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Drachiella liaoii sp. nov., a new member of the Schizoserideae (Delesseriaceae, Rhodophyta) from Taiwan and the Philippines

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A new member of Delesseriaceae (Ceramiales, Rhodophyta) is described from Southern Taiwan and the Philippines. On the basis of comparative vegetative and reproductive morphology, and phylogenetic analysis inferred from nuclear-encoded large-subunit ribosomal DNA sequences (LSU rDNA), we conclude that it belongs in the genus *Drachiella*, tribe Schizoserideae, subfamily Phycodryoideae. The new taxon shares with other *Drachiella* species the absence of macro- and microscopic veins; diffuse growth by marginal and intercalary meristematic cells; a polystromatic, lobed thallus; abundance of rhizoidal marginal proliferations used for attachment; convoluted plastids in surface cells; abundant secondary pit connections among adjacent vegetative cells; large intercellular spaces between surface cells; procarps confined to the upper side of the thallus, circular in outline, consisting of a supporting cell bearing a strongly curved carpogonial branch and two sterile groups that remain undivided; vertical division of gonimoblast initial from auxiliary cell, and unilateral, monopodial branching of gonimoblasts; and mature cystocarps with a massive candelabrum-like fusion cell of fused gonimoblasts bearing carposporangia in branched chains. It is distinguished from the other members of the genus by thalli that consist of extensive tangled mats of prostrate and overlapping decumbent blades, procarps confined to the upper side of the thallus, and the lack of basal stalks or stipes. Whereas the Schizoserideae is predominantly a Southern Ocean tribe, one of the tribe's four genera, *Drachiella*, was known only from the eastern Atlantic and Mediterranean. We herein report the first record of the genus for the Indo-Pacific Ocean, and describe *Drachiella liaoii*, sp. nov., as a fourth species in the genus.

Key words: algae, Ceramiales, Delesseriaceae, *Drachiella liaoii* sp. nov., LSU rDNA, Philippines, phylogeny, Rhodophyta, Schizoserideae, Taiwan

Introduction

The overall phylogeny of the Delesseriaceae at the subfamily and tribal level was recently revised by Lin *et al.* (2001) on the basis of evidence inferred from sequence analysis of the nuclear-encoded large-subunit ribosomal RNA gene (LSU rDNA) and chloroplast-encoded *rbc*L, and from a re-assessment of a suite of morphological characters. Lin *et al.* (2001) identified three subfamilies in the Delesseriaceae, thus emending the two-subfamily system of Kylin (1924, 1956) that consisted of the Delesserioideae and Nitophylloideae. A new subfamily, the Phycodryoideae, was proposed to include four natural assemblages, equivalent to tribes, that were traditionally placed in the Nitophylloideae. The Phycodryoideae consists of the Phycodryeae (formerly known as the Phycodrys Group; Kylin, 1924), the Cryptopleureae (formerly known as the Cryptopleura Group; Kylin, 1924), the Myriogrammeae (Hommersand & Fredericq, 1997*a*) and the Schizoserideae (Hommersand & Fredericq, 1997*b*; Lin *et al.*, 2001).

The predominantly Southern Hemisphere tribe Schizoserideae has been well characterized morphologically (Maggs & Hommersand, 1993; Hommersand & Fredericq, 1997*b*; Lin & Kraft, 1999) and consists of four non-parasitic genera: *Schizoseris* Kylin 1924, *Neuroglossum* Kützing 1843, *Abroteia* J. Agardh 1876 and *Drachiella* Ernst *et* J. Feldmann 1957 (Hommersand & Fredericq, 1997*b*). The eastern Atlantic and Mediterranean genus *Drachiella* can be separated from the other three genera by its polystromatic thallus, lack of macro- and microscopic veins, procarps confined to the upper side of the thallus, a strongly curved carpogonial branch with the trichogyne passing beneath sterile group 1, and two sterile groups remaining undivided after fertilization (Maggs & Hommersand, 1993; Hommersand & Fredericq, 1997*b*).

The genus *Drachiella* includes three species: the type *D. spectabilis* Ernst *et* J. Feldmann (1957)

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known from the British Isles to N. France, *D. heterocarpa* (Chauvin *ex* Duby) Maggs *et* Hommersand (1993) recorded from the British Isles to N. Spain, and *D. minuta* (Kylin) Maggs *et* Hommersand (1993) known from the British Isles to Morocco and the Mediterranean. An undescribed species of *Drachiella* was collected in the southern Philippines and southern Taiwan. In this paper we describe the new species on the basis of its vegetative and reproductive morphology, and provide further evidence of its taxonomic placement as inferred from comparative gene sequence analysis of selected members of the Phycodryoideae.

Materials and methods

Collections were made by either SCUBA or snorkelling. Algal samples for the molecular study were desiccated in silica gel or preserved in 95% alcohol. Voucher specimens and materials used in the morphological study were fixed in 10% formalin/seawater, and then stored in 5% formalin/seawater or pressed as herbarium sheets, and deposited in the Herbarium of the Taiwan National Museum of Marine Biology and Aquarium (NMMBA), National Taiwan Ocean University (NTOU) and the University of Louisiana at Lafayette (LAF). Whole-mount material and hand-sections were stained in 1% aniline blue acidified with 1% HCl and mounted in glycerol or were treated with Wittmann's aceto–iron–haematoxylin–chloral hydrate (Wittmann, 1965) and mounted in 50% Hoyer's mounting medium (Lin & Kraft, 1999). Type specimens were scanned using a Microtek Scanmaker III. Microphotographs were taken on an Olympus BX60 microscope with a Polaroid DMC Ie digital camera. Digital images were edited and assembled in plates using Photoshop v.4.0. Photographic plates were printed on an Epson Stylus Color 900 inkjet printer.

DNA samples were prepared using the DNeasy Plant Mini Kit (QIAGEN, Valencia, CA, USA) following the instructions of the manufacturer. The gene selected is the nuclear-encoded large-subunit ribosomal DNA gene (LSU rDNA). The primers and protocols for gene amplification and automated sequencing used in this study are listed in Lin *et al*. (2001).

The sequence data, first generated in Lin *et al*. (2001), were compiled and aligned with Sequencher (Gene Codes Corp., Ann Arbor, MI, USA) and exported for phylogenetic analysis. The LSU rDNA data set alignment was done first by using the online program ClustalW 1.8 (http://dot.imgen.bcm.tmc.edu:9331/multi-align/multi-align.html), and then this alignment was revised manually. Phylogenetic analyses of the LSU rDNA sequence data were performed using the Minimum Evolution (Distance) Neighbor-Joining program with the Kimura 2-parameter, and Maximum Parsimony algorithms available in the computer program PAUP (v. 4.0b4a*: Swofford, 2000). Parsimony heuristic searches consisted of 500 random stepwise additions, MULPARS (but holding only five trees at each step) and Tree-Bisection-Reconnection (TBR) swapping algorithm until swapping was complete. The searches were done on each data set under the criterion of equal weights for all substitutions. Consistency (CI) and retention (RI) indices (Kluge & Farris, 1989) were calculated excluding uninformative characters. Support for nodes of parsimony trees was assessed by calculating 1000 bootstrap resamplings (Felsenstein, 1985) of the heuristic searches based on random stepwise additions, MULPARS and TBR.

Material examined in this study includes *Drachiella liaoii* sp. nov. Lin, Lewis *et* Fredericq from Southern Taiwan: Wan Lee Dong Bay (21°59′N; 120°42′E), Kenting National Park, coll. S.-M. Lin & M.-L. Qiu, tetrasporophytic, 1–5 m depth, 26.i.92; Banana Bay (21°55′N; 120°49′E), coll. S.-M. Lin, cystocarpic and tetrasporophytic, 1–5 m depth, 19.viii.00; and from the Southern Philippines: Little Santa Cruz Is. (6°55′N; 122°05′E), Zamboanga City, coll. S.-M. Lin, tetrasporophytic, 1–10 m depth, 28.iv.98.

Results

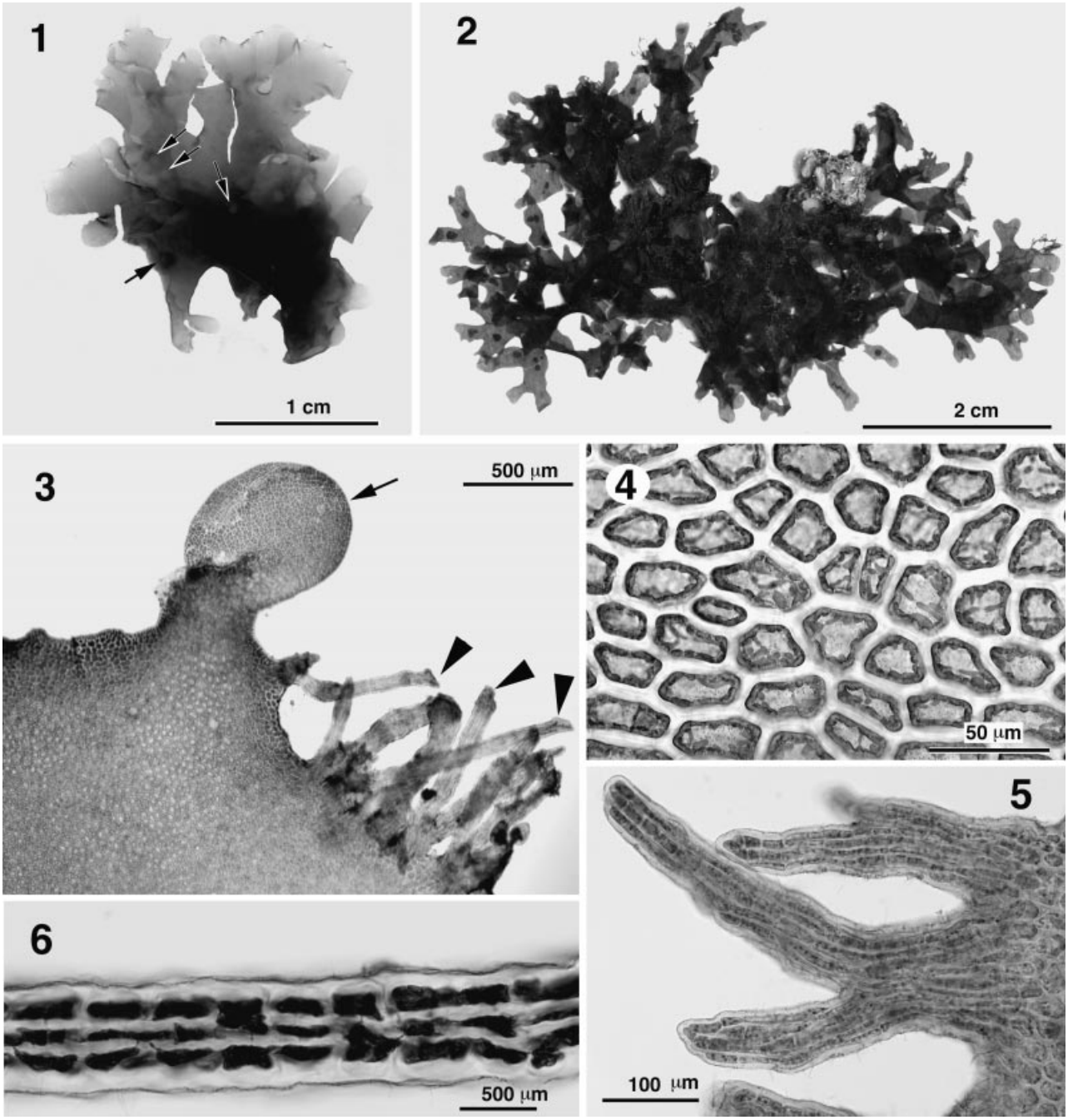
Diagnosis and observations

Drachiella liaoii Lin, Lewis *et* Fredericq, sp. nov. (Figs 1–20)

Thalli constantes ex ramosis laminis prostratis versus decumbentes rhizoideis marginalibus filamentosis; laminae usque ad 1·5 cm longaeque 2–3 mm latae, polystromaticae omnino; macroscopicae microscopicae venae absentes; thalli masculini incogniti; cystocarpia dispersa secus marginem laminae fertilis, hemisphaerica; procarpia formantia supra laminarum fertilium, gonimoblasti initio exorientes unilaterales e cellula fusionalis ramosa ampla multinucleata; tetrasporangia disposita in soros discoideos versus ovalia, sporangia abscissa lateralia e cellulis subsuperficialibus formantes duo series transsectiones laminarum fertilium.

Thalli consisting of extensive tangled mats composed of prostrate and overlapping, decumbent, lobed blades lacking stipe and holdfast; lobed blades each up to 1·5 cm in length by 2–3 mm in width, mats reaching up to 6 cm width, attached to the substratum by uniseriate, marginal rhizoidal proliferations; blades otherwise polystromatic; macro- and microscopic veins absent; male gametophytes unknown; procarps restricted to the upper side of fertile blades, when unfertilized consisting of a supporting cell bearing a strongly curved carpogonial branch and two sterile groups that remain undivided; vertical division of gonimoblast initial from auxiliary cell; mature cystocarps hemispherical, scattered over the dorsal surface, with a massive candelabrum-like fusion cell of fused inner gonimoblasts bearing carposporangia in branched chains, auxiliary and central cells in the floor of the cystocarp; tetrasporangia arranged in discoid to oval sori, the sporangia cut off laterally from subsurface cortical cells and forming two rows in cross-sections of fertile blades.

ETYMOLOGY: 'liaoii', is dedicated in honour of Dr Lawrence Liao, prominent phycologist in the Philip-



Figs 1–6. *Drachiella liaoii* Lin, Lewis *et* Fredericq, sp. nov. Habit and vegetative morphology (Figs 1, 3–6: Banana Bay, Kenting National Park, Fig. 2: Wan Lee Dong, Kenting National Park). Fig. 1. Part of holotype (cystocarpic). Arrows point to cystocarps. Fig. 2. Syntype (tetrasporic). Fig. 3. Portion of vegetative thallus showing a young blade (arrow) and marginal rhizoidal proliferations (arrowheads). Fig. 4. Surface cells with convoluted plastids. Fig. 5. Close-up of rhizoidal proliferations from the margin. Fig. 6. Cross-section through the upper, tristromatic portion of the thallus.

pines, who organized the 1998 collecting trip to Little Santa Cruz Island in Zamboanga.

HOLOTYPE: NMMBA, 8-19-2000-S1 (Fig. 1). Isotypes in NTOU and LAF, 92-6231-32.

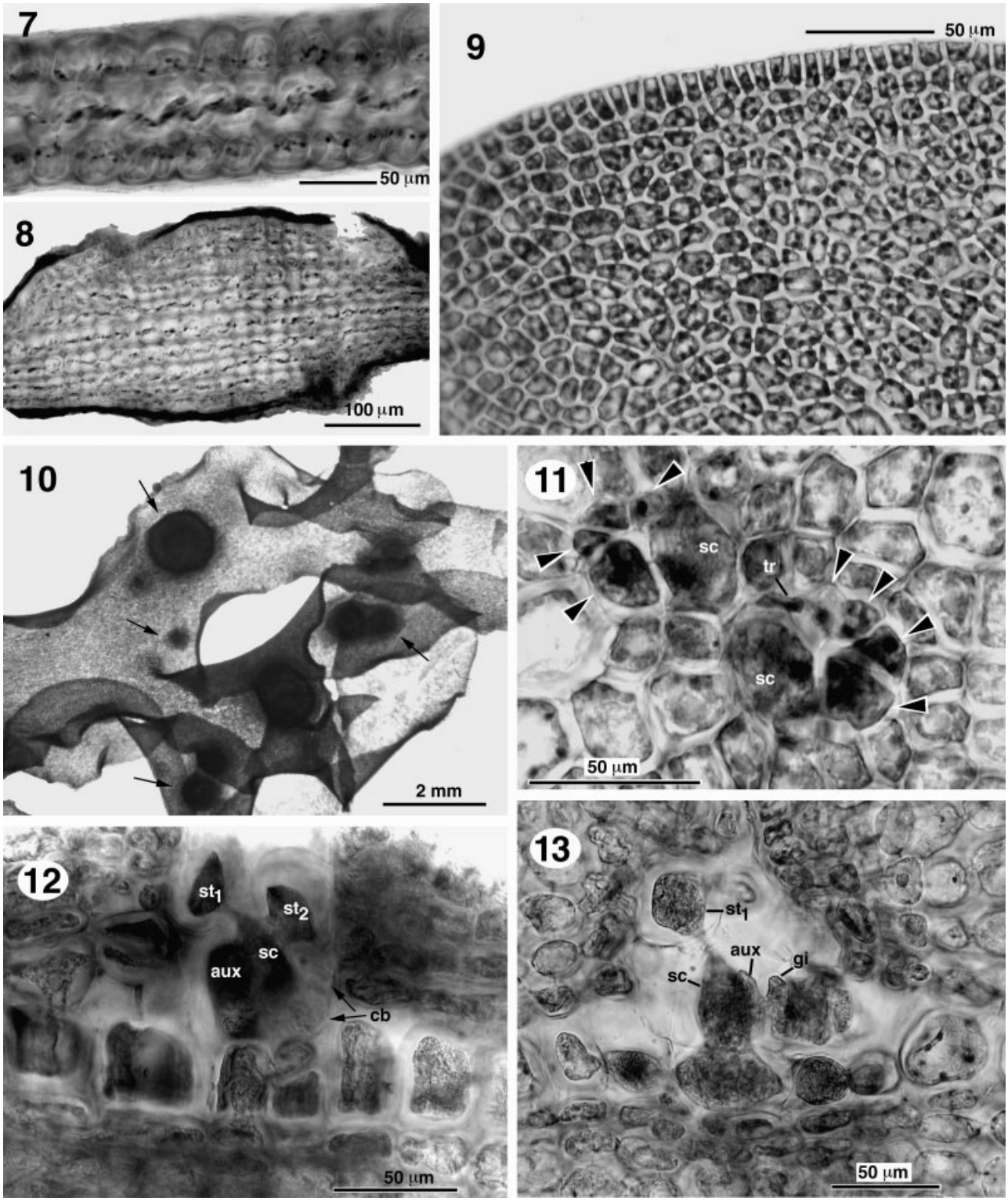
TYPE LOCALITY: Banana Bay, Kenting National Park, southern Taiwan (21°55′N; 120°49′E).

DISTRIBUTION: Known from Kenting National Park, southern Taiwan and Little Santa Cruz Island, Zamboanga, southern Philippines.

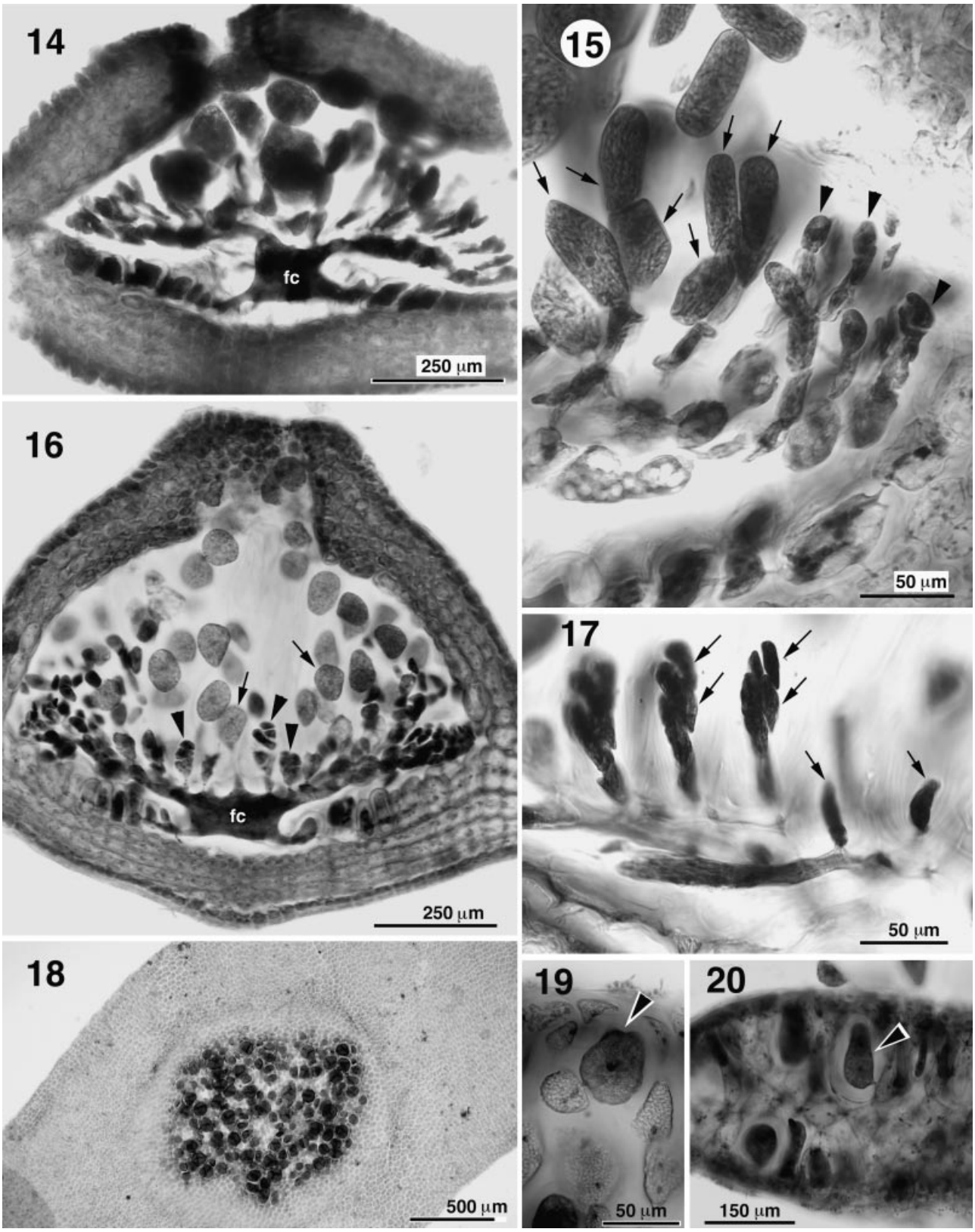
HABITAT AND SEASONALITY: Collections were seasonally made in April, August, September and January. Lack of perennial stipes indicates that this taxon may be an annual. Plants were growing at 1–10 m depths on coral reefs, or were epiphytic on the coralline *Cheilosporum acutilobum* (Decaisne) Piccone.

Habit and vegetative structure

Thalli are composed of prostrate and overlapping decumbent membranous, lobed blades (Fig. 1), forming mats 1–2 cm high and up to 6 cm wide (Fig. 2). Blades are bright-red to pink, often with brilliant pink and blue iridescence. A holdfast or



Figs 7–13. *Drachiella liaoii* Lin, Lewis *et* Fredericq, sp. nov. Vegetative and reproductive morphology (Banana Bay, Kenting National Park). Fig. 7. Cross-section through the blade showing nuclei organized in the median plane of young surface cells. Fig. 8. Cross-section through a polystromatic, old blade. Fig. 9. Young blade margin showing uni-, bi- and multinucleate surface cells, abundant secondary pit connections and large interstitial spaces. Fig. 10. Close-up of a cystocarpic blade. Arrows point to hemispherical cystocarps. Fig. 11. Focus at the subsurface plane showing a young pre-fertilization procarp with supporting cell (sc) bearing a young, strongly curved, 4-celled carpogonial branch (arrowheads) with trichogyne initial (tr). Fig. 12. Cross-section through a young cystocarp showing a supporting cell (sc) bearing two undivided sterile groups (st_1, st_2), auxiliary cell (aux) and degenerated carpogonial branch fusion cell (cb). Fig. 13. Cross-section through a young cystocarp showing an auxiliary cell (aux) with gonimoblast initial (gi). In focus is the undivided sterile group 1 (st_1) borne on a supporting cell (sc).



Figs 14–20. *Drachiella liaoii* Lin, Lewis *et* Fredericq, sp. nov. Cystocarp and tetrasporangial features (Banana Bay, Kenting National Park). Fig. 14. Cross-section through a nearly mature cystocarp showing a massive fusion cell (fc) bearing highly branched gonimoblast filaments. Fig. 15. Close-up of gonimoblasts showing carposporangia in branched chains (arrows) and immature carposporangia (arrowheads). Fig. 16. Cross-section through a fully mature cystocarp showing carposporangia (arrows) and initials of secondary carposporangia (arrowheads). fc, fusion cell. Fig. 17. Close-up of initials of secondary carposporangia (arrows). Fig. 18. Surface view of a tetrasporangial sorus. Fig. 19. Cross-section through a young tetrasporangial sorus showing a tetrasporangial initial (arrowhead) cut off laterally from the inner cortical cells. Fig. 20. Cross-section through a mature tetrasporangial sorus showing tetrasporangia (arrowhead) arranged in two rows.

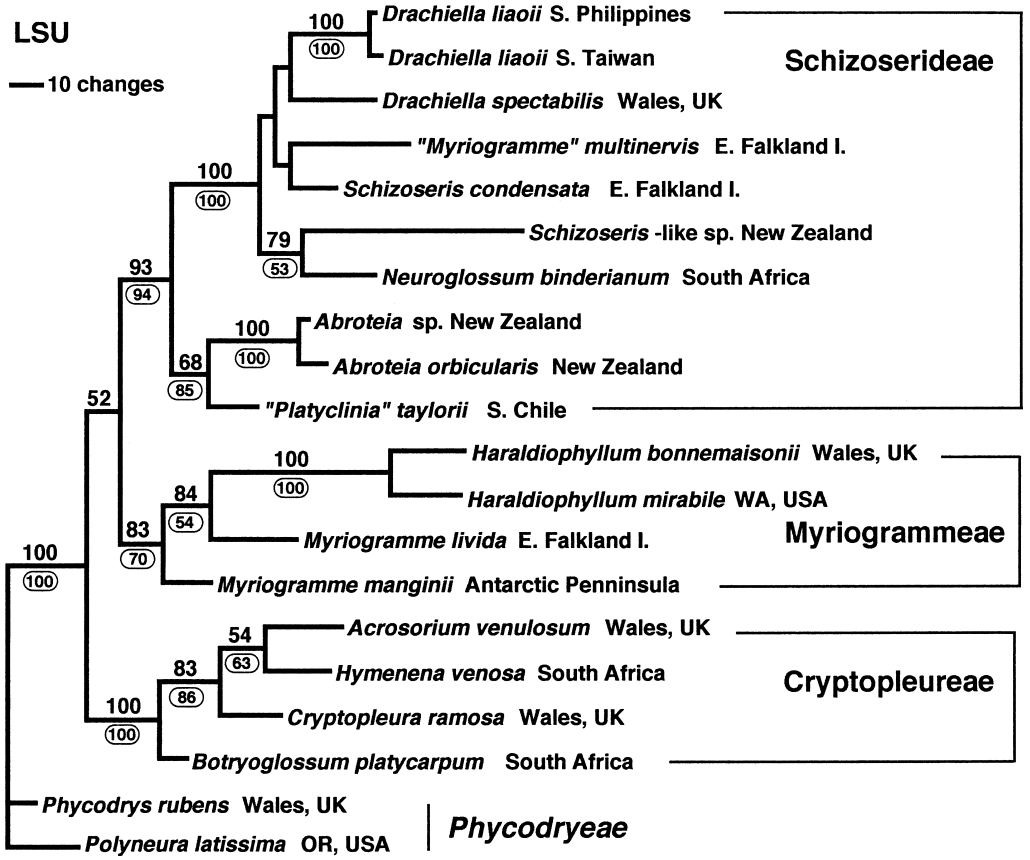


Fig. 21. One of two equally most parsimonious LSU rDNA trees showing the inter- and intra-generic relationships of the Schizosorideae in the subfamily Phycodryoideae. Tree length = 738 steps, CI = 0·6477, RI = 0·6601, informative characters = 219 of 1170 included sites. Bootstrap proportion values (1000 replicates, > 50%) derived from parsimony and neighbor joining analyses are shown, respectively, above and below the nodes. Branch lengths are proportional to the amount of sequence change.

recognizable stipe are absent, and the blades are anchored directly to the substratum by multicellular, uniseriate, multinucleate rhizoidal proliferations extending from marginal surface cells or from the blade's undersurface (Figs 3, 5). Decumbent blades are subdichotomously to irregularly lobed, with the free ends unevenly 1–3 mm wide, giving most plants highly irregularly outlines (Fig. 2). New bladelets are formed from marginal cells as small blade proliferations, 0·5–3 mm in width by 1–5 mm long, and may be irregularly rounded apically (Fig. 3). Margins are otherwise smooth and entire. Seen from above, there are several plastids per surface cell, variously convoluted in outline (Fig. 4).

Blades are polystromatic throughout from within one or two cells of the leading margins. Initially the prostrate blades are tristromatic (Figs 6, 7), 70–100 μm in thickness, but increase in thickness up to 300 μm reaching 10–12 cell layers thick (Fig. 8). Micro- and macroscopic veins are absent throughout.

Growth is diffuse by meristematic activity of marginal and intercalary cells (Fig. 9). Marginal meristematic cells of prostrate and decumbent blades (Fig. 9) are initially uninucleate, becoming bi- or multinucleate. In cross-sections, nuclei within young surface cells are arranged in a median plane (Fig. 7). Secondary pit connections are abundant between adjacent multinucleate cells (Fig. 9). The intercellular spaces among the surface cells are large (Fig. 10).

Reproductive structures

Male gametophytes are unknown. Mature cystocarps are scattered over the fertile blade (Fig. 10). Procarps (Fig. 11) are abundant near the blade margins and restricted to the upper blade surface. Unfertilized procarps consist of a fertile central cell, cutting off a fertile pericentral cell which becomes the large supporting cell that cuts off laterally a strongly curved 4-celled carpogonial branch (Fig. 11) followed by two 1-celled sterile groups. The uninucleate trichogyne initial is at first isodiametric (Fig. 11, left) before it starts narrowing and elongating (Fig. 11, right). The outline of such a young procarp is typically circular. The supporting cell and unfertilized carpogonium remain uninucleate, whereas the second and third cells of the carpogonial branch become multinucleate (Fig. 11). The first cell of the carpogonial branch is large, typically half the size of the supporting cell (Fig. 11).

Table 1. List of species analysed for the molecular study with their LSU rDNA accession numbers previously deposited in GenBank (from Lin *et al.*, 2001). The number after the accession number is the percentage of the fragment (1170 bp) sequenced

Species	GenBank accession no.
Abroteia orbicularis J. Agardh	AF259402, 100%
Abroteia sp.	AF259403, 100%
Acrosorium venulosum (Zanardini) Kylin	AF259405, 100%
Botryoglossum platycarpum (Turner) Kützing	AF259408, 100%
Cryptopleura ramosa (Hudson) Kylin *et* Newton	AF259420, 100%
Drachiella liaoii sp. nov.[a]	AY033510, 97%
Drachiella liaoii sp. nov. (as *Drachiella*-like sp. in Lin *et al.*, 2001)	AF259480, 100%
Drachiella spectabilis Ernst & Feldmann	AF259427, 100%
Haraldiophyllum bonnemaisonii (Kylin) Zinova	AF312313, 95%
Haraldiophyllum mirabile (Kylin) Zinova	AF312314, 87%
Hymenena venosa (Linnaeus) Krauss	AF259438, 100%
Myriogramme livida (Hooker *et* Harvey) Kylin	AF259443, 100%
Myriogramme manginii (Gain) Skottsberg	AF259455, 100%
'*Myriogramme*' *multinervis* (Hooker *et* Harvey) Kylin	AF259483, 100%
Neuroglossum binderianum Kützing	AF259456, 100%
Phycodrys rubens (Linnaeus) Batters	AF259470, 100%
'*Platyclinia*' *taylorii* Levring	AF259474, 100%
Polyneura latissima (Harvey) Kylin	AF259475, 100%
Schizoseris-like sp.	AF259485, 91%
Schizoseris condensata (Reinsch) Ricker	AF259484, 100%

[a] Newly produced sequence from *D. liaoii* collected from Banana Bay, Kenting National Park by S.-M. Lin, 19.viii.00.

Direct fertilization was not seen in our material. Following presumed fertilization, the supporting cell cuts off the auxiliary cell (Fig. 12); all four cells of the carpogonial branch fuse after diploidization of the auxiliary cell as the pit connection between them break down, resulting in a carpogonial fusion cell in which the nuclei and cell contents degenerate (Fig. 12). The auxiliary cell in turn cuts off on one side a gonimoblast initial vertically (Fig. 13) that continues to divide anticlinally to produce young gonimoblasts. The two sterile groups remain undivided. As gonimoblast development progresses, the pit connection linking each sterile cell to the supporting cell breaks down, resulting in partially fused sterile cells that retain their shape but become slightly enlarged (Figs 12, 13). Cells in the floor of the cystocarp are typically enlarged and become darkly staining (Figs 12, 13). The gonimoblasts at first develop on one side, and then continue to branch and radiate in all directions upwardly into the cystocarp cavity. The gonimoblasts branch monopodially in short chains that branch towards the upper side only. A massive and highly branched multinucleate fusion cell is formed primarily due to the breakdown of primary pit connections between the supporting cell and the remnant of the auxiliary cell, and the innermost gonimoblast cells. In addition, fusions extend laterally at the base of the cystocarp, incorporating central cells (Figs 14, 16). Pyriform carposporangia, 50–70 μm by 45–65 μm, are formed continually terminally in short branched chains (Figs 15, 16), and secondary carposporangia are frequently formed in small clusters below primary carposporangia on the branched arms of the fusion cell (Figs 16, 17). The carposporophyte is housed within a pericarp 4 or 5 cell layers thick, 100–130 μm in thickness, with a slightly protuberant central ostiole (Fig. 16).

Tetrasporangial sori, formed on ordinary blades, are rounded to ovoid in shape (Fig. 18), 500–750 μm by 700–800 μm in diameter, solitary or aggregated, and scattered over both sides of the fertile blades. Tetrasporangial initials are cut off laterally from inner cortical cells (Fig. 19). Mature tetrasporangia are tetrahedrally divided, 50–65 μm by 50–75 μm in diameter, mature at an irregular rate, and are arranged on both sides of the central cells (Fig. 20).

Molecular analyses

Partial LSU rDNA sequences of *D. liaoii* sp. nov. were generated from two collections: one from Banana Bay, Kenting National Park, Southern Taiwan (type locality) and one from Little Santa Cruz Is., southern Philippines. A set of 18 additional representative taxa belonging to the four tribes in the subfamily Phycodryoideae (Table 1), with the tribe Phycodryeae serving as the outgroup, was selected for the analysis (Fig. 21). The LSU rDNA alignment initially included 1563 sites. Due to questionable homology of sites in the 5′ and 3′ ends of these sequences having a large number of insertions/deletions, they were excluded from the analysis. Additionally, sites encompassing indels in

the interior portions of the sequences were not included, so that the final data matrix was restricted to 1170 total sites that included 219 parsimony-informative characters (18·7%). Although a distance tree is not presented, it is congruent with the parsimony tree, and distance bootstrap values > 50 have been included on the parsimony tree below the nodes (Fig. 21).

The Schizoserideae, Myriogrammeae and Cryptopleureae, using the Phycodryeae as the outgroup, are well-supported monophyletic clades, each receiving strong bootstrap support, respectively 93/83/100 in the parsimony analysis and 94/70/100 in the distance analysis (Fig. 21). The undescribed specimens from the Philippines and Taiwan clearly belong in the Schizoserideae, and are conspecific, differing by 7 bp (< 0·6% divergence). Although there is no bootstrap support, the new taxon consistently is sister to the type species of *Drachiella*, *D. spectabilis*. There are two major groups within the Schizoserideae: one strongly supported (100/100) clade consisting of *Drachiella*, *Schizoseris* and *Neuroglossum*, and a second, weakly to moderately supported clade (68/85) consisting of *Abroteia* and the taxon currently known as *Platyclinia taylorii*. *Drachiella* is sister to *Schizoseris*, and this assemblage is sister to *Neuroglossum*. However, this topology shows only low to moderate bootstrap support (Fig. 21).

Discussion

Lin *et al*. (2001) recently revised the systematics of the Delesseriaceae and proposed a three-subfamily system for the family rather than Kylin's (1924, 1956) two-subfamily system. On the basis of both morphological and molecular evidence, they proposed a new subfamily, the Phycodryoideae, to contain four tribes, namely the Schizoserideae, Myriogrammeae, Cryptopleureae and Phycodryeae, all formerly placed in the subfamily Nitophylloideae by Kylin (1924, 1956). The diagnostic character for separating the Phycodryoideae from the Nitophylloideae pertains to carposporophyte development. In the Phycodryoideae, a post-fertilization fusion cell is large and multinucleate due to the fusion of the auxiliary cell with inner gonimoblast cells and neighbouring gametophytic cells, as the pit connections linking gonimoblast cells degenerate. In contrast, in the Nitophylloideae, a fusion cell or fusion products is lacking, and the basal gonimoblast cell remains small and uninucleate, with the pit connection linking each gonimoblast cell persisting and expanding in size.

The Schizoserideae have been characterized by Hommersand & Fredericq (1997*b*) by such features as the presence of single dissected parietal plate-like or convoluted ribbon-like plastids in older vegetative cells; procarps consisting of two 1-celled sterile groups, a strongly curved 4-celled carpogonial branch and absence of cover cells; gonimoblast filaments at first developing unilaterally to one side, later radiating in all directions and bearing carposporangia in simple chains; a large fusion cell that is branched through the incorporation of cells of inner gonimoblast filaments and central floor cells; and the formation of carposporangia in branched chains. On the basis of our morphological observations, our new taxon clearly belongs to this tribe.

The Schizoserideae, Myriogrammeae and Cryptopleureae, using the Phycodryeae as the outgroup, are strongly supported monophyletic clades, as was already noted by Lin *et al*. (2001) from phylogenetic sequence analyses inferred from both chloroplast-encoded *rbc*L and LSU rDNA. Although bootstrap support for the Schizoserideae was strong, with *Abroteia* from New Zealand and '*Platyclinia*' from Chile well separated from the cluster of the genera *Drachiella*, *Neuroglossum* and *Schizoseris*, these three genera are weakly differentiated (Fig. 21). However, *Drachiella* can be distinguished from the other genera on the basis of its procarps being confined to the upper side of the thallus only. Since no other species from these three genera have been sequenced and analysed, we suggest maintaining these three genera at this point and call for a detailed morphological study of the type species of *Neuroglossum*, *N. binderianum*, and *Drachiella*, *D. spectabilis*, to clarify their relationships with *Schizoseris*.

The new taxon shares with *Drachiella* as currently circumscribed (Maggs & Hommersand, 1993) the absence of macro- and microscopic veins; diffuse growth by marginal and intercalary meristematic cells; a polystromatic, lobed thallus; abundance of rhizoidal marginal proliferations used for attachment; convoluted plastids in surface cells; abundant secondary pit connections among adjacent vegetative cells; large intercellular spaces between surface cells; procarps confined to the upper side of the thallus, circular in outline, consisting of a supporting cell bearing a strongly curved carpogonial branch and two sterile groups that remain undivided; vertical division of gonimoblast initial from auxiliary cell, and unilateral, monopodial branching of gonimoblasts; and mature cystocarps with a massive candelabrum-like fusion cell of fused gonimoblasts bearing carposporangia in branched chains. It is distinguished from the other members of the genus by thalli that consist of extensive tangled mats of prostrate and overlapping decumbent blades, and lack of basal stalks or stipes.

Kylin (1924) stressed the diagnostic importance of a strongly curved carpogonial branch with the trichogyne extending beneath sterile group-1 and

Table 2. Relevant features separating the four species of *Drachiella*. Data from *D. spectabilis*, *D. minuta* and *D. heterocarpa* are adapted from Maggs & Hommersand (1993)

Features	*D. liaoii*	*D. spectabilis*	*D. minuta*	*D. heterocarpa*
Habit	Entangled mats of prostrate and overlapping, decumbent, lobed, entire blades	Erect, semi-peltate blades	Erect to mainly prostrate	More or less erect when young, blades formed either singly or in small groups
Attachment mode	Marginal uniseriate, rhizoidal proliferations	Solid lobed holdfast with prostrate rhizome-like outgrowths	Prostrate rhizome-like cylindrical axes forming rhizoidal haptera	Branched holdfast consisting of discoid primary holdfast and rhizome-like prostrate axes
Stipe	Absent	Erect, cylindrical to compressed	Compressed	Cylindrical, branched when old, cartilaginous
Thallus size	Mats up to 1–6 cm wide, 2 cm high	2–14 cm wide	0·5–5 cm wide, 0·7–5 cm high	Up to 9 cm wide, 5–7 cm high
Blade shape	Fan-shaped when single, irregular subdichotomous mats with lobed apices	one or more fan-shaped, entire blades with pointed apices	Lanceolate to ovate, becoming fan-shaped, sometimes deeply divided with lobed apices	Fan-shaped, dichotomously or irregularly lobed or deeply divided with entire or toothed margins
Blade thickness	3–12 cell-layered; 70–300 μm	1–10 cell-layered; 65–450 μm	3–5 cell-layered; 50–130 μm	1–20 cell layered; 55–1100 μm
Tetrasporangial sori	On ordinary blades, on both sides of thallus	On specialized bladelets, developing on blade remnants along margins on upper surface	Subapical, just inside marginal lobes	On specialized bladelets, developing on old stipes and thickened blade remnants

emerging distally from it in *D. minuta* (as *Myriogramme minuta*), but this stage was not seen in our material due to lack of many functional prefertilization stages. Likewise, the diploidization of the auxiliary cell by means of the connecting cell as shown by Hommersand & Fredericq for *Schizoseris condensata* (1997*b*) was not observed.

Morphological features separating *D. liaoii* from the other species in the genus, namely *D. spectabilis*, *D. heterocarpa* and *D. minuta*, are listed in Table 2 (from Magne, 1957; Maggs & Hommersand, 1993). *D. liaoii* can easily be misidentified in the field as '*Acrosorium venulosum*' (Zanardini) Kylin (1924), which occurs in the Indo-Pacific Ocean (see Silva *et al.*, 1996), due to similar entangled clumps and prostrate habit. However, *D. liaoii* can be distinguished from *A. venulosum* by the lack of microscopic veins that characterize *A. venulosum*, and by its polystromatic thallus. On the basis of the morphological and molecular results, our new species fits well within the description of the genus *Drachiella* (see Maggs & Hommersand, 1993) and is the first record of the genus *Drachiella* from the Indo-Pacific Ocean and also the first record outside the northeastern Atlantic Ocean.

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