The terete and sub-terete members of the red algal tribe Amansieae (Ceramiales, Rhodomelaceae)

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Abstract — The tribe Amansieae is composed mostly of genera with dorsiventrally flattened thalli with only a few species that are terete or sub-terete in cross-section. Two of these comprise the monotypic genera Rytiphlaea and Halopithys, both natives of the Mediterranean Sea and the northeastern Atlantic Ocean. An investigation of the relationships of these two species to each other and to the remaining terete or sub-terete species, Enantiocladia schottii and Protokuetzingia australasica, was carried out. The monotypic genus Digeneopsis from Mozambique and South Africa, which has been previously placed in the tribe Polysiphonieae, was also studied. No generic distinction was supported between Digeneopsis subopaca, Enantiocladia schottii and Halopithys incurva, and consequently all species have been included in Halopithys. Rytiphlaea tinctoria was shown to be generically distinct. Using molecular phylogenetic analysis, Rytiphlaea and Halopithys were shown to be closely related to each other but to have no particularly close affinity to Protokuetzingia.

Amansieae / anatomy / Ceramiales / Digeneopsis / Halopithys / marine algae / phylogeny / Rhodomelaceae / Rytiphlaea


Algues marines / Amansieae / anatomie / Ceramiales / Digeneopsis / Halopithys / phylogénie / Rhodomelaceae / Rytiphlaea

Dedicated to Izzie Abbott on the occasion of her 85th birthday.
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INTRODUCTION

Most members of the Amansieae form lateral wings as an integral part of their thalli. However, three monotypic genera (*Rytiphlaea*, *Halopithys* and *Protokuetzingia*), as well as *Enantiocladia schottii* (W.R. Taylor) S.M. Wilson et Kraft, have thalli that are terete or ovoid in cross-section showing little or no evidence of lateral wing formation. As part of an ongoing study of the genera of the Amansieae (Phillips, 2002a, b, 2005) these taxa were investigated to establish their relationship to one another and the rest of the tribe.

The genus *Rytiphlaea* is one of the oldest of all red algal genera, having been described in 1817 by C. Agardh to accommodate four species; *R. complanata* (Clemente) C.Agardh, *R. purpurea* C.Agardh, *R. pinastroides* (S.G.Gmel.) C.Agardh and *R.? lineata* (Turner) C.Agardh. *Rytiphlaea complanata* is now known as *Pterosiphonia complanata* (Clemente) Falkenb. The identity and status of *R.? lineata* from New Zealand is uncertain. By 1824, C. Agardh considered the genus to consist of only three species, *R. complanata*, *R. obtusiloba* (Mert.) C.Agardh and *R. tinctoria* (Clemente) C.Agardh. The latter is a younger but legitimate name for *R. purpurea* based on *Fucus tinctoria* Clemente (1807), and it was on this species, *R. tinctoria*, that the genus was lectotypified by Schmitz (1889: 447).

A plethora of species (almost 50; Tab. 1), now included in other genera of the Rhodomelaceae, have at one time or another been attributed to *Rytiphlaea*, but currently only *R. tinctoria* is considered to truly belong to the genus (Kylin, 1956; Wilson & Kraft; 2000). *Rytiphlaea tinctoria* is distributed throughout the Mediterranean Sea and in warmer parts of the eastern Atlantic Ocean. The genus is characterized by five pericentral cells, sub-terete axes with strongly incurved apices, and indeterminate branching that is alternate to irregular (Kylin, 1956). Reproductive structures are formed on unmodified axes.

Like *Rytiphlaea*, *Halopithys* is a monospecific genus largely from the northeastern Atlantic. *Halopithys* was described in 1843 by Kützing based on *Fucus pinastroides* S.G.Gmel. (1768). Batters (1902), however, realized that *F. pinastroides* was a superfluous and hence illegitimate name as Gmelin had cited *Fucus incurvus* Hudson (1762) in the protologue. Consequently Batters made the new combination *Halopithys incurva*. The genus is characterized by terete axes with five pericentral cells, irregularly-spaced determinate and indeterminate branches, strongly incurved apices, and reproductive structures on paired or clustered branchlets arising in the axils of laterals (Maggs & Hommersand, 1993).

Kützing also included in *Halopithys* the Australian *Rhodomela australasica* (Mont.) Kütz. (1847) and *Rhodomela elata* (Sond.) Kütz. (1865). *Halopithys elata* is now known as *Cladurus elata* (Sond.) Falkenberg (1901) of the Chondrieae, and *H. australasica* was made the type species of *Protokuetzingia* Falkenberg (1901), characterised by six rather than five pericentral cells. The anatomy of *Protokuetzingia* was detailed by Wilson & Kraft (2000), who noted the endogenous, opposite laterals that may be determinate or indeterminate, the marginal to submarginal position of the reproductive structures, and the trichoblast-bearing stichidia. A second species of *Protokuetzingia*, *P. schottii*, had been described from Caribbean South America by Taylor (1941), but Wilson & Kraft (2000) removed it from that genus on the basis of its five instead of six pericentral cells, provisionally placing it in *Enantiocladia*. Their reasons for choosing *Enantiocladia* were the opposite position of the laterals and the geographic proximity of the type localities of *Protokuetzingia schottii* and...
Table 1. Details of publication and current status of all *Rytiphlaea* species. Underlined species names indicate that current status is uncertain. In the right hand column bold lettering indicates current placement.

<table>
<thead>
<tr>
<th>Rytiphlaea species</th>
<th>Basionym</th>
<th>Type Locality</th>
<th>Taxonomic History and Current Placement</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>R. aculeata</em> C.Agardh msr., J.Agardh 1841:26 nom. nud., J.Agardh 1863:1087</td>
<td>Western Australia</td>
<td>= <em>Endosiphonia spinulosa</em> (Harv.) Womersley et M.J. Parsons 2003: 251. (see also Harv. 1863:xviii; Silva et al. 1996:551) &quot;This is most likely a representative of <em>Endosiphonia</em>&quot; Wilson &amp; Kraft 2000:330 (of <em>R. aculeata</em>)</td>
<td></td>
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<tr>
<td><em>R. angusta</em> Okamura 1896:26</td>
<td>Japan</td>
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<tr>
<td><em>R. belangeri</em> Mont. 1857:138</td>
<td>Martinique</td>
<td>Description suggests possible links with <em>Halopithys incurva</em> and given locality should be investigated with regard to <em>H. schottii</em> = <em>Lophurella caespitosa</em> (fide Falkenberg 1901:436)</td>
<td></td>
</tr>
<tr>
<td><em>R. caespitosa</em> (Hook.f. et Harv.) J.Agardh 1863:1091</td>
<td>Oceopoto and Parimahu, New Zealand</td>
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<tr>
<td><em>R. canaliculata</em> Grev. 1831:149, fig. 1-4</td>
<td>Swan River, Western Australia</td>
<td>→ <em>Kuetzingia canaliculata</em> (Grev.) Sond. 1845:54</td>
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<tr>
<td><em>R. capensis</em> Kütz. 1843:448</td>
<td>Cape of Good Hope, South Africa</td>
<td>= <em>Pterosiphonia cloiophylla</em> (C.Agardh) Falkenb. (fide Hommersand 1963:261)</td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>Synonymy</td>
<td>Location</td>
<td>Notes</td>
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<tr>
<td><em>R. cloiophylla</em></td>
<td><em>Rhodomela cloiophylla</em></td>
<td>Cape of Good Hope, South Africa</td>
<td>→ <em>Pterosiphonia cloiophylla</em> (C.Agardh) Falkenb. 1901:271</td>
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<tr>
<td>(C.Agardh)</td>
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<tr>
<td>J.Agardh 1841†:26</td>
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<tr>
<td><em>R. complanata</em></td>
<td><em>Fucus complanata</em></td>
<td>“in Mari Mediterraneo et Atlantico ad oras” Spain</td>
<td>→ <em>Pterosiphonia complanata</em> (Clemente) Falkenb. 1901:271</td>
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<tr>
<td>(Clemente)</td>
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<tr>
<td>C.Agardh 1817xxv</td>
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<tr>
<td>J.Agardh 1885:106</td>
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<td>“shows no relationship to the Amansieae” Wilson &amp; Kraft 2000:330</td>
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<tr>
<td><em>R. corymbosa</em></td>
<td></td>
<td>Cape of Good Hope, South Africa</td>
<td>= <em>Pterosiphonia cloiophylla</em> (C.Agardh) Falkenb. (fide Silva <em>et al.</em> 1996:549)</td>
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<tr>
<td>Kütz. 1849:844</td>
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<tr>
<td><em>R. delicatula</em></td>
<td><em>Husseya delicatula</em></td>
<td>D’Urville Island, Cook Straits, Akaroa, New Zealand</td>
<td>→ <em>Aphanocladia delicatula</em> (Hook.f. et Harv.) Falken. *in Schmitz &amp; Falkenberg 1897:444</td>
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<tr>
<td>Hook.f. et Harv. in Harvey</td>
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<tr>
<td>1855b:224</td>
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<tr>
<td><em>R. dumosa</em></td>
<td></td>
<td>False Bay, near Muysevenberg, Cape of Good Hope, South Africa</td>
<td>= <em>Pterosiphonia cloiophylla</em> (C.Agardh) Falkenb. (Delf &amp; Michell 1921:114 place in synonymy with <em>Polysiphonia acanthina</em> J.Agardh which is in synonymy with <em>Pterosiphonia cloiophylla</em> fide Papenfuss 1943:89)</td>
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<td>Harv. 1847:33</td>
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<tr>
<td><em>R. duperreyi</em></td>
<td></td>
<td>Martinique</td>
<td>→ <em>Odonthalia</em> Postels et Rupr. 1840:14</td>
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<tr>
<td>C.Agardh 1828:52</td>
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<td></td>
<td>→ <em>Amansia</em> J.Agardh 1841:26</td>
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<td></td>
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<td>→ <em>Enantiocladia duperreyi</em> (C.Agardh) Falken. *in Schmitz 1889:447</td>
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<tr>
<td>1855a:538</td>
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<td>“…material is insufficient for identification” Wilson &amp; Kraft 2000:330</td>
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<tr>
<td><em>Rhodomela pinastroides</em></td>
<td><em>Pinastroides</em></td>
<td>Canary Islands</td>
<td>= <em>H. pinastroides</em> (fide Falkenberg 1901:436)</td>
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<tr>
<td>var. <em>episcopalis</em> Mont.</td>
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<td>= <em>Halopithys incurva</em> (Huds.) Batters</td>
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<td>Endligher 1843:48</td>
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<tr>
<td><em>R. firma</em></td>
<td></td>
<td>Cape of Good Hope</td>
<td>= <em>Pterosiphonia cloiophylla</em> (C.Agardh) Falkenb. (see Silva <em>et al.</em> 1996:549)</td>
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<tr>
<td>C.Agardh 1828:54</td>
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<tr>
<td>Rytiphlaea species</td>
<td>Basionym</td>
<td>Type Locality</td>
<td>Taxonomic History and Current Placement</td>
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</tbody>
</table>
| *R. fruticulosa* (Wulfen) Harv. 1849:81 | *Fucus fruticulosus* Wulfen 1786-1790:159, pl. 16, fig. 1; 1803:56 | UK? | → *Polysiphonia* Sprengel 1827:350  
 → *Boergeseniella fruticulosa* (Wulfen) Kylin 1956:507 |
| *R. glomerata* (C.Agardh) Decne. 1842:358 | *Amandia glomerata* C.Agardh 1822:194 | Hawaii | → *Odonthalia* Endlicher 1843:47  
 → *Fimbriaria* Trévisan 1845:30  
 → *Amandia glomerata* C.Agardh (see Masuda & Abe 2002) |
 = *Osmundaria obtusiloba* (C.Agardh) R.E.Norris 1991:14 |
| *R. kuetzingioides* Sond. 1857:331 | | Geographe Bay, Western Australia | = *Amandia serrata* (Harv.) Womersley 2003:394  
 (J.Agardh 1885 refers this species to *Ryt. merrifieldiae*) |
| *R. latiuscula* Harv. 1857:331 | *Fucus lineatus* Turner 1817:10, pl. 201 | New Zealand (Banks) | → *Epineuron lineatum* (Turn.) Hook.f. et Harv. 1845:532  
 current status unknown |
| *R. lineata* (Turner) C.Agardh 1817:xxv | *Fucus lineatus* C.Agardh 1824:161 | Western Australia | → *Nanopera merrifieldiae* (J.Agardh) S.M.Wilson et Kraft 2000:341 |
 → *Wormskioldia* Spreng. 1827:332  
 → *Amandia* Grev. 1830:xxvi  
 → *Odonthalia* Postels et Rupr. 1840:14  
 → *Vidalia* J.Agardh 1863:1123  
 → *Eurostylis* Kuntze 1891:894  
 → *Osmundaria obtusiloba* (C.Agardh) R.E.Norris 1991:14  
 → *Halophyta incisa* (Huds.) Batters 1902:78  
 = *Halophyta incisa* (Huds.) Batters 1902:78 |
| *R. pinastroides* C.Agardh 1817:xxv nom. illeg. | *Fucus pinastroides* S.G.Gmel. 1768:127, pl. XI, fig. 1 nom. illeg. | England | “the identity of this species is unknown. Voucher material is apparently not in existence. C. Agardh (1828: 53) listed the names as a likely synonym of ... *R. tinctoria*, but the presence of this species in the Red Sea is somewhat doubtful.” Papenfuss (1968:28) |
| *R. plana* (Forssk.) Kuntze 1898:424 | *Confervula plana* Forsskål 1775:188 | | |

→ Amansia J.Agardh 1863:1116

→ Enantiocladia prolifera Falkenb. in Schmitz & Falkenberg 1897:467

R. pumila C.Agardh 1827†:639

R. pumila Zanardini 1841:181, pl. II, fig. 4 non C.Agardh

R. purpurea C.Agardh 1817:xxv nom. nov

Fucus purpureus Turner 1817:67, pl. 224 nom. illeg. non Hudson 1762:471 (= Cystodonium purpureum (Huds.) Batters 1902:68)

R. rhodantha (Harv.) Decne. 1842:358

Delesseria rhodantha Harv. 1834:151, pl. CXXVI

→ Amansia rhodantha (Harv.) J.Agardh

R. rigidula Kütz. 1843:448

R. semicristata J.Agardh 1842:145

R. seminuda Kütz. 1865:6, pl. 14a-c

R. simplicifolia Harv. 1860:298

R. spinulosa (Harv.) P.C.Silva in Silva et al. 1996:551

Alsidium spinulosa Harv. 1855a:538

Western Australia

→ Odonthalia floccosa (Esp.)” De Toni 1903:1099

R. sinensis Debeaux 1875:49 (also 1873†, nom nud.)

“du camp de Tché-fou, et non loin de la rade de Yan-taï (Prov. Du Chang-tong)” China (imperfecte descripta et tantum quoad habitum caespitis ficta) [imperfectly described and of the size and habit of turf] videtur, suadente quoque loco natali, h.c. Tscifu maris sinensis, cadem species ac Symphyocladia gracilis (Mart.) Falk. Vix comparanda videtur cum Odonthalia floccosa (Esp.)” De Toni 1903:1099

= Endosiphonia spinulosa (Harv.) Womersley et M.J. Parsons 2003:251, “The genus to which it truly belongs cannot positively be known till its tetrasporic fruit shall be found.” Harv. 1860:pl. CXXIX. Illustrations show 4 pericentral cells.

Dasyopsis pumila f. zanardiniana (Zanardini) Mazza 1922-1926:1670

= Rytiphlaea tinctoria (Clemente) C.Agardh

= Rytiphlaea tinctoria (Clemente) C.Agardh (fide Falkenberg 1901:437)

= Rytiphlaea tinctoria (Clemente) C.Agardh (see J. Agardh 1863:1093, Falkenberg 1901:437)

= Rytiphlaea tinctoria (Clemente) C.Agardh (fide De Toni 1903:1093)

= Epiglossum proliferum (C.Agardh) L.E.Philips 2002b:

L. E. Phillips & O. De Clerck
<table>
<thead>
<tr>
<th>Rytiphlaea species</th>
<th>Basionym</th>
<th>Type Locality</th>
<th>Taxonomic History and Current Placement</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>R. stangeri</em> Harv. mscr.</td>
<td></td>
<td>Port Natal (Durban), South Africa</td>
<td>→ <em>Polysiphonia stangeri</em> Harv. ex J. Agardh 1863:937</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>→ <em>Pterosiphonia stangeri</em> (Harv.) Falkenb. 1901:270</td>
</tr>
<tr>
<td><em>R. thuyoides</em> (Harv.) Harv. 1849:81</td>
<td><em>Polysiphonia thuyoides</em> Harv. ex Mackay 1836:205</td>
<td>Miltown Mal Bay, Co. Clare, Ireland</td>
<td>→ <em>Pterosiphonia</em> Batters 1902:82</td>
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<td></td>
<td></td>
<td></td>
<td>→ <em>Boergeseniella thuyoides</em> (Harv.) Kylin 1956:508</td>
</tr>
</tbody>
</table>
| *R. truncata* Kütz. 1865:5, pl. 11e-h | | Cape of Good Hope, South Africa | “R. uncialis, cespitosa, angustissima, parum complanata, alterne et distiche ramosa, ramis bi-tripinnatis, pinnis apice truncatis, dichotome-multifidis, laciniiis terminalibus brevissime articulatis, articulis unicellularibus – Ad Caput bonae spei.” (Kütz. 1865:5)  
Looks to have 6 pericentral cells from the illustration. |
| *R. umbellata* J.Agardh ex Wilson 1892:166 nom. nud.; Tisdall 1898:513 nom. nud. | | Port Phillip Heads, Victoria, Australia | same as *R. umbellifera = Cladurus elatus* ? |
E. duperreyi (the type species of Enantiocladia). They also noted the common abaxial positions of the procarps and the number of pericentral cells, although these can hardly be considered unique generic characters of Enantiocladia within the Amansieae. They did not discuss any possible relationship to the other semi-terete members of the Amansieae, particularly Rytiphlaea and Halopithys, despite citing the pronounced flattening of the winged thallus as a generic character of Enantiocladia, a feature not present in E. schottii.

Simons (1970) established another monotypic rhodomelaceous genus, Digeneopsis, for the newly collected D. subopaca from Mozambique. Simons’ descriptions of both the genus and species briefly characterized members as erect and having corticated stems densely covered with determinate branches, these branched near the base and with rounded apices. Tetrasporangia were said to be formed two per segment in stichidia, but gametophytic plants were unknown. The pericentral cell number was not specified, but Simons’ illustrations (1970, fig. 11F) suggest that there are five. The genus name refers to the similarity in overall habit to the widespread Digenea simplex (Wulfen) C.Agardh of the Polysiphonieae. Simons (1976) also included Digeneopsis within the Polysiphonieae although a number of features appear to be at odds with characteristics of that tribe.

New material of Digeneopsis, including female gametophytic plants, have prompted the investigation of this genus and its comparison to genera of the Amansieae that are similar in pericentral cell number and in the terete to sub-terete profiles of the axes in cross-section. Material of Rytiphlaea tinctoria suitable for DNA extraction was also obtained, allowing analysis of both molecular and morphological characters and comparison with the previously published sequences of Halopithys incurva (Phillips, 2000) and the non-winged amansioid species Protokuetzingia australasica (Phillips, 2002a).

**MATERIALS AND METHODS**

Anatomical observations were made from herbarium specimens or formaldehyde-preserved material. Sections were cut by hand with a single-edged razor blade, rehydrated where necessary in a weak detergent solution, stained in 1% acidified aniline-blue solution, and mounted on glass slides in 20%-50% Karo™ corn syrup (CPC International Inc., Englewood Cliff, NJ).


Halopithys (Enantiocladia) schottii: 1. Cartagena, Columbia (Schott

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1. Culture collections of J.A. West, School of Botany, The University of Melbourne, Australia.
The non-winged Amansieae (Rhodomelaceae)


Herbarium specimens were scanned using a UMAX Astra 2100s flatbed scanner (Umax Systems GmbH, Willich, Germany), low-power habit micrographs were photographed using a WILD photoautomat MPS 55 macroscope (Leica, Heidelberg, Germany), and photomicrographs were taken on ZEISS Axioskop2 microscope (Carl Zeiss, Oberkochen, Germany).

Sequences of the 18S rRNA gene were obtained for five species (Tab. 2) following the methods described in Phillips et al. (2000). Using SeqPup (Gilbert, 1995), the sequences were added by eye to an alignment of 12 previously published species (Tab. 3).

The alignment was converted into an unordered character state matrix (A, G, T, C, − = gap, × = missing data) using the PAUP computer package version 4.0b8 (Swofford, 2000). All characters were equally weighted and gaps were treated as missing data. Most-parsimonious trees were obtained using the branch-and-bound search option. Once obtained, trees were rooted with reference to two species of the genus *Polysiphonia*. One thousand bootstrap replicates were performed to obtain a measure of the robustness of the phylogeny.

The maximum likelihood analysis was conducted using a likelihood model estimated from the data set and refined through successive tree searches. The result corresponded to the Hasegawa-Kishino-Yano model (Hasegawa et al., 1985) with a transition/transversion ratio of 2, a proportion of invariant sites estimated as 0.66, with rates (for variable sites) assumed to follow a gamma distribution with shape parameter 0.80. This combination of parameters produced the tree with the highest log-likelihood.

Table 2. Collection information for species included in 18S rRNA gene sequencing.

<table>
<thead>
<tr>
<th>Species</th>
<th>Collection Details (Location, Collector, Date, Voucher)</th>
<th>Genbank Accession Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kuetzingia canaliculata (Grev.) Sond.</td>
<td>Cervantes, Western Australia, M &amp; F Hommersand, 20.ix.1995, MELU A000054</td>
<td>AY237283</td>
</tr>
<tr>
<td>Rytiphlaea tinctoria (Clemente) C.Agardh</td>
<td>Brucoli, Syracuse, Eastern Sicily, Furnari, 24.x.2000, MELU LEP-R170</td>
<td>AY237284</td>
</tr>
<tr>
<td>Vidalia colensoi (Hook.f et Harv.) J.Agardh</td>
<td>Farmer Rocks, Three Kings Islands, New Zealand, Knight, 25.xi.1998, MELU LEP-R112</td>
<td>AY237285</td>
</tr>
<tr>
<td>Vidalia fimбриata (J.V.Lamour.) J.Agardh</td>
<td>Yule Point, Port Douglas, Queensland, West, 12.vi.1987, JAW 2841</td>
<td>AY237286</td>
</tr>
<tr>
<td>Vidalia spiralis (C.Agardh) J.Agardh</td>
<td>Cottesloe, Western Australia, McKernan, 24.mi.1999, MELU LEP-R125</td>
<td>AY237287</td>
</tr>
</tbody>
</table>
Distance analysis was conducted using the Hasegawa-Kishino-Yano model (Hasegawa et al., 1985), the trees constructed using the neighbor-joining algorithm. One thousand bootstrap replicates of the data set were analysed to assess the robustness of the resultant phylogeny.

### RESULTS AND DISCUSSION


**Etymology**: “*rytis*” = a wrinkle, “*phloios*” = cortex, referring to the transversely furrowed or striate appearance of the surface.

**Lectotype and only species**: *R. tinctoria* (Clemente) C.Agardh (Schmitz, 1889)

**Distribution**: Mediterranean Sea, Atlantic coasts of Spain, Portugal, northern Africa and Macaronesia (Fig. 1).

### Table 3. 18S rRNA gene sequences used in alignment and not generated in this study

<table>
<thead>
<tr>
<th>Species</th>
<th>Reference</th>
<th>Genbank Accession Number</th>
</tr>
</thead>
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<tr>
<td><em>Adamsiella melchiori</em> L.E.Phillips et W.A.Nelson</td>
<td>Phillips, 2002a (as <em>Lenormandia</em> sp. 1)</td>
<td>AF339897</td>
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<tr>
<td><em>Melanamansia glomerata</em> (C.Agardh) R.E.Norris</td>
<td>Phillips, 2000</td>
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<td><em>Melanamansia mamillaris</em> (J.V.Lamour. ex C.Agardh) R.E. Norris</td>
<td>Phillips et al. 2000</td>
<td>AF203889</td>
</tr>
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<td><em>Epiglossum smithiae</em> Hook.f. et Harv.</td>
<td>Phillips, 2002a (as <em>Lenormandia smithiae</em>)</td>
<td>AF339895</td>
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<td><em>Aneurianna dentata</em> L.E.Phillips</td>
<td>Phillips, 2003</td>
<td>AY237280</td>
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<td><em>Halophyts incurva</em> (Huds.) Batters</td>
<td>Phillips, 2000</td>
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<td><em>Osmundaria prolifera</em> J.V.Lamour.</td>
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<td><em>Polysiphonia savatieri</em> Hariot</td>
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<td>AF203885</td>
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<td><em>Protokuetzingia australasica</em> (Mont.) Falkenb.</td>
<td>Phillips, 2002a</td>
<td>AF339901</td>
</tr>
</tbody>
</table>
The non-winged Amansieae (Rhodomelaceae)


*Fucus tinctorius* Clemente, 1807†: 316.

*Fucus purpuratus* Turner, 1817: 67, pl. 224 *nom. illeg.*; Bertolini, 1819: 222, 306, pl. 5, fig. 7a,ab. non *Fucus purpureus* Hudson, 1762: 471; Esper, 1798: 114, pl. LVIII [= *Cystoclonium purpureum* (Huds.) Batters, 1902: 68].

*Rytiphlaea purpurea* C.Agardh, 1817: xxv *nom. nov.*

*Fucus striatus* Draparn. *mcr.* (fide De Toni, 1924: 1095).

*Fucus phenax* Sprengel, 1809: 191, pl. 7, fig. 15.

*Polyisophonia campanulata* Delle Chiaje, 1829†: 68 (fide Falkenberg, 1901:438).

*Rytiphlaea tinctoria* var. *horridula* J.Agardh, 1842: 145.


*Rytiphlaea rigidula* Küting, 1843: 448; 1849: 845; 1865: 6, pl. 13a-d.

*Rytiphlaea seminuda* Küting, 1865: 6, pl. 14a-c.

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**Fig. 1.** Distribution of the non-winged Amansieae. Arrows indicate type localities of *Halopithys* species. *inc* – *H. incurva*, *sch* – *H. schottii*, *sub* – *H. subopaca*. 

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*Fucus tinctorius* Clemente, 1807†: 316.

*Fucus purpuratus* Turner, 1817: 67, pl. 224 *nom. illeg.*; Bertolini, 1819: 222, 306, pl. 5, fig. 7a,ab. non *Fucus purpureus* Hudson, 1762: 471; Esper, 1798: 114, pl. LVIII [= *Cystoclonium purpureum* (Huds.) Batters, 1902: 68].

*Rytiphlaea purpurea* C.Agardh, 1817: xxv *nom. nov.*

*Fucus striatus* Draparn. *mcr.* (fide De Toni, 1924: 1095).

*Fucus phenax* Sprengel, 1809: 191, pl. 7, fig. 15.

*Polyisophonia campanulata* Delle Chiaje, 1829†: 68 (fide Falkenberg, 1901:438).

*Rytiphlaea tinctoria* var. *horridula* J.Agardh, 1842: 145.


*Rytiphlaea rigidula* Küting, 1843: 448; 1849: 845; 1865: 6, pl. 13a-d.

*Rytiphlaea seminuda* Küting, 1865: 6, pl. 14a-c.
**Lectotype:** MA-Algae 1473 (Cremades, 1993: 23-24, fig. 8) (not seen).

**Type Locality:** Castillo de St Catalina and Punto de St Maria, Andalucia, Spain

**Distribution:** As for genus (Fig. 1). There are also isolated reports of this species from the Red Sea (Turner, 1817: 68; Muschler, 1908: 217; Farghaly, 1980: 165), but its presence there has not been confirmed (Papenfuss, 1968:101).

**Habit and Anatomy:** Plants are found from the intertidal to depths of 60 metres (Falkenberg, 1901 and observations of specimens in GENT) in a variety of habitats but mostly on sandy or muddy substrate, maerl banks or shell debris. Thalli arise from a discoid holdfast with one to several erect axes being produced from a single holdfast (Fig. 2). Plants reach up to 18 cm in height (Kylin, 1956), are

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**Figs 2-7. Rytiphlaea tinctoria** (Clemente) C.Agardh (2 = GENT HEC 1679, 3-7 = MELU LEP-R170).

2. Habit. Scale = 1 cm. 3. Habit showing regular alternate branching, incurved apices, transverse striations (arrows) and vegetative trichoblasts. Axes are more heavily pigmented at the apices. Scale = 1 mm. 4. Strongly incurved branch apices with vegetative trichoblasts. Scale = 250 µm. 5. Detail of branch apex. Young trichoblasts are formed within a gelatinous vesicle (arrow) but elongate once erupted. Scale = 100 µm. 6-7. Cross-sections through young and mature axes showing central-axial cells (asterisks), five pericentral cells (dots), further medullary cells and darkly pigmented cortex. Scales 5 = 100 µm, 6 = 200 µm.
yellowish to dark red-brown in colour becoming darker towards the tips of the axes, and coriaceous to cartilaginous in texture. Endogenous laterals are formed alternately (Figs 2, 3) or irregularly from the lateral margins of the bearing axes. Apices are strongly incurved (Figs 3-5) and bear a row of dorsal exogenous trichoblasts, which are formed one per segment (Figs 4, 5). Initially the trichoblasts are small and enclosed within a vesicle (Fig. 5), but once the vesicle erupts they elongate considerably (Figs 4, 5) before becoming deciduous and leaving an inconspicuous scar.

Mature axes are 0.5-1.0 mm in width and are dorsiventrally flattened but without true wings, the outline in cross-section being sub-terete to oval (Figs 6, 7). In cross-section the axis is composed of a central-axial cell, five pericentral cells (two dorsal, two lateral and one ventral) and further medullary cells formed from the pericentral cells. The cortex forms a single layer, one or two cells thick, of small isodiametric cells. Although the cortex is heavily pigmented, striations are visible through it (Fig. 3), indicating the position of the axial segments. This feature is responsible for the generic name.

Reproductive material was not available for examination. Kylin (1956) reports procarps, cystocarps and stichidia to be like those of Halopithys. Falkenberg (1901) reported procarps to be formed in a dorsal row at the apex of ultimate axes. Cystocarps are said to be subspherical (Gayral, 1958).

Falkenberg (1901) reported male gametophytes to produce spermatangial branches in a dorsal series from the apex of otherwise unmodified axes. The spermatangial branches are formed on reduced trichoblasts in which the basal segment is sterile and the three distal segments are fertile. The spermatangial capitula are incurved when developing, but become straight when mature.

Remarks: Although Rytiphlaea tinctoria was described long ago and is widely recorded throughout its distribution, there is surprisingly little information about this species. It is distinguished from most members of the Amansieae by its lack of extended wings and from the other non-winged members by the dorsiventrally compressed axes and the presence of rudimentary wings.

As mentioned above, almost 50 species have been attributed to Rytiphlaea (Tab. 3). In most cases these species have been moved to other genera or were species subsequently reduced to synonymy with other species. In some cases, however, it has not been possible to establish the status of the species; such cases require further investigation.


Etymology: “Halo” = salt, “pitus” = pine tree, for the pine-like habit of the plant (Newton 1931).

Type species: H. pinastroides (S.G.Gmel.) Kütz. [= H. incurva (Huds.) Batters].

Distribution: Faroe Islands, southern England and Ireland, Channel Islands, Atlantic coasts of Spain, France and Portugal, Mediterranean and Adriatic Seas, Morocco, Canary Islands, Mozambique, northern Natal, South Africa, Caribbean coast of Columbia and Brazil (Fig. 1).

Thalli erect, arising from a discoid holdfast, composed of apically incurved indeterminate axes with indeterminate and paired determinate laterals. All axes terete, laterals arising endogenously or adventitiously. Reduced exogenous vegetative trichoblasts may be present in a dorsal series at the apex. Axes
composed in cross-section of a central-axial cell, five pericentral cells (two dor-
sal, two lateral and one ventral) and a cortex of small isodiametric cells. In lower
axes additional pseudoparenchymatous cells may be present between the peri-
central cells and the cortex. Secondary cortication absent. Tetrasporangia pro-
duced in stichidia that are modified axes produced singly or in clusters on
primary indeterminate axes. Two tetrasporangia are formed per fertile segment
from the 3rd and 4th (lateral) pericentral cells. Two to five cover cells are pro-
duced. Gametophytes are dioecious, and reproductive structures arise on fertile
trichoblasts formed in a dorsal series from the apices of fertile branchlets. Fertile
branchlets are formed singly or in clusters on or in place of indeterminate axes,
or sometimes in the axes of determinate axes. Procarps are typical for the
Amansieae and comprise a fertile pericentral cell that acts as a supporting cell, a
four-celled carpogonial branch terminating in a trichogyne, and two sterile-cell
groups (basal and lateral). Cystocarps are ovoid to globose. Spermatangial capit-
ula are ovoid to globose.

Remarks: Halopithys is distinguished in the Amansieae by the completely
terete axes. The genus to which it bears the closest resemblance is Rytiphlaea,
which differs in having dorsiventrally compressed axes and rudimentary wings.
The type species, H. incurva, has been known from the Mediterranean since at
least the eighteenth century. The other two species, H. schottii and H. subopaca,
have been here included in Halopithys on the basis of their terete axes and paired
determinate laterals.

Key to the species of Halopithys.

1a. Lateral branch formation very dense - indeterminate axes not visible between
determinate laterals; ratio of central-axial to pericentral cell diameters (c:p)
= 1:3-4; distribution restricted to southeastern Africa ......... H. subopaca
1b. Lateral branch formation sparse to dense - indeterminate axes visible between
determinate laterals; c:p = 1:1.0-2.0; distribution in Atlantic Ocean, 
Mediterranean and Caribbean Seas ......................... 2
2a. Lateral branch formation sparse; c:p = 1:1.5-2.0; distribution restricted to
Caribbean Sea ............ H. schottii
2b. Lateral branch formation moderate to dense; c:p = 1:1; distribution in
Mediterranean Sea and eastern Atlantic Ocean ............. H. incurva

1. Halopithys incurva (Huds.) Batters, 1902: 78; Newton, 1931: 340, fig. 210;
Gerloff & Geissler, 1971: 784; Levring, 1974: 104; Cooke, 1975†: 200; Tsekos &
Haritonidis, 1977: 61; Guiry, 1978: 127; Nizamuddin et al., 1979: 475; Meñez &
Mathieson, 1981: 49; Giaccone et al., 1985: 681; South & Tittley, 1986: 54;
Boudouresque & Perret-Boudouresque, 1987: 30; Aleem, 1993: 99; Maggs &
Hommersand, 1993: 305, fig. 93; Silva et al., 1996: 495; Desikachary et al., 1998: 324;
Carrillo & Sansón, 1999: 68, 92, 205.
Fucus incurvus Hudson, 1762: 470.
Ceramium incurvum (Huds.) Lamarck et Candolle, 1815: 43.
Fucus pinastroides S.G.Gmelin, 1768: 127, pl. XI, fig. 1 nom. illeg.;
Stackhouse, 1797: 74, pl. XIII (incl. var. α pinastroides and var. β incurvus);
Sphaerococcus pinastroides Stackhouse, 1797: xxiv nom. illeg.
Rytiphlaea pinastroides C.Agardh, 1817: xxv nom. illeg.; J.Agardh, 1842:
145; 1863: 1088; Endlicher, 1843: 48; Harvey, 1847: 32; 1849: 80, pl. IID; 1855b: 224
Gigartina pinastroides Lyngbye, 1819: 45 nom. illeg.

Rhodomela pinastroides C.Agardh, 1822: 381 nom. illeg.; 1824: 200; Sprengel, 1827: 343; Naccari, 1828: 76 (Rodomela pinastroide); Greville, 1830: li, 104, pl. 13; Richard, 1832: 1; Mackay, 1836: 197; Zanardini, 1841: 182; Hooker & Harvey, 1845: 533; Bertoloni, 1862: 130.

Halopithys pinastroides Kützing, 1843: 433, pl. 52, fig. 7-8; 1845: 327; 1849: 840; 1865: 10, pl. 27a-d; Frauenfeld, 1855: 63; Martens, 1868: 4,98; Holmes & Batters, 1890: 94; Bornet, 1892: 303; Schmitz & Falkenberg, 1897: 466; Falkenberg, 1901: 472, pl. 9, figs 1-5; De Toni, 1903: 1081; 1924: 426; Mazza, 1905-1911: 364; Preda, 1908: 190; van Heurck, 1908: 74; Schmidt, 1924: 97; Børgeresen, 1930: 117, fig. 48; Kylin, 1956: 544; Gayral, 1958: 496, pl. CL, fig 72B; Haritonidis & Tsekos, 1974: 37; 1975: 217; 1976: 281; Tsekos & Haritonidis, 1977: 61. non Halopithys pinastroides sensu Seagrief, 1984: 34 (= H. subopaca, see De Clerck et al., 2002).

Rhodomela pinastroides var. episcopalis Montagne, 1840†: 153, pl.8, fig. 3. Rhodomela episcopalis Montagne, 1842: 253.

Rytiphlaea episcopalis (Mont.) Endlicher, 1843: 48.

Lophura episcopalis (Mont.) Kützing, 1849: 851; 1865: pl. 40d-h; Falkenberg, 1901: 472.


Type Locality: Sussex, England

Distribution: Faroe Islands, southern England and Ireland, Channel Islands, Atlantic coasts of Spain, France and Portugal, Mediterranean and Adriatic Seas, Morocco, Madeira and the Canary Islands. There have been isolated reports from New Zealand [Richard, 1832:1, “Banks, fide Turner... probably some mistake” Harvey, 1855b: 224], Sri Lanka [“Ceylon nach Smith” Martens, 1868] and Brazil (Schmidt, 1924) although it is probable that the latter record may be referable to H. schottii (Fig. 1).

Habit and Anatomy: Plants are erect, reaching to 30 cm in height (Fig. 8), and are found in a variety of habitats including intertidal pools, “infra-littoral; on sand and mud on sheltered coasts” (Haritonidis & Tsekos, 1974) and to depths of 30 metres (Falkenberg, 1901). Plants are composed of one or several indeterminate axes 0.8-1.0 mm in diameter that are terete and arise from a discoid holdfast. The indeterminate axes branch alternately to irregularly (Fig. 9). The major axes and their lateral branches bear opposite pairs of simple or compound determinate laterals, 0.5-0.9 mm in diameter. Where compound, the secondary laterals are formed in opposite pairs. Apices are strongly to weakly incurved (Figs 8, 9) and may produce exogenous trichoblasts in a dorsal row.

In cross-section the axes are composed of a central-axial cell, 125-150 μm in diameter, and five pericentral cells equal to or only slightly larger than the central-axial cell (Fig. 10). In younger branches the pericentral cells are surrounded only by a cortex, one to two cells thick, of small isodiametric heavily pigmented cells. In older branches the cortex may be thicker and up to 4 layers of pseudoparenchymatous cells may be found between the pericentral cells and the heavily pigmented cortex (Fig. 10).

Reproductive material was not available for examination but has been described by Maggs & Hommersand (1993). Tetrasporangia are formed, two per fertile segment, in stichidia that take the place of branches on determinate laterals. It has not been reported whether the stichidia bear trichoblasts from their...
Gametophytes are dioecious, procarps forming on trichoblasts produced in a dorsal series in the same manner as vegetative trichoblasts. Procarps arise on the epibasal segment of the trichoblast with the ventral pericentral cell acting as the supporting cell. One to two mature cystocarps are found on a fertile branchlet and are ovoid to slightly urceolate and approximately 750 µm in diameter (Maggs & Hommersand, 1993, fig. 93F). Male gametophytes produce spermatangial branches in a dorsal series on determinate laterals. The spermatangial branches consist of one to two sterile basal segments terminated by spherical to ovoid spermatangial capitula (Maggs & Hommersand, 1993, fig. 93D, E).

Remarks: Although this species is widely reported to possess five pericentral cells around the central-axial cell, both Kützing (1865, pl. 10d) and Maggs & Hommersand (1993, fig. 93C) clearly illustrate cross-sections with six cells surrounding the central-axial cell. The illustration of Falkenberg (1901, pl. 9, fig. 3) shows a cross-section with five pericentral cells and a trichoblast initial making a sixth cell in the pericentral ring. This may explain the apparent sixth pericentral cells in the illustrations of Kützing (1865) and Maggs & Hommersand (1993).

This species is distinguished from most other members of the Amansieae by its terete axes. It differs from the other two species in the genus in branching density and in the comparative diameters in cross-section of central-axial to pericentral cells (see below). In habit it is most like Rytiphlaea tinctoria, the distribution of the two species overlapping over most of their ranges. They differ in the profile of the cross-section, Rytiphlaea's being ovoid compared with the strictly circular profile of Halopithys. They also differ in the position of the repro-
ductive branchlets, which are often found in the axils of laterals in *Halopithys incurva* and positioned irregularly in *Rytiphlaea*.


**Holotype:** F980817 **Isotype:** MICH (not seen).

**Type Locality:** Cartagena, Columbia (*Schott*, No.19, Nov. 1857).

**Distribution:** Caribbean coast of Columbia and Brazil (Fig. 1).

**Habit and Anatomy:** Plants are erect and up to 18 cm in height. Habitat details are not known. The axes are terete and arise from a discoid holdfast 2-4 mm in diameter. Major axes are apparently indeterminate, 1-2 mm in diameter, and branch alternately to irregularly (Figs 11, 12). Apices are strongly to weakly incurved and may produce compound exogenous trichoblasts in a dorsal row (Fig. 13). The indeterminate axes bear opposite determinate laterals approximately 0.5 mm in diameter and up to 1.5 (-2.0) mm in length (Figs 12, 14). Pairs of determinate laterals are fairly regularly spaced, being separated by 1-3 mm (4-10 segments) (Fig. 12). Determinate laterals may be compound and may be accompanied by adventitious branchlets that arise near the base of the axes (Fig. 14).

In cross-section axes are composed of a central-axial cell and five pericentral cells (Fig. 15). The pericentral cells are 180-200 µm in diameter, which is approximately 1.5-2.0 times the diameter of the central-axial cell. In moderately old branches the pericentral cells are surrounded by a layer of pseudoparenchymatous cells and a cortex, one cell thick, of small, darkly pigmented, isodiametric cells (Fig. 15).

Tetrasporophytes were described by Joly et al. (1966) as bearing stichidia 2 mm in length by approximately 250 µm in width that produce two sporangia per fertile segment. The stichidia are formed on determinate branchlets and apparently bear vegetative trichoblasts from their apices (see Joly et al., 1966, p. 53 and pl. 3, figs 5-7). Gametophytes are dioecious. Female gametophytes produce sessile globular to urceolate cystocarps in a dorsal row on determinate laterals (Fig. 16). Mature cystocarps were not seen. Male gametophytes produce spermatangial branches in a dorsal series on determinate laterals (Fig. 17). Spermatangial capitula are ovoid, 200-250 µm in length and subtended by a single sterile segment (Fig. 17).

**Remarks:** Taylor (1941) discussed at some length the possible generic affiliations of this species. He considered the only possibilities to include *Protokuetzingia* and *Halopithys*, rejecting *Rytiphlaea* and the remainder of the Amansieae as all possessing a winged thallus. He rejected *Halopithys* on the basis of sparse branching [*H. pinastroides* (= *incurva*) being densely branched] and the size of the pericentral cells [all being of equal size in *H. pinastroides* (=*incurva*) compared with two being a little smaller (according to his interpretation) in *P. schottii*]. Taylor (1941) noted the disparity in pericentral cell number between *P. australasica* and *P. schottii* but considered the habit of the two species to be similar enough to include them in the same genus.

Wilson & Kraft (2000), in their study of the genus *Protokuetzingia*, transferred *P. schottii* to *Enantiocladia*, emphasising the importance of pericentral cell number as a generic character in the Amansieae. Their choice of *Enantiocladia* was provisional. This species does not conform to the generic description of
Enantiocladia sensu Wilson & Kraft (2000, p. 332) where the thalli are described as being flattened and with medullary wings.

Taylor (1941) objected to placing *P. schottii* in *Halopithys* because of the difference in density of the branching. Branching density, however, is a character that can be influenced by a variety of factors including age, health and environmental conditions. The Caribbean species has been collected so infrequently that the range of variability in this character is not known, and the density of branching, which may ultimately prove to be a useful species character, should not be given undue emphasis at this stage. The other difference between the Caribbean species and *Halopithys* was described (Taylor 1941, p.102) as a difference in the diameters of pericentral cells. Taylor’s illustration (1941, Pl. II, fig.9) and the material examined here (Fig. 15) shows all pericentral cells to have virtually identical sizes, agreeing very well with the condition seen in *Halopithys incurva*.

Although thorough investigation of more specimens of this species would be desirable, it is clear that its generic affinities lie with neither *Protokuetzingia* nor *Enantiocladia* but with *Halopithys*.

### 3. Halopithys subopaca (Simons) L.E.Phillips et De Clerck, comb. nov.


**Holotype**: BOL [Isaac B. 273 sub. Simons 2748 (*parte*)].

**Type Locality**: Santa Maria, Inhaca, Mozambique.

**Distribution**: known only from Mozambique and northern Natal, South Africa (Fig. 1).

**Habit and Anatomy**: Thalli are erect and reach up to 10 cm in height (Figs 18-20), and are found in intertidal pools and the shallow subtidal. Plants are composed of one or several major indeterminate axes 1.0-1.5 mm in diameter that are terete and arise from a discoid holdfast (Figs 18-20). The indeterminate axes are irregularly and infrequently branched and densely clothed for their entire lengths in compound determinate laterals. These determinate laterals are formed endogenously and oppositely (Fig. 21) and are 3-4(-6) mm in length. Where compound, the secondary laterals are formed oppositely near the base (Fig. 21) and are usually endogenous although adventitious secondary laterals may also be formed from cortical cells. Apices are strongly to weakly incurved, and may produce small exogenous trichoblasts in a dorsal row. The first pericentral cell is produced always to the left of the trichoblast initial (i.e. anticlockwise if looking down on the apex from above).

In cross-section axes are composed of a central-axial cell and five pericentral cells (Fig. 22). The central-axial cell, at approximately 30-40 µm in diameter, is considerably smaller than the pericentral cells, all of which are approximately 150 µm in diameter. In younger indeterminate branches and in all determinate laterals the pericentral cells are surrounded only by a cortex, one to two cells thick, of small isodiametric heavily pigmented cells. In older branches the cortex may be thicker and layers of pseudoparenchymatous cells may be found between the pericentral cells and the heavily pigmented cortex (Fig. 22).

Tetrasporangia are produced in stichidia (Fig. 23) found on the determinate laterals. Two tetrasporangia are produced in each segment from the 3rd and 4th pericentral cells. Trichoblasts are not produced from apices of stichidia. Gametophytes are presumably dioecious. Procarps are formed on the epibasal cells of reduced trichoblasts produced in a dorsal series on determinate laterals. The fertile trichoblast cell produces five elongate pericentral cells (Figs 24, 25), the
fifth (ventral) one acting as the supporting cell. The trichoblast segments proximal and distal to the procarp become polysiphonous before fertilisation (Fig. 25) and contribute to the formation of the pericarp. Cystocarps and male gametophytes have not been recorded for this species.

**Remarks:** This species is similar to the other species of *Halopithys* in the terete profile of the axes. The major difference between them is in overall habit, *H. subopaca* having distinctive indeterminate axes that are densely clothed with strictly determinate laterals of uniform length. They differ also in the relative sizes of the central-axial cell and pericentral cells in cross-section. In *H. incurva* the central-axial cell is of similar diameter to the pericentral cells (c:p = 1:1). In *H. schottii* the central-axial cell is a little smaller than the pericentral cells (c:p = 1:1.5-2.0), whereas in *H. subopaca* the central-axial cell is much smaller than the pericentral cells (c:p = 1:3-4).

When Simons (1970) originally described *Digeneopsis*, he failed to compare it with any genus apart from *Digenea*. The suite of small differences between this species and the type species of *Halopithys, H. incurva*, does not warrant separate generic status for *Digeneopsis subopaca* although they do, in combination with the disjunct distributions, provide good characters for specific separation and identification.
MOLECULAR RESULTS

The molecular analyses resulted in the phylogenetic trees shown in Fig. 26. In all analyses Halopithys incurva and Rytiphlaea tinctoria formed a highly supported, monophyletic group to the exclusion of all other included members of the Amansieae. The relationships within the Amansieae were, in general, not highly resolved, but the close link between these two species was universally supported. The clade containing Rytiphlaea and Halopithys showed no particular affinity to the other non-winged species, Protokuetzingia australasica, which instead grouped with high support with Kuetzingia canaliculata. The latter is a winged species that, like Protokuetzingia, produces six pericentral cells (Wilson & Kraft, 2000).

DISCUSSION AND CONCLUSIONS

The non-winged members of the Amansieae include four species with five, and one species with six pericentral cells. The molecular analyses have confirmed the long-held belief (Falkenberg, 1901; Kylin, 1956; Hommersand, 1963; Wilson & Kraft, 2000) that pericentral cell number is of fundamental importance in determining relatedness within the Amansieae, as Protokuetzingia was shown not to be closely related to Halopithys and Rytiphlaea. The remaining four non-winged species have been separated into two genera based on the compressed versus terete profiles of the axes in cross-section. This is a distinction that was first made in 1843 when Kützing established Halopithys. The molecular analyses, however, suggest that the two genera are very closely related, and as they are two of only three amansioid species found in the eastern Atlantic Ocean.
Mediterranean Sea [the other being Osmundaria (Vidalia) volubilis (Linnaeus) R.E.Norris], it is not unreasonable to assume that they are derived from a common ancestor.

The terete profile of Halopithys and its simple axial construction suggest that it may be a primitive form within the Amansieae. The molecular results, however, do not necessarily support this. The six-pericentral-celled Amansieae form a clade sibling to the remainder of the Amansieae. The resolution of other genera and species in the tribe is not clear from these analyses, but the Halopithys and Rytiphlaea clade is not basal in the tribe. This suggests the possibility that the terete/sub-terete nature of the axes in these genera may be a derived condition, resulting from the loss of wings.

Inclusion of the other two species of Halopithys in the molecular analyses may help to clarify the position of this clade, as would a molecular investigation using a less-conserved gene than the 18S rRNA gene used here. If Rytiphlaea were found, in these further analyses, to be positioned within a clade containing the three Halopithys species, there may be grounds for including all four species within a single genus. Although there are few morphological characters separating Rytiphlaea and Halopithys (compressed versus terete axes and presence/absence of rudimentary wings), these are considered significant enough to retain generic separation at this time. The formation of wings is a feature typical
of the Amansieae, and whether the absence of wings is ancestral or derived, the intermediate state exhibited by *Rytiphlaea* must be considered significant in the evolutionary development of the tribe.

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