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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***

Résumé — Les algues rouges cylindriques ou subcylindriques de la tribu des Amansieae (Ceramiales, Rhodomelaceae). La tribu des Amansieae est principalement composée de thalles aplatis dorsiventralement avec quelques espèces qui sont cylindriques ou subcylindriques en section transversale. Deux d’entre elles forment les genres monotypiques *Rytiphlaea* et *Halopithys*, tous deux natifs de la Méditerranée et de l’Océan atlantique NE. Les relations entre ces deux espèces et les autres espèces cylindriques ou subcylindriques, *Enantiocladia schottii* et *Protokuetzingia australasica,* ont été étudiées. Le genre monotypique *Digeneopsis* du Mozambique et d’Afrique du Sud, précédemment placé dans la tribu des Polysphonieae a aussi été étudié. Il n’y a aucune distinction générique entre *Digenopsis subopaca, Enantiocladia schottii* et *Halopithys incurva* : toutes ces espèces ont donc été incluses dans le genre *Halopithys*. *Rytiphlaea tinctoria,* en revanche, appartient à un genre distinct. Les analyses phylogénétiques moléculaires montrent des liens étroits entre *Rytiphlaea* et *Halopithys* mais aucune affinité particulière avec *Protokuetzingia*.

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 characterised 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.

Rytiphlaea *species*	*Basionym*	*Type Locality*	*Taxonomic History and Current Placement*
R. aculeata C.Agardh mscr., J.Agardh 1841†:26 *nom. nud.,* J.Agardh 1863:1087		Western Australia	= ***Endosiphonia spinulosa*** (Harv.) Womersley et M.J. Parsons 2003: 251. (see also Harv. 1863:xviii; Silva *et al.* 1996:551) "This is most likely a representative of Endosiphonia" Wilson & Kraft 2000:330 (of *R. aculeata*)
R. angusta Okamura 1896†:26		Japan	= ***Symphyocladia gracilis*** (Martens) Falkenb. 1901:282, 736
R. australasica (Mont.) Endl. *in* Harv. 1847:32	*Rhodomela australasica* Mont. 1840†:154	"in littoribus Van Diemen" [= Storm Bay, Tasmania fide Ducker, 1979:20]	→ *Halopithys* Kütz. 1849:841 → *Lophura* Kütz. 1849:851 → ***Protokuetzingia australasica*** (Mont.) Falkenb. *in* Schmitz & Falkenberg 1897:469
R. australis (Mont.) Endlicher 1843:48		Australia	*err. cit. pro. R. australasica* Mont. = ***Protokuetzingia australasica*** (Mont.) Falkenb.
R. australis Kütz. 1849:845		Falkland Islands	= *Rhodomela patula* (*fide* De Toni 1903:1094) = ***Lophurella patula*** (Hook.f. & Harv.) De Toni
R.? baileyi Harv. 1853:29		Monterey Bay, California, U.S.A.	→ *Polysiphonia* J.Agardh 1863:937 → Vertebrata Kuntze 1891:928 → ***Pterosiphonia baileyi*** (Harv.) Falkenb. 1901:270
R. belangeri Mont. 1857:138		Martinique	Description suggests possible links with *Halopithys incurva* and given locality should be investigated with regard to *H. schottii*
R. caespitosa (Hook.f. et Harv.) J.Agardh 1863:1091	*Rhodomela caespitosa* Hook.f. et Harv. *in* Harvey 1855b:225	Occepoto and Parimahu, New Zealand	= ***Lophurella caespitosa*** (*fide* Falkenberg 1901:436)
R. canaliculata Grev. 1831:149, fig. 1-4		Swan River, Western Australia	→ ***Kuetzingia canaliculata*** (Grev.) Sond. 1845:54
R. capensis Kütz. 1843:448		Cape of Good Hope, South Africa	= ***Pterosiphonia cloiophylla*** (C.Agardh) Falkenb. (*fide* Hommersand 1963:261)

R. cloiophylla (C.Agardh) J.Agardh 1841†:26	*Rhodomela cloiophylla* C.Agardh 1822:375	Cape of Good Hope, South Africa	→ ***Pterosiphonia cloiophylla*** (C.Agardh) Falkenb. 1901:271
R. complanata (Clemente) C.Agardh 1817:xxv	*Fucus complanata* Clemente 1807†:316	"in Mari Mediterraneo et Atlantico ad oras Hispaniae et Hiberniae" C.Agardh 1828:54	→ ***Pterosiphonia complanata*** (Clemente) Falkenb. 1901:271
R. compressa J.Agardh 1885:106		Geographe Bay, Western Australia	= ***Husseya rubra*** (Harv.)Silva in Silva *et al.* 1996:501 (*fide* Womersley 2003: 420). "shows no relationship to the Amansieae" Wilson & Kraft 2000:330
R. corymbosa Kütz. 1849:844		Cape of Good Hope, South Africa	= ***Pterosiphonia cloiophylla*** (C.Agardh) Falkenb. (*fide* Silva *et al.* 1996:549)
R. delicatula Hook.f. *et* Harv. *in* Harvey 1855b:224		D'Urville Island, Blind Bay, Cook Straits, Akaroa, New Zealand	→ ***Aphanocladia delicatula*** (Hook.f. *et* Harv.) Falkenb. *in* Schmitz & Falkenberg 1897:444
R. dumosa Harv. 1847:33		False Bay, near Muysenberg, Cape of Good Hope, South Africa	= ***Pterosiphonia cloiophylla*** (C.Agardh) Falkenb. (Delf & Michell 1921:114 place in synonymy with *Polysiphonia acanthina* J.Agardh which is in synonymy with *Pterosiphonia cloiophylla* fide Papenfuss 1943:89)
R. duperreyi C.Agardh 1828:52		Martinique	→ *Odonthalia* Postels et Rupr. 1840:14 → *Amansia* J.Agardh 1841:26 → ***Enantiocladia duperreyi*** (C.Agardh) Falkenb. *in* Schmitz 1889:447
R. elata (Sond.) Harv. 1855a:538	*Rhodomela elata* Sond. 1853:699	Lefevre Peninsula, South Australia	→ ***Cladurus elatus*** (Sond.) Falkenb. 1901:223 see also Silva *et al.* 1996:485-6. "…material is insufficient for identification" Wilson & Kraft 2000:330
R. episcopalis (Mont.) Endlicher 1843:48	*Rhodomela pinastroides* var. *episcopalis* Mont. 1840†: 153, pl. 8, fig. 3	Canary Islands	= *H. pinastroides* (*fide* Falkenberg 1901:436) = ***Halopithys incurva*** (Huds.) Batters
R. firma C.Agardh 1828:54		Cape of Good Hope	= ***Pterosiphonia cloiophylla*** (C.Agardh) Falkenb. (see Silva *et al.* 1996:549)

Rytiphlaea *species*	*Basionym*	*Type Locality*	*Taxonomic History and Current Placement*
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	*Amansia glomerata* C.Agardh 1822:194	Hawaii	→ *Odonthalia* Endlicher 1843:47 → *Fimbriaria* Trévisan 1845:30 → *Melanamansia* R.E. Norris 1995:66 → ***Amansia glomerata*** C.Agardh (see Masuda & Abe 2002)
R. hilariana Grev. 1833†:423		Brazil	→ *Vidalia obtusiloba* (C.Agardh) J.Agardh (*fide* Taylor 1960:609) = ***Osmundaria obtusiloba*** (C.Agardh) R.E.Norris 1991:14
R. kuetzingioides Sond. 1880:33 *nom. illeg.*		Geographe Bay, Western Australia	= ***Amansia serrata*** (Harv.) Womersley 2003: 394. (J. Agardh 1885 refers this species to *Ryt. merrifieldiae*)
R. latiuscula Harv. 1857:331		Japan	→ *Enantiocladia* Okamura 1907:42, pl. IX, fig. 1, pl. X, figs 1-17 → ***Symphyocladia latiuscula*** (Harv.) Yamada 1941:215
R.? lineata (Turner) C.Agardh 1817:xxv	*Fucus lineatus* Turner 1817:10, pl. 201	New Zealand (*Banks*)	→ *Epineuron lineatum* (Turn.) Hook.f. *et* Harv. 1845:532 current status unknown
R. merrifieldiae J.Agardh 1885:107 *(merrifieldii)*		Western Australia	→ ***Nanopera merrifieldiae*** (J.Agardh) S.M.Wilson *et* Kraft 2000:341
R. multifida (J.V.Lamour.) Decne. 1842:358	*Amansia multifida* J.V.Lamour. 1809:332	Santo Domingo, Dominican Republic	***Amansia multifida*** J.V.Lamour. 1809:332
R. obtusiloba C.Agardh 1824:161		Brazil	→ *Wormskioldia* Spreng. 1827:332 → *Amansia* Grev. 1830:xlvi → *Odonthalia* Postels *et* Rupr. 1840:14 → *Vidalia* J.Agardh 1863:1123 → *Euspiros* Kuntze 1891:894 → ***Osmundaria obtusiloba*** (C.Agardh) R.E.Norris 1991:14
R. pinastroides C.Agardh 1817:xxv *nom. illeg.*	*Fucus pinastroides* S.G.Gmel. 1768:127, pl. XI, fig. 1 *nom. illeg.*	England	→ *Halopithys* Kütz. 1843:433 = ***Halopithys incurva*** (Huds.) Batters 1902:78
R. plana (Forssk.) Kuntze 1898:424	*Conferva plana* Forsskål 1775:188		"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. prolifera Grev. mscr.		"ad oras Indiae orientalis (Wight! Sub n:o 146)" J.Agardh 1863:1116	→ *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			→ ***Dasyopsis pumila* f. *zanardiniana*** (Zanardini) Mazza 1922-1926:1670
R. purpurea C.Agardh 1817:xxv *nom. nov.*	*Fucus purpureus* Turner 1817:67, pl. 224 *nom. illeg.* *non* Hudson 1762:471 (= *Cystoclonium purpureum* (Huds.) Batters 1902:68)	U.K.	= ***Rytiphlaea tinctoria*** (Clemente) C.Agardh
R. rhodantha (Harv.) Decne. 1842:358	*Delesseria rhodantha* Harv. 1834:151, pl. CXXVI	Cap Malheureux, Mauritius	→ ***Amansia rhodantha*** (Harv.) J.Agardh
R. rigidula Kütz. 1843:448		Adriatic Sea	= ***Rytiphlaea tinctoria*** (Clemente) C.Agardh (*fide* Falkenberg 1901:437)
R. semicristata J.Agardh 1842:145		Mediterranean	= ***Rytiphlaea tinctoria*** (Clemente) C.Agardh (see J. Agardh 1863:1093, Falkenberg 1901:437)
R. seminuda Kütz. 1865:6, pl. 14a-c		Adriatic Sea	= ***Rytiphlaea tinctoria*** (Clemente) C.Agardh (*fide* De Toni 1903:1093)
R. simplicifolia Harv. 1860:298		Australia	= ***Epiglossum proliferum*** (C.Agardh) L.E.Phillips 2002b:
R. sinensis Debeaux 1875:49 (also 1873†, *nom nud.*)		"du camp de Tché-fou, et non loin de la rade de Yan-taiï (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.e. Tscifu maris sinensis, eadem species ac *Symphyocladia gracilis* (Mart.) Falk. Vix comparanda videtur cum *Odonthalia floccosa* (Esp.)" De Toni 1903:1099
R. spinulosa (Harv.) P.C.Silva *in* Silva *et al.* 1996:551	*Alsidium spinulosa* Harv. 1855a:538	Western Australia	= ***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. CXXX. Illustrations show 4 pericentral cells.

Rytiphlaea *species*	*Basionym*	*Type Locality*	*Taxonomic History and Current Placement*
R. stangeri Harv. mscr.		Port Natal (Durban), South Africa	→ *Polysiphonia stangeri* Harv. ex J. Agardh 1863:937 → ***Pterosiphonia stangeri*** (Harv.) Falkenb. 1901:270
R. thuyoides (Harv.) Harv. 1849:81	*Polysiphonia thuyoides* Harv. *ex* Mackay 1836:205	Miltown Mal Bay, Co. Clare, Ireland	→ *Pterosiphonia* Batters 1902:82 → ***Boergeseniella thuyoides*** (Harv.) Kylin 1956:508
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, laciniis terminalibus brevissime articulatis, atriculis 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 ?*
R. umbellifera J.Agardh 1894:77		Port Phillip Heads, Victoria, Australia	= ***Cladurus elatus*** (Sond.) Falkenb. (*fide* Wilson & Kraft 2000:330)
R. undulata (Decne) Decne 1842:358 *nom nud.*	*Amansia undulata* Decne 1841:173 *nom. nud.*		

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).

Specimens examined: *Rytiphlaea tinctoria*: 1. Le Dramont, Colanque du Pin, France, shaded crevices, 30 cm depth (*Coppejans*; 19.ix.1975, GENT HEC 2610). 2. Calvi, Pointe de la Revellata, Corsica, 40 m depth (*Coppejans*; 8.iv.1981, GENT HEC 4778). 3. Brucoli, Syracuse, Eastern Sicily, 50 cm depth (*Furnari*; 24.x.2000, MELU LEP R170). 4. Split, Croatia, at the base of *Cytoseira* spp., 1 m depth (*Coppejans*; 2.xi.1976, GENT HEC 2766). 5. Sikinos, Greece, 50 cm depth (*Coppejans*; 10.xiii.1972, GENT HEC 1679). *Halopithys incurva*: 1. Le Dramont, Colanque du Pin, France, 50 cm depth (*Coppejans*; 22.ix.1974, GENT HEC 2301). 2. Brest, Anse du Caro, France, infralittoral fringe (*Coppejans*; 28.iii.1975, GENT HEC 2464). 3. Calvi, Grottes de Veaux, Corsica (*Coppejans*; 9.xii.1977, GENT HEC 3260). 4. Bembridge, Isle of Wight, United Kingdom, mediolittoral (*Coppejans*; 9.iv.1977, GENT HEC 2913). 5. Tabarka, Tunisia, 2 metres depth, (*West*; 14.iv.1975, JAW1547[1]). *Halopithys (Enantiocladia) schottii*: 1. Cartagena, Columbia (*Schott*

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No. 19; xi.1857, F980817, female, HOLOTYPE) (*Schott*; no date, F1013299, male). *Halopithys (Digeneopsis) subopaca*: 1. Santa Maria, Inhaca, Mozambique (*Isaac* B. 273 sub. Simons 2748 (*parte*), BOL) 2. Bangha Nek, Rabbit Rock, Kwazulu Natal, South Africa, intertidal (*Coppejans*, *De Clerck, Bolton, Anderson, Leliaert, Muylle & De Smet*; 13.viii.1999, GENT KZN 569) 3. Kosi Bay, Kwazulu Natal, South Africa, intertidal pools (*Coppejans et al.*; 16.viii.1999, GENT KZN 748, tetrasporophyte) 4. Mabibi, Mabibi Point, 30 km N of Sodwana Bay, Kwazulu Natal, South Africa, intertidal pools (*Coppejans et al.*; 9.viii.1999, GENT KZN 368A) (*De Clerck & Cocquyt*; 13.viii.2000, GENT KZN 1641, female) 5. Cape Vidal, Kwazulu Natal, South Africa, shallow intertidal pools (*De Clerck & Cocquyt*; 18.viii.2000, GENT KZN 1809) 6. Crayfish Point, Mapelane, Kwazulu Natal, South Africa, shallow mid intertidal pools (*De Clerck & Cocquyt*; 20.viii.2000, GENT KZN 1843)

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 invariable 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.

Species	*Collection Details (Location*, Collector*, Date, Voucher)*	*Genbank Accession Number*
Kuetzingia canaliculata (Grev.) Sond.	Cervantes, Western Australia, *M & F Hommersand*, 20.ix.1995, MELU A000054	AY237283
Rytiphlaea tinctoria (Clemente) C.Agardh	Brucoli, Syracuse, Eastern Sicily, *Furnari*, 24.x.2000, MELU LEP-R170	AY237284
Vidalia colensoi (Hook.f *et* Harv.) J.Agardh	Farmer Rocks, Three Kings Islands, New Zealand, *Knight*, 25.xi.1998, MELU LEP-R112	AY237285
Vidalia fimbriata (J.V.Lamour.) J.Agardh	Yule Point, Port Douglas, Queensland, *West*, 12.vi.1987, JAW 2841	AY237286
Vidalia spiralis (C.Agardh) J.Agardh	Cottesloe, Western Australia, *McKernan,* 24.iii.1999, MELU LEP-R125	AY237287

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

Species	*Reference*	*Genbank Accession Number*
Adamsiella melchiori L.E.Phillips *et* W.A.Nelson	Phillips, 2002a (as *Lenormandia* sp. 1)	AF339897
Melanamansia glomerata (C.Agardh) R.E.Norris	Phillips, 2000	AF251512
Melanamansia mamillaris (J.V.Lamour. *ex* C.Agardh) R.E. Norris	Phillips *et al.* 2000	AF203889
Epiglossum smithiae Hook.f. *et* Harv.	Phillips, 2002a (as *Lenormandia smithiae*)	AF339895
Aneurianna dentata L.E.Phillips	Phillips, 2003	AY237280
Halopithys incurva (Huds.) Batters	Phillips, 2000	AF251513
Lenormandia spectabilis Sond.	Phillips, 2002a	AF339896
Neurymenia fraxinifolia (Mert. ex Turner) J.Agardh	Phillips, 2002a	AF339899
Osmundaria prolifera J.V.Lamour.	Phillips, 2002a	AF339900
Polysiphonia howei Hollenb.	Phillips, 2003	AY237282
Polysiphonia savatieri Hariot	Phillips et al., 2000	AF203885
Protokuetzingia australasica (Mont.) Falkenb.	Phillips, 2002a	AF339901

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

Genus *Rytiphlaea* C.Agardh, 1817: xxv; 1828: 50; Harvey, 1847: 31; 1849: 77; 1853: 28; 1855b: 224; Kützing, 1849: 844; Bertoloni, 1862: 131; J. Agardh, 1863: 1084; 1885: 106; Ardissone, 1883: 420; Schmitz, 1889: 447; Schmitz & Falkenberg, 1897: 467; Falkenberg, 1901: 436; De Toni, 1903: 1093; 1924: 427; Preda, 1908: 188; Kylin, 1956: 544; Wilson & Kraft, 2000: 330.

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).

***Rytiphlaea tinctoria* (Clemente) C.Agardh**, 1824: 160; 1828: 52; Naccari, 1828: 64 (*Ritiflea tintoria*); Zanardini, 1841: 181; J.Agardh, 1842: 145; Endlicher, 1843: 48; Kützing, 1843: 448; 1849: 845; 1865: 6, pl.13e-i; Zanardini, 1843: 51; Frauenfeld, 1855: 64 + pl.; Bertoloni,1862: 131; Ardissone & Strafforello, 1878: 218; Ardissone,

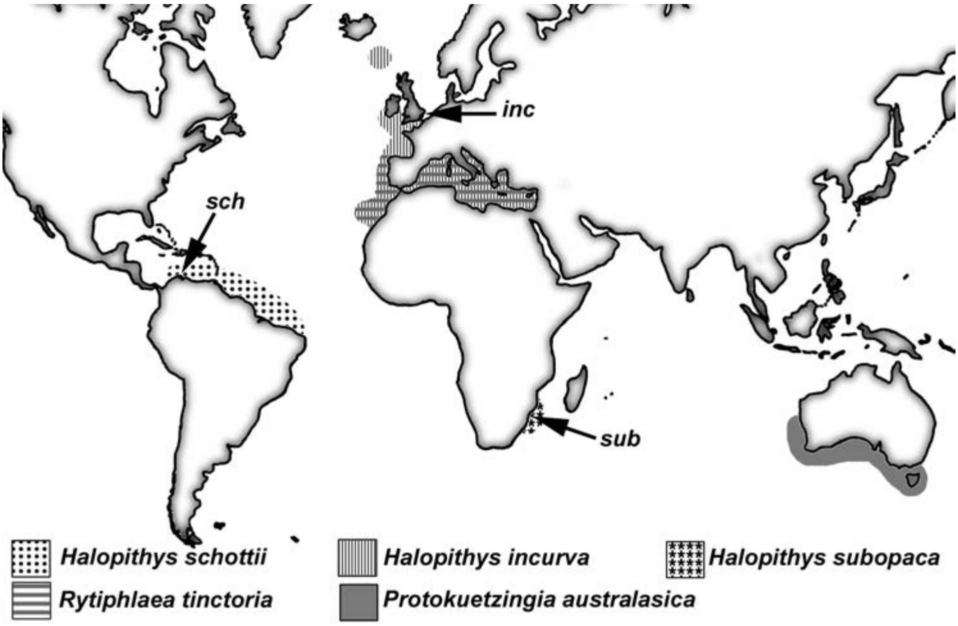


Fig. 1. Distribution of the non-winged Amansieae. Arrows indicate type localities of *Halopithys* species. *inc – H. incurva, sch – H. schottii, sub – H. subopaca.*

1883: 422; Hauck, 1885: 247, fig. 100; Schmitz, 1889: 447; Bornet, 1892: 302; Schmitz & Falkenberg, 1897: 467; Reinbold-Itzehoe, 1898: 90; Falkenberg, 1901: 438; De Toni,1903: 1095; 1924: 427; Mazza, 1905-1911: 371; Preda, 1908: 189; Børgesen, 1930: 116; J.Feldmann, 1942: 92; J.Feldmann & Tixier, 1947: 341; Kylin, 1956: 544; Gayral, 1958: 498, pl. CLI, fig. 72C; Papenfuss, 1968: 101, Ardré, 1970: 220; Nizamuddin & Lehnberg,1970: 128, pl. XIX, fig. 44; Gerloff & Geissler, 1971: 788; Haritonidis & Tsekos, 1974: 38; 1975: 219; 1976: 283; Levring, 1974: 104; Tsekos & Haritonidis, 1974: 405; 1977: 63; Nizamuddin *et al.*, 1979: 475; Meñez & Mathieson, 1981: 52; Weisscher, 1983: 76; Audiffred & Weisscher, 1984: 26; Giaccone *et al.*, 1985: 695; South & Tittley, 1986: 56; Boudouresque & Perret-Boudouresque, 1987: 34; Aleem, 1993: 102; Carrillo & Sansón, 1999: 68,92,207.

Fucus tinctorius Clemente, 1807†:316.

Fucus purpureus 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. *mscr.*(fide De Toni, 1924: 1095).

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

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

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

Rytiphlaea semicristata J.Agardh,1842: 145; 1863: 1092; Kützing, 1849: 845.

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

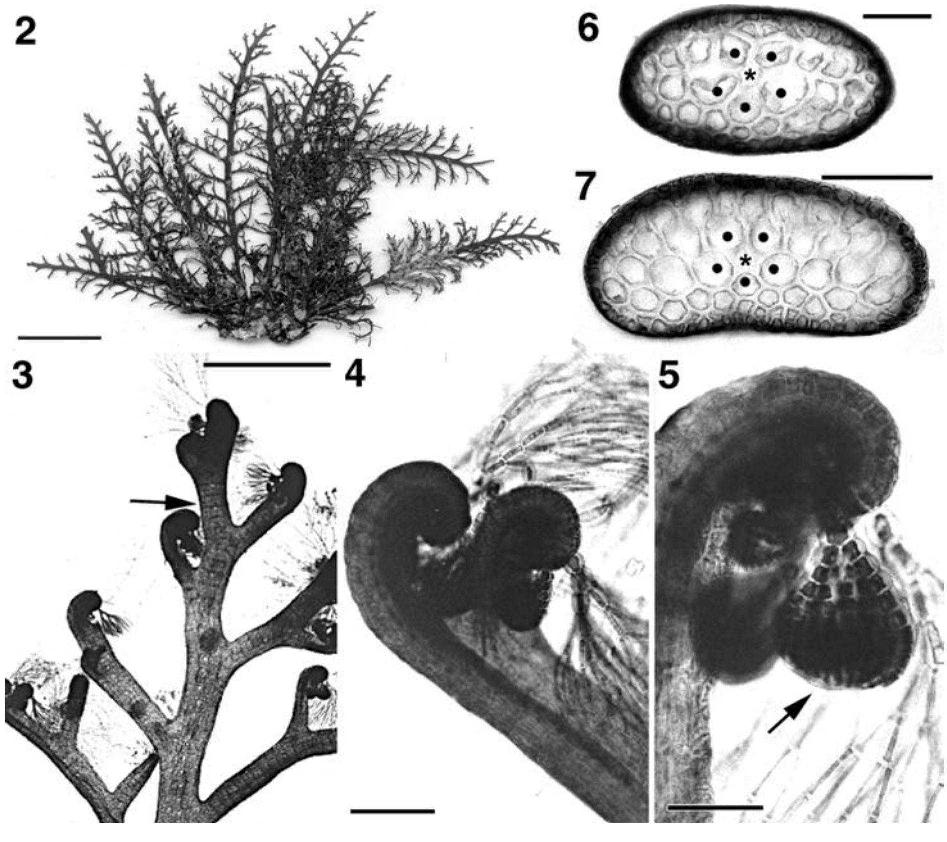
Rytiphlaea seminuda Kützing, 1865: 6, pl. 14a-c.

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



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.

Genus *Halopithys* Kützing, 1843: 433; 1849: 840; Schmitz & Falkenberg, 1897: 466; Falkenberg, 1901: 471; De Toni, 1903: 1080; 1924: 426; Preda, 1908: 190; Newton, 1931: 340; Kylin, 1956: 544; Ardré, 1970: 220; Maggs & Hommersand, 1993: 304; Desikachary *et al.*, 1998: 323; Wilson & Kraft, 2000: 327.

Digeneopsis Simons, 1970:13; 1976:90.

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 dorsal, two lateral and one ventral) and a cortex of small isodiametric cells. In lower axes additional pseudoparenchymatous cells may be present between the pericentral cells and the cortex. Secondary cortication absent. Tetrasporangia produced 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 produced. 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 axils 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 capitula 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; J.Feldmann, 1942: 92; J.Feldmann & G.Feldmann, 1946: 176, fig. 6; Ardré, 1970: 220; 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*); Esper, 1800: 146, pl. XCIX; Turner, 1808: 22-23, pl. 11; Bertoloni, 1819: 223, 307.

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

("probably some mistake"); Derbès & Solier, 1856: 74, pl. XXI, fig. 3-7; Ardissone & Strafforello, 1878: 217; Le Jolis, 1880: 147; Ardissone, 1883: 421; Hauck, 1885: 248.

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. II *nom. illeg.*; 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; Børgesen, 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.

Lectotype: BM ex Herb. Pulteney, England, unlocalized (Maggs & Hommersand, 1993: 305) (not seen).

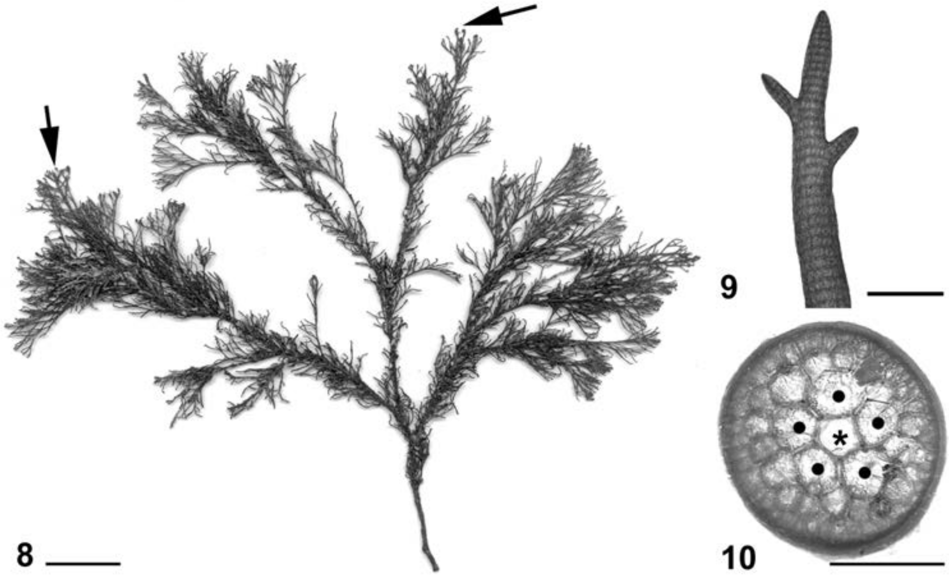
Type Locality: Sussex, England

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 referrable 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, "infralittoral; 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



Figs 8-10. *Halopithys incurva* (Huds.) Batters. (8 = GENT HEC 3260, 9 = JAW 1547, 10 = GENT HEC 4778). **8.** Habit. Scale = 2 cm. **9**. Branch apex with alternate laterals and obvious transverse striations. Scale = 1 mm. **10**. Cross section showing central-axial cell (asterisk), five pericentral cells (dots), further pseudoparenchymatous cells and darkly pigmented cortex. Scale = 500 mm.

apices. 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 reproductive branchlets, which are often found in the axils of laterals in *Halopithys incurva* and positioned irregularly in *Rytiphlaea*.

2. ***Halopithys schottii*** **(W.R.Taylor) L.E.Phillips *et* De Clerck, *comb. nov.***

Protokuetzingia schottii W.R.Taylor, 1941: 100, pl. II; 1960: 607; Joly *et al.*, 1966: 52, pl. III, figs 3-7.

Enantiocladia schottii (W.R.Taylor) S.M.Wilson *et* Kraft, 2000: 338, fig. 5.

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

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

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

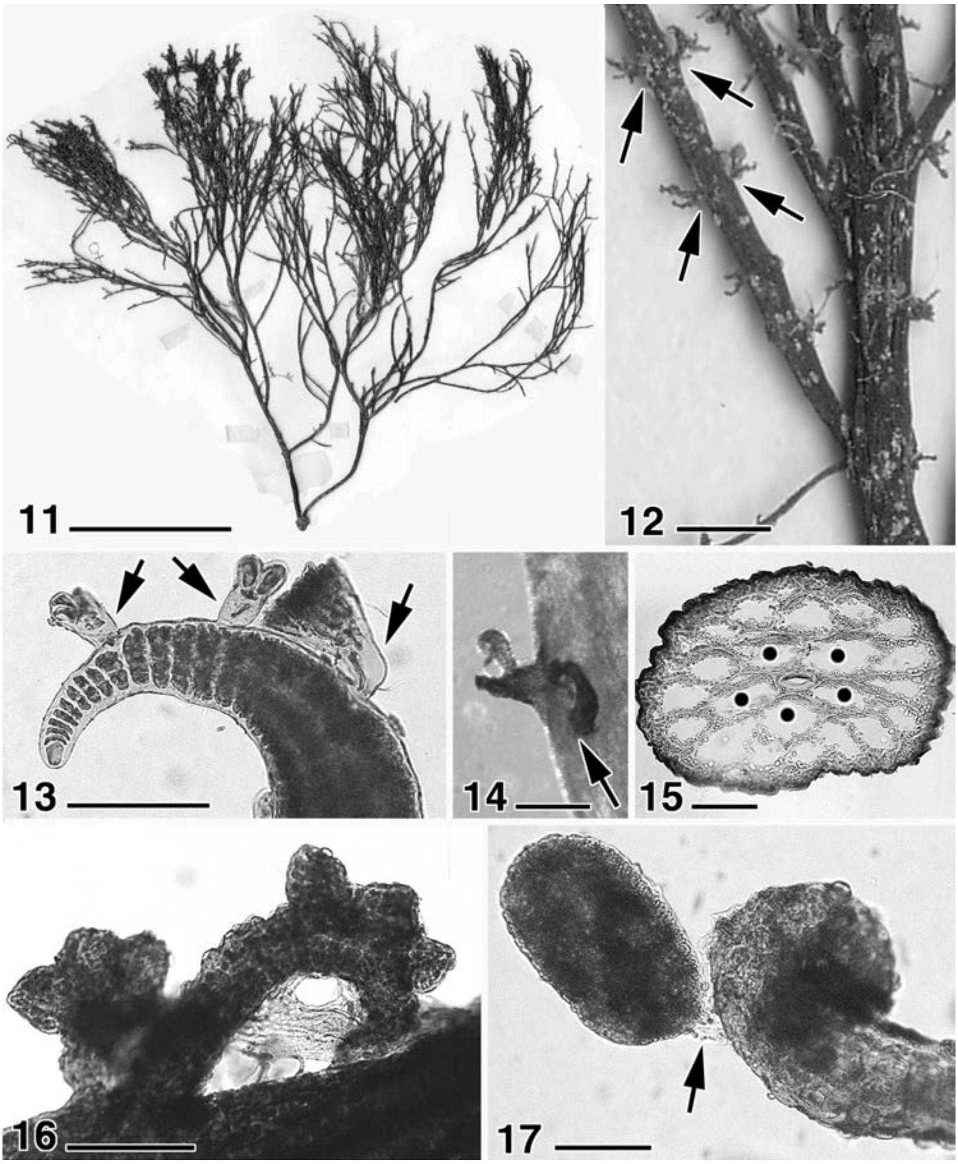
Habit and Anatomy: Plants are erect and up to 18 cm in height. Habitat details are not known. The axes are terete and arise from a discoid holdfast 2-4 mm in diameter. Major axes are apparently indeterminate, 1-2 mm in diameter, and branch alternately to irregularly (Figs 11, 12). Apices are strongly 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 mm 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



Figs 11-17. *Halopithys schottii* (W.R.Taylor) L.E.Phillips *et* De Clerck. (11-16 = F980817, 17 = F1013299). **11**. Habit. Scale = 5 cm. **12**. Detail of branching showing indeterminate axes with paired compound determinate laterals (arrows). Scale = 2 mm. **13**. Branch apex with exogenous trichoblasts (arrows). Scale = 100 µm. **14**. Detail of compound indeterminate axis with adventitious branchlet arising near its base (arrow). Scale = 500 µm. **15**. Cross-section showing central-axial cell surrounded by five pericentral cells (dots), pseudoparenchymatous cells and darkly pigmented cortex. Scale = 200 µm. **16**. Incurved branchlets bearing dorsal series of procarps. Scale = 200 µm. **17**. Spermatangial branch borne dorsally on tightly incurved branchlet. A single sterile segment (arrow) subtends the ovoid spermatangial capitulum. Scale = 100 µm.

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.*

Digeneopsis subopaca Simons, 1970: 13, figs 10, 11E-G; Seagrief, 1984: 24; Silva *et al.*, 1996: 491; De Clerck *et al.*, 2002: 421, fig. 34.

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

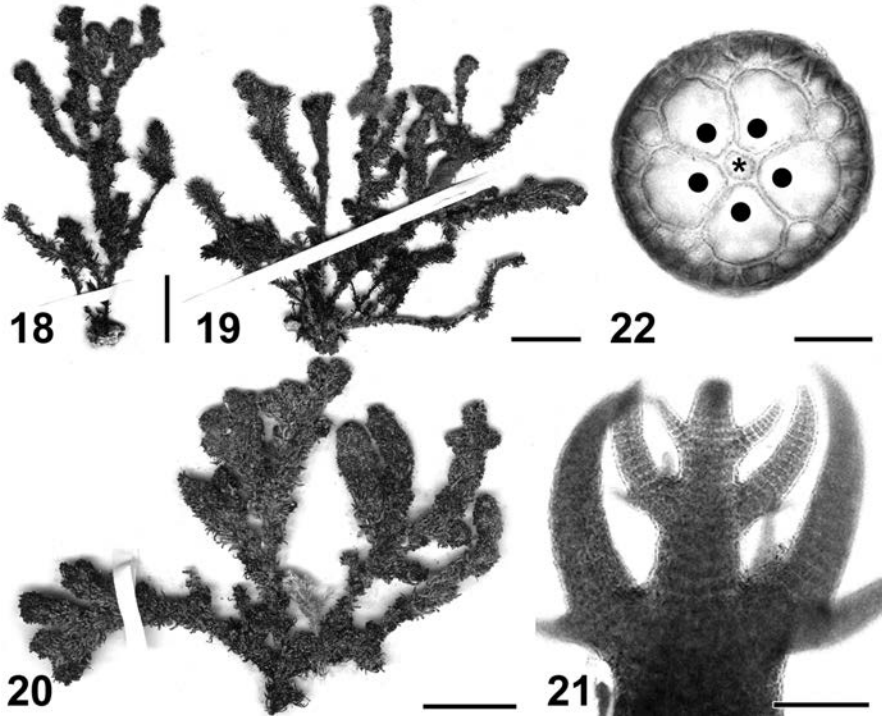
Type Locality: Santa Maria, Inhaca, Mozambique.

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

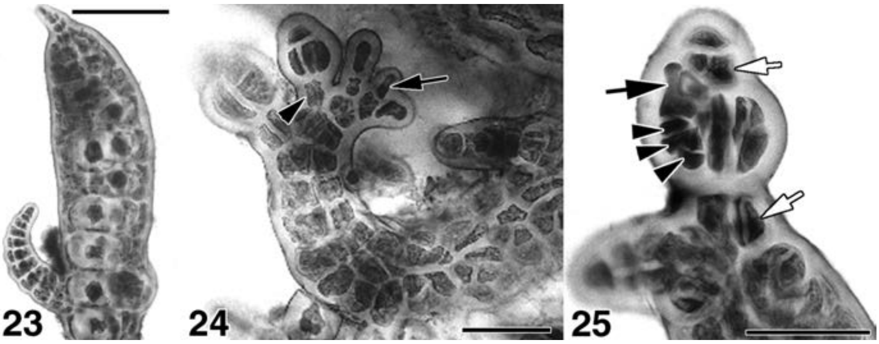


Figs 18-22. *Halopithys subopaca* (Simons) L.E.Phillips et De Clerck. (18-20 = GENT KZN368A, 21-22 = GENT KZN1641). **18-20**. Habits. Scale = 2 cm. **21**. Apical portion showing opposite determinate laterals. Scale = 200 µm. 22. Cross-section through axes showing central-axial cell (asterisk), five pericentral cells (dots) and small-celled cortex. Scale = 100 µm.

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.



Figs 23-25. *Halopithys subopaca* (Simons) L.E.Phillips *et* De Clerck. (23 = GENT KZN748A, 24-25 = GENT KZN1641). **23**. Lateral view of tetrasporangial stichidia with immature tetrasporangia. Scale = 200 µm. **24**. Incurved branchlet bearing dorsal series of fertile trichoblasts. Trichoblasts are derived exogenously (arrow). The basal segment is initially monosiphonous (arrowhead) while the epibasal segment divides. Scale = 50 µm. **25**. Procarp showing the four-celled carpogonial branch (arrowheads and black arrow) terminating in a developing trichogyne (black arrow). Both the trichoblast segment above and below the fertile segment have become polysiphonous (white arrows). Scale = 50 µm.

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 and

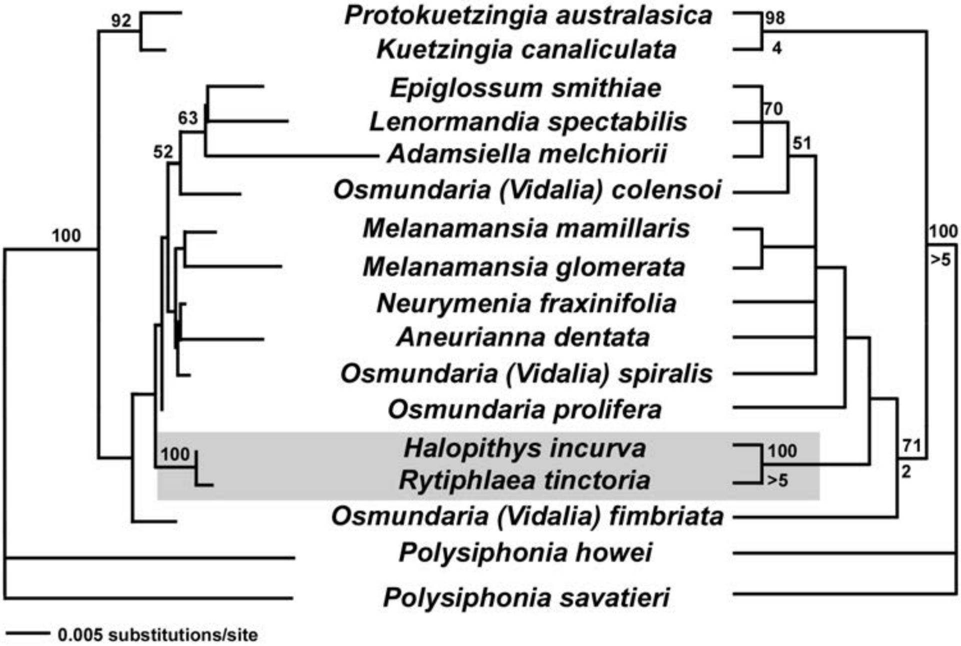


Fig. 26. Maximum Likelihood Phylogram (left) and Strict Consensus Cladogram of 10 Most-Parsimonious Trees (right) [Length = 297 steps, CI = 0.798, RI = 0.610] inferred from analyses of the 18S rRNA gene. Numbers above nodes indicate bootstrap support for the phylogenies over 1000 bootstrap replicates using Neighbor-Joining (left) and Parsimony (right) criteria. Values less than 50 are omitted. Values below the nodes (right) indicate Bremer support (decay indices).

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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