



Reproductive Morphology in Mediterranean *Seirospora giraudyi* (Ceramiales, Rhodophyta)

Conxi Rodríguez-Prieto¹ & Max H. Hommersand²

¹University of Girona, Faculty of Sciences, Department of Environmental Sciences, Campus de Montilivi, 17071 Girona, Spain

²Department of Biology, Coker Hall, University of North Carolina, Chapel Hill, North Carolina 27599-3280, USA

e-mail: conxi.rodriguez@udg.edu (corresponding author)

Manuscript received: 25.04.2011; Revised: 12.05.2011; Accepted: 25.05.2011

ABSTRACT

This paper presents a detailed description of the reproductive characters of Mediterranean *Seirospora giraudyi* based on fresh material collected in the northwestern coast of Spain. Vegetative cells are uninucleate. The plant is monoecious. Spermatangial parent cells are clustered on modified dwarf determinate filaments, usually situated on adaxial surfaces of branches. One to four spermatia are formed by elongation and proximal divisions of the spermatangial parent cells. Spermatium with a nucleus situated in a meiosis. The thallus is procarpic. The four-celled carpogonial branch is initially L-shaped, and it is situated on a periaxial supporting cell. When the carpogonial branch is either initiated or fully differentiated, a second periaxial cell forms on the opposite side of the fertile axial cell. The mature carpogonial branch is U-shaped and the supporting cell and second periaxial cell enlarge and divide transversely to produce a pair of uninucleate auxiliary cells. The nucleus in the fertilized carpogonium divides twice and the carpogonium cleaves vertically into two cells that, in turn, cut off a pair of uninucleate connecting cells that fuse with the auxiliary cells on opposite sides; the diploid nuclei in the connecting cells divide at the site of fusion and one of the nuclei enters the auxiliary cell while the other is extruded. Each auxiliary cell gives rise to a terminal primary gonimoblast cell containing the diploid nucleus and a narrow foot cell with two distal lobes. The haploid nucleus remains in the lower lobe of the foot cell and divides, whereas the extruded diploid nucleus resides next to the upper lobe of the foot cell. The two primary gonimoblasts elongate and divide transversely to form terminal gonimolobe initials, followed by several lateral gonimolobe initials. Gonimolobes form lax chains of carposporangia. As the gonimoblasts mature, both lobes of the foot cell which is situated on the supporting cell elongate, the upper one secondarily connecting with the supporting cell, and the lower one with the fertile axial cell. The gonimoblasts are subtended at maturity by one to several clusters of involucrel filaments. *Seirospora* is currently placed in the tribe Euptiloteae; however, the reproductive characters of *S. giraudyi* are identical to those described for the Callithamnieceae. Molecular studies are needed to confirm the taxonomic position of *S. giraudyi* as well as that of the other species placed in *Seirospora*.

Keywords : Callithamnieceae / Ceramiales / Euptiloteae / Nuclear behaviour / Reproduction / Taxonomy

(ABBREVIATIONS: ac1 = first auxiliary cell; ac2 = second auxiliary cell; c = carposporangia; c1 = first carpogonial branch cell; c2 = second carpogonial branch cell; c3 = third carpogonial branch cell; cc = connecting cell; cp = carpogonium; dcp = divided carpogonium; dn = diploid nucleus; edrn = extruded diploid residual nucleus; fac = fertile axial cell; fc = foot cell; gl = gonimolobe; gli = gonimolobe initial; hn = haploid nucleus; if = involucrel filament; n = nucleus; pg = primary gonimoblast cell; s = spermatium; sc = supporting cell; sdpc = second pericentral cell; sn = sperm nucleus; spc = spermatangial parent cell; t = trichogyne)

Thanks are due to Jordi, Pere, Toni, Andrés, Lali, Jordi II, Joan, and the other diving friends. We thank Dr Marc Verlaque, Technologique de Luminy, 13288, Marseille Cedex 9, France for his review, which has improved the quality of the article. This project was supported by two grants from the Spanish Ministry of Science and Technology (CGL2004-05556-C02-01 and CGL2008-00932).

INTRODUCTION

This study focuses on the male and female reproductive structures and early postfertilization events in Mediterranean *Seirospora giraudyi* (Kützinger) De Toni, and is based on fresh material collected in the northwestern coast of Spain. *Seirospora giraudyi* was first described by Kützinger (1849) as *Phlebothamnion giraudyi* Kützinger, and transferred to the genus *Seirospora* Harvey by De Toni (1903). *Seirospora*, together with *Euptilota* Kützinger and *Sciurothamnion* O. De Clerck *et al.* Kraft in O. De Clerck, Kraft & Coppejans, is currently recognized as a member of the Euptiloteae in the Callithamnioideae, Ceramiaceae (Hommersand *et al.* 2006). These three genera share several important reproductive characters in common with the Callithamnieae. All three form clusters of spermatangial branchlets on determinate axes; their carpogonial branch is four-celled and born on a periaxial cell that functions as the supporting cell; sterile groups on periaxial cells are absent; two auxiliary cells are typically cut off, one from the supporting cell that bears the carpogonial branch, and the other from a second periaxial cell born on the opposite side of the same axial cell; and finally, they produce tetrahedrally-divided tetrasporangia borne on cells of determinate branchlets (Feldmann-Mazoyer 1941, Kylin 1956, Wollaston & Womersley 1959, Hommersand 1963, Wollaston 1968, Dixon 1971, Maggs & Hommersand 1993, De Clerck *et al.* 2002, McIvor *et al.* 2002, Hommersand *et al.* 2004, 2006). On the other hand, Hommersand *et al.* (2006) separated the Euptiloteae from the Callithamnieae mainly on the basis that the carpogonium does not divide after fertilization in the former, but expands and forms a pair of tube-like protuberances directed toward the auxiliary cells that are cut off as connecting cells. In the Callithamnieae, in contrast, the fertilized carpogonium normally divides into two cells, each of which cuts off a small connecting cell that fuses with the auxiliary cells. Moreover the nucleus is terminal in the spermatangia of Euptiloteae whereas it is medial in spermatangia of the Callithamnieae (McIvor *et al.* 2002; Hommersand *et al.* 2004, 2006). Finally, the position of the carpogonial branch in relation to the vegetative filament in the fertile axial segment is different in the two tribes: directly below or on opposite sides in the Euptiloteae and at right angles to the vegetative cells in the Callithamnieae (Hommersand *et al.* 2006). *Sciurothamnion* is an exception to this rule (De Clerck *et al.* 2002).

Seirospora is presently represented by nine species distributed both in the Northern and Southern Hemispheres (Guiry & Guiry 2011). The morphology of the female reproductive structures and some postfertilization events have been described in detail in *S. interrupta* (Smith) F. Schmitz (Maggs & Hommersand 1993), *S. occidentalis* Børgesen (Itano 1977, Kraft 1988, Aponte & Ballantine

1991), *S. orientalis* Kraft (Kraft 1988), and *S. viridis* Aponte & D.L. Ballantine (Aponte & Ballantine 1995). Male, carposporophytic and tetrasporophytic stages have been described and illustrated previously in the Mediterranean species, *S. giraudyi* (Feldmann-Mazoyer 1941). Moreover, G. Feldmann-Mazoyer showed that the carpogonial branch is situated laterally above the intercalary vegetative cell, and that it is representative of the *Callithamnion corymbosum* type (Feldmann-Mazoyer 1941, Fig. 176 b); however, she did not describe the details of the early postfertilization events. In as much as the development of the male and female reproductive structures and particularly the organization of the carpogonial branch and its associated cells in the fertile axis before fertilization and the mechanisms by which derivatives of fertilized nuclei are transferred to the auxiliary cells are important taxonomically in Ceramiales (Hommersand *et al.* 2004), we investigate these characters in *S. giraudyi*.

MATERIALS AND METHODS

Specimens of *Seirospora giraudyi* were collected by SCUBA from the deep infralittoral and shallow circalittoral northwestern Mediterranean coasts of Spain. Material was observed in surface view and stained with a solution of hematoxylin according to the method of Rodríguez-Prieto & Hommersand (2009). Habit pictures were taken with a Canon EOS 350D (Canon, Tokyo, Japan) and photomicrographs were made with an AxioCam MRC attached to an Axioskop 2 plus microscope (Zeiss, Berlin, Germany). Herbarium abbreviations follow Thiers (2011, continuously updated) Index Herbariorum: <http://sweetgum.nybg.org/ih/>.

OBSERVATIONS

Seirospora giraudyi (Kützinger) De Toni 1903: 1349

Figs. 1A-1O, 2A-2O, 3A-3I, 4A-4D

BASYONIM — *Phlebothamnion giraudyi* Kützinger 1849: 656

TYPE LOCALITY — Ad oras gallicas leg. Giraudy (in coll. Lenormand) [France] (Kützinger 1849: 656).

DISTRIBUTION — Mediterranean (Guiry & Guiry 2011).

ILLUSTRATIONS — Feldmann-Mazoyer 1941, Figs. 175, 176.

MATERIAL STUDIED — Spain: Canons d'Aiguagelida, Palafrugell, -30 m, 29 May 2005, C. Rodríguez-Prieto, HGI-A 9931 male, female and tetrasporophyte. Formigues Islands, Palamós, -15 m, 30 June 2001, C. Rodríguez-Prieto HGI-A 6239 male, female and tetrasporophyte; -30 m, 30 May 2009, C. Rodríguez-Prieto, HGI-A 9256 male, female and tetrasporophyte; -35 m, 04 July 2010, C. Rodríguez-Prieto HGI-A 9244 male, female and tetrasporophyte. Món

de Fora, Palamós, -30 m, 22 May 2005, C. Rodríguez-Prieto HGI-A 9930 male and female.

HABITAT — Specimens occur in small aggregates, usually epiphytic on encrusting corallines, in deep infralittoral zones or in the shallow circalittoral.

DESCRIPTION — *Seirospora giraudyi* presents a rosy delicate uniseriate filamentous thallus, up to 6 cm high, fixed to the substratum by a rhizoidal discoid holdfast (Fig. 1A). Main axes and branches alternately or slightly irregularly branched in one plane, with branches arising from the distal ends of the axial cells (Figs. 1A-1C). Thallus progressively more corticated toward the base by rhizoidal filaments issuing from basal cells of lateral branches (Figs. 1D-1G). Axes can be up to 400 μm in diameter at the base of the thallus while distal cells taper to 7.5-10.0 μm , and occasionally terminate in hairs 4-5 μm in diameter and up to 170 μm in length (Fig. 1H, arrow). All vegetative cells uninucleate (Figs. 1B-1D, 1G), with a nucleus up to 4.0-8.4 μm in diameter in gametophytic cells and up to 5.9-8.7 μm in tetrasporophytic cells. Growth of an indeterminate axis maintained by transverse division of the apical cells but at times also by slightly oblique divisions (Figs. 1B, 1H).

The life cycle is triphasic with isomorphic gametophytes and tetrasporophytes. Plants are monoecious and postfertilization events have been observed in all the fertile specimens examined. Mixed gametophytic and tetrasporophytic phases often occur on the same thallus. Spermatangial parent cells arising from the distal end of axial cells (Figs 1I-1K), occasionally two per bearing cell (Fig. 1L), and clustered on modified dwarf determinate branches usually situated on the adaxial surface of the branches (Fig. 1I). Spermatangial cells uninucleate, with a nucleus 3.7-5.9 μm in diameter situated in a medial position (Figs 1J-1M). Spermatia formed by elongation (Fig. 1M, arrows) and proximal divisions of the spermatangial parent cells. One to four vacuolate spermatia are formed per bearing cell that are ovoid after release, 6.7-10.6 μm long \times 3.5-6.5 μm wide, with a terminal nucleus 2.3-4.3 μm in diameter, and a proximal vesicle (Figs 1N, 1O).

Female reproductive structures procarpic. Procarps solitary or in series formed near the apices on indeterminate axes. Fertile axial cells initiating a single periaxial cell that will function as the supporting cell of the carpogonial branch (hereafter supporting cell) (Fig. 2A). The supporting cell divides and gives rise first to a two-celled (Fig. 2B), and then a three-celled carpogonial branch whereupon the third cell forms a protuberance that will become the initial of the trichogyne (Fig. 2C). Mature carpogonial branch four-celled and L-shaped, with the first three cells horizontal and the carpogonium vertical (Figs 2D-2G). After presumed fertilization the carpogonium expands horizontally occupying the space between the supporting cell and the second periaxial cell (Figs 2D-2F). At the same time, the

nuclei in the third and second cells of the carpogonial branch, and sometimes that of first cell, divide, so that they contain two nuclei (Figs 2E-2G). Nuclei of the first three cells of the carpogonial branch are 3.3-7.0 μm in diameter, both in uninucleate and binucleate cells, and the nucleus of the unfertilized carpogonium is 2.8-4.8 μm in diameter (Figs 2A-2G). Aborted disintegrating carpogonial branches are commonly seen (Figs 2H, 2I). When the carpogonial branch is either initiated or fully differentiated, a second periaxial cell forms on the fertile axial cell opposite the supporting cell of the carpogonial branch (Fig. 2G). Unfertilized carpogonial branches are evanescent and soon disappear; however, the paired periaxial cells may persist and their presence indicates the former position of a procarp. Although, in general, a determinate branch may have several or even seriate fertile cells with paired periaxial cells, usually only one procarp develops a gonimoblast on an axis.

A spermatium was seen nearby or attached close to the tip of the trichogyne in every instance in which the trichogyne had elongated (Fig. 2J) or a sperm nucleus was observed inside the trichogyne (Fig. 2K). As suggested by Hommersand *et al.* (2006) in *Aristoptilon mooreanum* (Lindauer) Hommersand & W.A. Nelson, it is conceivable that trichogyne elongation takes place only in the presence of a compatible spermatium. After fertilization, the diploid nucleus of the carpogonium divides twice (Fig. 2L) and the carpogonium partly divides vertically (Fig. 2M). The fertilized carpogonial branch is displaced towards the supporting cell acquiring a U-shaped form (*sensu* Miranda 1934) (Fig. 2M). Meanwhile, the supporting cell and the second periaxial cell enlarge and divide transversely such that each cuts off a uninucleate auxiliary cell with nuclei 3.2-6.7 μm in diameter (hereafter called the first and second auxiliary cell) (Fig. 2N). Each of the two cells derived from the division of the carpogonium cuts off a small connecting cell, and in turn, each of these connecting cells fuses close to the base of one of the enlarging paired auxiliary cells (Figs 2O, 3A, 3B). Pit connections containing pit plugs were never formed in association with the connecting cells. Connecting cells are situated in the same plane as the fused carpogonial branch cells but in a different plane from the auxiliary cells, so that it is difficult to bring both structures into focus at the same time (Fig. 3B). Concurrently, the cells of the carpogonial branch fuse and fade, and then disappear (Fig. 3B, arrowhead).

The auxiliary cells grow becoming bell-shaped, and their haploid nuclei move to the external bases of the auxiliary cells (Fig. 3C). The diploid nuclei of the connecting cells divide at the surface of each auxiliary cell with one nucleus entering and moving towards its center and the other extruded to the base of the auxiliary cell (Fig. 3C). Each auxiliary cell then cuts off a terminal primary gonimoblast cell containing the diploid nucleus, and a flattened foot cell

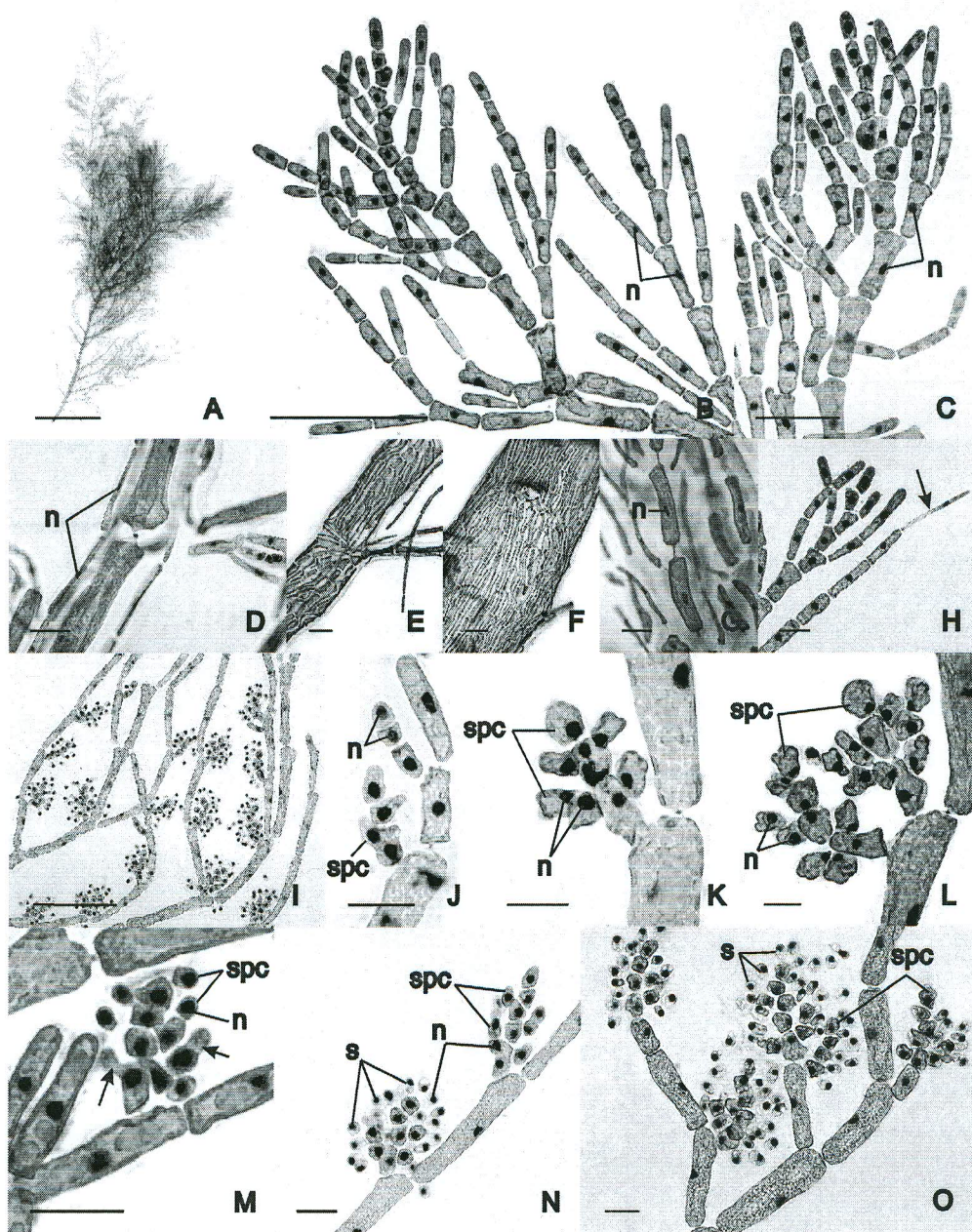


Fig. 1 — **A-O.** *Seirospora giraudyi*. Habit, vegetative structure and male reproductive structures. Figs B-O stained with hematoxylin. **A.** Habit (HGI-A 9256). **B-C.** Vegetative uniseriate filaments of uninucleate cells (HGI-A 9244). **D.** Detail of main axes near apex of thallus (HGI-A 6239). **E-F.** Heavily corticated main axes at middle and base of thallus (HGI-A 9256). **G.** Structure of the rhizoidal cortical filaments (Fig. 6239). **H.** Filament prolonged into a slender hair (arrow) (Fig. 9244). **I.** Spermatangial axes with several determinate spermatangial branchlets (HGI-A 9256). **J.** Uninucleate spermatangial branchlets developing adaxially (HGI-A 6239). **K.** Cluster of spermatangia developing singly at distal ends of spermatangial filaments. (HGI-A 9256). **L.** Occasional paired clusters of spermatangia per vegetative axial cell (HGI-A 9256). **M.** Uninucleate spermatangial parent cell (arrows) elongating to cut off a spermatium (HGI-A 9244). **N.** Young (upper) and mature (lower) spermatangial branchlets cutting of spermatia. Spermatia appearing ovate and vacuolate, each with a terminal nucleus and proximal vesicle (HGI-A 9256). **O.** Mature spermatangial branchlets with abundant terminal spermatangial parent cells giving rise to spermatia (HGI-A 9256). Abbreviations: n = nucleus, spc = spermatangial parent cell; s = spermatium. Scale bars: Fig. 1A = 1 cm; Figs 1B, 1C, 1E, 1F, 1I = 100 μ m. Figs 1D, 1G, 1H, 1J-1O = 20 μ m.

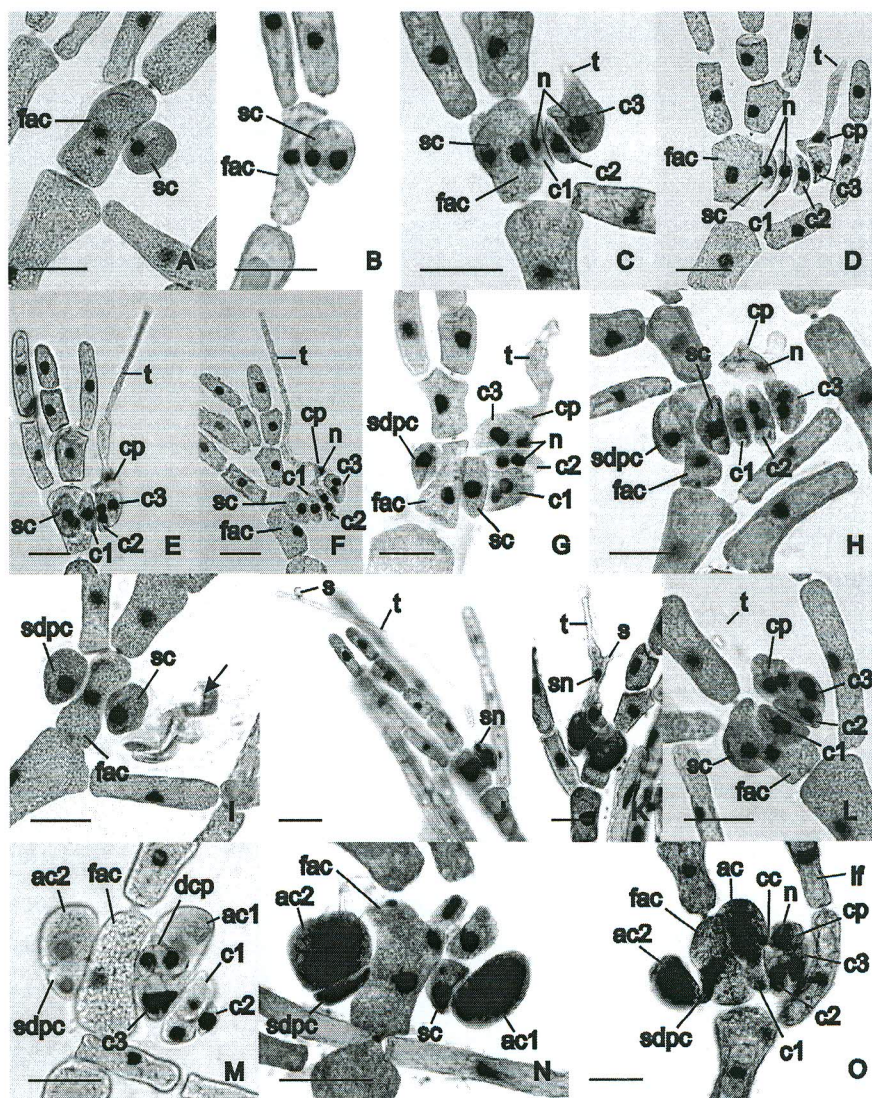


Fig. 2 — A-O. *Seirospora giraudyi*. Female reproductive structures and young postfertilization stages. Hematoxylin. **A.** Fertile axial cell bearing a single uninucleate periaxial cell (supporting cell) (HGI-A 9244). **B.** As above, with the supporting cell bearing a binucleate first cell of a carpogonial branch (HGI-A 6239). **C.** Three-celled carpogonial branch in which the third cell has initiated a trichogyne (HGI-A 9244). **D.** L-shaped four-celled carpogonial branch with the carpogonium bearing an extended trichogyne (HGI-A 6239). **E.** As in Fig. D but with a binucleate second cell of the carpogonial branch (HGI-A 6239). **F.** The same but with binucleate third and second cells of the carpogonial branch (HGI-A 6239). **G.** Procarp with a second periaxial cell developed on the fertile axial cell, and with binucleate first, second and third cells of the carpogonial branch (HGI-A 9244). **H.** Aborted carpogonial branch with the carpogonium disintegrating (HGI-A 9244). **I.** Disintegrating carpogonial branch (HGI-A 9244). **J.** Carpogonial branch with an attached spermatium and sperm nucleus inside the trichogyne (HGI-A 6239). **K.** Carpogonial branch with an empty spermatium attached to the trichogyne and a sperm nucleus just inside the carpogonium (HGI-A 9244). **L.** Carpogonial branch in which the nucleus of the carpogonium has divided (HGI-A 6239). **M.** U-shaped carpogonial branch in which the carpogonium has divided vertically and given rise to two derivative cells (HGI-A 6239). **N.** Paired auxiliary cells cut off from the supporting cell and the second periaxial cell (HGI-A 9931). **O.** Divided carpogonium which has produced a connecting cell that is in the process of fusing with the auxiliary cell. Note: an involucreal filament has originated from the cell beneath the fertile axial cell (HGI-A 9931). Abbreviations: ac1 = first auxiliary cell; ac2 = second auxiliary cell; c1 = first cell of the carpogonial branch; c2 = second cell of the carpogonial branch; c3 = third cell of the carpogonial branch; cc = connecting cell; cp = carpogonium; dcp = divided carpogonium; fac = fertile axial cell; if = involucreal filament; n = nucleus; s = spermatium; sc = supporting cell; sdpc = second periaxial cell; sn = sperm nucleus; t = trichogyne. Scale bars: Figs 2A-2O = 20 μ m.

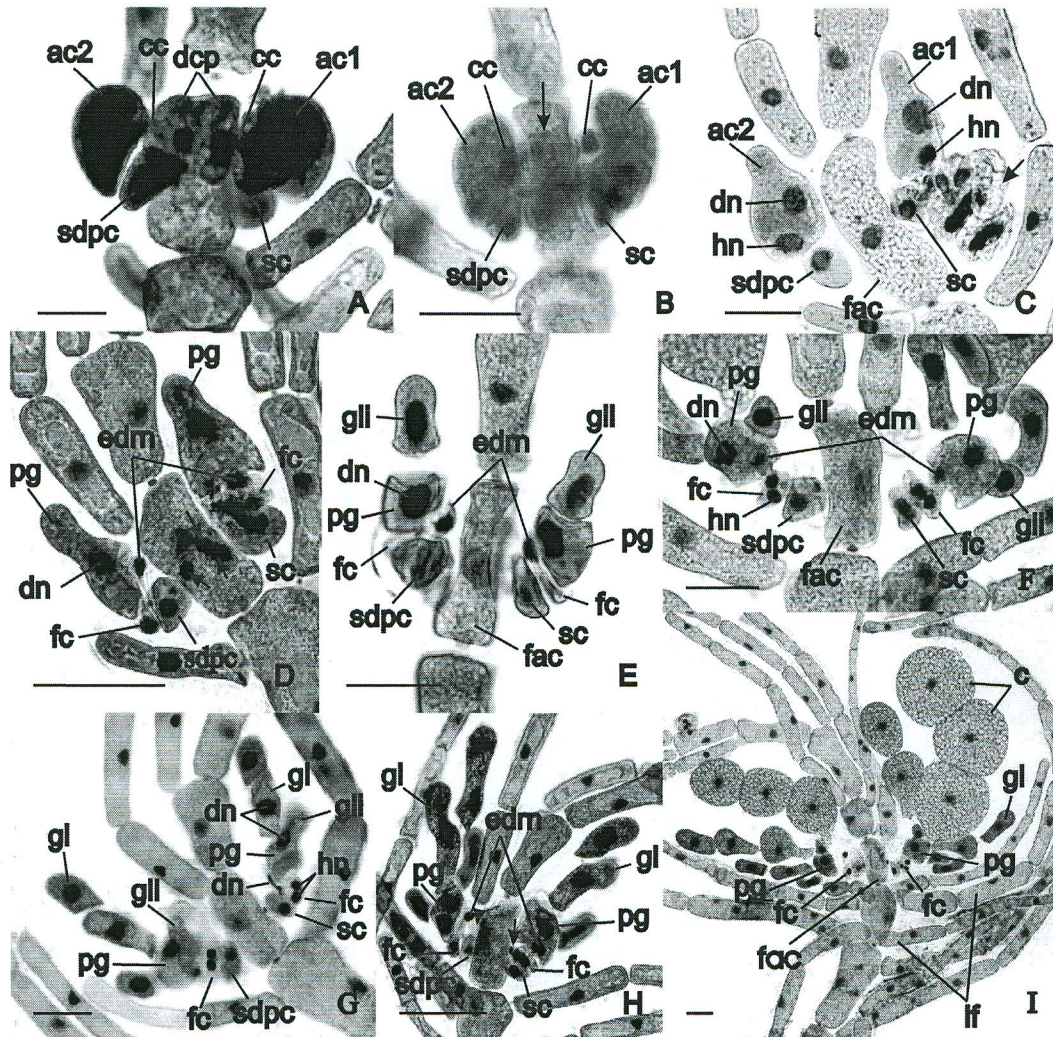


Fig. 3 — A-I. *Seirospora giraudyi*. Postfertilization stages and gonimoblast development. Hematoxylin. **A.** Divided carpogonium in which each derived cell contains a nucleus and has cut off a connecting cell that is fusing with the auxiliary cell on each side (HGI-A 9930). **B.** After diploidization of the auxiliary cells the remnant cells of the carpogonial branch cells fade and disintegrate (arrow). Connecting cells are still distinguishable. Auxiliary cells are out of focus (HGI-A 6239). **C.** Paired bell-shaped diploidized auxiliary cells that have elongated (HGI-A 6239). **D.** Bell-shaped primary gonimoblast cells elongating to give rise to the primary gonimolobe cell. The foot cell (fc) situated above the second periaxial cell is typically flattened with distal inflated lobes. The carpogonial branch nuclei are still intact (arrows) (HGI-A 9244). **E.** As in Fig. 3D, but with the primary gonimoblast cells already divided and showing a foot cell with an extruded diploid residual nucleus in its upper lobe (HGI-A 6239). **F.** As above, with the primary gonimoblast cell lobed and giving rise to several gonimolobe initials, and with both foot cells containing a large diploid residual nucleus in the upper lobe and two small haploid nuclei in the lower lobe (HGI-A 6239). **G.** As above, but with the foot cell situated above the supporting cell secondarily fused onto the supporting cell (HGI-A 9244). **H.** Young carposporophyte in which the upper lobe of the foot cell situated above the supporting cell has elongated and fused secondarily to the supporting cell, and the lower lobe has fused secondarily with the fertile axial cell (arrow). In turn, the upper lobe of the foot cell over the second periaxial cell is still fused with the faded carpogonial branch (arrowhead) (HGI-A 9244). **I.** Mature gonimoblasts with gonimolobes at different stages of development, some of them showing files of carposporangia, and involucrel filaments arising from the cell situated below the fertile axial cell and the one beneath it (HGI-A 9244). Abbreviations: ac1 = first auxiliary cell; ac2 = second auxiliary cell; c = carposporangia; cc = connecting cell; dcp = divided carpogonium; dn = diploid nucleus; edm = extruded diploid residual nucleus; fac = fertile axial cell; fc = foot cell; gl = gonimolobe; gll = gonimolobe initial; hn = haploid nucleus; lf = involucrel filament; n = nucleus; pg = primary gonimoblast cell; sc = supporting cell; sdpc = second periaxial cell. Scale bars: Figs 3A-3I = 20 μ m.

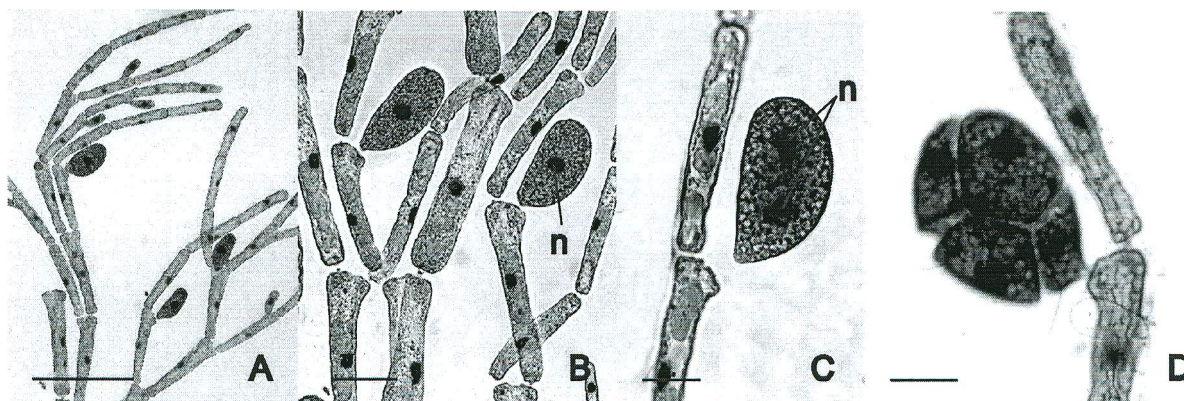


Fig. 4—A-D. *Seirospora giraudyi*. Tetrasporangia. Hematoxylin. **A.** Sessile tetrasporangial primordia attached to the adaxial surface of determinate axes (HGI-A 9256). **B.** Detail of a uninucleate tetrasporangial primordium (HGI-A 6239). **C.** Tetrasporangial primordium in which the nucleus has undergone the first division (HGI-A 6239). **D.** Mature tetrahedrally divided tetrasporangium (HGI-A 9931). Abbreviation: n = nucleus. Scale bars: Fig. 4A = 100 μ m; Figs 4B–4D = 20 μ m.

with two conspicuous distal lobes (Figs 3D–3F), the upper lobe containing the diploid extruded nucleus remaining after the division of the connecting cell, 4.0–5.3 μ m in diameter, and the lower one containing the original haploid nucleus of the auxiliary cell which typically divides with the derived nuclei being 3.1–4.8 μ m in diameter (Fig. 3F).

The two foot cells follow different postfertilization patterns. The upper lobe of the cell situated above the supporting cell elongates and also fuses secondarily with the supporting cell (Fig. 3G). In addition, the lower lobe of this fusion cell, which contains two nuclei, connects secondarily with the fertile axial cell in a proximal position (Fig. 3H, arrow). Pit plugs were never formed in association with these secondary connections. Subsequently the upper lobe of the foot cell situated over the second periaxial cell occasionally appears fused with the faded carpogonial branch in a distal position, just over the connection between the second periaxial cell and the fertile axial cell (Fig. 3H, arrowhead).

Finally, the primary gonimoblast cells elongate, often becoming bell-shaped (Fig. 3D), and first give rise to a terminal gonimolobe initial (Fig. 3E). Subsequently the primary gonimoblast cells become irregular in shape and cut off several lateral gonimolobe initials (Figs 3F–3I) which develop gonimolobes composed of chains of carposporangia (Fig. 3I). The primary gonimoblast cells contain large diploid nuclei 6.2–8.7 μ m in diameter (Figs 3D–3I). Carposporangia develop simultaneously in any given gonimolobe but the carposporangia mature at different rates in separate gonimolobes (Fig. 3I). Cells of the immature gonimolobes bear nuclei 4.3–6.0 μ m in diameter (Figs 3G–3I). Mature carposporangia are ovoid and 40–65 μ m in

diameter with nuclei 4.8–6.1 μ m in diameter (Fig. 3I). At maturity the gonimoblasts contain several gonimolobes inside a common outer envelope, and are laxly subtended by one (Figs 3C, 3D, 3G, 3H) or two (Fig. 3I) clusters of involucral filaments that arise after fertilization from the cell situated immediately below the fertile axial cell and, at maturity, the one below it (Fig. 3I).

Tetrasporangia are sessile, borne adaxially on determinate branches (Fig. 4A). Young primordia have large nuclei 7.1–9.9 μ m in diameter (Fig. 4B) that divide (Fig. 4C) and give rise to tetrahedrally arranged tetrasporangia 60–80 μ m in length, with nuclei 5.2–7.6 μ m in diameter (Fig. 4D). Bisporangia and seirosporangia were not observed.

DISCUSSION

Our results demonstrate that *Seirospora giraudyi* possesses two reproductive features that are characteristic of the Callithamnidae and Euptiloteae among the Ceramiales: the carpogonium expands and auxiliary cells are cut off from the supporting cell and opposite periaxial cell, and the diploid nucleus undergoes two divisions and ultimately cuts off a pair of connecting cells that fuse with the auxiliary cells. No other tribes in the Ceramiales undergo these processes in exactly the same way (Hommersand *et al.* 2006). Although *Seirospora* was assigned to the Euptiloteae based on molecular evidence (Hommersand *et al.* 2006), *S. giraudyi* stands closer to the Callithamnidae based on its morphological and reproductive features. These distinguishing characters have been described previously in *Callithamnion corymbosum* (Smith) Lyngbye (Oltmanns

1898), *Aglaothamnion cordatum* (Børgesen) Feldmann-Mazoyer (O'Kelly & Baca 1984, as *Callithamnion caudatum*), and *Aglaothamnion halliae* (F.S. Collins) N.E. Aponte, D.L. Ballantine & J.N. Norris (Hommersand 1997) including the medial position of the nucleus in spermatangial cells and a fertilized carpogonium that divides into two cells, each of which cuts off a small connecting cell that fuses with one of the paired auxiliary cells (Hommersand *et al.* 2004, 2006).

S. giraudyi differs from the other species placed in the Euptiloteae for which early postfertilization stages are well documented: *Euptilota fergusonii* A.D. Cotton, *E. formosissima* (Montagne) Kützinger and *E. molle* (Wollaston) O. De Clerck (Hommersand *et al.* 2004), and *Sciurothamnion stegengae* O. De Clerck & Kraft (DeClerck *et al.* 2002) in which the carpogonium does not divide after fertilization but forms a pair of tube-like protuberances that are cut off as connecting cells directed toward the auxiliary cells. They also bear spermatangia with terminal nuclei (De Clerck *et al.* 2002; Hommersand *et al.* 2004).

In other species of *Seirospora* in which postfertilization events have been described, namely, *S. interrupta* (Maggs & Hommersand 1993), *S. occidentalis* (Itono 1977; Kraft 1988; Aponte & Ballantine 1991), *S. orientalis* (Kraft 1988), and *S. viridis* (Aponte & Ballantine 1995), division of the fertilized carpogonium has not been described. In our opinion early postfertilization events and the transfer of diploid nuclei from the carpogonium to the auxiliary cells needs to be reinvestigated in *Seirospora*, since *S. giraudyi* shares a carposporophyte structure in which the gonimoblasts form carposporangia in chains rather than in tightly branched clusters as is typical of *Callithamnion* and *Aglaothamnion*. (Feldmann-Mazoyer 1941; Dixon 1971; Kylin 1956; Kraft 1988; Maggs & Hommersand 1993; Womersley & Wollaston 1998). Indeed, Feldmann-Mazoyer (1941) insisted in that the genus *Aglaothamnion* has spherical and lobed gonimoblasts. The present work may be sufficiently detailed to permit new comparisons to be made between species and genera placed either in the Callithamnieae or the Euptiloteae.

The behaviour of mature foot cells described here is new both for the Callithamnieae and the Euptiloteae. In the foot cells that lie above the supporting cells, the upper lobes elongate and secondarily connect with the supporting cells, and the lower lobes, each of which contains two nuclei, secondarily connect with the fertile axial cell. Pit plugs have not been seen in any of these connections.

LITERATURE CITED

- Aponte NE & Ballantine DL 1991 The life history in culture of *Seirospora occidentalis* (Ceramiaceae, Rhodophyta) from the Caribbean, *Crypt. Bot.* **2** 261-268
- Aponte NE & Ballantine DL 1995 *Aglaothamnion flexibile* sp. nov. and *Seirospora viridis* sp. nov. (Ceramiaceae, Rhodophyta) from Puerto Rico, *Phycologia* **34** 102-112
- De Clerck O Kraft GT & Coppejans E 2002 Morphology and systematics of *Sciurothamnion stegengae* gen. et sp. nov. (Ceramiaceae, Rhodophyta) from the Indo-Pacific, *J. Phycol* **38** 1176-1189
- De Toni GB 1903 *Sylloge algarum omnium hucusque cognitarum. Vol. IV. Florideae. Sectio III* (Sumptibus auctoris: Patavii [Padua], Italy)
- Dixon PS 1971 Studies of the genus *Seirospora*, *Botaniste* **54** 35-48
- Feldmann-Mazoyer G 1941 ['1940'] *Recherches sur les Céramiacées de la Méditerranée occidentale* (Minerva: Alger, Algeria)
- Guiry MD & Guiry GM 2011 *AlgaeBase. World-wide electronic publication, National University of Ireland, Galway*, <http://www.algaebase.org>; searched on 29 February 2011
- Hommersand MH 1963 The morphology and classification of some Ceramiaceae and Rhodomelaceae, *Univ Calif Publ Bot* **35** vii+165-366
- Hommersand MH 1997 Postfertilization development and the nature of the connecting cell in *Aglaothamnion halliae* (Callithamnieae, Ceramiales), *Crypt Algol* **18** 263-271
- Hommersand MH De Clerck O & Coppejans E 2004 A morphological study and taxonomic revision of *Euptilota* (Ceramiaceae, Rhodophyta) from South Africa, *Eur J Phycol* **39** 369-394
- Hommersand MH, Freshwater DW, Lopez-Bautista JM & Fredericq S 2006 Proposal of the Euptiloteae Hommersand et Fredericq, trib. nov. and transfer of some southern hemisphere Ptiloteae to the Callithamnieae (Ceramiaceae, Rhodophyta), *J Phycol* **42**: 203-225
- Itono H 1977 Studies on the ceramiaceous algae (Rhodophyta) from southern parts of Japan, *Bibl Phycol* **35** 1-499
- Kraft GT 1988. *Seirospora orientalis* (Callithamnieae, Ceramiales), a new red algal species from the southern Great Barrier Reef, *Jpn J Phycol (Sôru)* **36** 1-11
- Kützinger FT 1849 *Species algarum* [FA Brockhaus: Lipsiae (Leipzig), Germany]
- Kylin H 1956 Die Gattungen der Rhodophyceen (CWK Gleerups Förlag: Lund, Sweden)
- Maggs CA & Hommersand MH 1993 Seaweeds of the British Isles. Volume 1. Rhodophyta. Part 3A. Ceramiales (HMSO: London, UK)
- McIvor L Maggs CA & Stanhope MJ 2002 *RbcL* sequences indicate a single evolutionary origin of multinucleate cells in the red algal tribe Callithamnieae, *Mol Phylog Evol* **23** 433-446

- Miranda F 1934. Materiales para una flora marina de las rías bajas gallegas, *Bol R Soc Esp Hist Nat* **34** 165-180
- O'Kelly CJ & Baca BJ 1984 The time course of carpogonial branch and carposporophyte development in *Callithamnion cordatum* (Rhodophyta, Ceramiales), *Phycologia* **23** 404-417
- Oltmanns F 1898 Zur Entwicklungsgeschichte der Florideen, *Bot Zeit* **56** 99-140
- Rodríguez-Prieto C & Hommersand MH 2009 Behaviour of the nuclei in pre- and post-fertilization stages in *Kallymenia* (Kallymeniaceae, Rhodophyta), *Phycologia* **48** 138-155
- Thiers B 2011 (continuously updated) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium, <http://sweetgum.nybg.org/ih/>
- Wollaston EM 1968 Morphology and taxonomy of Southern Australian genera of Crouanieae Schmitz (Ceramiales, Rhodophyta), *Aust J Bot* **16**: 217-417
- Wollaston EM & Womersley HBS 1959 The structure and reproduction of *Gulsonia annulata* Harvey (Rhodophyta), *Pac Sci* **13**: 55-62
- Womersley, H.B.S. & Wollaston E.M. 1998. Tribe Callithamnieae, In Womersley HBS *The marine benthic flora of southern Australia - Part IIIC. Ceramiales - Ceramiales, Dasyaceae*, pp 231-269 (Australian Biological Resources Study & State Herbarium of South Australia : Canberra & Adelaide, Australia)