000-01-28, coll. K. Yang); LYP-1611 (Jongdal, Jeju Island 2000-02-13); LYP-1612 (Jongdal, Jeju Island 2000-03-25, Phyco. Res. 52, fig. 23); LYP-1614 (Jongdal, Jeju Island 2000-05-21, analysis); LYP-1615 (Hamdeog, Jeju Island 2002-05-23); LYP-1616 (Jongdal, Jeju Island 2000-06-29); LYP-1618 (Jongdal, Jeju Island 2000-12-19, @); LYP-1620 (Jongdal, Jeju Island 2001-02-11); LYP-1621 (Jongdal, Jeju Island 2001-03-03); LYP-1622 (Boogchon, Jeju Island 2001-07-05, @); LYP-1623 (Seogeondo, Jeju Island 2001-06-24); LYP-1624 (Hamdeog, Jeju Island 2002-06-19); LYP-1625 (Jongdal, Jeju Island 2001-01-11); LYP-1626 (Jongdal, Jeju Island 2000-04-22); LYP-1629 (Boogchon, Jeju Island 2001-07-05, @, analysis); LYP-1630 (Jongdal, Jeju Island 2000-12-19, @); LYP-1631 (Jongdal, Jeju Island 2000-07-16, analysis); LYP-1638 (Jongdal, Jeju Island 2000-05-21); LYP-1655 (Jongdal, Jeju Island 2001-01-11); LYP-1656 (Jongdal, Jeju Island 2002-03-24, coll. B. Kim); LYP-1659 (Jongdal, Jeju Island 2000-12-19, analysis); LYP-1914 (Hamdeog, Jeju Island 2003-04-27, analysis); LYP-1925 (Ham, Jeju Island 2003-04-27, coll. B. Kim); LYP-1926 (Hamdeog, Jeju Island 2003-07-04, @); LYP-1931 (Guideog, Jeju Island 2002-06-23, coll. M. Kim); LYP-1940 (Hamdeog, Jeju Island 2003-06-05, analysis); LYP-1941 (Ham, Jeju Island 2003-06-05, analysis); LYP-1946 (Jongdal, Jeju Island 2003-06-05); LYP-1957 (Hamdeog, Jeju Island 2003-06-05); LYP-1961 (Jongdal, Jeju Island 2000-07-16, @).

Remarks: *Martensia bibarii* is quite distinct in terms of the latticework and pilose tufts on the terminal region of every lateral lobe and the apex of the blades, and the long, linear, twisted blades with several lobes along the entire margins. The pilose tufts are derived from the longitudinal lamellae of the latticework. As in the latticeworks of other species of *Martensia*, the latticeworks of *M. bibarii* also comprise narrow leading margins and coarse mesh consisting of longitudinal lamellae and cross-connecting strands. However, the latticeworks of *M. bibarii* retain the network organization early in latticework development, but later leave the longitudinal lamellae free because the leading margins and cross-connecting strands of the latticework are fragmented. Occasionally, some cross-connecting strands persist near the base of the pilose tufts. The blades of *M. bibarii* are usually ribbon-shaped, more or less twisted, with highly dentate margins, and occasionally transform into narrow and thick stipe-like structures (Fig. 6A). The lateral lobes of the stipe-like blade become flabellate with short stalk-like structure. Thus, the thallus morphology of *M. bibarii* is not related to that of the other described species of *Martensia*. The second-order latticework in *M. jejuensis* also transforms into pilose tufts. However, *M. bibarii* is easily distinguished from *M. jejuensis*, which has flabel-
Fig. 5. Martensia bibarii Y. Lee. A. Holotype (LYP-1594). B. Thallus (LYP-1612) in liquid preserved condition. C. Thallus (LYP-1598) with stipe-like blades.
late blades.

The specimens (LYP-1603, LYP-1606) from Haye and Jongdal, Jeju Island, are identical to *M. jejuensis* in molecular analyses of the ITS 1 region in the nrDNA. However, the specimens were identified as *M. bibarii* on the basis of morphological characters.

*Martensia elegans* Hering 1841: 92.

*Fig. 6. Martensia bibarii* Y. Lee. A. Stipe-like structure (arrow, LYP-1612). B. Latticework (LYP-1629).

*Capraella elegans* (Hering) J. De Toni 1936; Papenfuss 1942: 449.


**Korean Name:** Gounbidanmangsa (고운비단망사)

**Type:** ? Isotypes UC1025434; UC1468396 (Millar 1990).

**Type Locality:** Port Natal [Durban], South Africa (Hering 1841: 92).

**Distribution:** Korea, Australia, Mauritius, and other localities (see Silva *et al.* 1996).

**Vegetative morphology:** Thalli are epiphytic, solitary, grow in bunches of several blades, pale purplish white or purplish red, and 6-8 cm high (Fig. 7A, D). The blades are flabellate, simple or furcated, with entire or dentate margins, slightly undulate along the margins, two to four layers in the central regions and up to ten layers at the base, and 100-300 µm thick (Fig. 7G, H). The cortical
cells of the membranous sections are flat, 40-80 μm long, 20-50 μm wide, and 20-50 μm thick; they are usually 5-7-angled with obtuse corners or somewhat round in the surface view and usually ellipsoid or oblong in the transverse section (Fig. 7F, Fig. 8A). The walls of the cortical cells are more or less thickened in the region facing the surface of the blades (Fig. 7G). Medullary cells are ellipsoid to oblong and somewhat thicker than the cortical cells. The vegetative cells in the lower region of the membranous section are more regularly stacked in anticlinal lines. Chloroplasts are numerous, assembled near the cell branous section are more regularly stacked in anticlinal lines. Chloroplasts are numerous, assembled near the cell walls, small, ellipsoid, and ca. 2 μm long (Fig. 8A). Latticeworks are formed early in the development of the blade, generally flabellate or rarely ellipsoid, comprise coarse and large mesh, retain the entire form, and are almost the same size as the membranous section. The leading margins of the latticeworks are entire or with spinelike projections and 30-50 μm wide (Fig. 7B, C). The longitudinal lamellae of the latticeworks are long, ribbon-shaped, with entire margins, and 40-60 μm wide. The cross-connecting strands are of usually unidirectional or rarely bidirectional orientation and often arranged in double rows (Fig. 7E).

**Reproductive morphology:** Tetrasporangia are borne in roundish and biconvex sori with a common envelope, on both the longitudinal lamellae and membranous sections; they are globose, with tetrahedral divisions, and 80-100 μm in diameter. The tetrasporangia are borne more dominantly in the latticeworks than in membranous sections. Spermatangial sori are principally formed along both surfaces of the longitudinal lamellae and rarely in the marginal region of the membranous sections, and they are ellipsoid and discolored. Spermatangia attaching to the spermatangial mother cells are ellipsoid, 5-6 μm long and 2-3 μm wide. Cystocarps are formed mainly in the latticework and rarely along the margins of the membranous sections and are globose, with a slightly protruding ostiole, and are 0.9-1.3 mm in diameter (Fig. 8B, E). Gonimoblasts comprise irregularly inflated cells that are rather pellucid, dichotomous in three-dimensional orientation, and form carpospores on every tip (Fig. 8H). Carpospores are dark red, pyriform to ellipsoid, and 100-120 μm long and 50-60 μm in diameter (Fig. 8D). Immature carpospores are also dark red, D-shaped or rectangular, borne in chains of two, and are 70-90 μm in diameter (Fig. 8G).

**Habitats:** The plants of *M. elegans* grow on rocks or on other algae in 5-8-m-deep subtidal regions from June to August while the male and female gametangial plants are found in June and July.

**Specimens examined:** TCD Herb. Harvey (Port Natal, South Africa, coll. Dr. Krauss, Dr. Stanger, and Dr. Gueinzius); SAP 060953 (Rocky Bay, South Africa, 1988-02-20, coll. T. Horiguchi); SAP 060954 (Palm Beach, South Africa, 1987-05-14, coll. T. Horiguchi); SAP 060955 (Rocky Bay, South Africa, 1987-10-25, coll. T. Horiguchi); LYP-1561 (Jongdal, Jeju Island 2000-07-16, ♂, ♀, analysis); LYP-1562 (Jongdal, Jeju Island 2000-08-03, ♀); LYP-1577 (Moonseom, Jeju Island, 2005-06-26, ♂, ♀, ♂♂, coll. Y. Ko); LYP-1657 (Hamdeog, Jeju Island, 2003-07-04, ♀, ♀♀, analysis); LYP-1950 (Hamdeog, Jeju Island, 2003-06-05).

**Remarks:** The examined plants of *M. elegans* from Jeju Island agreed quite well with specimens from Port Natal, South Africa (deposited in TCD Herbarium and the Herbarium Hokkaido University, Sapporo, Japan [SAPI]) in terms of the features and color of the blade and latticework. However, the leading margins of the latticework in the gametangial plants of *M. elegans* from Jeju Island have numerous spinelike projections on the outer edges although no second-order bladelets are formed (Figs. 7B, 8B). The tetrasporangial sori are borne on both the membranous sections and the latticework in plants from Jeju Island as in plants from Mauritius and Port Natal, South Africa (SAP 060954), although they are borne only on the latticework in plants from Australia and Japan (Børgesen 1952; Millar 1990; Yoshida and Mikami 1996). Moreover, cystocarps or spermatangial sori are borne in the latticework and rarely on the membranous sections of the plants from Jeju Island, although no sexual reproductive structures are observed on the membranous sections of plants from South Africa (Figs. 7B, D, 8B, E). As indicated by Millar (1990), the thalli of *M. elegans* are similar to the juvenile thalli of *M. australis*. The peculiarity of *M. elegans* is that the membranous sections are purplish white and the latticework is flabellate with a narrow leading margin. However, the plants from Jongdal, Jeju Island (LYP-1562), have an ellipsoid latticework comprising coarse and large mesh.

*Martensia flammifolia* sp. nov.

Fig. 9.

**Diagnosis:** Thalli epilithici, membranacei, ruberis, lamina una constatit, per rhizoides exortes base thalli ad substratum affixi, reticulum deficientes, 15-25 cm alti. Bases thalli cuneatae, eliquum rhizoidea emittentes. Laminae supra hapteron basale expansae, maximam partem uninistratae, tristratae ad regionem basalem, marginibus integris, plerunque lacer-
Fig. 7. *Martensia elegans* Hering. A. Thallus (sterile, LYP-1594). B. Spinelike projections on the leading margin of latticework. C. Leading margin with entire edge. D. Female thallus bearing cystocarps (black dots). E. Unidirectional orientation of the cross-connecting strands in latticework. F. Cortical cells in surface view. G. Transverse section of the middle part of blade. H. Transverse section of the lower part of blade.
atae vel divergentes, ad regionem mediam pertusae, subdichotome ramificantes, 40-100 μm crassae. Cellulae aspectu paginali 5-7-angulae, oblongae in sectione transversali, aliquot pit-connexionibus, 50-75 μm longae, 30-45 μm latae, 30-40 μm crassae. Chloroplasti numerosi, discoidei vel lineares, 4-8 μm longi, 3-5 μm diametro. Tetrasporangia globose divisione tetraedrica, 70-80 μm diametro. Structurae reproductivae ceterae ignotae.

Thalli are epilithic, membranous, red, composed of one blade, attached to the substratum by several rhizoids arising from the base of the thallus, lack latticework, and are 15-25 cm high. The base of the thallus is cuneate and gives rise to several rhizoids. Blades are expanded above the basal holdfast, mostly one-layered, three-layered in the basal region, with entire margins, generally lacerated or diverging, perforated at the center region, branch sub-

dichotomously, and are 40-100 µm thick. Cells are 5-7-angled in the surface view, oblong in the transverse section, with several pit-connections, 50-75 µm long, 30-45 µm wide, and 30-40 µm thick. Chloroplasts are numerous, ellipsoid to linear, 4-8 µm long and 3-5 µm in diameter. Tetrasporangia are globose with tetrahedral division and 70-80 µm in diameter. Other reproductive structures are unknown.

**Korean name:** Minbidanmangsa (민비단망사).

**Holotype:** LYP-1969 Biyangdo, 2004-04-13, ♂, S. Cho; The Herbarium of Cheju National University.

**Type locality:** On the artificial substratum in the subtidal region at 12 m depths off Biyangdo, Jeju Island.

**Vegetative morphology:** Thalli are epilithic, membranous, comprise a single blade, attach to the substratum with several rhizoids arising from the base, highly perforated at the middle portion, lack a latticework, and are 15-25 cm high (Fig. 9A). The base of the thallus is cuneate and gives rise to several rhizoids that are mono- or polysiphonal (Fig. 9B). The haptera are not formed on the surface of the blades. The blades are expanded immediately above the base and acquire a flabellate form, simple or occasionally furcated or lacerated into two to three segments at the lower regions, perforated and tattered in the middle regions, give rise to several branches, one layer thick except in the lower portion and the tetrasporangial sori, and are 40-100 µm thick. The perforation occurred only in the middle region of the blades in all specimens observed in this study. The perforation may result in tatters of the middle portion of the blade and partial fragmentation of the upper parts of the blade. Also, the margins of the middle regions of the blade are ragged. The branches are borne laterally and terminally from the margins of the upper parts of the blade, horn-shaped, and with rather acute apices. The margins of the blade are generally smooth or occasionally with one or two cell protrusions and slightly undulate. The lower part of the blade and the tetrasporangial sori comprise three cell layers (Fig. 9G, H). The vegetative cells in the monolayered parts are pentagonal to heptagonal with obtuse corners in the surface view, oblong in transverse sections, 50-75 µm long, 20-30 µm wide, and 30-40 µm thick (Fig. 9D, F). The cells in the multilayered part are the same shape in the surface view as those in the monolayered part, but transversely ellipsoid to oblong in transverse section and are 20-25 µm thick (Fig. 9H).

Several granules are observed in the vegetative cells near the margins of the blade, which are rather glossy, ellipsoid, 7-15 µm long and 3-7 µm in diameter (Fig. 9C).

However, further studies are needed to determine whether the granules are species-specific because they do not occur in all cells near the margins of the blade. The chloroplasts are discoid to ellipsoid, numerous, aggregated near the cell walls, 4-8 µm long, and 3-5 µm in diameter (Fig. 9D).

**Reproductive morphology:** Several tetrasporangia are borne in a common envelope as small and roundish sori in the upper portion of the blade, globose with tetrahedral divisions, 70-80 µm in diameter (Fig. 9E). The tetrasporangial sori are biconvex in transverse section, and are absent in the perforate middle and basal multilayer portions of the blade (Fig. 9G).

**Habitats:** Plants of *M. flammifolia* grow on artificially constructed concrete substratum in the 12-15-m-deep sand bottom off Biyangdo Islet, Jeju Island.

**Specimens examined:** LYP-1969 (Biyangdo, Jeju Island 2004-04-13, ♂, 2004-209, analysis).

**Remarks:** Martensia flammifolia lacks a latticework. Thus, this taxon is more related to *Opephyllum* than to *Martensia*. Schmitz (in Schmitz and Hauptfleisch 1897) established the genus *Opephyllum* on the basis of plants from Mindanao Island, the Philippines, of which the monotypic species is *O. martensii* (De Toni 1900; Kylin 1956). Papenfuss (1962) suggested that *Opephyllum* may be synonymous with *Martensia*. Wynne (1996) distinguished the genus *Martensia* as having fairly regular latticeworks compared to the genus *Opephyllum*, which has numerous openings of various sizes. Recently, Lin *et al.* (2001) neotypified the species *O. martensii* based on topotype collections and synonymized the genus *Opephyllum* with *Martensia* based on the results of molecular analyses of *rbcL* and LSU rDNA. The thalli of *M. flammifolia* differ from those of the other species of *Martensia* in lacking the latticework, comprising a single blade that is mostly monolayered, having perforations of various sizes, a cuneate base, and large chloroplasts. Consequently, it seems to be an artificial classification that a taxon with such different characteristics is considered a member of the genus *Martensia*. Some characters, such as the shape of the vegetative cells, the formation of tetrasporangial sori, and the molecular analyses of *rbcL* and LSU rDNA, are similar to characters of the tribe Martensiae. Pending further studies on the relationship between *Martensia* and *Opephyllum*, this taxon is described in the genus *Martensia* following the suggestion of Lin *et al.* (2001).

*Martensia flammifolia* is closely related to *M. martensii* in having almost monolayered blades, perforations in the middle region of the blades, and the absence of the lat-
ticework (Lin et al. 2001b). However, *M. flammifolia* is easily distinguished from *M. martensii* by its flabellate blades without branches. *Martensia flammifolia* is also similar to *M. projecta* in the form of the blades and the scarcely visible latticeworks (Lee 2005). However, the former is easily distinguished from the latter by the perforations on the blades, the smooth margins, and somewhat irregular branching.

*Martensia fragilis* Harvey 1854: 145.

Figs 10, 11.

*Martensia fragilis* Harvey 1854: 145; J. Agardh 1863 [1851-1863]: 829; Kützing 1869: 22, pl. 59; De Toni 1900: 617; Svedelius 1908; Børgesen 1919: 348; De Toni 1924:
capillaries along the margins, two to four cell layered, grad-
dichotomously branching, generally with spinelike pro-
Firstly, we observe the anatomical structure of the thallus. The membranous sections are flabellate, simple or
latticework distally and the membranous sections proxi-
trichotomously; they are subspherical, consist of pellucide and fusiform cells, and form a car-
sporophore on every branch tip (Fig. 11D). Carpospores are
dark red, pyriform, 90-100 \( \mu m \) long and 40-50 \( \mu m \) in
diameter (Fig. 11B). Spermatangial sori are formed on
both surfaces of the longitudinal lamellae of the lattice-
work, circular to ellipsoid, and appear as faintly colored
spots in the surface view. Spermatangial sori are also
formed on the leading margins of the latticeworks. The
spermatangial mother cells are ovoid with a sharp point
outward, bear a spermatangium on the tip, and are 12-15
\( \mu m \) long and 2-3 \( \mu m \) in diameter (Fig. 11E). The sper-
matangia attaching to the tip of the spermatangial mother
cells are ovoid to ellipsoid and 2-3 \( \mu m \) in diameter. Tetrasporangia are borne in sori on the longitudinal lamellae and leading margins of the latticeworks, globose, with tetrahedral divisions, and 80-90 \( \mu m \) in diame-
ter (Fig. 11F). The tetrasporangial sori are small, discoid in
the surface view, with a common envelope, and bicon-
 vex in transverse sections (Fig. 11G).

**Habitats:** The plants grow solitarily on rocks and
shells in the lower tidal mark or 5-8-m-deep subtidal
regions along the coast of Jeju Island. *Martensia fragilis*
occurring in April, matures from May to July, and disap-

**Reproductive morphology:** The tetrasporophytes and
gametophytes of *M. fragilis* are isomorphic and the
gametophytes are dioecious. Cystocarps are borne along
the margins of the longitudinal lamellae of the lattice-
works, globose with slightly protruding ostioles, and ca.
1.5 mm in diameter. The carposporophytes are filament-
ous and branch trichotomously; they are subspherical,
consist of pellucide and fusiform cells, and form a car-
spore on every branch tip (Fig. 11D). Carpospores are
dark red, pyriform, 90-100 \( \mu m \) long and 40-50 \( \mu m \) in
diameter (Fig. 11B). Spermatangial sori are formed on
both surfaces of the longitudinal lamellae of the lattice-
work, circular to ellipsoid, and appear as faintly colored
spots in the surface view. Spermatangial sori are also
formed on the leading margins of the latticeworks. The
spermatangial mother cells are ovoid with a sharp point
outward, bear a spermatangium on the tip, and are 12-15
\( \mu m \) long and 2-3 \( \mu m \) in diameter (Fig. 11E). The sper-
matangia attaching to the tip of the spermatangial mother
cells are ovoid to ellipsoid and 2-3 \( \mu m \) in diameter. Tetrasporangia are borne in sori on the longitudinal lamellae and leading margins of the latticeworks, globose, with tetrahedral divisions, and 80-90 \( \mu m \) in diam-
ter (Fig. 11F). The tetrasporangial sori are small, discoid in
the surface view, with a common envelope, and bicon-
 vex in transverse sections (Fig. 11G).

**Habitats:** The plants grow solitarily on rocks and
shells in the lower tidal mark or 5-8-m-deep subtidal
regions along the coast of Jeju Island. *Martensia fragilis*
occurring in April, matures from May to July, and disap-
Fig. 11. *Martensia fragilis* Harvey. A. C. Transverse section of membranous section. B. Carpospores. D. Carposporophyte. E. Transverse section of the longitudinal lamella bearing spermatangial sori. F. Hapteron with a tuft of rhizoids. G. Transverse section of the longitudinal lamella bearing tetrasporangia. H. Cortical cells in surface view. I. Longitudinal section of basal holdfast.
pears in August on the coast of Jeju Island. The juvenile plants of *M. fragilis* are seldom found in March and September. The tetrasporangial plants are found from April to July, the male gametangial plants only in April, and the cystocarpic plants from May to July. The cystocarpic plants are dominant in July, whereas the tetrasporangial and the cystocarpic plants from May to July. The cystocarpic plants are rare at this time.

**Specimens examined:** Lectotype in TDC Harvey Algae of Ceylon, Harvey Alg. Ceylon Exsic. #5; LYP-1966 (Oahu, Hawaii 1978-02, cultured J. A. West); LYP-1553 (Daryeodo, Jeju Island 2001-07-05, ♂, ♀); LYP-1564 (Hengwon, Jeju Island 1988-05-29, ♂, ♂); LYP-1565 (Jongdal, Jeju Island 2000-04-22, ♂); LYP-1566 (Seongsan, Jeju Island 2000-07-17, coll. B. Kim); LYP-1567 (Hansu, Jeju Island 2000-07-06, ♂, ♂); LYP-1568 (Bugcheon, Jeju Island 2001-07-05, ♂); LYP-1569 (Hamdeog, Jeju Island 2002-04-07, ♂, ♀, coll. B. Kim); LYP-1570 (Hamdeog, Jeju Island 2002-04-11, ♂, ♀, ♀, ♂); LYP-1571 (Hamdeog, Jeju Island 2002-05-11, ♂, ♀, ♀); LYP-1572 (Hamdeog, Jeju Island 2002-06-19, ♂, ♀); LYP-1573 (Hamdeog, Jeju Island 2002-05-23, ♂, ♀); LYP-1574 (Hamdeog, Jeju Island 2002-06-19, ♂, ♀); LYP-1575 (Seongsan, Jeju Island 2002-06-15, ♂, ♀); LYP-1583 (Haengwon, Jeju Island 2000-06-04, ♂, coll. B. Kim); LYP-1588 (Haengwon, Jeju Island 2000-06-04, ♂, coll. B. Kim); LYP-1587 (Jongdal, Jeju Island 2000-09-03, ♀); LYP-1592 (Moonjuranseom, Jeju Island 2001-06-23); LYP-1613 (Hamdeog, Jeju Island 2002-04-11); LYP-1632 (Hamdeog, Jeju Island 2003-07-04, ♂, ♀); LYP-1672 (Jongdal, Jeju Island 2000-03-25); LYP-1693 (Hamdeog, Jeju Island 2003-07-04); LYP-1915 (Yonggoondo, Jeju Island 2002-04-11, ♂); LYP-1916 (Hansoo, Jeju Island 2003-05-11, ♂); LYP-1917 (Yongdang, Jeju Island 2003-06-13, ♂, ♂); LYP-1927 (Hamdeog, Jeju Island 2003-07-04, ♂, ♀); LYP-1935 (Hamdeog, Jeju Island 2003-06-05, ♂, ♂); LYP-1943 (Ongpo, Jeju Island 2004-04-25, 2004-04-25, 2004-04-25); LYP-1953 (Hamdeog, Jeju Island 2003-06-17, ♂, coll. H. Kang, MBC); LYP-1956 (Sinchang, Jeju Island 2003-06-15, 2003-06-15); LYP-1967 (Hamdeog, Jeju Island 2003-06-05).

*Martensia denticulata* Harvey; Syntype in TCD Herb. from Rottnest, West Australia, Harvey Alg. Aust. Exsic. #112.

*Martensia pavonia* (J. Agardh) J. Agardh; Lectotype in LD Herb. Agardh #36296, Guadeloupe, Duchassaing #72.

**Remarks:** The examined plants of *M. fragilis* from Jeju Island agreed well with the lectotype specimen of *M. fragilis* Harvey. However, the plants from Jeju Island are more variable in morphology than the type collections in TCD. The membranous sections of the blades are generally flabellate, simple or dichotomously branching, and occasionally have spinelike projections along the margins. The latticework of the thalli from Jeju Island comprises small mesh, and the latticework is three to five times larger than the membranous section; this character is more related to *M. australis*. Whether the second-order blades are present or absent on the leading margins of the latticework is one of the main aspects used to distinguish *M. fragilis* from *M. australis* in this paper. In *M. fragilis*, the lobes that are formed along the outer edges of the leading margins of the latticeworks develop the latticeworks along the distal margins and appear to be identical to juvenile blades in shape. Thus, the juvenile blades derived from the lobes are termed second-order bladelets. The second-order bladelets are rare on some thalli and numerous on others (Fig. 10A-D).

Okamura (1909, pl. 53) described and illustrated *M. elegans* Hering. However, more than one species of *Martensia* seem to have been included in Okamura’s (1909) plate; his Fig. 1 may be regarded as *M. australis*, Figs. 2 and 3 as *M. bibarii*, and Fig. 4 as *M. fragilis*. Okamura (1936) later described *M. denticulata* and reillustrated all figures except Figs 1 and 3 in the new plate. Millar (1990, p. 417) seemed to regard Fig. 1 as *M. australis*, although the number of the figure may have been miread as Fig. 4 (see Okamura 1909, pl. 53, fig. 4). Yoshida and Mikami (1996) and Yoshida (1998) regarded all figures in the plate (Okamura 1909, pl. 53) as *M. fragilis*.

Kang (1966, 1968) described and presented a figure of *M. denticulata* based on thalli from Mokdo (40323), Bijindo (40321), Chujado (40322), and Jeju Island (40319-20, 40324). Specimens (LYP-1917, LYP-1927, LYP-1956) similar to the figure by Kang (1968, pl. 69, fig. 264) are somewhat rare and are found only in June and July.


Figs. 12.


**Korean Name:** Jejubidanmangsa (제주비단망사)

**Holotype:** CNU (LYP-1586, Cheju National University, Jeju. Herb. Y. Lee).

**Type Locality:** Subtidal regions at 6-8 m depths off Jongdal, Jeju Island, Korea, 2000-08-03 (Lee 2004: 256).

**Distribution:** Korea.

**Vegetative morphology:** Thalli are epiphytic, comprise initial blades and linear axes, yellowish brown, slightly fluorescent, and are 6-25 cm high (Figs. 12A, B). However, the thalli turn red when dried. The initial blades are membranous, flabellate to cuneiform, simple
or furcated at the base, and comprise four to five cell layers. Several discoid haptera are formed on the surfaces of the initial blades. The latticeworks of *M. jejuensis* comprise coarse mesh and thin leading margins, are generally fragmented at the upper part, and leave several longitudinal lamellae free. The free upper parts of the longitudinal lamellae of the latticework elongate, slightly expand, form a long axis with a riblike thickness at the center, and give rise to several projections laterally; the projections are spatulate or spinelike. Occasionally, sev-

eral lobes arise along the margins of the axes. The spatulate projections develop into flabellate blades with second-order latticeworks. Frequently, the free upper parts of the second-order latticeworks elongate continuously and become hair tufts. Juvenile thalli of \textit{M. jejuensis} may differ in morphology from mature thalli because the second-order bladelets and the free axes develop late.

\textbf{Reproductive morphology:} Tetrasporangial sori are borne on the initial blade and the second-order bladelets as well as the axes. The tetrasporangial sori are produced more abundantly on the membranous section and latticework than on the axes. The tetrasporangial sori include several bladelets and the free axes develop late.

\textbf{Habitats:} The plants of \textit{M. jejuensis} grow on other algae, including \textit{Lomentaria catenata} Harvey, \textit{Gelidiwm amansii} (Lamouroux) Lamouroux, and \textit{Pterocladiella capillacea} (Gmelin) Santelices \textit{et} Hommersand, and articulate coralline algae in the subtidal region of Jongdal and Hamdeog, Jeju Island, from May to August. Plants of \textit{M. jejuensis} also occur in rock pools at Seogeondo, Jeju Island, in June.

\textbf{Specimens examined:} LYP-1586 (Jongdal, Jeju Island 2000-08-03, ♂, analysis); LYP-1589 (Haye, Jeju Island 2001-12-20, ♂, coll. B. Kim); LYP-1591 (Hamdeog, Jeju Island 2002-05-23); LYP-1595 (Haye, Jeju Island 2002-08-22, ♂, coll. B. Kim); LYP-1596 (Haye, Jeju Island 2002-08-22, ♂, analysis); LYP-1601 (Jongdal, Jeju Island 2000-06-29, ♂); LYP-1602 (Jongdal, Jeju Island 2000-07-16); LYP-1923 (Hamdeog, Jeju Island 2003-07-04, ♂); LYP-1955 (Hamdeog, Jeju Island 2003-07-04, ♂, analysis).

\textbf{Remarks:} The conspicuous characteristics defining \textit{M. jejuensis} are the flabellate shape of the thallus in broad outline, partially fragmented latticeworks, several long axes derived from the free upper parts of the longitudinal lamellae of the latticeworks, second-order bladelets arising from the axes and the leading margins of the second-order latticeworks, and spatulate or spatulate projections formed along the outer edges of the leading margins of the latticeworks. Generally, no projections are formed along the longitudinal lamellae of the intact latticeworks although several spatulate projections arise in the intact latticeworks in some thalli from Haye, Jeju Island (LYP-1596). Occasionally, the free longitudinal lamellae of the latticeworks on the second-order bladelets do not become the second-order axes but become hairy tufts, which are similar to those of \textit{M. bibarii} (Lee 2004).

The specimens from Haye (LYP-1596) are identical to \textit{M. bibarii} in the molecular analysis of the ITS 1 region in the nrDNA. However, the specimens were identified as \textit{M. jejuensis} on the basis of morphological characters.


\textbf{Fig. 13.}


\textbf{Korean Name:} Jomagsonbidanmangsa (조막손비단망사)


\textbf{Type Locality:} Subtidal regions at 4-6 m depths off the northern slope of Moonseom, Jeju Island, Korea.

\textbf{Distribution:} Korea.

\textbf{Vegetative morphology:} Thalli are epilithic or epiphytic, membranous, flabellate, comprise one to four blades, purplish red, and are 5-7 cm high (Fig. 13A, B). The holdfasts are composed of rhizoids that arise from the lowermost portion of the thalli. Small discoid haptera are additionally formed on various parts of the lower portion of the membranous sections. The blades form several lobes along the distal margins of the membranous sections and have numerous projections along the lateral margins. The membranous sections of the blades comprise two to four cell layers and are 50-120 µm thick. The lobes elongate linearly, are sometimes furcated, and form a latticework on the distal margins. The vegetative cells are generally oblong and stacked in anticlinal lines. Chloroplasts are small, discoid, and congregate along the inside of the cortical cell walls. The latticeworks are formed only on the distal margins of the lobes in the early developmental stages of the lobes, retain the intact figure, and rarely exceed the length of the membranous sections. The leading margins of the latticework are narrow and give rise to numerous spinelike projections along the outer edges. All projections give rise to additional short projections radially on the tips, which are composed of one to several cells. Occasionally, these projections become membranous, grow up to 2-3 mm long, and are furcated two or three times. No second-order bladelets are found on the latticeworks. The longitudinal lamellae of the latticeworks are long, ribbon-shaped, with dentate margins. The cross-connecting strands of the latticeworks are of bidirectional orientation. Double rows of cross-connecting strands occur at some intervals along the longitudinal lamellae of the latticeworks.

\textbf{Reproductive morphology:} The tetrasporophyte of \textit{M. palmata} is isomorphic with the gametophyte. Male and female gametangial thalli are also morphologically simi-
lar. The membranous sections of the female thalli are somewhat undulate and have more projections than those of male or tetrasporangial thalli. Cystocarps may be formed preferentially along the margins of the membranous sections rather than in the latticeworks. Also, they are formed along the edges of the openings of the membranous section when the membranous section is perforated. Spermatangial sori are formed in the middle to upper portions of the membranous sections as well as on the longitudinal lamellae of the latticeworks. Tetrasporangial sori are formed on the whole part of the blade except the lower portions. A mixed-phase plant forming tetrasporangial sori together with spermatangial sori on the blade was found. The tetrasporangial sori are borne in the proximal region of the membranous section and the latticework whereas the spermatangial sori are

in the distal region. The two reproductive sori are slightly intermingled at the borders in the blade.

**Habitats:** Plants of *M. palmata* are epilithic or epiphytic on other algae, such as *Acanthopeltis longiramulosa* Y. Lee or *Cladophora wrightiana* Harvey in 4-6-m-deep subtidal regions off the northern slopes of Moonseom and Seobseom. Plants of *M. palmata* also grow on rocks at depths of 18 m at Hwasoon, Jeju Island. They grow from March to August and generally reproduce between May and June.

**Specimens examined:** LYP-1588 (Moonseom, Jeju Island 2005-06-26, ♂, ♂, 2005-198, coll. Y. Ko); LYP-1627 (Hwasoon, Jeju Island 2005-05-225, ♂, 2005-55, coll. Y. Ko); LYP-1668 (Moonseom, Jeju Island 2002-08-04, coll. B. Kim, analysis); LYP-1669 (Moonseom, Jeju Island 2002-07-31, ♂, ♂, ♂, coll. B. Kim); LYP-1670 (Moonseom, Jeju Island 2001-06-21, ♂, ♂, ♂, analysis); LYP-1671 (Seobseom, Jeju Island 2002-06-09, ♂, coll. B. Kim); LYP-1673 (Seobseom, Jeju Island 2002-03-24, ♂, ♂, coll. B. Kim); LYP-1911 (Moonseom, Jeju Island 2002-08-04, coll. B. Kim); LYP-1924 (Seobseom, Jeju Island 2005-06-12, ♂, 2005-112); LYP-1942 (Seobseom, Jeju Island 2004-05-16, ♂, ♂, 2004-321); LYP-1968 (Moonseom, Jeju Island 2005-06-11, ♂, ♂, ♂, 2005-83, coll. Y. Ko); LYP-1970 (Seobseom, Jeju Island 2004-05-14, 2004-324); LYP-1971 (Seobseom, Jeju Island 2004-05-14, 2004-323, analysis).

**Remarks:** *Martensia palmata* is related to *M. fragilis* and *M. indica* in terms of the branching blades (Harvey 1860, as *M. denticulata*; Millar 1990; Krishnamurthy and Thomas 1977). However, *M. palmata* is easily distinguished from the latter species by the absence of second-order bladelets or lobes along the outer edges of the primary latticework. Moreover, the blades of *M. fragilis* and *M. indica* are somewhat regularly dichotomous. *Martensia palmata* shares the characteristic of forming cystocarps along the margins of the membranous sections with *M. lewisiae* (Lin et al. 2004). However, the two species are quite distinct in all other respects, including growth habits, blade shape, branching patterns, and latticework formation.


Fig. 14.


**Korean Name:** Dotolbidanmangsa (도돌비단망사)


**Type Locality:** Subtidal regions at 4-6 m depths off the northern slope of Seobseom, Jeju Island, Korea.

**Distribution:** Korea.

**Vegetative morphology:** Thalli grow on rocks, comprise several blades in a bunch, and are 10-15 cm high (Fig. 14A, B). The holdfasts consist of the haptera of many filamentous cells that originate from the lowermost cells of the blade and conglutinate together. The blades are membranous, flabellate, branch subdichotomously at obtuse angles, with undulate margins and spinelike projections along the margins, and occasionally with wartlike projections at the surfaces. The segments of the branches are linear and slightly expanded upwards. The terminal segments are gradually attenuated toward the apex, appear to be horn-shaped, and have the latticeworks in the terminal regions. The membranous sections comprise one to four cell layers, gradually thickening toward the base, occasionally perforated in the lower portions, and have a parenchymatous structure near the base. The cortical cells are 5-7-angled with obtuse corners in the surface view. Chloroplasts are very small, discoid, and generally aggregate near the cell walls. Latticeworks develop late and are weak, retain the intact shape, and are up to 3 mm high. The latticeworks are very inconspicuous, rare, and are not always formed on all branches of a thallus. The majority of thalli observed in this study lacked the latticeworks.

**Reproductive morphology:** Tetrasporophytes and gametophytes of *M. projecta* are generally isomorphic. Male gametangial thalli are also similar to female gametangial thalli. Cystocarps are generally borne on the surfaces near the margins or rarely in the central regions of the membranous sections. Spermatangia are borne in roundish and faintly colored sori in the middle regions of the membranous sections. Indusia of the spermatangial sori are formed. Tetrasporangial sori are formed on the membranous sections, discoid in the surface view, biconvex in transverse section, and with a monolayer envelope. A thallus bearing cystocarps and tetrasporangial sori on the same blade was found at Moonseom in July. The cystocarps are borne along the margins and the edges of the openings, and the tetrasporangial sori are borne in the middle region of the membranous section.

**Habitats:** The thalli of *M. projecta* are epilithic or epiphytic on other algae growing at 6-18 m depths off Seobseom, Moonseom and Hwasoon, Jeju Island from March to July. These plants were all mature.

**Specimens examined:** LYP-1619 (Moonseom, Jeju Island 2002-07-31, ♂, ♂, ♂, coll. B. Kim); LYP-1918 (Moonseom, Jeju Island 2005-06-11, ♂, 2005-84, coll. B. Kim); LYP-1933 (Seobseom, Jeju Island 2004-04-10, ♂, ♂, ♂, ♂, coll. B. Kim); LYP-1619 (Moonseom, Jeju Island 2002-07-31, ♂, ♂, ♂, coll. B. Kim).
Fig. 14. *Martensia projecta* Y. Lee. A. Holotype (LYP-1959). Note the arrows indicate the latticeworks. B. Female gametangial thallus (LYP-1918). Note latticeworks (arrows).

Remarks: Martensia projecta is distinct in having terminal branches, wartlike projections in the membranous sections, indusia of the spermatangial sori, and very inconspicuous latticeworks. The wartlike projections on the surfaces of the blades and the indusia of the spermatangial sori are peculiar characteristics that are not found in other described species to date. This species is easily falsely described as having blades lacking the latticeworks because thalli bearing latticeworks were only observed in 20% of the specimens examined in this study. Consequently, this species may be in a transitional stage between M. flammifolia and M. palmata (Lee 2005). However, M. projecta has latticeworks, whereas M. flammifolia lacks the latticeworks (Lee 2005). Martensia projecta is somewhat related to M. le wisiae in terms of the inconspicuous latticeworks (Lin et al. 2004). However, M. projecta is easily distinguished from M. le wisiae by the branching and robust blades.

Martensia projecta is somewhat related to M. fragilis, M. indica, and M. palmata in terms of the thalli with branching blades. However, M. projecta is easily distinguished from the latter species by the terminal, horn-shaped branches and the inconspicuous latticeworks.

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