European Journal of Phycology

ISSN: 0967-0262 (Print) 1469-4433 (Online) Journal homepage: https://www.tandfonline.com/loi/tejp20

Reappraisal of the type species of *Polysiphonia* (Rhodomelaceae, Rhodophyta)

Myung-Sook Kim , Christine Maggs , Lynne McIvor & Michael Guiry

To cite this article: Myung-Sook Kim , Christine Maggs , Lynne McIvor & Michael Guiry (2000) Reappraisal of the type species of *Polysiphonia* (Rhodomelaceae, Rhodophyta), European Journal of Phycology, 35:1, 83-92, DOI: 10.1080/09670260010001735661

To link to this article: https://doi.org/10.1080/09670260010001735661

Reappraisal of the type species of *Polysiphonia* (Rhodomelaceae, Rhodophyta)

MYUNG-SOOK KIM[1], CHRISTINE A. MAGGS[2], LYNNE McIVOR[2] AND MICHAEL D. GUIRY[1]

[1]*The Martin Ryan Marine Science Institute and Department of Botany, National University of Ireland Galway, Galway, Ireland*
[2]*School of Biology & Biochemistry, Queen's University of Belfast, Belfast BT9 7BL, N. Ireland*

(*Received 5 March 1999; accepted 13 December 1999*)

The genus *Polysiphonia* Greville, nom. cons., has had a long and confused nomenclatural history. At present, *Polysiphonia* has a wide circumscription, including at least 200 species, but it is heterogeneous in many vegetative and reproductive developmental features. Central to any re-evaluation of the genus is a detailed examination of the type species of *Polysiphonia*, *P. urceolata* (Lightfoot *ex* Dillwyn) Greville, which is conspecific with *P. stricta* (Dillwyn) Greville. We here report on the vegetative and reproductive morphology of *P. stricta*, including *P. urceolata*, based on type and other material from the British Isles. Thalli consist of prostrate and erect ecorticate axes with four pericentral cells, attached by unicellular rhizoids remaining in open connection with pericentral cells. Prostrate axes lack vegetative trichoblasts; trichoblasts occur seasonally on erect axes. Branch initials are cut off from the subapical cell at intervals of four or five segments in dichotomous and alternating pairs rather than being formed from each axial cell in the spiral pattern typical of most species of *Polysiphonia*. Spermatangial branch initials, which are trichoblast homologues, are produced directly from each axial cell at the tips of erect branches, not subtended by trichoblasts, and have two- to five-celled sterile tips when mature. The mature carpogonial branch is four-celled with a two-celled first sterile group and a one-celled second sterile group. Following presumed fertilization, direct fusion apparently takes place between carpogonium and auxiliary cell; mature cystocarps are usually urceolate. Tetrasporangia are formed from the third pericentral cell, in straight series, and have two pre-sporangial cover cells. Previous accounts of a third, post-sporangial cover cell could not be substantiated. *P. stricta* and a small group of other *Polysiphonia* species differ in several important respects from most members of the genus, which have rhizoids cut off from pericentral cells by a cell division, abundant trichoblasts, spirally arranged tetrasporangia and a post-sporangial cover cell. The branching pattern of *P. stricta* highlights the difficulties of distinguishing between the tribes Polysiphonieae and Pterosiphonieae.

Key words: morphology, *Polysiphonia*, *Polysiphonia stricta*, *Polysiphonia urceolata*, Polysiphonieae, red algae, taxonomy, type materials

Introduction

The common and widespread red algal genus *Polysiphonia* Greville has had a long and confused nomenclatural history. It was originally described by C. Agardh (1817) under the name *Hutchinsia*, but this name was invalid as it was predated by the flowering plant genus *Hutchinsia* R. Brown *in* Aiton (1812), both genera having been named for Miss Ellen Hutchins who collected widely in Bantry Bay, Co. Cork, Ireland, in the early 1800s. Greville (1823, pl. 90) therefore proposed the new name *Polysiphonia* as a substitute for *Hutchinsia*. Several older generic names for species of *Polysiphonia* exist, however (Silva, 1952), and in the International Code of Botanical Nomenclature (Greuter *et al.*, 1994), *Polysiphonia* has been conserved against *Vertebrata* S. F. Gray (1821), *Grammita* Bonnemaison (1822) and *Grateloupella* Bory de Saint-Vincent (1823, as *Gratelupella*). Silva (1952) chose *Polysiphonia urceolata* (Lightfoot *ex* Dillwyn) Greville (1824, p. 309, pl. II, fig. 19), based on *Conferva urceolata* (Dillwyn, 1809, p. 82, pl. G), as the type of the conserved genus. However, Taylor (1962) pointed out that Greville's original (1823) proposal of *Polysiphonia* was as an avowed substitute for *Hutchinsia*, hence *P. violacea* (Roth) Sprengel [(= *P. fucoides* (Hudson) Greville], chosen by Schmitz (1889) as the lectotype species, should not have been rejected as the type. Nevertheless, *P. urceolata* remains the type species of *Polysiphonia* because it is the designated lectotype of this conserved generic name (Taylor, 1962; Silva *et al.*, 1996, p. 921). *P. urceolata* has been placed in synonymy with *Polysiphonia stricta* (Dillwyn) Greville (Maggs & Hommersand, 1993).

The generic circumscription of *Polysiphonia* has been in an almost constant state of flux since C. Agardh's (1817) proposal of *Hutchinsia*. Sprengel (1827) was the first author to adopt the name *Polysiphonia* for the majority of the species placed by C. Agardh in *Hutchinsia* (Dixon & Irvine, 1970), and included 27 species altogether. J. Agardh (1863, p. 908) treated *Polysiphonia* as a diverse and speciose genus, which he divided primarily on the basis of thallus size into four subgenera: *Ptilosiphonia*, *Herpo-*

Correspondence to: C. A. Maggs, e-mail: c.maggs@qub.ac.uk

siphonia, *Oligosiphonia* and *Polysiphonia*. Schmitz & Falkenberg (1897) and Falkenberg (1901) completely revised the Rhodomelaceae, including the taxa referred to *Polysiphonia* by J. Agardh (1863). The tribes ('Familie') Pterosiphonieae and Herposiphonieae were proposed, and *Lophosiphonia* was described.

Falkenberg's (1901) circumscription of *Polysiphonia* was similar to that currently adopted by most workers (e.g. Maggs & Hommersand, 1993; Silva *et al*., 1996). Subsequently, Kylin (1941) segregated *Orcasia* (based on *Polysiphonia senticulosa* Harvey); Kylin (1956) resurrected the genera *Vertebrata* and *Carradoria* Kylin *non* Martius, now *Carradoriella* P. Silva *in* Silva *et al*. (1996: type species: *C. virgata* (C. Agardh) P. Silva from South Africa) and proposed *Boergeseniella* based on *Polysiphonia fruticulosa* (Wulfen) Sprengel. Kylin's proposals have not generally been widely accepted: Kudo & Masuda (1988) treated both Kylin's species of *Orcasia* as members of *Polysiphonia*; Wynne (1986) replaced *Carradoriella virgata* (as *Carradoria virgata*) in *Polysiphonia*; and Maggs & Hommersand (1993) recognized *Boergeseniella* but not *Vertebrata*. Hollenberg (1968*a*, *b*) divided the Pacific Ocean species of *Polysiphonia* into two groups (apparently without taxonomic rank): Oligosiphonia and Polysiphonia. He also proposed several new genera, e.g. *Womersleyella* Hollenberg (1967), based on *W. pacifica* Hollenberg, to which some species of *Polysiphonia* were later transferred (Norris, 1992).

At present, therefore, the genus *Polysiphonia* has a wide circumscription, including at least 200 species (Stegenga *et al*., 1997). However, as noted by Hommersand (1963), *Polysiphonia* is quite variable in its vegetative and reproductive developmental features. Maggs & Hommersand (1993) likewise listed alternate character states for features such as whether rhizoids are cut off from pericentral cells or remain in open connection with them. Hommersand (1963) described five different modes of vegetative branch origin in *Polysiphonia*, and commented on the presence or absence of branches of restricted growth. Tetrasporangial development varied, sporangia being derived from either the second or third pericentral cell, either in a regular spiral in species bearing trichoblasts, or in straight rows correlated with a lack of trichoblasts. Maggs & Hommersand (1993) and Stegenga *et al*. (1997) noted that tetrasporangia could have either two or three cover cells. Hommersand (1963) also drew attention to discrepancies between the commonly accepted four-celled state of the carpogonial branch in *Polysiphonia* and reports of functional three-celled carpogonial branches. Recently, Kim *et al*. (1994) and Kim & Lee (1997) have confirmed the existence of both three-celled and four-celled carpogonial branches in different Korean *Polysiphonia* species.

Molecular phylogenetic studies also indicate that species presently assigned to *Polysiphonia* represent several well-defined and divergent clades (McIvor *et al*., 1999). Central to any investigation of this morphological and molecular heterogeneity is the examination of the type species of *Polysiphonia*, *P. urceolata*. As noted above, *P. urceolata* is conspecific with *P. stricta*. *P. stricta* is a common lower intertidal and subtidal species in the North Atlantic Ocean (Kapraun & Rueness, 1983; Schneider & Searles, 1991; Maggs & Hommersand, 1993). Numerous morphological forms have been described throughout its range and variously treated taxonomically as varieties, species, or seasonal growth forms (Batten, 1923; Rosenvinge, 1923–4; Taylor, 1957). Although *P. stricta* (as *P. urceolata*) has also been reported from Korea (Kang, 1966) and Japan (Segi, 1951), Yoon (1986) referred these plants to *Polysiphonia morrowii* Harvey (1856). *P. stricta* therefore may be confined to the North Atlantic; other records from the Pacific (e.g. Scagel *et al*., 1989; Hansen, 1997) require reinvestigation.

Polysiphonia stricta sensu lato (including forms such as '*urceolata*', '*patens*' and '*spiralis*'; see Maggs & Hommersand, 1993) has previously been the subject of several investigations. Batten (1923) concentrated on gross morphological features, particularly the holdfast and spiralling of pericentral cells; Rosenvinge (1923–4) studied habitat, phenology and life history and made general observations on vegetative and reproductive development. The most detailed morphological study is that of Kylin (1937), who investigated the development of tetrasporangia and procarps. Taylor (1960) examined the variability in culture of several morphological features of an isolate from Atlantic Canada. There appear to be no studies to date on post-fertilization development in *P. stricta*. Recently, Kim *et al*. (1994), Kim (1995) and Kim & Lee (1996*a*) described the development of vegetative and reproductive structures of two Korean species: *P. atlantica sensu* Kim & Lee (1996*a*) (not conspecific with the type of *P. atlantica* Kapraun *et* J. Norris from Ireland) and *P. morrowii*, both of which have an obvious resemblance to *P. stricta*. These reports differed in one important feature, the absence of post-sporangial cover cells, from Kylin's observations on *P. stricta* (as *P. urceolata*).

Accurate information on the morphology of *P. urceolata*, including its post-fertilization development, is essential for any future revisions of the genus *Polysiphonia*. The aim of the present study was to document the morphology of *P. stricta* (including *P. urceolata*) for comparison with Kylin's (1937) findings, with particular emphasis on potentially phylogenetically informative characters such as mode of branch formation, female and post-fertilization development, and the origin of tetrasporangia.

Materials and methods

Type material of several forms of *Polysiphonia stricta*, including *P. urceolata*, *P. patens* and *P. stricta*, was located in the Natural History Museum, London (BM) and Botanical Museum, Lund, Sweden (LD). A wide range of forms of *P. stricta* was collected around the coasts of Britain and Ireland between 1979 and 1994, both intertidally and subtidally, and preserved in 4% formalin/seawater. Specimens covering the full range of vegetative and reproductive variation observed (*c*. 40 samples) were

prepared as permanent mounts by soaking overnight in 4% formalin/seawater with 1–2 drops of aniline blue, rinsing in fresh seawater, and mounting in dilute Karo corn syrup acidified with a small drop of 1% HCl. Measurements included the largest and smallest sizes observed for each feature, and exclude the cell wall thickness. Material from the British Isles that is similar to *P. subtilissima* Montagne (see Maggs & Hommersand 1993, fig. 111H, I), and may represent this species (B. Womersley, personal communication), is excluded from the following account.

Detailed anatomical studies were made on male, female, cystocarpic and tetrasporangial thalli of *P. stricta* collected from marina pontoons at Hayling Island, Hampshire, England, in February 1998, and fixed immediately in 4% formalin/seawater. The liquid-preserved material was cleared in 5–10% sodium hydroxide for 1–2 d, then rinsed in distilled water (Nam & Saito, 1991). Material was mounted directly in Karo containing 1% aniline blue for microscopic examination. To observe the formation of tetrasporangia, several tetrasporangial apices were squashed with the eraser end of a pencil, and good preparations were selected from these. The anatomy was reconstructed by drawing the cells of the squashed axes, using a camera lucida.

Representative herbarium specimens and slides have been placed in the Phycological Herbarium, National University of Ireland, Galway (GALW) and the Natural History Museum, London (BM).

Results

Type specimens

Conferva urceolata. The localities originally cited by Dillwyn (1809, p. 82, pl. G) in the protologue of *Conferva urceolata* included Devon, Scarborough, Isle of Wight, Brighton (all England) and near Forres in Moray (Scotland). No potential types were found in BM. Specimen no. 39962 in LD is a glass slide in a package labelled 'Conf. urceolata tab G. Forres. Sp. orig. Dillwyn'. Although Dillwyn did not mention fertile stages in the protologue, there is no reason to doubt the authenticity of this specimen, which is selected here as the lectotype of *Conferva urceolata*. It is characteristic of mature thalli of *P. stricta* growing on *Laminaria hyperborea* stipes, having relatively wide, dark-coloured axes without trichoblasts, and large urceolate cystocarps.

Conferva patens. The original collections cited by Dillwyn (1809, p. 82, pl. G) when describing *Conferva patens* ere from Bantry, made by Miss Hutchins, and from Seaton, Devon, made by Mrs A. W. Griffiths. A specimen in BM from Bantry was labelled by A. R. A. Taylor 'Type spec. of *Conferva patens* Dillwyn'. This specimen is designated here as the lectotype. It was collected by Miss Hutchins, and has a note from her dated 5 September 1809: 'I think you will find this only a variety of C. stricta: it grows in deep water'. She also noted that this or other material was found in April on the stalks of *Laminaria hyperborea* (Gunnerus) Foslie (as *Fucus digitatus*). The specimen had clearly been growing on kelp, and has wide, stiff axes with recurved branchlets, no trichoblasts and large tetrasporangia. A probable isotype is housed at LD 399981.

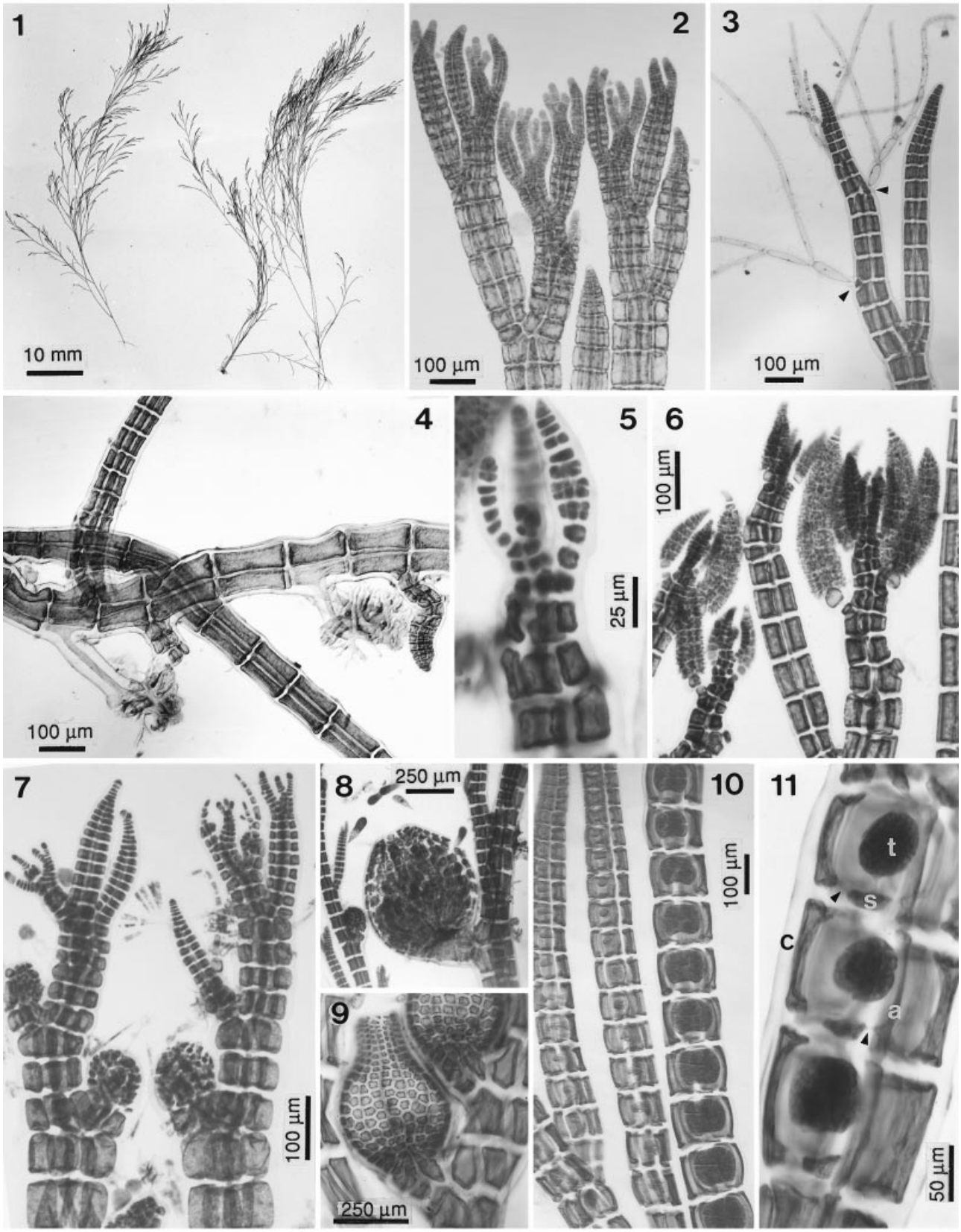
Conferva stricta. The protologue of *Conferva stricta* Dillwyn (1804, pl. 40) cited three localities, Swansea (Wales), Dover and Yarmouth (England). A lectotype of *C. stricta* was designated by Maggs & Hommersand (1993, p. 355). This specimen is from Swansea and is cystocarpic, with soft, relatively narrow axes, apparently lacking trichoblasts, and resembles material obtained from lower-shore rock pools and marina pontoons such as that described in detail below.

Habit

All collections have extensive prostrate axes. Thalli with a general appearance similar to type material of *Conferva stricta* (Fig. 1) intergrade in all vegetative and reproductive features with specimens resembling the type material of *C. patens* and *C. urceolata*. Even thalli collected on kelp stipes, as were the types of *C. patens* and *C. urceolata*, show considerable variation, associated with season and age. Kelp epiphytes were relatively soft and flaccid when young, and their older axes became harsh and rigid with recurved branches. Thalli collected in different habitats varied considerably in overall size (2–25 cm), colour (bright orange-red to dull brown), texture (flaccid to rigid) and branching pattern (narrow elongate tufts with lateral branching to broad dichotomously branched thalli; lower axes sometimes bearing series of short reflexed branchlets). In view of the continuous variation in all characters examined, no distinction is made between the different forms of *P. stricta* in the following description of vegetative and reproductive features.

Vegetative anatomy

Erect axes are little-branched, ecorticate, with four pericentral cells, 50–300 μm in diameter, with segments one to five diameters in length. They develop from domed apical cells 9–10 μm wide (Fig. 2), which divide slightly obliquely. Pericentral cells are formed in alternating sequence. Branches develop at intervals of four to five segments (Fig. 2). Trichoblasts, when present (Fig. 3), are composed of uninucleate cells, attached by small scar cells, but they are often absent. Branching is pseudodichotomous to alternate, and corymbose at the tips (Fig. 2). Branches are initiated by exogenous division of the subapical cell (Fig. 2), not associated with the rare trichoblasts. Prostrate axes (Fig. 4) are much branched, giving rise endogenously to erect axes and further prostrate axes. Mature prostrate axes are 50–100 μm in diameter, with segments 0.5–1.5 diameters long, and lack trichoblasts. Rhizoids, 30–40 μm in diameter, develop



Figs 1–11. Vegetative and reproductive structures of *Polysiphonia stricta*. Fig. 1. Habit of thalli from shallow subtidal bedrock, Ballyhenry Is., Strangford Lough, N. Ireland, 23 November 1988, leg. CAM. Fig. 2. Vegetative apices showing large apical cells with oblique divisions; note corymbose branching. Falmouth marina, Cornwall, England, 7 March 1989, leg. CAM. Fig. 3. Trichoblasts, composed of uninucleate cells, attached by small scar cells (arrowheads). Lower-shore pools, Fanad Head, Co. Donegal, Ireland, 5 May 1989, leg. CAM. Fig. 4. Prostrate axis attached by unicellular rhizoids in open connection with pericentral cells. Lower-shore, on *Mastocarpus stellatus* in tidal rapids, Kylesku, Sutherland, Scotland, 13 October 1988, leg. CAM. Figs 5, 6. Developing and mature spermatangial branches with sterile tips. Collection details as Fig. 3. Fig. 7. Tips of female thallus with procarps and early post-fertilization cystocarps. Lower-shore rock pool, Dart, Devon, England, 12 May 1987, leg. A. E. Little. Fig. 8. Mature globose cystocarp, with extruded pyriform carposporangia.

from the middle of little-pigmented pericentral cells of prostrate axes and lower parts of erect axes, and remain in open connection with them (Fig. 4). Although the attachment disc is usually highly digitate, the rhizoid remains unicellular (Fig. 4). Paired rhizoids are sometimes formed by two different pericentral cells in the same segment.

Spermatangia

In a fertile axis, a deciduous, determinate spermatangial branchlet is produced by most of the segments towards the apex of the branch in a spiral arrangement (Figs 5, 12, 13), so that mature branchlets are clustered spirally at apices (Fig. 6). Spermatangial branchlets are polysiphonous, except for two proximal and two or more distal segments which are monosiphonous. The basal segment is isodiametric and always embedded in the axis, whereas the suprabasal segment protrudes obviously. Each segment of the spermatangial branchlet produces four pericentral cells. All the terminal cells derived from the pericentral cell become spermatangial mother cells, each of which forms two or three spermatangia. Mature spermatangial branchlets (Fig. 6) are 200–480 μm long and 60–130 μm wide, straight or slightly incurved, conical or cylindrical, and terminate in two to five isodiametric to elongate sterile cells. Trichoblasts were rarely present in male gametophytes, and when present spermatangial branchlets usually replaced them rather than being borne on them.

Procarps

The procarp of *Polysiphonia stricta* (Fig. 7) develops on the second segment of a trichoblast (Fig. 14). The fertile segment cuts off five pericentral cells (Fig. 15), the first being formed abaxially. The second pericentral cell is formed either to the left or to the right (with the axis seen in face view) of the first. The other pericentral cells form alternately. The last-formed pericentral cell, the fifth, lies directly on the adaxial surface of the fertile segment of the trichoblast and becomes the procarp initial (Fig. 15). The first division of the fertile pericentral cell is a longitudinal one cutting off the first sterile group initial to the side towards the fourth pericentral cell (Fig. 16). The first sterile group initial undergoes a transverse division to produce two sterile cells (Fig. 17). The second division of the fertile pericentral cell cuts off a larger cell, the carpogonial branch initial (Fig. 17), to the side towards the third pericentral cell. The carpogonial branch initial divides twice to produce the first three cells of the carpogonial branch (Figs 18, 19). The basal part of the supporting cell then cuts off the second sterile group initial. About this time the third cell of the carpogonial branch divides to produce the carpogonium, the fourth cell of the branch, which has an elongate trichogyne. The mature carpogonial branch is four-celled with a two-celled first sterile group and a one-celled second sterile group (Fig. 20).

Post-fertilization development

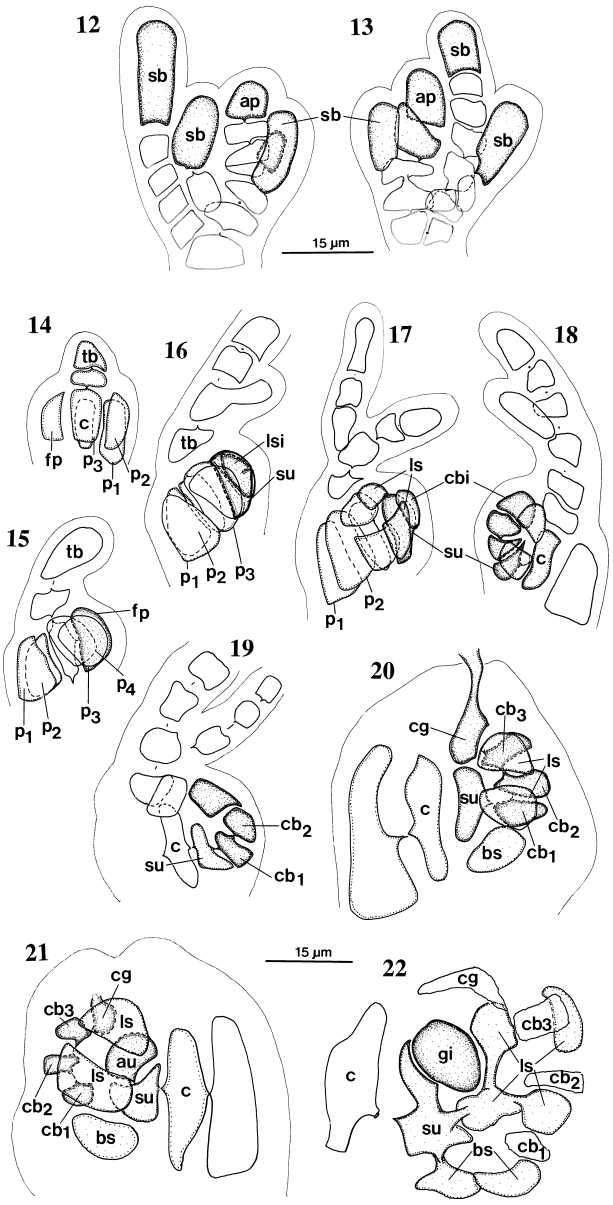
After putative fertilization, an auxiliary cell is formed from the supporting cell (Fig. 21). Each of the sterile cells of the procarp has divided once so that the first sterile group now consists of four cells and the second sterile group of two cells. There are no connecting cells linking the carpogonium and the auxiliary cell; instead an outgrowth from the carpogonium itself appears to grow towards the auxiliary cell and fuse with it. After putative diploidization of the auxiliary cell, the pit connection between the auxiliary and supporting cells begins to enlarge. The auxiliary cell cuts off a single primary gonimoblast cell (Fig. 22). The primary gonimoblast cell rapidly forms several secondary gonimoblast cells laterally. The pit connection between the auxiliary cell and supporting cell, and also the pit connections between the supporting cells and the sterile cell groups, continues to enlarge. Ultimately, a large fusion cell is formed that supports the gonimoblast filaments, the pit connections of which also widen so that the basal cells of the gonimoblast filaments become incorporated into the fusion cell (Fig. 22).

Mature cystocarps (Figs 8, 9) are borne on wide stalks, angled inwards so that they lie parallel to the axis, 300–700 μm high and 250–500 μm in diameter, and are usually distinctly urceolate, typically with a projecting ostiole. Considerable and apparently continuous variation in the shape of the pericarps was observed, some cystocarps being more or less globose (Fig. 8) while others have projecting ostioles of varying lengths up to 150 μm (Fig. 9). Carposporangia (Fig. 8) are clavate and 125–200 μm in length × 35–50 μm in diameter.

Tetrasporangia

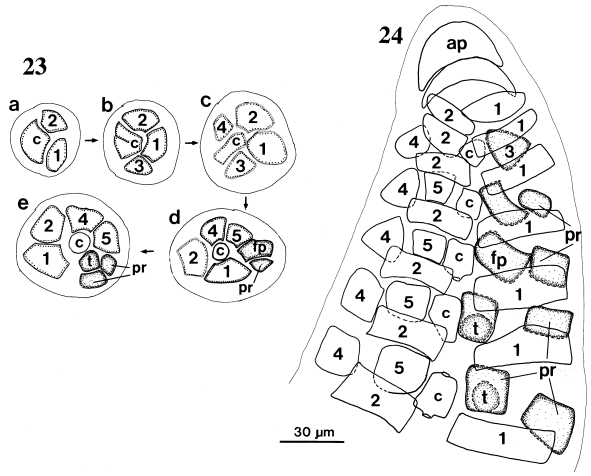
Tetrasporangia (Figs 10, 11) are borne in straight series of variable length in the last two to three orders of branching, fertile axes being shorter than vegetative ones. A single tetrasporangium is formed in each segment. In fertile axes five, rather than four, pericentral cells are formed in an alternating sequence and only the third pericentral cell becomes fertile (Figs 23, 24). The third pericentral cell is cut off clockwise or anticlockwise, in a non-random, possibly dorsiventral pattern, which might require nuclear staining to elucidate the orientation of successive divisions

Subtidal, Milford Haven, Pembroke, Wales, 18 July 1985, leg. A. E. Little. Fig. 9. Mature urceolate cystocarp. Collection details as Fig. 7. Fig. 10. Developing and mature tetrasporangia in long straight rows. Lower shore, wave-exposed rock pools, White Rocks, Co. Antrim, N. Ireland, 6 April 1989, leg. CAM. Fig. 11. Tetrasporangia (t), showing pit connections (arrowheads) between tetrasporangial stalk cells (s), central axial cells (a), and cover cells (c). Collection details as Fig. 3.



Figs 12–22. Male and female reproduction in *Polysiphonia stricta*. Figs 12, 13. Initial stage of formation of apical spermatangial branches; trichoblasts are absent. Figs 14–20. Development of procarp in *Polysiphonia stricta*. Figs 14, 15. Early stages of development of procarp-bearing segment showing formation of five pericentral cells. Figs 16–19. Stages following initiation of lateral sterile group (Figs 16, 17) and four-celled carpogonial branch (Figs 18, 19). Fig. 20. Mature four-celled carpogonial branch with basal sterile cell and two undivided sterile lateral cells. Fig. 21. Formation of the auxiliary cell after fertilization. Fig. 22. Gonimoblast initial formed; fusion taking place between auxiliary cell and supporting cell. All material from Hayling Island, England, February 1998, leg. R. L. Fletcher. Abbreviations: ap, apical cell; au, auxiliary cell; bs, basal sterile group; c, central axial cell; cb, carpogonial branch, with cell numbers; cbi, carpogonial branch initial; cg, carpogonium; fp, fertile pericentral cell; gi, gonimoblast initial; ls, lateral sterile group; lsi, lateral sterile initial; p, pre-sporangial cover cell, with cell numbers; sb, spermatangial branch; su, supporting cell; tb, trichoblast.

in pericentral cell formation prior to septation. Details of the sequence of cell formation are as follows: the first division of the fertile pericentral cell, which forms the



Figs 23, 24. Tetrasporangial development in *Polysiphonia stricta*. Fig. 23. Stages of development of tetrasporangia-bearing segments, not shown in sequential segments of a single axes. *a*, formation of pericentral cells 1 and 2; *b*, pericentral cell 3 (fertile pericentral cell) formed and pericentral cell 4 being formed; *c*, pericentral cell 4 cut off; *d*, pericentral cell 5 present and fertile pericentral has formed first pre-sporangial cover cell; *e*, both pre-sporangial cover cells and tetrasporangium formed (sporangial stalk cell lies under the tetrasporangium). Fig. 24. Squash of apex with developing tetrasporangia showing sequential formation of five pericentral cells. Pit connections are not visible due to squashing. The fertile pericentral cell divides obliquely to form the first pre-sporangial cover cell, then the second pre-sporangial cover cell is formed by a periclinal division; the tetrasporangial stalk cell has not yet been formed. Material from Hayling Island, England, February 1998, leg. R. L. Fletcher. Abbreviations: ap, apical cell; c, central axial cell; fp, fertile pericentral cell; pr, pre-sporangial cover cell; t, tetrasporangium.

first pre-sporangial cover cell, is oblique, towards the first pericentral cell of the segment; the second pre-sporangial cover cell is then formed by a periclinal division of the residual fertile pericentral cell (Figs 23, 24). The inner resultant cell then divides transversely to form the sporangial initial and a smaller stalk cell that remains pit-connected to the central cell of the segment (Fig. 11). The sporangium and cover cells become greatly enlarged and the axis expands to one side. Mature tetrasporangia (Fig. 10) are spherical, 50–150 μm in diameter, tetrahedrally divided, and covered by the two enlarged pre-sporangial cover cells.

In tetrasporangial thalli bearing trichoblasts, tetrasporangia sometimes appeared somewhat spiral in arrangement, because the row of sporangia changed position in the axis after formation of a trichoblast. However, a regular spiral was never observed.

Discussion

Polysiphonia is currently placed in the rhodomelacean subfamily Rhodomeloideae Hommersand (Maggs & Hommersand, 1993), within the tribe Polysiphonieae Schmitz (1889). Several characters, principally the details of female reproductive development, distinguish the Rhodomeloideae from the Bostrychioideae Hommersand (Hommersand, 1963; Maggs & Hommersand, 1993). As

far as these features are known for *Polysiphona stricta* (including *P. urceolata*), they generally accord with those of the subfamily Rhodomeloideae. However, the direct fusion of carpogonium with auxiliary cell in *P. stricta* reported here differs from Maggs & Hommersand's (1993) description of post-fertilization development in the Rhodomeloideae, which involves connecting cells. We acknowledge that nuclear staining would be required to confirm that direct fusion involves transfer of the diploid nucleus to the auxiliary cell.

Our observations on *P. stricta* also conflict to some extent with the present circumscription of the tribe Polysiphonieae. According to Hommersand (1963, pp. 340, 347), the Polysiphonieae, containing *Polysiphonia* and a large number of other genera, such as *Aphanocladia* Falkenberg, *Boergeseniella* and *Fernandosiphonia* Levring, is closely related to the Pterosiphonieae Falkenberg, containing *Pterosiphonia* and several other genera. The principal differences between the tribes, noted by Hommersand, were the absence of vegetative trichoblasts in the Pterosiphonieae and some details of branching. Vegetative trichoblasts have now been reported in *Pterosiphonia* (Uwai & Masuda, 1999), so the only difference between the tribes appears to lie in the branching pattern. In Polysiphonieae, the lateral-branch initials, including trichoblast initials, form on every segment and are arranged in a spiral. In Pterosiphonieae, by contrast, the segments that produce lateral-branch initials are separated by one or more naked internodal segments, and the branching is alternate-distichous (Hommersand, 1963). Hommersand (1963) acknowledged that the distinction between the two tribes was probably artificial, and the problems in circumscribing them are exemplified by the present position in synonymy with *Polysiphonia* in the Polysiphonieae of at least two genera, *Carradoriella* and *Vertebrata*, previously considered to be members of the Pterosiphonieae. Uwai & Masuda (1999) also noted that the only clear anatomical distinction between the Polysiphonieae and the Pterosiphonieae, the bilateral organization of non-trichoblastic laterals in the lattter, is compromised by the secondary bilaterality of several Polysiphonieae such as *Boergeseniella*. However, by contrast, Ardré (1970), showing that *Aphanocladia* exhibited characters seen in both *Polysiphonia* and *Pterosiphonia*, speculated that the Pterosiphonieae might be ancestral to the Polysiphonieae.

The following discussion will compare, firstly, the vegetative features and, secondly, the reproductive characters of *P. stricta* with those of other species of *Polysiphonia* and related genera. The branching pattern of *P. stricta* highlights the similarity between *Polysiphonia* and Pterosiphonieae. Growth is via a prominent apical cell that divides slightly obliquely. Branch initials are produced exogenously from the subapical cell at intervals of four or five segments in a dichotomous and alternating pattern rather than arising spirally, from each axial cell. *P. stricta* shows a pattern in which a pair of branches is borne on one side of the axis, then a pair on the other side, as seen in *Polysiphonia atlantica sensu* Kim & Lee (1996*b*). The pairs of branches are bilaterally arranged, even though the axis has a radial organization. Branches in the upper portion of the thallus all grow to the same level, resulting in a corymbose form, as in *P. atlantica sensu* Kim & Lee (1996*a*) and *P. subtilissima* (Womersley, 1979). The distinctive nature of the short branches seen in several species similar to *P. stricta* was commented on by Hommersand (1963). He noted their occurrence in *P. boergesenii* Baardseth and in the genus *Orcasia* (i.e. *P. senticulosa* and *P. morrowii*). *P. boergesenii* resembles *P. stricta* in many ways, and is likewise found on kelp stipes (Baardseth, 1941). The branching pattern of *P. stricta* and a small group of other *Polysiphonia* species thus differs markedly from that of the rest of the genus, in which branch initials form in a spiral sequence from every segment (Hommersand, 1963).

Hommersand (1963) noted that the formation of axes of limited growth appears to be correlated with the scarcity or absence of trichoblasts, which are formed regularly and abundantly in most species of *Polysiphonia* (Hommersand, 1963; Maggs & Hommersand, 1993). Absence of trichoblasts was considered to be an important character by Kylin (1956). It was one of the main features that led Kylin (1956) to resurrect *Vertebrata* for *P. lanosa* (as *P. fastigiata*), and he also mentioned scarcity of trichoblasts in the generic description of *Orcasia*. However, in *P. boergesenii* trichoblasts are abundant on main axes but absent on the short laterals (Baardseth, 1941), and in *P. stricta*, trichoblasts may be either absent (often) or present (Rosenvinge, 1923–4; Kylin, 1937; Maggs & Hommersand, 1993). Rosenvinge (1923–4) reported that trichoblasts in *P. stricta* (as *P. urceolata*) were formed only in autumn and winter and could still be present in July and August. They were always absent in the creeping branches. In the present study, trichoblasts were observed most frequently in spring.

A third feature correlated with the alternate-distichous branching pattern and scarcity of trichoblasts in *P. stricta* and similar species is the morphology of rhizoids. In *Polysiphonia*, rhizoid morphology has previously been considered to be an important taxonomic character at the species level (Hollenberg, 1968*a*; Yoon, 1986). Rhizoids are either cut off by cross-walls from pericentral cells or remain in open connection with them, as in *P. stricta*. Species with this type of rhizoid include *P. atlantica* (Maggs & Hommersand, 1993), *P. atlantica sensu* Kim & Lee (1996*a*), *P. abscissa* Hooker *et* Harvey (Womersley, 1979), *P. pacifica* Hollenberg (1942), *P. scopulorum* (Womersley, 1979), *P. subtilissima* (Womersley, 1979), *P. morrowii* (Kim *et al*., 1994) and the closely morphologically similar taxa *P. pungens* Hollenberg (1942) and *P. senticulosa* Harvey (Kudo & Masuda, 1988). These all have four pericentral cells and develop extensive prostrate axes but have sparse or absent trichoblasts. There are, however, other *Polysiphonia* species with open rhizoids, including *P. lanosa* (Rawlence & Taylor, 1970), *P. devoniensis* (Maggs & Hommersand, 1993) and *P. adamsiae* (Adams, 1991), which do not share the other vegetative

features of *P. stricta*. Although *P. lanosa* lacks trichoblasts, there is no prostrate system, and it has 12–24 pericentral cells. *P. devoniensis* and *P. adamsiae* both have extensive prostrate systems but differ from *P. stricta* in the formation of abundant trichoblasts and 10 pericentral cells, respectively.

With respect to the four vegetative morphological features discusssed above (branching pattern, scarce/absent trichoblasts, formation of non-septate rhizoids and presence of an extensive prostrate system) and the number of pericentral cells, *Polysiphonia stricta* groups with a few other Atlantic and Pacific *Polysiphonia* species. These include *P. abscissa*, *P. atlantica*, *P. atlantica sensu* Kim & Lee (1996*a*), *P. morrowii*, *P. pacifica*, *P. pungens*, *P. scopulorum*, *P. senticulosa* and *P. subtilissima*. The reproductive development of *P. stricta* also allies it with most of these species. Whereas spermatangial branches in *Polysiphonia* are normally produced from trichoblasts (Segi, 1951), typically borne adaxially at the first trichoblast dichotomy (Maggs & Hommersand, 1993), they are not subtended by trichoblasts in *P. stricta*, *P. atlantica* (Maggs & Hommersand, 1993), *P. atlantica sensu* Kim & Lee (1996*a*), *P. morrowii* (Kim *et al*., 1994), *P. scopulorum* or *P. subtilissima* (Womersley, 1979). *P. stricta* males resemble those of *Pterosiphonia parasitica* (Hudson) Falkenberg, in that there is a shift from the usual alternate-distichous vegetative branching to a spiral arrangement of spermatangial branches from every segment (Suneson, 1940). Although this type of spermatangial branch development is strikingly different from that of the majority of *Polysiphonia* species, the variation observed within some species, e.g. *P. fucoides* (Maggs & Hommersand, 1993), in which spermatangial axes can either replace trichoblasts, or form singly or in pairs at the first dichotomy, downgrades the importance of this character, which may nevertheless be significant at the species level in some groups. In *P. stricta* and related species, spermatangial branches terminate in sterile tips of two to five cells in *P. stricta*, four to six cells in *P. subtilissima*, five to eight cells in *P. morrowii* and one or two cells in *P. atlantica sensu* Kim & Lee (Womersley, 1979; Maggs & Hommersand, 1993; Kim *et al*., 1994). By contrast, authentic *P. atlantica*, which resembles these species in all major vegetative features, lacks sterile tips on spermatangial axes.

Our observations on procarp development in *P. stricta* are in accord with those on *P. urceolata* by Kylin (1937), who reported a four-celled carpogonial branch, a two-celled lateral sterile group and a one-celled basal sterile group, except that he apparently did not observe the final division of the sterile group cells. Procarp formation in *P. stricta*, including the development of four-celled carpogonial branches, is essentially identical to that in other genera of the Rhodomelaceae (Nam *et al*., 1994). Kim *et al*. (1994), Kim (1995) and Kim & Lee (1996*a*) likewise found four-celled carpogonial branches in *P. atlantica sensu* Kim & Lee and *P. morrowii* from Korea. However, they reported that four other Korean *Polysiphonia* species (*P. japonica* Harvey, *P. savatieri* Hariot, *P. yendoi* Segi and *P. harlandii* Harvey) have three-celled carpogonial branches. This finding was in accord with the reports of three-celled carpogonial branches in the related species *P. platycarpa* Boergesen from India (Iyengar & Balakrishnan, 1950) and *P. harveyi* Bailey from Atlantic North America (Hommersand & Fredericq, 1990). Broadwater & Scott (1982) found four-celled carpogonial branches in material identified as *P. harveyi*, but this may instead have been *P. fibrillosa* (Dillwyn) Sprengel, as these two species have often been confused (Maggs & Hommersand, 1993). Although carpogonial branch length has been documented in only a small proportion of *Polysiphonia* species, it appears that *P. stricta* and a group of similar species have typical rhodomelacean four-celled carpogonial branches, whereas *P. harveyi* and at least a few other species have three-celled branches.

Previous accounts of post-fertilization events in the genus *Polysiphonia* have also differed strikingly among investigators. Kylin (1923) reported that in *P. fucoides* (as *P. nigrescens*), direct fusion takes place between the carpogonium and the auxiliary cell. Broadwater & Scott's (1982) ultrastructural study of *Polysiphonia* sp. (as *P. harveyi*) also documented direct fusion. Iyengar & Balakrishnan (1949, 1950), by contrast, reported the existence of connecting cells in *P. platycarpa*. In *P. harveyi* Hommersand & Fredericq (1990) showed that two connecting cells were formed from the carpogonium; the auxiliary cell then expanded and fused with the connecting cells. Direct fusion between carpogonium and auxiliary cell has been demonstrated in *P. morrowii* and Korean '*P. atlantica*' (Kim *et al*., 1994; Kim & Lee, 1996*a*). We have now observed a similar type of fusion in *P. stricta*, although caution is required in its interpretation pending a study employing nuclear stains. *Polysiphonia* is thus confirmed to be heterogeneous in its post-fertilization development, exhibiting at least two patterns of development. The first of these, the direct fusion of carpogonium and auxiliary cell, has been observed in *P. stricta* and two related species: Korean '*P. atlantica*' and *P. morrowii*. It also occurs in *P. fucoides* (Kylin, 1923) and in *Boergeseniella fruticulosa* (as *P. fruticulosa*: de Valéra, 1938). The second type, in which connecting cells are formed by the fertilized carpogonium, has been documented only in *P. harveyi* and *P. platycarpa*.

The occurrence of five pericentral cells in fertile axes of *P. stricta* corresponds with the observations of Rosenvinge (1923–4, fig. 348C, D, as *P. urceolata*). Although Rosenvinge stated that there were six pericentral cells, he probably failed to distinguish between pericentral cells and cover cells (M. Hommersand, personal communication). The sequence of formation of the tetrasporangium and cover cells is of phylogenetic significance within the Ceramiales (Hommersand, 1963). In most of the Rhodomelaceae which have been investigated, the fertile pericentral cell initially cuts off two pre-sporangial cover cells which become large and rectangular. Next, the fertile pericentral cell divides transversely into a tetrasporangium and a stalk cell, and finally, after the formation of the

tetrasporangium, the stalk cell may cut off a small, triangular post-sporangial cover cell (Scagel, 1953, p. 12; Hommersand, 1963, pp. 277, 321). The third cover cell is absent in several genera including *Herposiphonia* and *Placophora* J. Agardh, and can be either present or absent in *Polysiphonia* (Maggs & Hommersand, 1993; Stegenga *et al*., 1997). In *P. atlantica sensu* Kim & Lee (1996*a*), *P. morrowii* (Kim *et al*., 1994; Stegenga, 1998) and our material of *P. stricta*, no post-sporangial cover cell was observed. However, Rosenvinge (1923–4) and Kylin (1937) both observed the occasional formation in *P. stricta* (as *P. urceolata*) of a small cell near the tetrasporangium. Rosenvinge did not comment on its formation. Kylin, referring to his own and Rosenvinge's observations, reported that this cell was cut off from the supporting cell of the sporangium and was therefore a third, post-sporangial cover cell. Rosenvinge noted that it was formed only when trichoblasts were present. However, in our material in which trichoblasts and tetrasporangia were formed in the same segments, no post-sporangial cover cell was ever observed. Either this feature can vary within *P. stricta*, or both Rosenvinge and Kylin based their observations on material of another species. The most likely candidate is *P. devoniensis*, but this has not been reported from Denmark or the west coast of Sweden although recently found in the Netherlands (Stegenga, 1998). Whether a post-sporangial cover cell is present can differ between otherwise similar species. As noted above, it is lacking in *P. atlantica sensu* Kim & Lee (1996a) and *P. morrowii* but present in *P. namibiensis* Stegenga & Engledow (Stegenga *et al*., 1997), which closely resembles *P. stricta* except that cystocarps are globose rather than urceolate. Studies on a larger number of species are required before the phylogenetic significance of this feature can be evaluated.

As noted by Falkenberg (1901) and Hommersand (1963), the arrangement of tetrasporangia differs according to whether trichoblasts are formed. In species with abundant trichoblasts, tetrasporangia develop from the second pericentral cell in a spiral arrangement (Kim, 1995; unpublished data). In *P. stricta* and other species usually lacking trichoblasts, such as Korean '*P. atlantica*' and *P. morrowii* (Kim *et al*., 1994; Kim & Lee, 1996*a*), the sporangia are seriate, being formed by the third pericentral cell. Detailed studies of tetrasporangial development have been made for relatively few other species as yet, but this generally seems to be true. Rosenvinge (1923–4) reported that in *P. urceolata* tetrasporangia were formed in a spiral arrangement when trichoblasts were present. In *P. boergesenii*, which lacks trichoblasts and otherwise closely resembles *P. stricta*, tetrasporangia are formed in straight rows (Baardseth, 1941).

In conclusion, we have shown that the type species of *Polysiphonia*, *P. stricta* (including *P. urceolata*), differs in several important respects from most members of the genus. *P. stricta* and a small group of other species including *P. abscissa*, *P. atlantica*, Korean '*P. atlantica*', *P. morrowii*, *P. pacifica*, *P. pungens*, *P. scopulorum*, *P. senticulosa* and *P. subtilissima*, all of which are ecorticate and have four pericentral cells, differ from all other *Polysiphonia* species in a suite of vegetative and reproductive characters. These features include the rarity or absence of trichoblasts, non-septate rhizoids, spermatangial branches not normally subtended by trichoblasts, and tetrasporangia formed in straight rows and lacking a post-sporangial cover cell. However, a few characters are variable amongst these species, such as the presence of sterile tips on spermatangial axes in all except *P. atlantica* and *P. scopulorum*. In addition, this group of species shares some, but not all, of these morphological features with a number of species such as *P. devoniensis*. Therefore, future revisions of *Polysiphonia*, based on *P. urceolata*, will require independent comparative evidence, such as DNA sequence data, to determine which of these features are relevant to generic circumscription.

Acknowledgements

We thank Dr R. L. Fletcher for providing material of this species. The first author would like to thank Professor I. K. Lee (Seoul National University, Korea) and Professor S. M. Boo (Chungnam National University, Korea) for support and encouragement. We are very grateful to Dr P. Silva for nomenclatural advice, to Prof. B. Womersley, and to Dr M. Hommersand and an anonymous reviewer for their contributions to the paper. This research was supported by a grant from The Korean Science and Engineering Foundation to M.-S.K. which is gratefully acknowledged.

References

Adams, N.M. (1991). The New Zealand species of *Polysiphonia* Greville (Rhodophyta). *New Zealand J. Bot*., **29**: 411–427.

Agardh, C.A. (1817). *Synopsis Algarum Scandinaviae* … Lund.

Agardh, J.G. (1863). *Species genera et ordines algarum* … **2** (3). Lund.

Aiton, W.T. (1812). *Hortus Kewensis*, 2nd edition, vol. 4. London.

Ardré, F. (1970). Observations sure le genre *Aphanocladia* Falkenberg (Rhodomélacées) et sur ses affinités. *Revue. Algol*., **1**: 37–54.

Baardseth, E. (1941). The marine algae of Tristan da Cunha. In *Results of the Norwegian Scientific Expedition to Tristan da Cunha* 1937–1938, no. 9. Oslo.

Batten, L. (1923). The genus *Polysiphonia* Grev., a critical revision of the British species, based upon anatomy. *J. Linn. Soc. Bot*., **46**: 271–311, pls. 22–25.

Bonnemaison, T. (1822). Essai d'une classification des hydrophites loculées, ou plantes marines articulées qui croissent en France. *J. Physique Chimie Hist. Nat. Arts*, **94**: 138–148, 174–203.

Bory de Saint-Vincent, J.B.G.M. (1823). Céramiaires. *Dictionnaire Classique d'Histoire Naturelle*, **3**: 339–341.

Broadwater, S.T. & Scott, J. (1982). Ultrastructure of early development in the female reproductive system of *Polysiphonia harveyi* Bailey. *J. Phycol*., **18**: 427–441.

De Valéra, M. (1938). On the anatomy and fruit-development of *Polysiphonia fruticulosa*. *K. Fysiogr. Sallsk. Lund Forh*., **8**: 145–152.

Dillwyn, L.W. (1802–9). *British Confervae*. W. Phillips, London. [1804, pls 39–44; 1809, pls 100–109, pls A-G]

Dixon, P.S. & Irvine, L.M. (1970). Miscellaneous notes on algal taxonomy and nomenclature: III. *Bot. Notiser*, **123**: 474–487.

Falkenberg, P. (1901). *Die Rhodomelaceen des Golfes von Neapel und der angrenzenden Meeresabschnitte*. R. Friedländer & Son, Berlin.

Gray, S.F. (1821). *A Natural Arrangement of British Plants*. 1. London.

Greuter, W., *et al*. (1994). *International Code of Botanical Nomenclature: Tokyo Code*. International Association for Plant Taxonomy, Berlin.

Greville, R.K. (1823). *Scottish Cryptogamic Flora* . . . , vol. 2(18): [i–iii], pl. 86–90. Edinburgh & London.

Greville, R.K. (1824). *Flora edinensis*. Edinburgh.

Hansen, G.I. (1997). A revised checklist and preliminary assessment of the macrobenthic marine algae and seagrasses of Oregon. In *Conservation and Management of Native Flora and Fungi* (Kaye, T.N., Liston, A., Love, R.M., Luoma, D.L., Meinke, R.J. & Wilson, M.V., editors), 175–200. Native Plant Society of Oregon, Corvallis.

Harvey, W.H. (1856). Algae, in Asa Gray, list of dried plants collected in Japan by S.W. Williams, Esq., and Dr. J. Morrow. *Mem. Am. Acad. Art Sci*., **2**: 331–332.

Hollenberg, G.J. (1942). An account of the species of *Polysiphonia* on the Pacific coast of North America. I. Oligosiphonia. *Am. J. Bot*., **29**: 772–785.

Hollenberg, G.J. (1967). New genera in the Rhodomelaceae from the central Pacific. *Bull. South. Calif. Acad. Sci*., **66**: 201–221.

Hollenberg, G.J. (1968*a*). An account of the species of *Polysiphonia* of the central and western tropical Pacific Ocean I. Oligosiphonia. *Pac. Sci*., 22: 56–98.

Hollenberg, G.J. (1968*b*). An account of the species of the red alga *Polysiphonia* of the central and western tropical Pacific Ocean II. Polysiphonia. *Pac. Sci*., **22**: 198–207.

Hommersand, M.H. (1963). The morphology and classification of some Ceramiaceae and Rhodomelaceae. *Univ. Calif. Publ. Bot*., **35**: 165–366.

Hommersand, M.H. & Fredericq, S. (1990). Sexual reproduction and cystocarp development. In *Biology of the Red Algae* (Cole, K.M. & Sheath, R.G., editors), 305–346. Cambridge University Press, Cambridge.

Iyengar, M.O.P. & Balakrishnan, M.S. (1949). Morphology and cytology of *Polysiphonia platycarpa* Boergs. Preliminary note. *Proc. Indian Acad. Sci*. B, **29**: 105–108.

Iyengar, M.O.P. & Balakrishnan, M.S. (1950). Morphology and cytology of *Polysiphonia platycarpa* Boergesen. *Proc. Indian Acad. Sci. B*, **31**: 135–161.

Kang, J.W. (1966). On the geographical distribution of marine algae in Korea. *Bull. Pusan Fish. Coll*. **7**: 1–125, pls. 1–12.

Kapraun, D.F. & Rueness, J. (1983). The genus *Polysiphonia* (Ceramiales, Rhodomelaceae) in Scandinavia. *Giorn. Bot. It*., **117**: 1–30.

Kim, M.S. (1995). A taxonomic revision of *Polysiphonia* (Rhodomelaceae, Rhodophyta) in Korea. PhD. thesis, Seoul National University.

Kim, M.S. & Lee, I.K. (1996*a*). Morphology and reproduction of *Polysiphonia atlantica* Kapraun *et* J. Norris (Rhodomelaceae, Rhodophyta). *J. Plant Biol*., **39**: 23–29.

Kim, M.S. & Lee, I.K. (1996*b*). Two species of *Polysiphonia*, *P. scopulorum* Harvey and *P. flaccidissima* Hollenberg (Rhodomelaceae, Rhodophyta), new to Korea. *Algae*, **11**: 141–148.

Kim, M.S. & Lee I.K. (1997). Morphology and reproduction of *Polysiphonia yendoi* Segi (Rhodomelaceae, Rhodophyta) in Korea. *Algae*, **12**: 73–81.

Kim, M.S., Lee, I.K. & Boo, S.M. (1994). Morphological studies of the red alga *Polysiphonia morrowii* Harvey on the Korean Coast. *Korean J. Phycol*., **9**: 185–192.

Kudo, T. & MAsuda, M. (1988). Taxonomic notes on *Polysiphonia senticulosa* Harvey and *P. pungens* Hollenberg (Ceramiales, Rhodophyta). *Jap. J. Phycol*. (*Sorui*), **36**: 138–142.

Kylin, H. (1923). Studien über die Entwicklungsgeschichte der Florideen. *K. Svensk Vetensk.-Akad. Handl*., **63**(11): 1–139.

Kylin, H. (1937). Über Anatomie und Fruchtentwicklung bei *Polysiphonia urceolata*. *Fysiogr. Sallsk. Forhandl*., **7**: 1–6.

Kylin, H. (1941) Californische Rhodophyceen. *Lunds Univ. Arsskr*., N.F., Avd. 2, **37**(2): 1–51.

Kylin, H. (1956). *Die Gattungen der Rhodophyceen*. CWK Gleerups Förlag, Lund.

Maggs, C.A. & Hommersand, M.H. (1993). *Seaweeds of the British Isles*, vol. 1, *Rhodophyta*, part 3A, *Ceramiales*. The Natural History Museum/HMSO, London.

McIvor, L., Maggs, C.A. & Stanhope, M.J. (1999). Molecular systematics of the red algal genus *Polysiphonia* Greville. *Phycologist*, **52**: 14.

Nam, K.W. & Saito, Y. (1991). *Laurencia similis* (Ceramiales, Rhodophyta), a new species from Queensland, Australia. *Br. Phycol. J*., **26**: 375–382.

Nam, K.W., Maggs, C.A. & Garbary, D.J. (1994). Resurrection of the genus *Osmundea* with an emendation of the generic delineation of *Laurencia* (Ceramiales, Rhodophyta). *Phycologia*, **33**: 384–395.

Norris, R.E. (1992). Ceramiales (Rhodophyceae) genera new to South Africa, including new species of *Womersleyella* and *Herposiphonia*. *S. Afr. J. Bot*., **58**: 65–76.

Rawlence, D.J. & TAaylor, A.R.A. (1970). The rhizoids of *Polysiphonia lanosa*. *Can. J. Bot*., **48**: 607–611.

Rosenvinge, L.K. (1923–4). The marine algae of Denmark. Contributions to their natural history. III. Rhodophyceae III (Ceramiales). *K. Danske Vidensk. Selsk. Skr*., **7**: 287–486.

Scagel, R.F. (1953). A morphological study of some dorsiventral Rhodomelaceae. *Univ. Calif. Publ. Bot*., **27**: 1–108.

Scagel, R.F., Gabrielson, P.W., Garbary, D.J., Golden, L, Hawkes, M.W., Lndstrom,. S.C., Oliveira, J.C. & Widdowson, T.B. (1989). *A Synopsis of the Benthic Marine Algae of British Columbia, Southeast Alaska, Washington and Oregon*. Phycological contribution no. 3. Department of Botany, University of British Columbia, Vancouver.

Schmitz, F. (1889). Systematische Ubersicht der bisher bekannten Gattungen der Floridеen. *Flora, Jena*, **72**: 435–456.

Schmitz, F. & Falkenberg, P. (1897). Rhodomelaceae. In *Die natürlichen Pflanzenfamilien* (Engler, A. & Prantl, K., editors), 1(2), 421–480. Leipzig.

Schneider, C.W. & Searles, R.B. (1991). *Seaweeds of the Southeastern United States, Cape Hatteras to Cape Canaveral*. Duke University Press, Durham, NC.

Segi, T. 1951. Systematic study of the genus *Polysiphonia* from Japan and its vicinity. *Rep. Fac. Fish. Mie Pref. Univ*., **1**: 169–272, pls. 1–16.

Sprengel, C. (1827). *Caroli Linnaei* . . . *Systema Vegetabilium* 4(1), 16th edition. Gottingen.

Silva, P.C. (1952). A review of nomenclatural conservation in the algae from the point of view of the type method. *Univ. Calif. Publ. Bot*., **25**: 241–324.

Silva, P.C., Basson, P.W. & Moe, R.L. (1996). Catalogue of the benthic marine algae of the Indian Ocean. *Univ. Calif. Publ. Bot*., **79**: 1–1259.

Stegenga, H. (1998). Nieuw gevestigde soorten van het geslacht *Polysiphonia* (Rhodophyta, Rhodomelaceae) in Zuidwest-Nederland. *Gorteria*, **24**: 149–156.

Stegenga, H., Bolton, J.J. & Anderson, R.J. (1997). *Seaweeds of the South African West Coast*. Bolus Herbarium publication no. 18. University of Cape Town.

Suneson, S. (1940). Studies on the structure and the reproduction of *Pterosiphonia parasitica*. *Svensk Bot. Tidskr*., **34**: 315–333.

Taylor, A.R.A. (1960). Variation in the genus *Polysiphonia* Greville. *Proc. Int. Seaweed Symp*., **5**: 209–216.

Taylor, A.R.A. (1962). The type species of *Polysiphonia* Greville. *Taxon*, **11**: 229.

Taylor, W.R. (1957). *Marine Algae of the Northeastern Coast of North America*, 2nd edition. University of Michigan Press, Ann Arbor.

Uwai, S. & Masuda, M. (1999). *Kintarosiphonia* (Rhodomelaceae, Ceramiales), a new red algal genus based on *Pterosiphonia fibrillosa* Okamura from Japan. *Phycologia*, **38**: 225–233.

Womersley, H.B.S. (1979). South Australian species of *Polysiphonia* Greville (Rhodophyta). *Aust. J. Bot*., **27**: 459–528.

Wynne, M.J. (1986). Report on a collection of benthic marine algae from the Namibian coast (southwestern Africa). *Nova Hedwigia*, **43**: 311–355.

Yoon, H.Y. 1986. A taxonomic study of genus *Polysiphonia* (Rhodophyta) from Korea. *Korean J. Phycol*., **1**: 3–86.