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Molecular phylogeny of the widespread *Martensia fragilis* complex (Delesseriaceae, Rhodophyta) from the Indo-Pacific region reveals three new species of *Martensia* from Taiwan

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The genus *Martensia* is characterized primarily by its unique thallus morphology, wherein a proximal membranous blade is interrupted distally by one to several bands of net-like tissue (networks). Among the known species, *M. fragilis* is characterized by fan-shaped, membranous blades with multiple bands of networks. The species has been frequently reported from warm temperate and tropical regions. Collections from various localities in the Indo-Pacific region included many specimens fitting this broad concept of *M. fragilis*, but differed in several aspects and were difficult to assign to any named species with confidence. In order to delineate the species boundaries within this suite of *M. fragilis*-like specimens and to clarify the phylogenetic significance of the morphological features used for separating species of *Martensia*, we used analyses of *rbc*L sequence to infer phylogenetic relationships among the available species with multiple bands of networks. Molecular analyses revealed that *M. fragilis* was restricted to its type locality Sri Lanka and that collections of *M.* '*fragilis*' from other regions were split into six clades. *Martensia* '*fragilis*' collections from Taiwan contained three cryptic species, which were described as new species (*M. leeii* W.-C. Yang & S.-M. Lin *sp. nov*., *M. kentingii* W.-C. Yang & S.-M. Lin *sp. nov.* and *M. taiwanifretensis* W.-C. Yang & S.-M. Lin *sp. nov.*) based on molecular and morphological evidence. *Rbc*L sequences of *M.* '*fragilis*' from Korea and Japan, as well as those of the recently described *M. bibarii* and *M. jejuensis*, were all virtually identical, indicating that previous records of *M. fragilis* from those regions should go under the name *M. jejuensis*, with *M. bibarii* placed in synonymy. Records of *M.* '*fragilis*' from other locations in the Indo-Pacific should be regarded as doubtful until detailed morphological studies and molecular analyses of freshly collected specimens become possible.

Key words: biogeography, Delesseriaceae, Indo-Pacific Oceans, *Martensia bibarii*, *Martensia fragilis*, *Martensia jejuensis*, *Martensia leeii*, *Martensia kentingii*, *Martensia taiwanifretensis*, molecular phylogeny, Rhodophyta, systematics, Taiwan

Introduction

Martensia (Hering 1841), the largest genus in the subfamily Nitophylloideae within the family Delesseriaceae, is primarily distributed in tropical to subtropical regions and includes 15 species in the western Pacific and Indian Oceans (see Millar, 1990; Lin *et al*., 2001*a*, 2004*a*, 2009; Lee, 2004, 2005, 2006) and only one species, *M. pavonia*, in the Caribbean Sea and warm water regions of the western Atlantic Ocean (Taylor, 1960, 1969; Littler & Littler, 2000; Wynne, 2011). The genus is primarily characterized by its membranous thalli with one (e.g. *M. elegans*, *M. australis*) or multiple bands (e.g. *M. fragilis*, *M. denticulata*) of net-like tissue (networks), although in a few species a network is absent (e.g. *M. martensii*). One of the most commonly recorded species is *M. fragilis*, which is thought to be widely distributed in both the Indian and western Pacific Oceans (see Guiry & Guiry, 2012).

Lin *et al*. (2004*a*, 2009) recently documented the morphology of the generitype, *M. elegans*, from South Africa, and described three species (*M. formosana*, *M. lewisiae* and *M. natalensis*). They concluded that the developmental pattern of the networks can be used as a taxonomic feature for delineating species, when coupled with *rbc*L sequence analysis. Our recent collections from the Indo-Pacific regions contained many

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M. fragilis-like specimens, which were difficult to assign to any named species. We therefore sequenced *rbc*L from these specimens, which came from the north-western Pacific Ocean (Japan, Korea, Taiwan), along with *M. fragilis* from Sri Lanka and *M. denticulata* from Western Australia, in order to infer their phylogenetic relationships, and we evaluated morphological features potentially useful for separating species. We then undertook a detailed morphological examination of *M. fragilis*-like specimens from Taiwan which, in combination with the *rbc*L analyses, led to the recognition of three new species.

Materials and methods

Specimens were collected in the shallow subtidal by snorkelling or SCUBA diving. Samples were preserved in 5% formalin in seawater or pressed on herbarium sheets and a fragment of each specimen was preserved in silica gel for subsequent DNA extraction. Voucher specimens have been deposited in the herbarium of the National Taiwan Ocean University, Taiwan (NTOU), the Herbarium of the Ghent University (GENT), and the Western Australian Herbarium (PERTH). Hand sections were stained with 1% aniline blue acidified with 1% HCl and mounted in 25–30% Karo® syrup (Englewood Cliffs, New Jersey, USA) or treated with Wittmann's aceto-iron-haematoxylin–chloral hydrate (Wittmann, 1965) and mounted in 50% Hoyer's mounting medium (Lin *et al*., 2004*b*). Photomicrographs were taken on an Olympus BX51 microscope with a Q-imaging digital camera (Burnaby, British Columbia, Canada), and habit images were reproduced with an Epson scanner (Tokyo, Japan) or a Nikon D300 digital camera (Nikon, Japan). DNA from silica gel-dried specimens was extracted using the DNeasy Plant Mini Kit (Qiagen, Valencia, California, USA) following the manufacturer's instructions. DNA sequencing procedures were as described by Lin *et al*. (2001*b*).

Phylogenetic analyses were performed using maximum-parsimony (MP), maximum likelihood (ML) and Bayesian analysis. MP and non-parametric bootstrapping followed Lin *et al.* (2011). We used PAUP* v4.0 (Swofford, 2003) for MP analyses and GARLI 1.0 (Zwickl, 2006) for ML analyses. Bootstrapping involved 1000 and 100 replicates for MP and ML analyses, respectively. The substitution model for ML was the General Time Reversible model with gamma distributed rate heterogeneity, which is the default model in GARLI 1.0. as used in Lin *et al.* (2009). A Bayesian analysis (BA) was performed in MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) using a GTR + I + Γ model, which allowed for rate variation among different codon positions. The analysis consisted of four chains (one hot and three cold), which were run for 10^6 generations with sampling every 100 generations. The first 1800 generations were discarded as burn-in. Stationarity was reached approximately at generation 18000. A 50% consensus tree (majority rule as implemented by PAUP* v4.0) was computed from the 9820 + 1 trees saved after the burn-in point. The genera *Nitophyllum* and *Augophyllum* was selected as outgroups in all analyses (Lin *et al*., 2004*a*, 2009).

Results

Molecular analyses

The multiple sequence alignment included 33 taxa of *Martensia*, including 18 newly generated *rbc*L sequences of *M. fragilis*-like specimens, from the Indian Ocean (Sri Lanka, Western Australia and South Africa) and western Pacific Ocean (Japan, Korea, Taiwan, the Philippines) (see Table 1 for the collection and GenBank accession number information). Because information was missing for the 5′ ends of many sequences the first 81 sites were excluded from the analyses, the final data matrix being restricted to 1386 base pairs, 370 of which were informative characters (26.7%).

The tree obtained by parsimony analysis via a heuristic search was largely congruent with tree topologies generated by ML and BA. Only the tree topology resulting from the ML is shown (Fig. 1), with the ML and MP bootstrap values and Bayesian posterior probabilities indicated on the branches. The earliest split in *Martensia* corresponds to the two recognized subgenera: subgenus *Martensia* which includes the generitype (*M. elegans*) from South Africa, *M. australis* from southern Philippines, and *M. formosana* and *M. flabelliformis* from Taiwan; and the subgenus *Mesotrema*, including the species with multiple bands of networks (*M. fragilis* from Sri Lanka, *M. fragilis*-like specimens from Hawaii, Japan, Korea, Taiwan and the Philippines, *M. denticulata* from Western Australia, *M. jejuensis* and *M. bibarii* from Korea, *M. natalensis* from South Africa, and *M. pavonia* from the Caribbean Sea), or with a weakly developed network (*M. lewisiae* from Taiwan), or lacking a network altogether (*M. martensii* from the southern Philippines). Molecular analyses demonstrated that the collections of *M. fragilis*-like specimens were subdivided into six lineages (see Fig. 1), comprising specimens from Hawaii (lineage V), Japan and Korea (lineage IV), Taiwan (three lineages: I, II and VII) and the Philippines (lineage III) which were all different from *M. fragilis* from the type locality, Sri Lanka (Fig. 1, lineage VI). Among the clades of *M.* '*fragilis*' from Taiwan, one was from northern Taiwan (I), one from southern Taiwan (II), and one from Penghu Island, Taiwan Strait (VII). The interlineage genetic distances of the seven clades of *M. fragilis* and *M.* '*fragilis*' from the Indo-Pacific region ranged from 1.33% to 11.59% (19–161 pairwise differences, Kimura 2-parameter model), whereas the intraspecific genetic divergence within the clades ranged from 0% to 0.3% (0–4 pairwise differences). The *rbc*L sequences of *M.* '*fragilis*' from Jeju Island, Korea, were identical to *M. jejuensis* and *M. bibarii* from the same island and differed only in four base pairs from *M.* '*fragilis*' collected from Chiba prefecture, central Japan.

Table 1. List of species used in *rbc*L analysis and accession numbers in GenBank. The number after the accession number is the percentage of the gene sequenced.

Species	Collection information	GenBank accession no.
Augophyllum kentingii S.-M. Lin, Fredericq & Hommersand	Chuanfanshi, Kenting National Park, Pingtung County, Taiwan, coll. S.-M. Lin, 14 March 2002	AY680694[4], 99%
Augophyllum wysorii S.-M. Lin, Fredericq & Hommersand	Galeta (STRI-research station), Colon, Caribbean Sea, Panama, coll. B. Wysor, 21 September 1999	AF257405[1], 97%
Martensia cf. *australis*	Little Santa Cruz Is., Zamboanga City, the Philippines, coll. S.-M. Lin, 29 April 1998	AF257374[1], 94%
Martensia bibarii Y.-P. Lee	Jongdal, Jeju Island, Korea, coll. S.-M. Lin, 25 June 2005 (KR-25vi2005-biba)	JX982269 [6], 95%
Martensia denticulata Harvey	Rottnest Island, Australia, coll. J. Huisman, 26 February 2011 (WAU-26.2.11.2.1-Mpav)	JX982270[6], 95%
Martensia denticulata	Rottnest Island, Australia, coll. J. Huisman, 26 February 2011 (WAU-26.2.11.2.2-Mpav)	JX982271[6], 95%
Martensia elegans Hering	Mzamba, E. Cape Province, South Africa, coll. S. Fredericq, 21 August 2005	FJ172367[5], 97%
Martensia elegans	Reunion Rocks, the Bluff, Natal, South Africa, coll. O. De Clerck, 17 August 2005	FJ172368[5], 97%
Martensia flabelliformis Harvey	Wanlitong, Kenting National Park, Pingtung County, coll. S.-M. Lin & M.-L. Qiu, 23 December 1996	AF257376[1], 80%
Martensia formosana S.-M. Lin, Hommersand & Fredericq	Sail Rock, Kenting National Park, Pingtung County, Taiwan, coll. S.-M. Lin, 2 October 2001	AY253663[3], 97%
Martensia formosana	Wan-Li-Dong, Kenting National Park, Pingtung County, Taiwan, coll. S.-M. Lin, 20 December 2001	AY253664[3], 98%
Martensia fragilis Harvey	Beruwala, Sri Lanka, coll. E. Coppejans, 8 February 2008 (HEC16356)	JX982272[6], 95%
Martensia '*fragilis*'	Chinaman's hat, Kameohe' Bay, Oahu, Hawaii, USA, coll. K. Cole, 29 May 1998	AF257377[1], 85%
Martensia '*fragilis*'	Little Santa Cruz Is., Zamboanga City, The Philippines, coll. S.-M. Lin, 28 April 1998	AF257382[1], 99%
Martensia '*fragilis*' [=*M. taiwanifretensis*, *sp. nov.*]	Jianshan, Penghu Archipelago, Taiwan, coll. S.-L. Liu, 13 January 2003 (TW-13i2003-Ms)	JX982273[6], 95%
Martensia '*fragilis*' [=*M. kentingii*, *sp. nov.*]	Hou Wan (#1), Kenting National Park, Pintung County, Taiwan, coll. S.-M. Lin, 7 February 2002 (HW1-07ii2002-Mmul)	JX982274[6], 95%
Martensia '*fragilis*' [=*M. kentingii*, *sp. nov.*]	How Wan (#2), Kenting National Park, Pintung County, Taiwan, coll. S.-M. Lin, 7 February 2002 (HW2-07ii2002-Mmul)	JX982275[6], 95%
Martensia '*fragilis*' [=*M. leeii*, *sp. nov.*]	Longdongwan, Taipei County, Taiwan, coll. S.-M. Lin, 30 June 2009 (#LDW-30vi2009-Mf1)	JX982276[6], 95%
Martensia '*fragilis*' [=*M. leeii*, *sp. nov.*]	Longdongwan, Taipei County, Taiwan, coll. S.-M. Lin, 24 June 2010 (LDW-24vi2010-Mf2)	JX982277[6], 95%
Martensia '*fragilis*' [=*M. leeii*, *sp. nov.*]	Longdongwan, Taipei County, Taiwan, coll. S.-M. Lin, 24 June 2010 (#LDW-24vi2010-Mf1)	JX982278[6], 95%
Martensia '*fragilis*' [=*M. leeii*, *sp. nov.*]	Shi-Cheng, Taipei County, Taiwan, coll. S.-M. Lin, 30 June 2009 (SC-30vi2009-Mf2)	JX982279[6], 95%
Martensia '*fragilis*' [=*M. leeii*, *sp. nov.*]	Yeliu, Taipei County, Taiwan, coll. S.-M. Lin, 7 July 1994	AF257378[1], 81%
Martensia '*fragilis*' [=*M. jejuensis*, *sp. nov.*]	Chochun, Jeju Island, Korea, coll. S.-M. Lin, 28 August 2008 (KR-28viii2008-inmat2)	JX982280[6], 95%
Martensia '*fragilis*' [=*M. jejuensis*, *sp. nov.*]	Seolim, Jeju Island, Korea, coll. S.-M. Lin, 24 June 2005 (#KR-24vi2005-pal)	JX982281[6], 95%
Martensia '*fragilis*' [=*M. jejuensis*, *sp. nov.*]	Okinoshima, Chiba Prefecture, Japan, coll. M. Suzuki, 25 March 2008 (JP-25iii2008-P)	JX982282[6], 95%
Martensia jejuensis Y.-P. Lee	Jongdal, Jeju Island, Korea, coll. S.-M. Lin, 25 June 2005 (#KR-24vi2005-jeju)	JX982283[6], 95%
Martensia lewisiae S.-M. Lin, Hommersand & Fredericq	Youzihu, Green I., Taitung County, Taiwan, coll. M.-F. Lin, 30 April 2005 (YZH-30iv2005- Mlew)	JX982284[6], 95%
Martensia lewisiae	Xianjiaowan, Kenting National Park, Pintung County, Taiwan, coll. S.-M. Lin, 14 March 2001	AY253661[3], 96%
Martensia lewisiae	Pool near Nuclear Waste Plant, Orchid Island, Taitung County, Taiwan, coll. S.-M. Lin, 28 March 2009 (NWP-28iii2009-Mlew)	JX982285[6], 95%
Martensia martensii (F. Schmitz) S.-M. Lin, Fredericq & L. M. Liao	La Vista Fel Mar, Upper Calarian, Zamboanga, the Philippines, coll. S.-M. Lin, 27 April 1998 (as *Opephyllum martensii*)	AF257406[7], 93%

(*continued*)

Table 1. Continued.

Species	Collection information	GenBank accession no.
Martensia martensii	La Vista Fel Mar, Upper Calarian, Zamboanga, the Philippines, coll. S.-M. Lin, 1 May 1998 (as *Opephyllum martensii*)	AF257407[1], 93%
Martensia natalensis S.-M. Lin, Hommersand, Fredericq & De Clerck	Umdloti Beach, Natal, South Africa, coll. S. Fredericq, 19 August 2005	FJ172361[4], 97%
Martensia natalensis	Mission Rocks, Natal, South Africa, coll. O. De Clerck, 13 May 2003 (KZN2234)	FJ172363[4], 97%
Martensia pavonia (C. Agardh) J. Agardh	Guanica, Puerto Rico, coll. D. Ballantine, 3 September 2003 (#PR-3ix2003-Mp)	JX982286[6], 95%
Martensia pavonia	Cayos Zapatilla, Bocas del Toro, Panama, Caribbean side, coll. B. Wysor, 21 October 1999	AF257378[1], 91%
Nitophyllum hommersandii S.-M. Lin & Fredericq	Xianjiaowan, Kenting National Park, Pingtung County, Taiwan, coll. S.-M. Lin, 19 August 2000	AY118270[2], 96%
Nitophyllum punctatum (Stackhouse) Greville	Asturias, Spain, coll. C. Maggs, 5 March 1999	AF257402[1], 97%

[1] Lin *et al.* 2001*a*; [2] Lin *et al.* 2003; [3] Lin *et al.* 2004*a*; [4] Lin *et al.* 2004*b*; [5] Lin *et al.* 2009; [6] this study; [7] Lin *et al.* 2001*a*.

Table 2. Morphological comparison of *Martensia* species with multiple bands of networks from the Indo-Pacific Oceans.

Species	Thallus habit	Blade morphology	Network structure	Distribution
M. fragilis[1, 2]	Bushy and erect, 5–9 cm high; epilithic	Blades fan-shaped, 1–3 cm wide, basal blades may bear 5–9 marginal bladelets, which again bearing several new marginal lobes, up to 5 alternation of producing marginal lobes	Mostly formed at distal ends of each branch; margins covered with numerous lobes or coarse tooth-like bladelets	Sri Lanka
M. denticulata[1, 3]	Erect or slightly prostrate, 5–8 cm high; epiphytic or epilithic	Blades ribbon-like initially, 1–3 cm wide, branched irregularly 2–3 orders; bearing fan-shaped, marginal bladelets with denticulate margins, or basal blades may bear 2–4 marginal bladelets, each of which again bearing 2–3 new marginal lobes	2–3 bands covered over the entire blade; margins covered with numerous fine, tooth-like bladelets	Rottnest Island, Western Australia
M. jejuensis[1, 4]	Bushy and erect, 8–15 (–30) cm high, epiphytic or epilithic	Blades linear, ribbon-like or fimbriate, 1–3 mm wide, or flabellate, 1–4 cm wide	Lobed networks numerous borne on distal ends of linear, ribbon-like axes, old networks often fragmented or becoming fimbriate	Korea and Japan
M. leeii[1]	Prostrate, 2–3 cm high, epiphytic or epilithic	Blades flabellate, 1.5–3 cm wide; bearing many marginal, membranous lobes	A conspicuous band of network across distal ends of blades, covering *c*. 30–60% of blades	Northern Taiwan in East China Sea
M. kentingii[1]	Prostrate, 2–3 cm high, mostly epiphytic	Blades flabellate, 1–2 cm wide; bearing few marginal, membranous lobes	A conspicuous band of network covering entire blades	Southern Taiwan
M. taiwanifretensis[1]	Prostrate, 2–4 cm high, mostly epilithic	Blades flabellate or slightly to deeply cleft, 2–3 cm wide; bearing many marginal, fan-shaped bladelets	1–3 conspicuous bands of networks across main blades; covering 60–80% of blades	Penghu Islands in Taiwan Strait

[1] This study; [2] Coppejans *et al.* (2009); [3] Harvey (1855); [4] Lee (2004).

Morphological observations

The *rbc*L sequence analyses revealed that the collections identified as *M.* '*fragilis*' from the Indo-Pacific were split into at least seven evolutionary lineages. We could not unequivocally demonstrate the occurrence of genuine *M. fragilis* outside its type locality. Accordingly, we recognize three new species, *Martensia leeii* W.-C. Yang & S.-M. Lin, *sp. nov.*, *Martensia kentingii* W.-C. Yang & S.-M. Lin, *sp. nov.*, *Martensia taiwanifretensis* W.-C. Yang & S.-M. Lin, *sp. nov.*, for the three clades detected by molecular analyses from northern, southern and western Taiwan, respectively. We studied the morphology of specimens with multiple bands of networks and summarize the diagnostic features that separate the species in Table 2. The other two clades of *M.* '*fragilis*' from the southern Philippines and Hawaiian Islands will be documented in detail once enough specimens become available.

A key to the three new species and the closely related species as detected from *rbc*L sequence analyses can be constructed using morphological characteristics, as follows:

Key to the species possessing multiple bands of network from the Indo-Pacific regions

1a. Thalli consisting of linear axes bearing flabellate bladelets..... 2

1b. Thalli flabellate bearing subdichotomously divided, lobed bladelets..... 3

2a. Thalli bushy, up to 15 (–30) cm long, old networks fragmented or becoming fimbriate, margins of networks covered with few teeth-like protrusions..... ..... ***M. jejuensis***

2b. Thalli ribbon-like initially, 5–8 cm long, old blade bearing 2–3 bands of network, margins of blades covered with numerous teeth-like or ligulate bladelets..... ..... ***M. denticulata***

3a. Thalli bushy, 5–9 cm long, each main blade bearing 5–9 bladelets, which also bearing several new marginal lobes, up to 5 orders of alternation of producing marginal bladelets or lobes..... ..... ***M. fragilis***

3b. Thalli prostrate, 2–4 long, blades bearing conspicuous bands of networks 4

4a. Thalli with thin membranous blades of 2–3 cell layers (less than 80 μm thick), network not fully covering the main blades..... 5

4b. Thalli with thick membranous blades, 4–5 cell layers (120–170 μm thick), network nearly fully covering the main blades..... ..... ***M. kentingii***

5a. Main blades slightly to deeply cleft, marginal bladelets mostly arising from the primary longitudinal lamellae..... ..... ***M. taiwanifretensis***

5b. Main blades mainly flabellate, marginal bladelets mostly arising from the membranous margins of blades..... ..... ***M. leeii***

Descriptions of new species

Martensia leeii* W.-C. Yang & S.-M. Lin, *sp. nov.

(Figs 2–12)

Description: Thalli fan-shaped, consisting of one to several blades, attached to the substratum by a short stipe, 1–3 mm in length; blades flabellate, 1–3 cm wide and 2–3 cm in length, with a conspicuous distal band of network and covered with many marginal, membranous lobes; each lobe may develop a new band of marginal network; network composed of primary longitudinal and cross-connecting lamellae enclosing needle-like, secondary cross-connecting and longitudinal lamellae; cross-connecting strands mostly developing unilaterally and linking unidirectionally to adjacent lamellae on the opposite side; gametophytes not found; tetrasporangial sori borne on primary longitudinal lamellae but not directly on membranous blades; tetrasporangial sori round to oval, 100–500 μm by 200–300 μm in diameter, solitary or aggregated, mature tetrasporangia 75–90 μm in diameter.

Holotype and isotypes: Holotype deposited at the herbarium of the Institute of Marine Biology, National Taiwan Ocean University, #NTOU-LDW-24vi10-05 (Fig. 2, holotype); isotypes #NTOU-LDW-24vi10-01 – #NTOU-LDW-24vi10-04 (Fig. 3).

Type locality: Lung Dong Wan, New Taipei County, north-eastern Taiwan (25°07.05′N, 121°54.57′E).

Etymology: The epithet '*leeii*' honours Professor Yongpil Lee (Cheju National University), who has made a significant contribution to the taxonomy of *Martensia* from Korea.

Distribution: Found along the coastline of northern Taiwan.

Habitat and seasonality: Plants were found in early summer from June through July; attached to rocky reefs at 1–12 m depths.

Specimens examined: **Taiwan:** New Taipei City: Yeliu, 1–12 m, coll. S.-M. Lin, sterile, 7 July 1994; Shi Cheng, coll. S.-M. Lin, tetrasporic, 30 June 2009; Lung Dong Wan, coll. L.-C. Liu, tetrasporic, 24 June 2010.

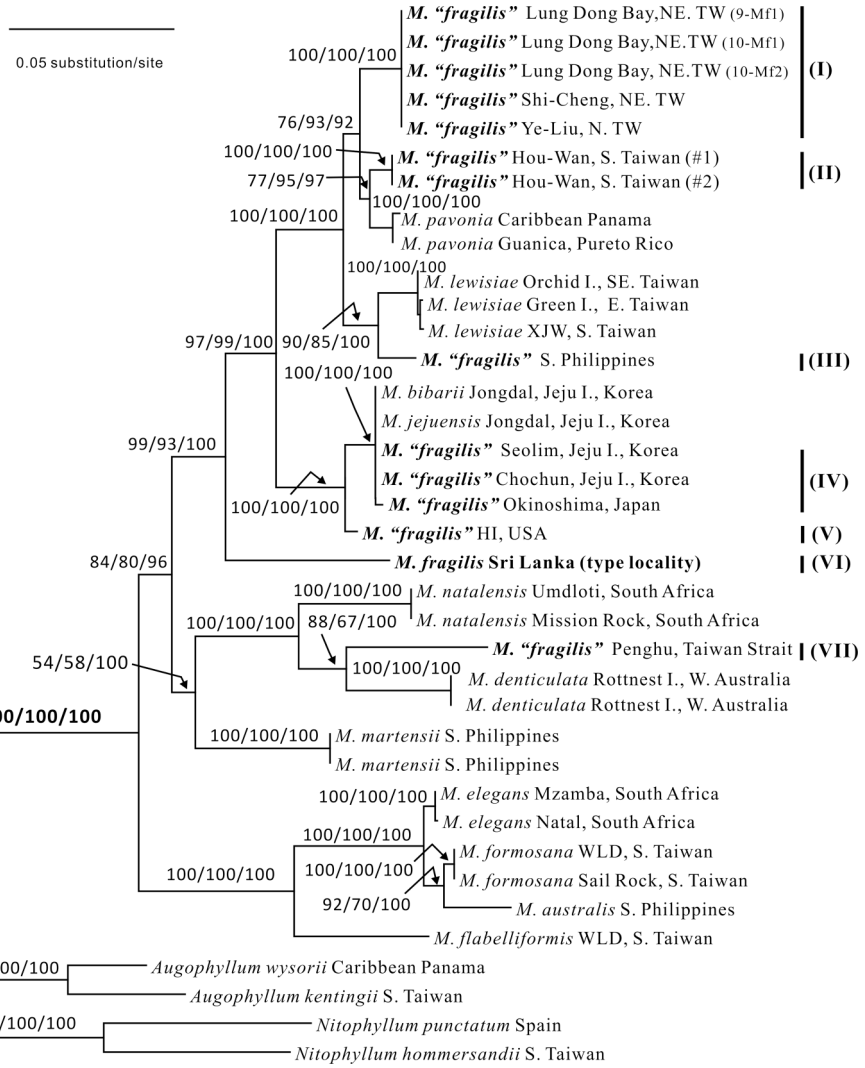


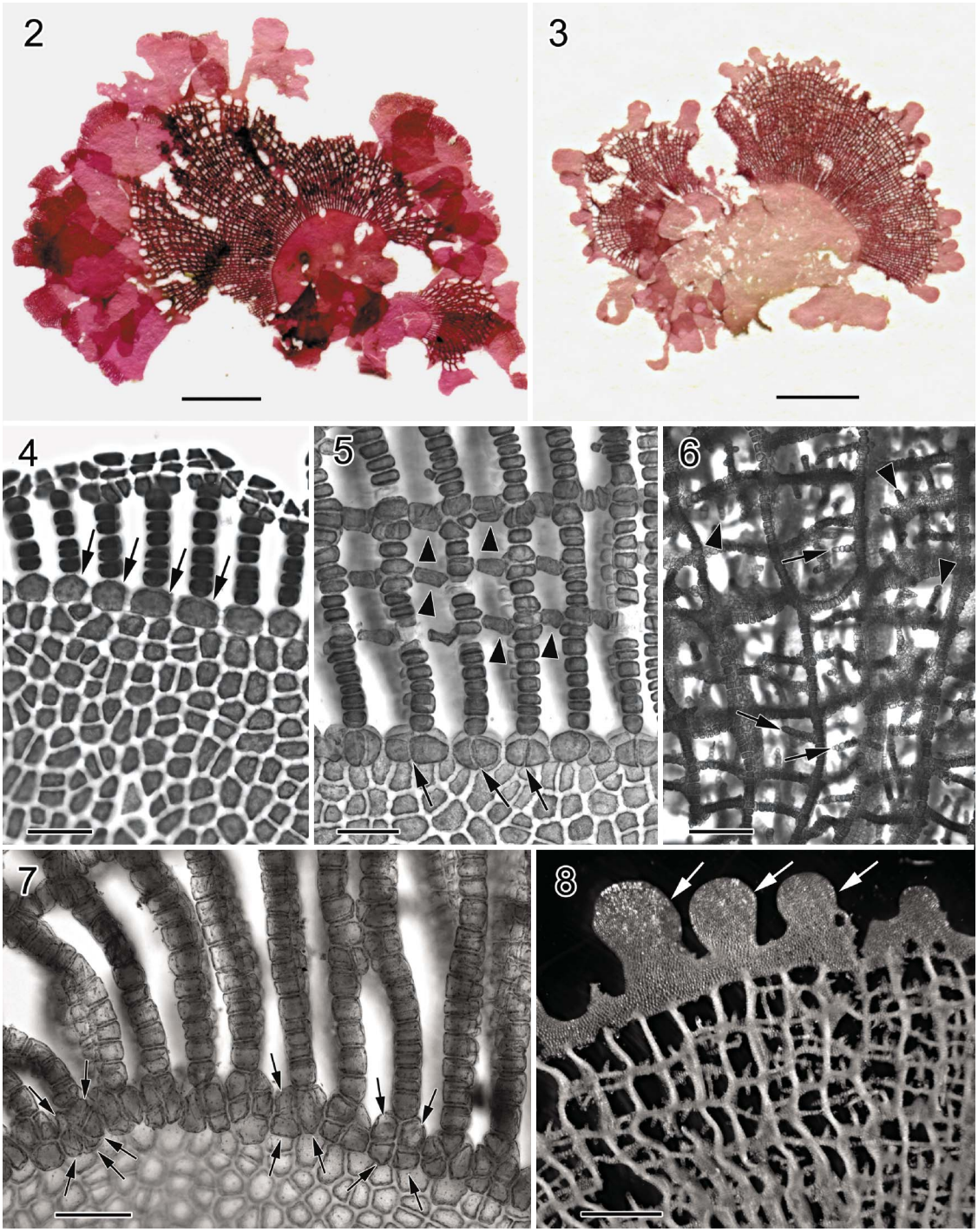
Fig. 1. *rbc*L phylogenetic tree of *Martensia* species from the Indo-Pacific region. Numbers on the branches are ML and MP bootstrap values and Bayesian posterior probabilities, respectively, all expressed as %.

Habit and vegetative morphology. Thalli (Figs 2, 3) are prostrate, pinkish to rose, consisting of one to several flabellate blades, 1–3 cm wide and 2–3 cm in length, attached to rocks by a short stipe, 2–3 mm. Several thalli usually grow together forming a floral-like cluster. Young blades consist of a conspicuous band of network and bear many marginal, membranous lobes (Figs 3, 8), which eventually become flabellate and bear distal networks (Fig. 2). Growth is diffuse and the network is initiated from a row of transformed marginal cells that divide transversely to form a membranous margin and intercalary longitudinal lamellae (Fig. 4). Cross-connecting strands mostly develop unilaterally and link unidirectionally to adjacent lamellae on the opposite side (Fig. 5). Expansion of the network is by intercalary cell divisions of primary longitudinal lamellae and the continued formation of cross-connecting strands (Figs 6, 8). Needle-like, secondary longitudinal (Fig. 6, arrowheads) and cross-connecting (Fig. 6, arrows) lamellae are initiated from the middle of the cross-linking lamellae, filling in the space created by the expansion of the primary network. The cells at the base of the network divide once or twice both anticlinally and longitudinally (Fig. 7, arrows). Primary longitudinal lamellae are sheet-like, 12–18 cells (300–700 μm) wide, and the basal membranous blades are composed of 2–3 cell layers (Fig. 9), 40–80 μm thick. Numerous secondary pit-connections are formed between cells of the membranous parts of the blades (Fig. 10).

Reproductive morphology. Tetrasporangial sori are round to ovoid in shape, 200–300 μm wide by 100–500 μm long, and are solitary or aggregated on primary longitudinal lamellae (Figs 11, 12). Tetrasporangial initials are transformed from multinucleate lamellar cells into tetrasporocytes, which become uninucleate through nuclear degeneration, leaving behind a single functional nucleus. Mature tetrasporangia are tetrahedrally divided and 70–100 μm in diameter.

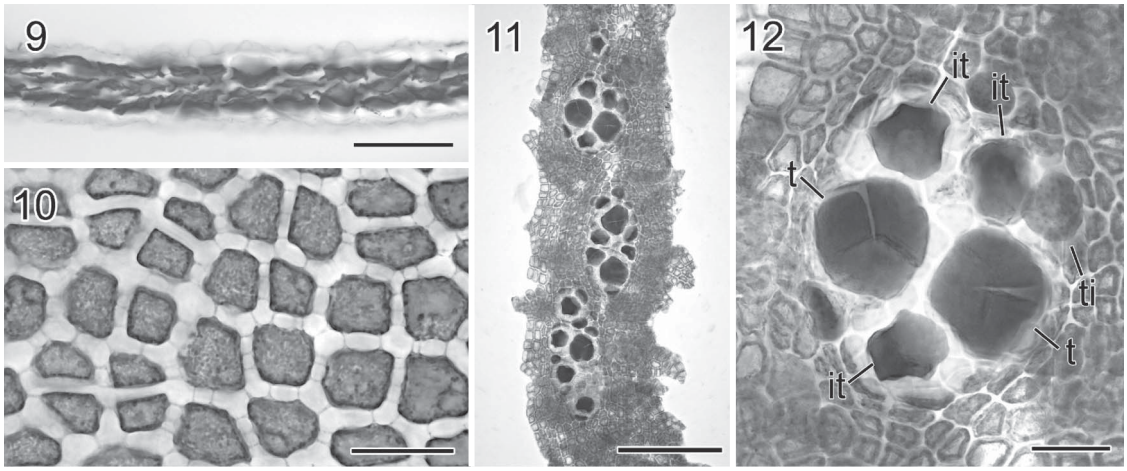
Martensia kentingii* W.-C. Yang & S.-M. Lin, *sp. nov.

(Figs 13–29)



Figs 2–8. *Martensia leeii* W.-C. Yang & S.-M. Lin *sp. nov.* Habit and network morphology (Lung Dong Wan, New Taipei City). **2**. Holotype, a tetrasporic plant. Scale bar = 5 mm. **3**. Isotype, a young plant. Scale bar = 5 mm. **4**. Early stage of network formation showing basal cells (arrows) of longitudinal lamellae. Scale bar = 50 μm. **5**. Basal part of a developing network showing connecting strands (arrowheads) and basal cells (arrows) of longitudinal lamellae. Scale bar = 100 μm. **6**. Proximal portion of a network showing secondary cross-connecting strands (arrows) and secondary longitudinal lamellae (arrowheads). Scale bar = 250 μm. **7**. Basal part of a developing network showing divided basal cells (arrows) of longitudinal lamellae. Scale bar = 100 μm. **8**. Proximal portion of thallus showing some lobes from the edge (arrows). Scale bar = 1 mm.

DESCRIPTION: Thalli fan-shaped, consisting of one to five flabellate blades, rose to dark red, attached to the substratum by rhizoidal haptera; blades 1–2 cm wide and 2–3 cm in length, with a conspicuous band of network when old and covered with many marginal, membranous rounded lobes; each lobe may develop a faint band of marginal network; network composed of primary longitudinal and cross-connecting lamellae, which develop bidirectionally and link to adjacent lamellae on the opposite side; needle-like, secondary, cross-connecting strands rare; tetrasporangial sori round to oval, 200–400 μm wide by 300–550 μm long, borne on primary longitudinal lamellae in network, mature tetrasporangia 60–100 μm in diameter;



Figs 9–12. *Martensia leeii* W.-C. Yang & S.-M. Lin *sp. nov.* Vegetative morphology and tetrasporangial formation (Lung Dong Wan, New Taipei City). **9**. Cross-section through basal part of a membranous blade. Scale bar = 100 μm. **10**. Close-up of surface cells showing discoid plastids and numerous secondary pit-connections. Scale bar = 50 μm. **11**. Close-up of tetrasporangial sori borne on a longitudinal lamella. Scale bar = 250 μm. **12**. Close-up of a tetrasporangial sorus showing multinucleate tetrasporangial initials (ti), immature tetrasporagia (it) and tetrahedrally divided tetrasporangia (t). Scale bar = 50 μm.

gametophytes dioecious, spermatangial sori irregularly oblong to rectangular and formed on primary longitudinal lamellae, each spermatangial parental cell bearing 1–2 spermatangia, 3–5 μm in diameter; cystocarps scattered over network, 800–1200 μm in diameter; procarps borne on membranous lobes derived from edges of longitudinal lamellae; carposporangia pyriform, 50–70 μm wide by 70–100 μm long, formed terminally.

Holotype and isotypes: Holotype deposited at the herbarium of the Institute of Marine Biology, National Taiwan Ocean University, #NTOU-HW-07ii2002-Mmul-1 (Fig. 13); isotypes #NTOU-HW-07ii2002-Mmul-2 (Fig. 14) to– #NTOU-HW-07ii2002-Mmul-7 and #NTOU-HW-07ii2002-Mmul-7mix.

Type locality: Hou Wan, Kenting National Park, Pintung County, southern Taiwan (22°02.79′N, 120° 42.14′E).

Etymology: The epithet '*kentingii*' refers to Kenting National Park, the type locality.

Distribution: Only found so far in Kenting National Park.

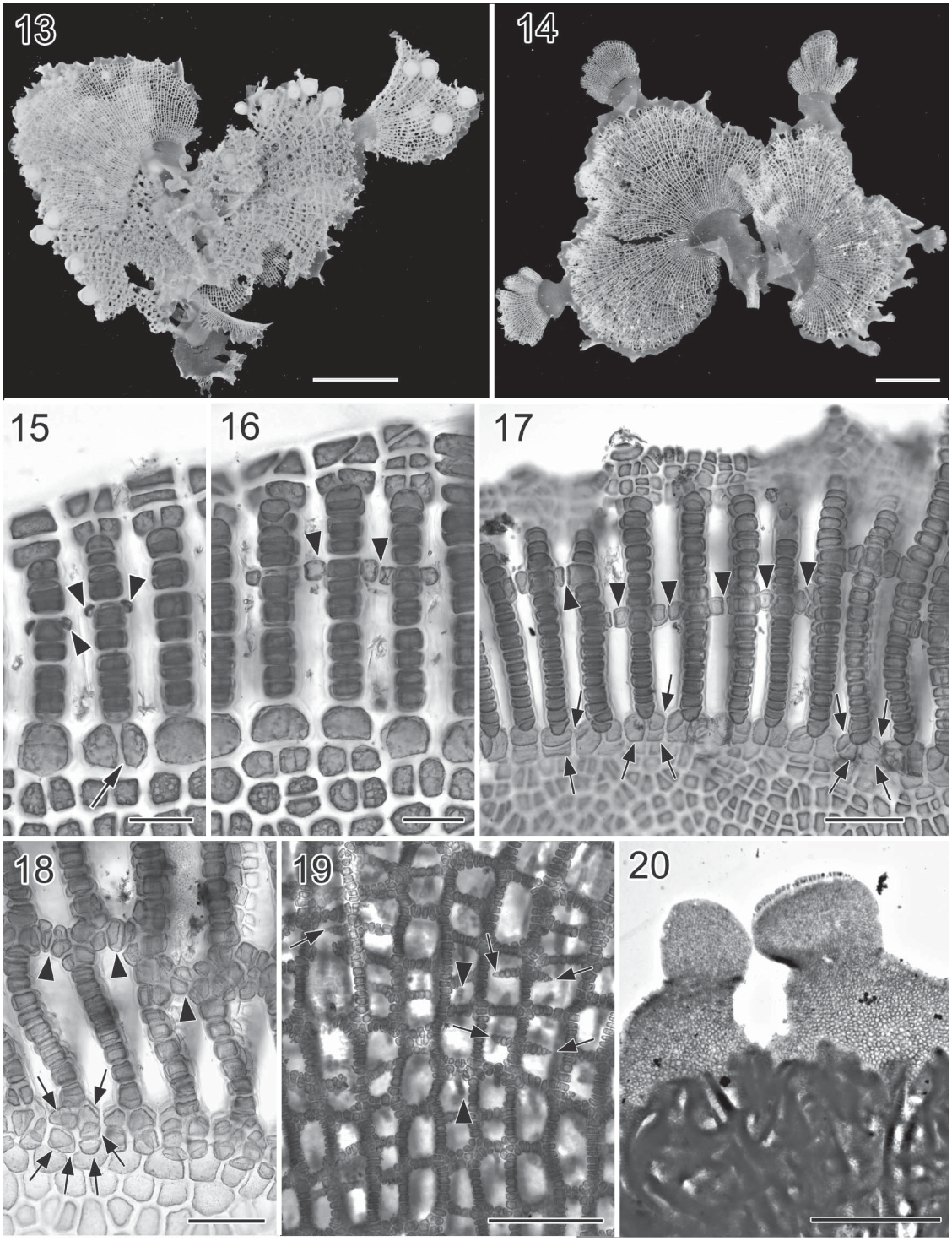
Habitat and seasonality: Plants were found from February through April; attached to rocky reefs at 1–3 m depths.

Specimens examined: **Taiwan:** Kenting National Park, Pingtung County: Hou Wan, 2–3 m deep, coll. S.-M. Lin, 7 February 2002; Sail Rock, 1–2 m deep, coll. S.-M. Lin, 1 April 2002.

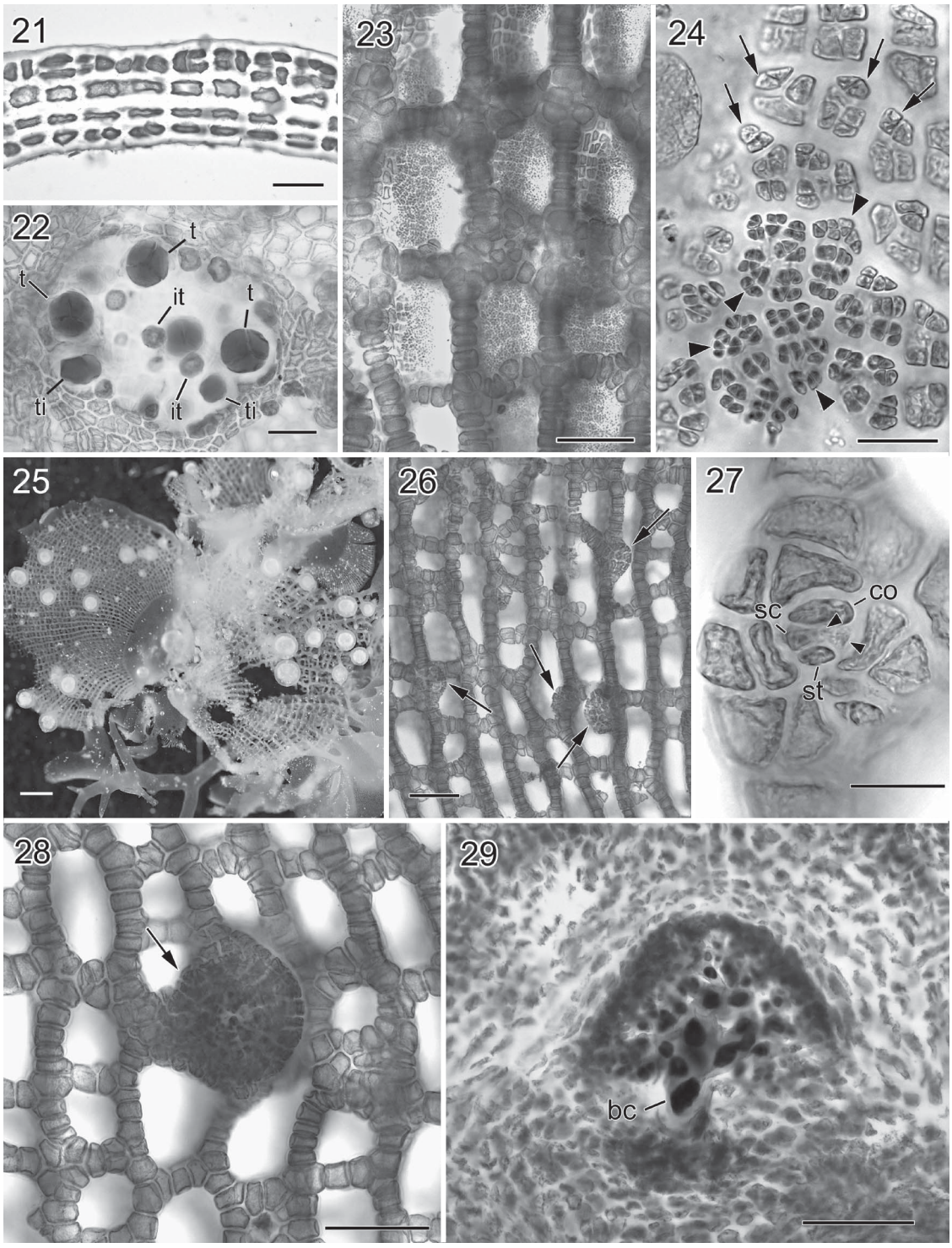
Habit and vegetative morphology. Thalli (Figs 13, 14) are slightly prostrate, pinkish to dark red, consisting of one to five, fan-shaped blades, 1–2 cm high and 2–3 cm wide, attached to rocks by rhizoidal haptera. Old blades consist of a conspicuous band of network, which almost covers the entire blade. Some lobes are produced along the blade margins, each lobe eventually developing into a flabellate blade, bearing a single band of network at the distal end (Figs 13, 14, 20).

Growth is diffuse and the network is initiated from a row of transformed marginal cells that divide transversely to form a membranous margin and intercalary longitudinal lamellae. Cross-connecting strands are initiated bidirectionally from the edges of longitudinal lamellae (Fig. 15) and are pit-connected to one another at the middle to adjacent lamellae on the opposite side (Fig. 16). Expansion of the network is by intercalary cell divisions of primary longitudinal lamellae and the continued formation of cross-connecting strands (Figs 17, 18). Secondary longitudinal lamellae are rare (Fig. 19, arrowheads), whereas cross-connecting strands are relatively common and gradually fill the space created by the expansion of the primary network (Fig. 20, arrows). The cells at the base of the network divide both anticlinally and longitudinally (Figs 17, 18) two or three times. Primary longitudinal lamellae and cross-connecting strands are sheet-like, 15–25 cells (450–900 μm) wide, and the basal membranous blades are composed of 4–5 cell layers (Fig. 21), 120–170 μm thick. Numerous secondary pit-connections are formed between cells of the membranous parts of the blades.

Reproductive morphology. Tetrasporangial sori are formed on primary longitudinal lamellae. Tetrasporangial sori are round to oval in shape (Fig. 22), 200–400 μm wide by 300–550 μm long and mostly solitary but sometimes aggregated. Tetrasporocytes are transformed from multinucleate lamellar cells. Mature tetrasporangia are



Figs 13–20. *Martensia kentingii* W.-C. Yang & S.-M. Lin *sp. nov.* Habit and network morphology (Hou Wan, Kenting National Park). **13**. Holotype, a female plant. Scale bar = 5 mm. **14**. Isotype, a young plant. Scale bar = 5 mm. **15**. Early stage of network formation showing cross-connecting strand initials (arrowheads) cut off bilaterally from longitudinal lamellae, and basal cells of longitudinal lamellae divided once. Scale bar = 50 μm. **16**. Another early development of network showing elongation of cell rows of longitudinal lamellae by intercalary cell divisions, and the formation of cross-connecting strands by pit connections between cells (arrowheads) derived from longitudinal lamellae on opposite sides. Scale bar = 50 μm. **17**. Further development of network showing the formation of cross-connecting strands by pit connections between cells (arrowheads) derived from longitudinal lamellae on opposite sides, and further cell division of basal cells (arrows). Scale bar = 125 μm. **18**. Basal portion of an older network showing cross-connecting strands (arrowheads) and transversely and oblique cell divisions of basal cells (arrows). Scale bar = 100 μm. **19**. Middle portion of an older network showing secondary cross-connecting strands (arrows) and secondary longitudinal lamellae (arrowheads). Scale bar = 500 μm. **20**. Close up of upper portion of network bearing lobed, membranous margin. Note that a new network band is already initiated along the margin of the lobe on the right. Scale bar = 1 mm.



Figs 21–29. *Martensia kentingii* W.-C. Yang & S.-M. Lin *sp. nov.* Vegetative and reproductive morphology (Hou Wan, Kenting National Park). **21**. Cross-section through basal part of membranous blade. Scale bar = 50 μm. **22**. Close up of a tetrasporangial sorus showing multinucleate tetrasporangial initials (ti), immature tetrasporangia (it) and tetrahedrally divided tetrasporangia (t). Scale bar = 50 μm. **23**. Spermatangial sori borne on longitudinal lamellae. Scale bar = 100 μm. **24**. Close up of a developing spermatangial sorus showing spermatangial parental cell initials (arrows) and spermatangial parental cells (arrowheads). Scale bar = 25 μm. **25**. Close up of cystocarps borne on network. Scale bar = 1 mm. **26**. Middle portion of network showing procarp-bearing lobes (arrows) derived from margins of longitudinal lamellae. Scale bar = 100 μm. **27**. Close up of a procarp composed of a supporting cell (sc), the one-celled sterile lateral (st), a carpogonial branch (arrowheads) and a cover cell (co). Scale bar = 25 μm. **28**. Surface view of a young cystocarp with an ostiole (arrow). Scale bar = 100 μm. **29**. Cross-section through a immature carposporophyte showing enlarged nuclei and newly formed basal cell (bc). Scale bar = 100 μm.

tetrahedrally divided and measure 60–100 μm in diameter.

Gametophytes are dioecious and are morphologically similar to the tetrasporophytes. Spermatangial sori are irregularly oblong to rectangular and are formed on primary longitudinal lamellae (Fig. 23). Spermatangial parental cell initials are cut off from surface cells of longitudinal lamellae (Fig. 24, arrows) and each parental cell bears one or two spermatangia, 3–5 μm in diameter. Cystocarps are scattered over the network, 800–1200 μm in diameter (Fig. 25). Procarps (Fig. 26) are abundant and borne on membranous lobes that arise from the edges of the longitudinal lamellae within the network. Fully developed procarps (Fig. 27) consist of a supporting cell bearing one four-celled carpogonial branch, a one-celled sterile group and a one-celled cover cell. Young cystocarps develop a central ostiole (Fig. 28). The nuclei of the supporting cell and inner gonimoblasts become enlarged (Fig. 29). Mature carposporangia are 50–70 μm wide by 70–100 μm long and pyriform, and are formed terminally.

Martensia taiwanifretensis* W.-C. Yang & S.-M. Lin *sp. nov.

(Figs 30–37)

Description: Thalli membranous and prostrate, consisting of several, slightly to deeply cleft blades, 2–3 cm wide and 2–4 cm long, attached to the substratum by rhizoidal haptera; blades with one to three bands of networks and bearing many marginal, membranous lobes derived from the distal ends of primary longitudinal lamellae; each lobe may develop a new band of marginal network; networks composed of primary longitudinal and cross-connecting lamellae enclosing secondary, needle-like filaments borne on primary longitudinal or on cross-connecting strands; tetrasporangial sori, round to oval, 170–200 μm wide by 200–300 μm long, borne on primary longitudinal lamellae in network only, mature tetrasporangia 75–100 μm in diameter; cystocarps, 800–1100 μm in diameter, mostly borne on edges of networks at distal ends of blades, pyriform carposporangia, 40–50 μm wide by 60–90 μm long.

Holotype and isotypes: Holotype deposited at the herbarium of the Institute of Marine Biology, National Taiwan Ocean University, #NTOU-PH-10316-1 (Fig. 30); isotypes #NTOU-PH-10316-2 to #NTOU-PH-10316-13, #NTOU-PH-10316-14 (Fig. 31), #NTOU-PH-10316-21.

Type locality: Li Jhen Gjiao, Penghu County, in the Taiwan Strait, western Taiwan (23°34.55′N, 119° 40.20′E).

Etymology: The epithet '*taiwanifretensis*' refers to the Taiwan Strait, where the type locality is located.

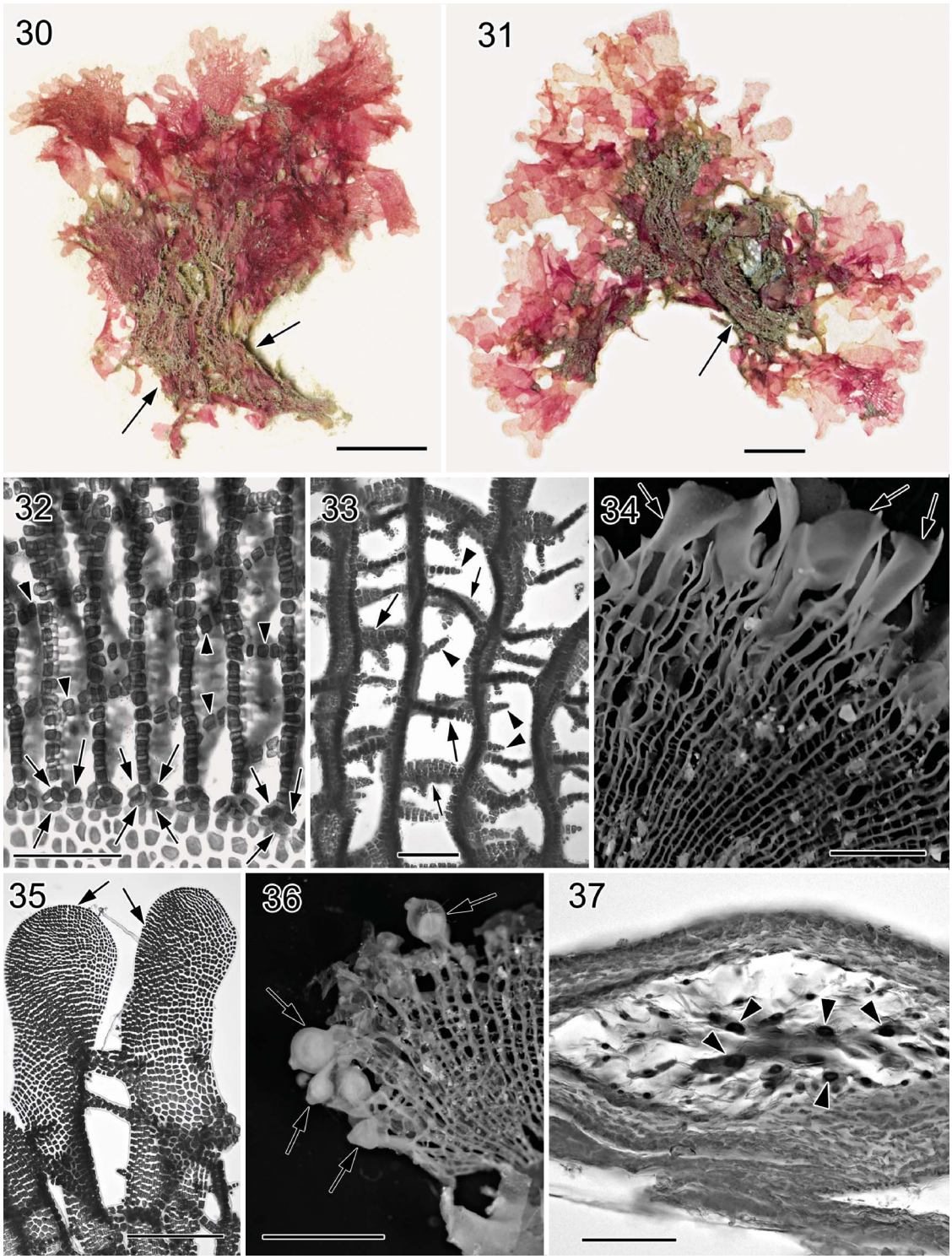
Distribution: Found only at Penghu in the Taiwan Strait.

Habitat and seasonality: Plants were collected from January through November; attached on coral reefs at 1–2 m depth.

Specimens examined: **Taiwan:** Penghu County in Taiwan Strait: (1) Makung Island: Li Jhen Gjiao, coll. S.-M. Lin & J. Lewis, 15 July 1992 (tetrasporic, females). Jai Shan, coll. S.-L. Liu, tetrasporic, 13 January 2003. Lin Tou Park, coll. S.-M. Lin & J. Lewis, 13 July 1992 (sterile), 13 November 1992 (tetrasporic). Pei Liao, coll. S.-M. Lin & J. Lewis, 16 July 1992 (tetrasporic). Guo Ye, coll. S.-M. Lin & J. Lewis, 16 July 1992 (tetrasporic). Da Liao, coll. S.-M. Lin & J. Lewis, 23 August 1993 (tetrasporic). (2) Won An Island: Won-An, coll. S.-L. Liu, 7 September 2012 (tetrasporic, sterile).

Habit and vegetative morphology. Thalli (Figs 30, 31) are slightly prostrate, pinkish to red, and consist of several, slightly to deeply cleft, membranous blades, 2–3 cm wide and 2–4 cm in length, attached to the substratum by rhizoidal haptera. Main blades consist of one to three bands of networks and bear many marginal bladelets (Fig. 31), which eventually become fan-shaped blades and bear distal networks (Fig. 30). Growth is diffuse and the network is initiated from a row of transformed marginal cells that divide transversely to form a membranous margin and intercalary longitudinal lamellae. Cross-connecting strands mostly develop bilaterally and link bidirectionally to adjacent lamellae on the opposite side (Fig. 32). Expansion of the network is by intercalary cell divisions of primary longitudinal lamellae and the continued formation of cross-connecting strands (Figs 33–35). Numerous needle-like filaments are initiated from primary longitudinal lamellae and cross-connecting strands (Fig. 33). The cells at the base of the network divide longitudinally first, then anticlinally (Fig. 32, arrows) once or twice. Primary longitudinal lamellae are sheet-like, 20–30 cells (300–650 μm) wide and the basal membranous blades are composed of 2–3 cell layers, 20–50 μm thick. Numerous secondary pit-connections are formed between cells of the membranous parts of the blades.

Reproductive morphology. Tetrasporangial sori are round to oval in shape, 170–200 μm wide by 200–300 μm long, and are formed on primary longitudinal lamellae only. Mature tetrasporangia are tetrahedrally divided and measure 75–100 μm in diameter. Male plants were not found in this study. Female gametophytes are morphologically similar to the tetrasporophytes, but are relatively smaller. Cystocarps are 800–1100 μm in diameter, mostly scattered over the



Figs 30–37. *Martensia taiwanifretensis* W.-C. Yang & S.-M. Lin *sp. nov.* Habit, vegetative and reproductive morphology (Makung Island, Penghu County). **30**. Holotype, a tetrasporic plant. Note that the network (arrows) at the basal part of the blade is covered by sand. Scale bar = 1 cm. **31**. Isotype, another tetrasporic plant with a basal network (arrow). Scale bar = 5 mm. **32**. Basal portion of developing network showing newly formed cross-connecting strands (arrowheads) and further cell division of basal cell (arrows). Scale bar = 250 μm. **33**. Middle portion of a fully developed network showing primary (arrows) and secondary, spine-like cross-connecting strands (arrowheads). Scale bar = 250 μm. **34**. A fully developed network showing the distal ends of longitudinal lamellae developed into wavy bladelets (arrows). Scale bar = 5 mm. **35**. Close up of the distal ends of two longitudinal lamellae (arrows) bridged by cross-connecting strands. Scale bar = 500 μm. **36**. Close up of cystocarps scattered along the margin of the network. Scale bar = 3 mm. **37**. Cross-section through a nearly mature cystocarp showing enlarged nuclei in inner cells (arrowheads) of gonimoblast filaments. Note that this section was made based on a compressed, dry specimen, so that the shape of the cells in the cystocarp is somewhat distorted. Scale bar = 100 μm.

edges of the networks at the distal ends of blades (Fig. 36). Procarps and early post-fertilization stages were not observed, but the nuclei of the inner gonimoblast filaments enlarged and become darkly stained in mature cystocarps (Fig. 37). Carposporangia are pyriform, measuring 40–50 μm wide by 60–90 μm long.

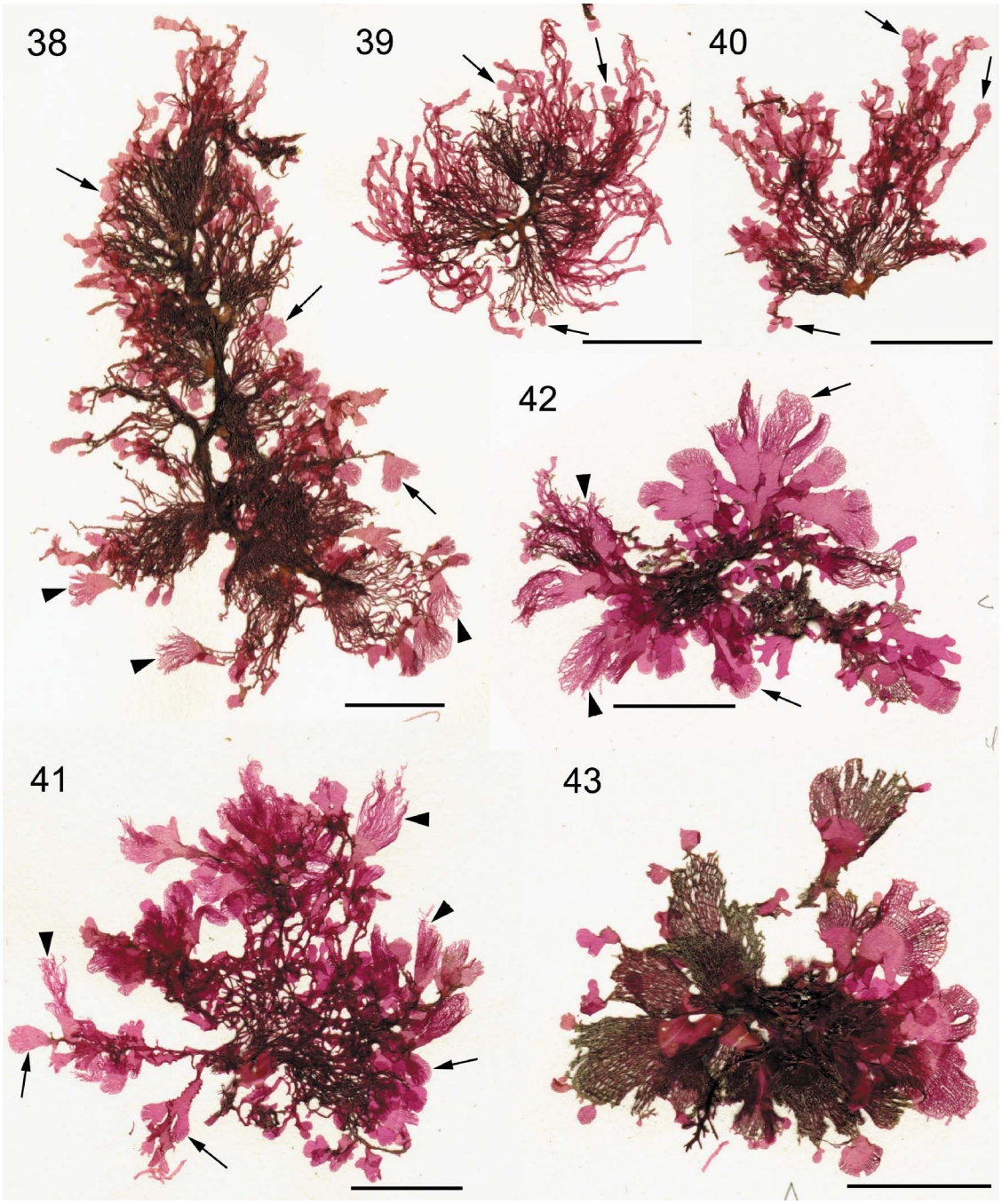
Discussion

Based on *rbc*L sequence analysis, Lin *et al.* (2004*a*, 2009) showed that *Martensia fragilis*, a supposedly widespread species with multiple network bands, may encompass several cryptic species that have thus far gone unrecognized. They also suggested the need for a detailed investigation of critical stages of vegetative and reproductive development in *M.* '*fragilis*' from different localities. Our analyses of additional *rbc*L sequences of *M. fragilis*-like specimens from the Indo-Pacific region, Korea and Japan in this study indicate that genuine *M. fragilis* may be restricted to Sri Lanka in the northern Indian Ocean. Unfortunately, Harvey (1854) did not provide an illustration when describing *M. fragilis* from Ceylon (=Sri Lanka), but the lectotype (TCD 0012254) is depicted at http://plants.jstor.org/specimen/tcd0012254, along with seven other plants from Harvey's collection from the type locality, Belligam (=Weligama). Our sequenced collection from Sri Lanka (the same taxon depicted in Coppejans *et al*., 2009. fig. 179a, b) agrees well with Harvey's description and the type material, and we provisionally recognize our material as authentic *M. fragilis* until a thorough taxonomic study of the genus around Sri Lanka can be undertaken. The genetic divergence distances among the six clades of *M.* '*fragilis*' varied from 1.33% to 11.59%, which exceeded the intraspecific divergence (less than 1%) (see Lin *et al*. 2004*a*, 2012). As a result, we recognize these six clades as independent species separate from *M. fragilis sensu stricto*.

On the other hand, the collections of *M.* '*fragilis*' from Japan and Korea turned out to be molecularly virtually identical to *M. jejuensis* (Lee, 2004, p. 256) and *M. bibarii* (Lee 2004, p. 258) from Jeju Island, Korea. Our analyses were based on two sets of seasonal collections of *Martensia jejuensis/bibarii* from the coasts of Jeju Island, including the type locality, Jongdal, that were made by the first author, S.-M. Lin, who also identified many forms intermediate between the type specimens of *M. jejuensis* and *M. bibarii* (see Figs 38–43). The pit-connections between linking cross-connecting strands and longitudinal lamellae in the networks can degenerate to varying degrees under differing environmental conditions or growth rates. Figs 38–40 show thalli with long, ribbon-like bladelets that were derived from the longitudinal lamellae of a broken network, whereas the networks of thalli shown in Fig. 43 remain intact. In some instances, the broadening longitudinal lamellae may bear marginal bladelets with hair-like networks (see Figs 41, 42, arrowheads). Thus it would appear environmental conditions can be a major factor affecting the morphology of *Martensia* in Jeju. In recent years, seashell culture has become popular around the coasts of Jeju Island and the ambient seawater is enriched. The changed environmental conditions might have considerable effects on the growth and thallus morphology of *Martensia* populations around Jeju Island. We obtained additional sequences from several collections of *Martensia*, displaying thallus morphologies similar to those of *M.* '*fragilis*', *M. jejuensis* and *M. bibarii* (data not shown; their thallus morphologies shown in Figs 38–43). These additional *rbc*L sequences are all identical to those of typical *M. jejuensis* and *M. bibarii*. Based on these results, we conclude that these two species are conspecific. As the two names appeared in the same publication (Lee, 2004) they have equal priority. Herein we choose to adopt the name *M. jejuensis* (thereby establishing priority, International Code of Nomenclature for algae, fungi and plants, Art. 11.5: McNeill *et al.*, 2012). Accordingly, the species bearing multiple bands of networks from Korea and Japan, i.e. *M.* '*fragilis*' and *M. bibarii*, should all be treated as *M. jejuensis*, and this taxonomic conclusion is made formal below.

The three new Taiwanese species, *M. leeii*, *M. kentingii* and *M. taiwanifretensis* described in this study can be separated from similar Indo-Pacific species such as *M. fragilis* from Sri Lanka, *M. denticulata* from Western Australia and *M. jejuensis* from Korea, by a combination of their thallus habit, blade morphology and network structure (see Table 2 for a morphological comparison). Among all the species with multiple bands of networks, *M. jejuensis* has the largest thallus (up to 30 cm) and shows a great variation of thallus habit (see Figs 38–43), whereas the thalli of genuine *M. fragilis* (see Coppejans *et al*., 2009. fig. 179a, b) and *M. denticulata* (Harvey 1855, pl. 127) are smaller, *c*. 5–10 cm in height. In contrast, the three new species from Taiwan are even smaller, ranging from 1–4 cm in height. *M. taiwanifretensis* can be separated from *M. leeii* and *M. kentingii* by its longer blades (up to 4 cm) with a conspicuous band of basal network (see Figs 40, 41). *Martensia kentingii* can be identified by its well-developed network, which almost covers the entire blade (see Figs 17, 18), whereas *M. leeii* can be characterized by the main blade having a wide band of network at the distal end and bearing numerous, fan-shaped, marginal lobes (see Figs 2, 3).

In this study, we have confirmed the observations by Lin *et al.* (2004*a*, 2009) that the morphology and the developmental patterns of networks are useful taxonomic features for delineating the species of *Martensia*. We anticipate that more new species of *Martensia* will be described when additional sequence analyses and careful, morphological comparison



Figs 38–43. *Martensia jejuensis.* Thallus morphology. **38–40**. Thalli representing *M. jejuensis* and *M.* '*bibarii*' and bearing lobed (arrows) and hairy (arrowheads) networks collected from Chochun, Jeju Island (coll. S.-M. Lin, 28 August 2008). **41–43**. Thalli representing *M.* '*bibarii*' and *M.* '*fragilis*' and bearing lobed (arrows) and hairy (arrowheads) networks collected from Seolim, Jeju Island (coll. S.-M. Lin & W.-J. Lee, 25 June 2005). Scale bars = 15 mm (Fig. 38) and 10 mm (Figs 39–43).

based on well-preserved specimens from warm water regions become available.

Taxonomic conclusion

***Martensia jejuensis* Y. Lee [(2004), *Phycological Research* 52: 256, figs 2–21] *sensu emend*. S.-M. Lin, W.-C. Yang, Huisman, De Clerk & W.J. Lee**

Holotype: tetrasporic, LYP-1586 in the Herbarium of the Department of Biology, Cheju National University (CNU).

Type locality: Subtidal zone (6–8 m deep), Jongdal, Jeju Island, Korea, 7 August 2000.

Proposed synonym: *Martensia bibarii* Y. Lee (2004), *Phycological Research* **52**: 258, figs 22–27. [Holotype: tetrasporic, LYP-1594 in the Herbarium of the Department of Biology, Cheju National University (CNU); Type locality: subtidal zone (6–8 m deep), Jongdal, Jeju Island, Korea, 3 August 2000.]

Distribution: **Korea:** Jeju Island, Korea (Lee, 2004; this study). **Japan:** Seto Inland Sea; Okinoshima,

Chiba Prefecture (this study). Previous records of *M. fragilis* (e.g. Yoshida & Mikami, 1996) and *M. denticulata* (Okamura, 1936) from Japan should be treated as *M. jejuensis*.

Acknowledgements

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