

Ditria expleta (Rhodophyta: Rhodomelaceae) a new red algal species from Western Australia

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Ditria expleta sp. nov. (Rhodophyta: Rhodomelaceae) is described from Western Australia, where it occurs epiphytically on the fronds of *Lobophora variegata* (Lamouroux) Womersley. Main axes and vegetative lateral branches are prostrate and dorsi-ventral, with five pericentral cells. Cells of the ventral pericentral siphon (which is aligned adjacent to the substratum) produce digitate holdfasts. Branch initials arise exogenously from each segment and are arranged in a spiral pattern with a 1/5 divergence between successive initials. The dorsal branch initial remains dormant, while the remainder produce lateral branches that lie flush with the substratum. The resultant thallus has a pattern of alternating pairs of lateral branches, with every fifth segment naked except for the dormant branch initial. Cytocarps are borne terminally on determinate lateral branches. Spermatangia arise on reduced branchlets near the apices of lateral branches. Tetrahedrally-divided tetrasporangia are produced in linear series of up to 10 sporangia in terminal portions of determinate lateral branches. *Ditria expleta* differs from the previously described species of the genus in the production of branches from both of the lateral branch initials. In *Ditria reptans* and *Ditria zonaricola* the ventral lateral initial remains dormant, with the resultant branching pattern that of alternating single branches. *Ditria* is included in the tribe Polysiphonieae. A comparison of the mode of branch formation in *Ditria expleta* with that found in the superficially similar *Dipterosiphonia* and *Herposiphonia* suggests that the latter two genera are incorrectly placed in the Polysiphonieae and should be transferred to a resurrected Herposiphonieae.

Key Index Words: algae—Australia—Dipterosiphonia—Ditria—Ditria expleta sp. nov.—Herposiphonia—Rhodomelaceae—Rhodophyta—taxonomy.

The red algal genus *Ditria* was established by Hollenberg (1967) for a prostrate rhodomelaceous plant from Hawaii. *Ditria reptans* Hollenberg was characterised by the production of determinate lateral branches in a regular sequence in which the branches were separated by alternating intervals of 2 and 3 segments. This branching pattern was described in greater detail by Yoshida & Yoshida (1983) when adding a second species (*D. zonaricola* (Okamura) Yoshida & Yoshida) to the genus, and they also described the previously unknown reproductive structures. In the two known species of *Ditria* the production of branch initials is in a spiral sequence in which only the more dorsal of the lateral initials develops into a branch, the rest remaining dormant (occasionally the dorsal initial

will produce a trichoblast). The resultant branching pattern is repeated every five segments. In a single sequence two lateral branches will be produced, separated from each other by a dormant dorsal branch initial and from subsequent lateral branches by two dormant ventral branch initials. The present paper adds a third species from materials collected in Western Australia. The new species differs in the production of additional branches from the lateral initials, resulting in a five segment sequence that includes four lateral branches arranged in alternating pairs and a single naked segment bearing only the dormant dorsal branch initial.

Materials and Methods

All specimens examined were preserved in approximately 4% formalin/seawater. Portions of plants for microscopical examination were mounted directly on slides in a solution of 1% aniline blue, 50% 'Karo' corn syrup (CPC International) and 49% water. Pressed specimens are lodged in the herbarium of the School of Biological and Environmental Sciences, Murdoch University, with isotypes distributed to PERTH, MELU, and NSW (abbreviations follow Holmgren *et al.*, 1990).

Observations

Ditria expleta Huisman sp. nov.

Plantae dorsiventralia prostratae axibus ecorticatis ad substratum per rhizoidiis digitatis affixae, axibus cum cellulis quinque pericentralibus. Ramulorum initia spiralter 1/5-divergentia producentia, initio dorsali laterali non-dividenti sed initiis caeteris ramos lateralia determinatos producentia. Axes principales et rami indeterminati laterales 5-110 μm diametro, ramis lateralibus determinatis simplicibus et pro longitudine 15-20 segmentis et 40-60 μm diametro. Cystocarpia terminalia in ramis determinatis lateralibus. Ramuli spermatangiales lanceolati 180-300 μm longi et 34-45 μm diametro, ramorum lateralium determinatorum in apice portati. Tetrasporangia tetrahedraliter divisa, 60-100 μm diametro, ramorum lateralium determinatorum partibus distalibus sporangia maturescentia deinceps in series lineares cum usque ad 10 sporangiis.

Prostrate, dorsiventral plants with ecorticate axes attached to the substatum by digitate rhizoids. Axes with five pericentral cells. Branch initials produced in a spiral sequence with a one fifth divergence; dorsal lateral initial remaining undivided, the remainder producing determinate or indeterminate lateral branches. Diameter of main axes and indeterminate lateral branches 50-110 μm . Determinate lateral branches simple, 15-20 segments in length, with a di-

ameter of 40-60 μm . Cytocarps terminal on determinate lateral branches. Spermatangial branchlets lanceolate, 180-300 $\mu\text{m} \times 34-45 \mu\text{m}$, borne on the distal ends of determinate lateral branches. Tetrasporangia tetrahedrally-divided, 60-110 μm in diameter, in linear series of up to ten successively maturing sporangia in the distal portions of determinate lateral branches.

Holotype: Goss Passage, adjacent to Beacon Island, Wallabi Group, Houtman Abrolhos. Epiphytic on *Lobophora variegata* (Lamouroux) Womersley at 15 m depth. (J. M. Huisman, 13.vii.1993; Murdoch HA 313a) (Fig. 1).

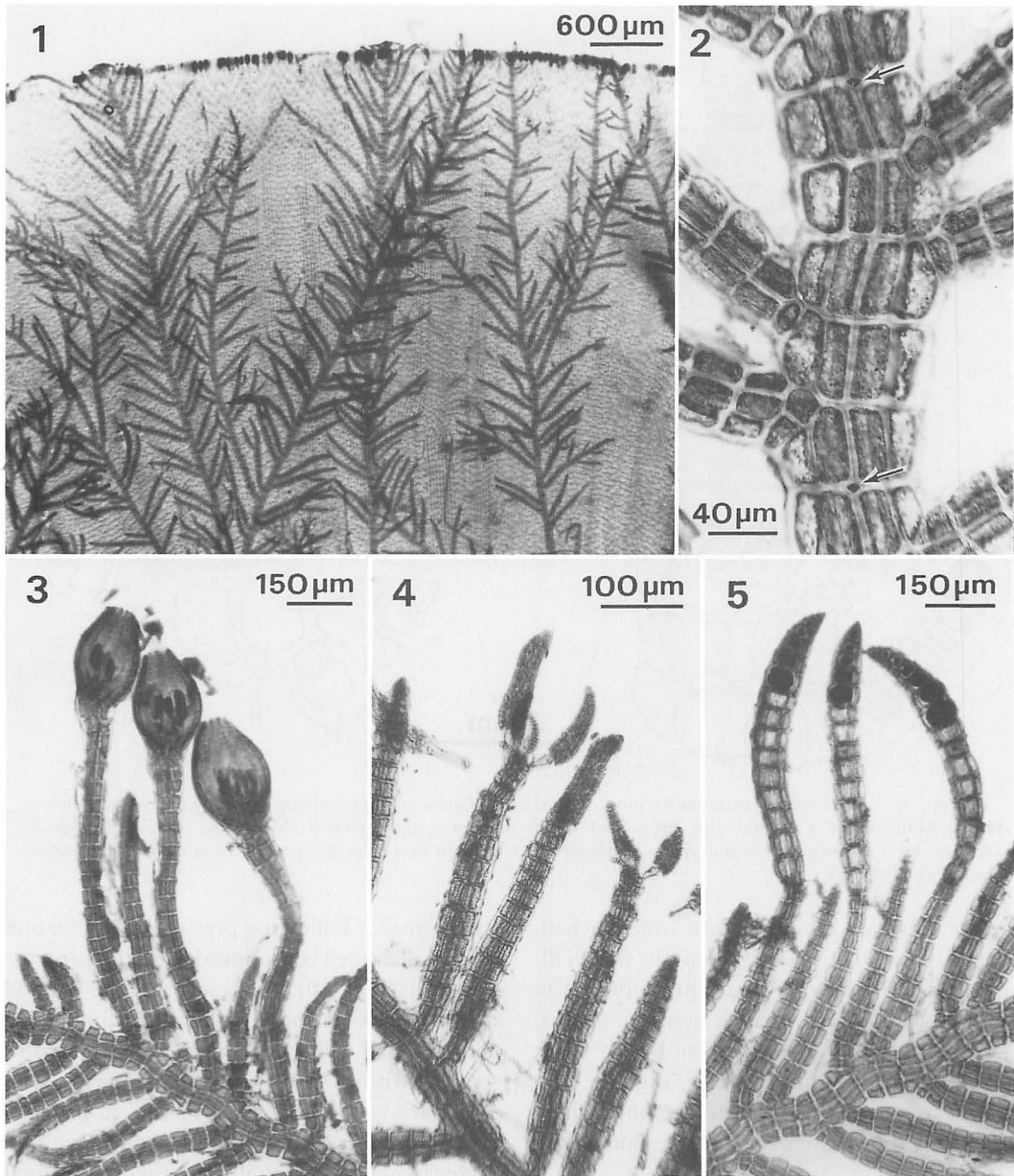
Etymology: The name 'expleta' is latin for 'complete' and is in reference to the additional lateral branches produced by the new species.

Habitat and Distribution: Thalli are apparently restricted to the fronds of *Lobophora variegata*, where they are found mainly on the upper surface, with apices often curling around the margins of the host (Fig. 1). Collections have been made from several locations in the Houtman Abrolhos and from Rottneest Island.

Specimens examined: Jackson I., Pelsaert Group, Houtman Abrolhos. On *Lobophora variegata* (J. M. Huisman, 14.x.1990; Murdoch HA 311; 30.ix.1991; Murdoch HA 312). Off Charlotte Point, Rottneest Island. On *Lobophora variegata* (J. M. Huisman, 20.xii.1992; Murdoch JH 271).

Vegetative structure

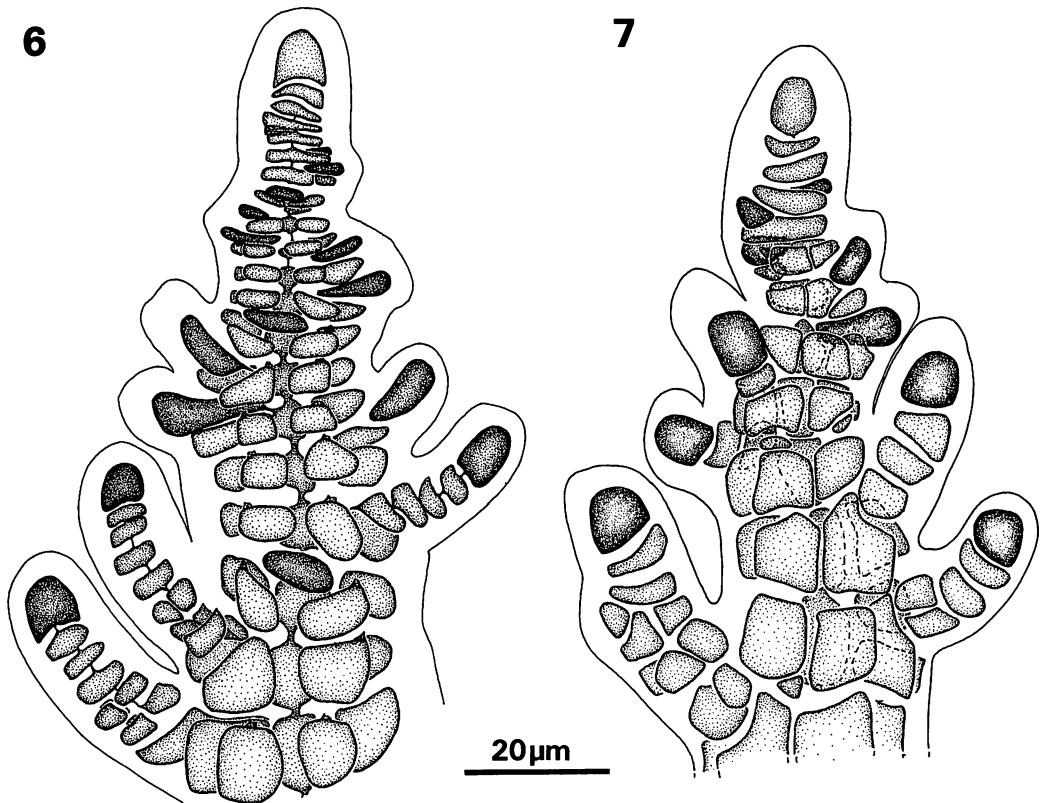
Plants minute, prostrate, with percurrent main axes. All axes are ecorticate and terete with five pericentral cells. Growth is via a prominent apical cell that divides slightly obliquely (Fig. 6). Branch initials are produced exogenously from each axial cell in a spiral sequence, with a one fifth divergence between subsequent initials (Fig. 6). Of the five branch initials, the dorsal initial remains dormant, with the remainder producing either indeterminate or determinate lateral branches. Despite the 1/5 divergence between the origin of adjacent branches, the prostrate nature of



Figs. 1–5. *Ditria expleta* Huisman sp. nov. Fig. 1. Plant from the type collection growing epiphytically on *Lobophora variegata* (Murdoch, HA 313). Fig. 2. Dorsal view of a mature indeterminate axis showing the sequence of production of lateral branches and dorsal primordia (arrows) (Murdoch, HA 311). Fig. 3. Cytocarps borne at the apices of determinate lateral branches (Murdoch, HA 312). Fig. 4. Spermatangial branches (Murdoch, HA 313). Fig. 5. Tetrasporangia arising in linear sequences near the apices of lateral branches (Murdoch, HA 313).

the thallus forces the lateral branches to remain horizontal and thus appear to occupy similar positions (Figs. 1, 2). The resultant branching pattern is a regular sequence of alternating pairs of branches (Fig. 2), with ev-

ery fifth segment naked (i.e. the segment bearing the undivided dorsal branch initial). Diameter of main axes 50–110 μm , with L/B of segments 0.1–1.3. Indeterminate lateral branches are identical to main axes. Deter-



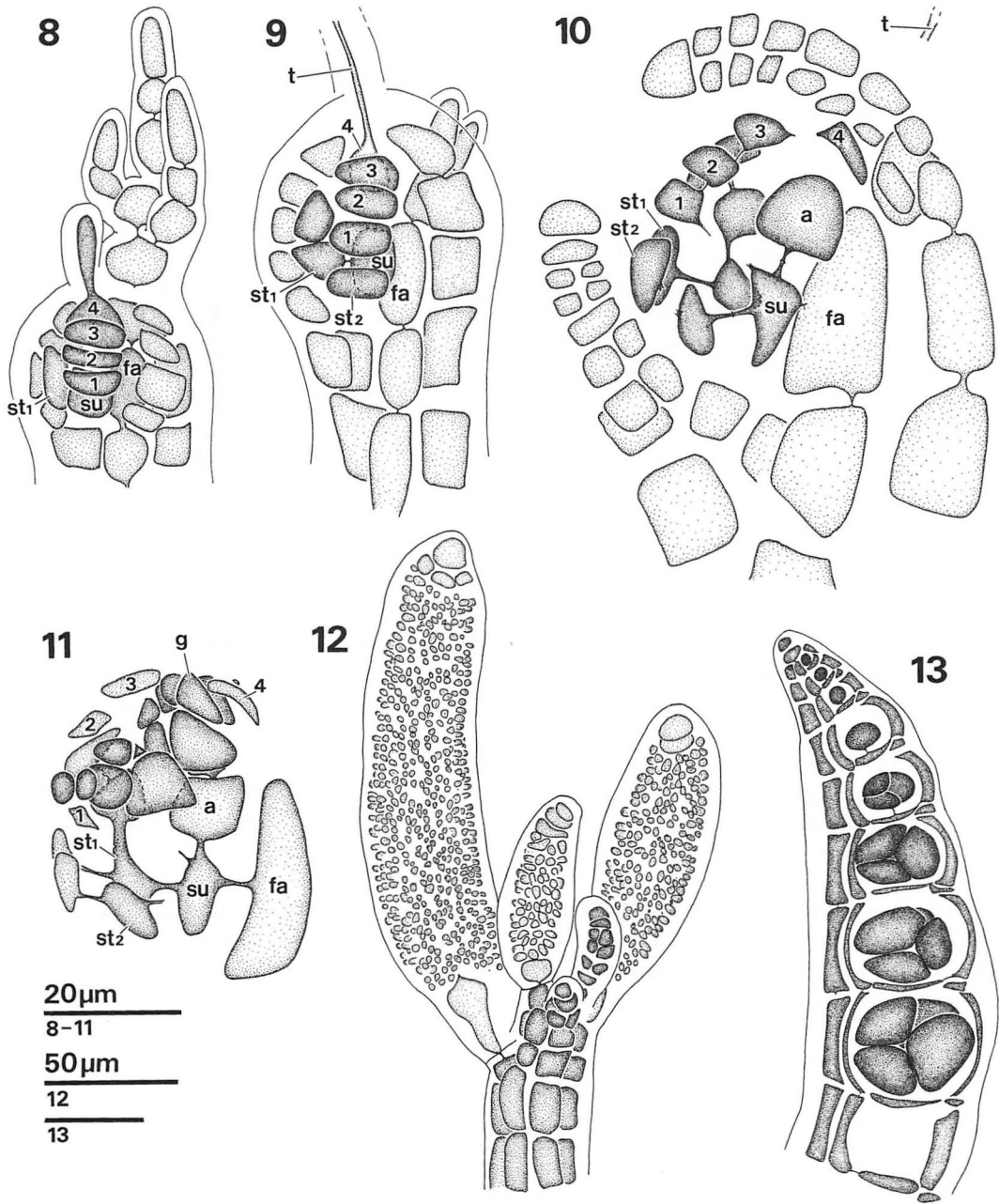
Figs. 6. *Ditría expleta* Huisman sp. nov. Dorsal view of apex of indeterminate axis showing the initiation of lateral branches in a spiral, with the dorsal initial remaining undeveloped (Murdoch, JH 271). Fig. 7. *Dipterosiphonia dendritica*. Ventral view of apex of indeterminate axis showing the initiation of lateral branches (Murdoch, JH 272).

minate lateral branches are unbranched, generally 15–20 segments in length, with a diameter of 40–60 μm . Thalli are attached to the host by rhizoids arising from the ventral pericentral cell. These rhizoids are short with a branched, multicellular, digitate pad. Their frequency is irregular, but where numerous they arise every 2–4 segments.

Carpogonial branch and cytocarp

Carpogonial branches arise near the apices of determinate lateral branches. Usually two trichoblasts are produced near the apex, with the most distal becoming fertile (Fig. 8). One of the pericentral cells on the epibasal cell becomes fertile and produces a four-celled carpogonial branch and two sterile branches (of one and two cells length) (Fig. 9). The carpogonial branch is curved with a terminal

trichogyne. Following presumed fertilization an auxiliary cell is produced from the supporting cell (Fig. 10). Transfer of the diploid nucleus was not observed, but on one occasion a small cell was seen in a position compatible with it being a connecting cell. The auxiliary cell divides transversely to produce 1–2 gonimoblast initials, which continue to divide (Fig. 11), eventually producing terminal carposporangia. During this process all of the cells of the two sterile branches on the supporting cell divide once to produce an additional cell, resulting in a two-celled branch and a three-celled branch with a lateral cell on the basal cell (Figs. 9–11). The connections between these cells widen during gonimoblast development and the cells apparently lose their contents, suggesting a nutritive function. The carpogonial branch gradually



Figs. 8-13. *Ditria expleta* Huisman sp. nov. Fig. 8. Developing carpogonial branch (Murdoch, HA 312). Fig. 9. Mature, four-celled carpogonial branch with sterile branches borne on the supporting cell (Murdoch, HA 312). Fig. 10. Initiation of the auxiliary cell from the supporting cell (Murdoch, HA 312). Fig. 11. Detail of gonimoblast initiation (Murdoch, HA 312). Fig. 12. Spermatangial branches (Murdoch, HA 313). Fig. 13. Optical section of tetrasporangial bearing branch, showing developing and mature sporangia (Murdoch, HA 313). Abbreviations: a=auxiliary cell; fa=fertile axial cell; g=gonimoblast; st1, st2, sterile branches on supporting cell; su=supporting cell; t=trichogyne; 1,2,3,4=cells of the carpogonial branch.

withers. Prior to gonimoblast initiation the carpogonial branch is curved around the auxiliary cells, with the trichogyne emerging in an apical position (Fig. 9). The constituent cells remain in this position, and the developing gonimoblast causes the branch to stretch before it is eventually lost. Remnants of the carpogonial branch can often be seen bordering the developing gonimoblast (Fig. 11), with the remains of the trichogyne projecting laterally from the pericarp (Fig. 10). The pericarp develops from pericentral cells surrounding the fertile axial cell, and the ostiole forms opposite the position of the supporting and auxiliary cells. In the mature cystocarp the auxiliary and supporting cells have merged to form a fusion cell that subtends the gonimoblast. Mature cystocarps are spherical to slightly ovoid, terminal on determinate lateral branches (Fig. 3).

Spermatangia

Spermatangial branchlets occur in clusters of up to six branchlets from the distal ends of determinate lateral branches (Figs. 4, 12). The branchlets arise in place of lateral branches (or primordia) and are initially monosiphonous and unbranched. Mature spermatangial branchlets have 11-14 axial cells and pericentral cells are produced from all cells with the exception of the basal, suprabasal, apical, and (often) subapical cells. The pericentral cells divide several times to become spermatangial mother cells, which in turn produce superficial spermatangia. Mature spermatangial branchlets are lanceolate in outline, measuring $180\text{--}3000 \times 35\text{--}45 \mu\text{m}$.

Tetrasporangia

Tetrasporangia occur in linear series of up to ten successively maturing sporangia in the distal portions of determinate lateral branches (Fig. 5). Initially the fertile pericentral cell divides to cut off two cover cells which take on the appearance of normal pericentral cells. A third cover cell is produced laterally from the fertile pericentral cell and remains small with the appearance of a dormant branch initial.

The sporangial initial arises on the distal side of the fertile pericentral cell and divides tetrahedrally. Mature sporangia are spherical to slightly flattened (Fig. 13) and measure $60\text{--}100 \mu\text{m}$ in diameter, markedly distending the bearing branch (Fig. 5).

Discussion

The genus *Ditria* includes prostrate, dorsoventral species with five pericentral cells and branch initials produced on every segment in a spiral sequence. As shown by Yoshida & Yoshida (1983), the arrangement of the pericentral cells is such that a single pericentral siphon lies immediately adjacent to the substratum. Attachment rhizoids arise from this line of cells. *Ditria expleta* displays all of these features and is clearly a member of the genus. In *D. reptans* (the type species) and *D. zonicicola*, however, the dorsal branch initial and the ventral lateral branch initials remain dormant, with only the dorsal lateral branch initials growing out to produce branches. The resultant branching sequence (in dorsal view) is therefore: right dorsal lateral branch, 'bare' segment (i.e., the segment bearing the dormant dorsal initial), left dorsal lateral branch, two 'bare' segments (i.e. the segments bearing the dormant ventral lateral initials). Occasionally the dorsal branch initial produces a trichoblast, and the sequence is repeated every five segments. The pattern was clearly described by Yoshida & Yoshida (1983) and has also been seen in eastern Australian material¹. In *D. expleta*, however, the ventral lateral initials also produce branches, resulting in a branching sequence of: right dorsal lateral branch, 'bare' segment, left dorsal lateral branch, left ventral lateral branch, right ventral lateral branch (Fig. 2). Only the dorsal branch initials are suppressed in *D. expleta*, and they have never been observed to produce trichoblasts.

Clearly such a branching pattern has arisen

¹ Epiphytic on *Lobophora variegata* at 1-2 m depth, Ned's Beach Channel, Lord Howe Island, N. S. W. (G. T. Kraft & A. J. K. Millar, 19.xii. 1986; MELU, A040314).

from the suppression of certain lateral branches due to the adoption of a prostrate habit. In *Ditria expleta* the pairs of lateral branches can be both determinate or indeterminate, or a mixture. Where there is a mixture, the indeterminate lateral branches commonly (although not always) arise from the ventral lateral initial, with the result being that the position of the indeterminate branch varies from being the distal member of a pair to the proximal member of a pair, depending on the side of the thallus from which the branches are produced. This pattern would appear to be a response to the adoption of a prostrate habit, as it is the branches adjacent to the substratum that become indeterminate, while those more dorsal in origin remain determinate. Although this suggests that *Ditria* is derived from an erect, spirally organised thallus, it is interesting to note that the direction of the spiral in indeterminate lateral branches changes depending on the side of the thallus from which they originate (also described for *D. zonaricola* by Yoshida & Yoshida, 1983). It is difficult to imagine that such a change is merely the result of the adoption of a prostrate habit, and is perhaps indicative of more substantial morphological changes.

The tribe Polysiphonieae was characterized by Hommersand (1963, p. 340) as including plants with "lateral branch initials"... "arranged in a spiral". *Ditria* clearly displays such a branching pattern and can be comfortably placed in the tribe. Of the other prostrate rhodomelaceae included in the Polysiphonieae, *Ditria expleta* shows remarkable similarities to the genus *Dipterosiphonia* Falkenberg, especially the type species *D. dendritica* (C. Agardh) Falkenberg. Both produce five pericentral cells and alternating pairs of lateral branches in a regular sequence. On closer examination, however, it can be seen that the similarities are superficial. In *Dipterosiphonia*, two pericentral siphons lie adjacent to the substratum and produce attachment rhizoids, an inversion of the situation found in *Ditria*. While *Dipterosiphonia* is generally included in the tribe Polysiphonieae (e.g. Hommersand, 1963; Schneider & Walde, 1992) an examina-

tion of its apical development suggests that such a placement is incorrect. As was pointed out by Yoshida & Yoshida (1983), branch initials in *Dipterosiphonia* do not arise in a spiral pattern. In *Dipterosiphonia dendritica* (Falkenberg, 1901; Yoshida & Yoshida, 1983; Schneider, 1975; pers. obs. on Western Australian material², Fig. 7) lateral branches are initiated on every segment and are arranged in alternating pairs, with the distal member of each pair forming an indeterminate branch and the proximal member remaining determinate (the sequence is reversed in *D. reversa* Schneider). Although one branch of each pair is displaced relative to the other, their initiation does not follow a spiral sequence (Yoshida & Yoshida, 1983, and pers. obs., Fig. 7). The proximal branch of each pair is always displaced dorsally relative to the distal branch (in *D. dendritica* at least), which means that either the direction of rotation changes between successive pairs of branches, or the degree of rotation between successive branches follows the sequence: 1/5, 2/5, 4/5, 3/5. Clearly the former cannot be considered to be spiral and the latter is highly unlikely. Obviously this arrangement of alternating pairs of lateral branches is not homologous to that found in *Ditria expleta*, and the two taxa have arrived at a similar branching pattern via different methods. Schneider & Walde (1992) also examined the branching pattern of several closely related dorsi-ventral Rhodomelaceae and concluded (as did Hommersand (1963) before them) that the dorsi-ventral Rhodomelaceae are derived from a number of different ancestors. Although they believed that *Dipterosiphonia* was spiral, they concluded from other features that the genus probably arose from a distichously branched ancestor, and that the Polysiphonieae represents the "independent development of a minimum of two radially organized lines". From the results of the present study and that of Yoshida and Yoshida (1983), however, it is

² Epiphytic on *Amphibolis antarctica* (Labillardiere) Sonder & Ascherson ex Ascherson, Eglinton Rocks, Ocean Reef. From 2 m depth (*T. Bell*, 28.i. 1993; Murdoch JH 272).

clear that *Dipterosiphonia* is not in fact spiral. This feature alone is sufficient to exclude the genus from the Polysiphonieae.

A similar situation can be seen in *Herposiphonia* Nägeli, where the branch initials arise in a regular, but not spiral, sequence. *Herposiphonia* produces a sequence of branches that includes alternating ventrally directed indeterminate branches separated by three dorsally directed determinate branches. The second of the three determinate branches is displaced relative to the others, which arise in a line. Most of the branching is therefore dorsal in origin and much of the thallus is unilateral. Clearly *Herposiphonia* must also be excluded from the tribe Polysiphonieae as defined by Hommersand (1963). In the past *Dipterosiphonia* and *Herposiphonia* have been included in the "*Herposiphonia*-Gruppe" by Kylin (1956) and the tribe Herposiphonieae by Scagel (1953). Hommersand (1963) subsumed the Herposiphonieae into the Polysiphonieae, based on the belief that all of the included genera displayed spirally arranged branch initials, but perhaps it is time to reconsider the tribe. *Herposiphonia* and *Dipterosiphonia* appear to be closely related, despite some differences in their branching patterns. The initiation of lateral branches in *Herposiphonia* is similar to that found in *Dipterosiphonia* but with the intercalation of two additional determinate branches per sequence. Schneider & Walde (1992) suggested that the line of evolution including *Dipterosiphonia* and *Herposiphonia* possibly arose from a distichous ancestor, perhaps during the separation of (and intermediate between) the distichous Pterosiphonieae and the spiral Polysiphonieae. Several authors have acknowledged the presence of an "evolutionary continuum between the *Pterosiphonia* and *Polysiphonia* levels of organization" (Kraft & Wynne, 1992) and the intermediate nature of *Herposiphonia* and *Dipterosiphonia* supports this. It is clear, however, that the two genera can no longer be maintained in the Polysiphonieae *sensu stricto*, nor are they compatible with the distichously-branched Pterosiphonieae. The evidence presented here and that of Schneider & Walde

(1992) suggest that *Herposiphonia* and *Dipterosiphonia* should be placed in a resurrected Herposiphonieae. While the Herposiphonieae can be separated from the Polysiphonieae on the basis of apical development, the production of vegetative trichoblasts and the displacement (although not spiral) of lateral branches in both *Herposiphonia* and *Dipterosiphonia* suggests a close relationship between the two tribes, perhaps more so than with the Pterosiphonieae.

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John M. Huisman : 西オーストラリア産シノブゴケ属の一新種 *Ditria expleta* (紅藻, フジマツモ科)

Lobophora variegata (Lamouroux) Womersley の着生する紅藻 *Ditria expleta* (紅藻・フジマツモ科) を新種として記載した。主軸と側生する栄養的な枝はほふくし、背腹性を持ち、5個の周心細胞を有する。基物と近接して配列する腹部の周心管の細胞は掌状の付着器を生ずる。分枝のイニシャルはそれぞれの分節から外生的に生じ、隣合うイニシャルの間で5分の1の開度で螺旋状のパターンを描いて形成される。背側の枝のイニシャルは休止状態にとどまり、一方そのほかのイニシャルは基物と同じ平面に配列する側枝に発達する。その結果生じる葉状体は互生する側枝を生じ、5番目毎の分節は休止状態にある背部の枝のイニシャルを除いて裸である。嚢果は有限成長の側枝に頂生する。造精器嚢は側枝の付近の退化した小枝に形成される。4面体の四分孢子嚢は有限成長の枝の上に10個程度まで線状に頂生する。*Ditria expleta* は本属のこれまでに記載されている種とは側枝のイニシャルの両側から枝を形成する点において異なる。*Ditria reptans* と *D. zonaricola* (シノブグサ) では腹部の枝のイニシャルは休止状態にとどまり、その結果1つおきに枝を生じる分枝のパターンをもたらす。*Ditria* はイトグサ族に含まれる。*Ditria expleta* と表面上類似する *Dipterosiphonia*, *Herposiphonia* を分枝形成過程において比較すると、これらの属がイトグサ族に含まれていることが不適切であり、復活したヒメゴケ族に含めるべきであることが明らかになる。(School of Biological and Environmental Sciences, Murdoch University, Murdoch, Western Australia, 6150, Australia).

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