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Vegetative and reproductive morphology of *Gloiocladia repens* (C. Agardh) Sánchez et Rodríguez-Prieto comb. nov. (Rhodymeniales, Rhodophyta), with a taxonomic re-assessment of the genera *Fauchea* and *Gloiocladia*

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A morphological and molecular study of *Fauchea repens*, the type species of *Fauchea*, (Faucheaceae, Rhodymeniales) and its comparison with *Gloiocladia furcata*, the type species of *Gloiocladia*, establishes that the two are closely related and belong in the same genus. Accordingly, we propose a new combination, *Gloiocladia repens* (C. Agardh) Sánchez et Rodríguez-Prieto, comb. nov., for the plant presently known as *Fauchea repens* (C. Agardh) Montagne et Bory *in* Montagne and designate a lectotype. We provide an emended description of the genus *Gloiocladia*, and transfer all the species presently placed in *Fauchea* to *Gloiocladia*.

Key words: 18S rDNA, *Gloiocladia*, Faucheaceae, *Gloiocladia furcata*, *Gloiocladia repens*, reproduction, Rhodymeniales, Rhodophyta, taxonomy

Introduction

The red algal family Faucheaceae Strachan, Saunders & Kraft is currently placed in the Rhodymeniales (Rhodophyta) (Saunders *et al*., 1999). The genus *Fauchea* Montagne et Bory (in Montagne, 1846: 64) includes 13 species, widely distributed in tropical, subtropical and temperate seas (Bornet, 1890; Weber-van Bosse, 1928; Baardseth, 1941; Segawa, 1941; Yamada, 1941; Børgesen, 1944; Taylor, 1945, 1960; Sparling, 1957; Norris & Aken, 1985; Xia & Zhang, 1999), of which *F. repens* (C. Agardh) Montagne et Bory (in Montagne, 1846) is the type species. Generic delineation of the genus *Fauchea* has been based primarily on vegetative characters, presence of a *tela arachnoidea* (network of erect persistent filaments surrounding the procarp and the gonimoblast and developing from a basal nutritive tissue) in the cystocarp, cystocarp position and morphology, and by the arrangement and division pattern of the tetrasporangia (Montagne, 1846; Kylin, 1931; Irvine & Guiry, 1980; Norris, 1991). The absence of detailed information on the reproductive structures in the type species has prevented the realization of a clear concept of *Fauchea* and its relationship with *Gloiocladia* J. Agardh (Irvine & Guiry, 1980; Norris, 1991). Based on sequence analyses, Saunders *et al*. (1999) included both genera in the family Faucheaceae, together with *Gloioderma fructiculosa* (Harvey) J. Agardh reported as *Gloiocladia fruticulosa* (Harvey) R.E. Norris.

This paper presents a detailed description of *F. repens* (as *Gloiocladia repens* (C. Agardh) Sánchez et Rodríguez-Prieto comb. nov.) based on fresh material collected during a study of the Faucheaceae of the Iberian Peninsula (Sánchez, 2005), along with a reinvestigation of original material housed in the Agardh Herbarium at Lund (LD) and material from other herbarium collections. We report new morphological data relating to vegetative and reproductive characters of *G. repens*, and have selected a lectotype for this species and reinvestigated the generic boundaries between *Fauchea* and *Gloiocladia*. We also generated 18S rRNA gene sequences from specimens of *G. repens* and *G. furcata* (C. Agardh) J. Agardh, and compared them with sequences from other Faucheaceae available in GenBank. Taxonomic changes include: a re-assessment of the genus *Gloiocladia* and transfer of *Fauchea* species to

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Gloiocladia, and further support for the reinstatement of the genus *Gloioderma*.

Materials and methods

Morphological analyses

Herbarium acronyms follow Holmgren *et al.* (1990). Specimens of *G. repens* were collected by SCUBA from the Mediterranean coasts of Spain. Preserved specimens from the original collection of C. Agardh housed at LD, and others from HGI, MA, MGC, SANT, VAL and the personal herbarium of J.J. Rodríguez y Femenías, located in the Ateneu of Maó, Minorca (Spain), were also examined. Sections were made with a razor blade or a freezing microtome, stained with acidified aqueous 1% aniline-blue and mounted in 50% Karo(r) corn syrup (Bestfoods, Englewood Cliffs, NJ, USA). Habit photographs were taken with a Pentax Program camera (Pentax, Golden, CO, USA). Photomicrographs were taken with a Spot Insight digital camera (Diagnostic Instruments, Sterling Heights, MI, USA) attached to an Axioskop 2 plus microscope (Zeiss, Berlin, Germany). Voucher specimens and slides were deposited in the Herbarium of the University of Girona, Spain (HGI).

Molecular analyses

Total genomic DNA was extracted from specimens of *G. repens* from Columbretes Islands, Spain and of *G. furcata* from Formigues Islands, Spain (desiccated in silica gel or in 95% ethanol) following Hughey *et al.* (2001), with a final cleaning step using the Gene Clean II kit (Bio 101, Vista, CA, USA). The nuclear-encoded 18S ribosomal RNA gene was amplified and sequenced as described in Freshwater *et al.* (2005) using the oligonucleotide primers published by Saunders & Kraft (1994). Sequencing reactions were run on an ABI 3100 Genetic Analyzer (DNA Analysis Core Facility, Centre for Marine Science, UNCW) and the reaction results edited and sequence contigs created using Sequencher (Gene Codes Corp., Ann Arbor, MI, USA). The resulting sequences have been deposited in GenBank under the accession numbers DQ790749 and DQ790750.

An 18S rDNA alignment including the two newly generated sequences, seven Faucheaceae sequences available in GenBank and a *Lomentaria baileyana* (Harvey) Farlow sequence as the outgroup, was assembled using MacClade (v. 4, Maddison & Maddison, 2000). *Lomentaria baileyana* was chosen as the outgroup for a number of reasons: (i) The Lomentariaceae and Faucheaceae are sibling groups in all published SSU analyses (Saunders *et al.*, 1999; Freshwater *et al.*, 2005); (ii) the topological arrangement of species within the Faucheaceae is basically the same in all published SSU trees and our unpublished analyses including 49 non-Faucheaceae Rhodymeniales whether or not *L. baileyana* is the only outgroup; (iii) various permutations of non-Faucheaceae species as outgroups did not change the basic Faucheaceae topology; and (iv) uncertain homology among sites was small when *L. baileyana* was the only outgroup included in the alignment. GenBank accession numbers for previously published sequences are shown under the relevant species names in Fig. 38. Alignment of these sequences was straightforward and performed by eye. Sites from the 5′ and 3′ ends of the alignment were removed due to missing data, so that the final alignment included 1,676 sites. Two internal regions of the alignment totalling 10 sites were excluded from analyses because the homology of these sites was uncertain. Data set characteristics and rate models were determined using MacClade, Modeltest (Posada & Crandall, 1998) and PAUP (Swofford, 2002). The aligned sequence data set and model parameters are available from the second author (DWF). Phylogenetic analyses using maximum likelihood (ML), maximum parsimony, and distance algorithms were performed using PAUP. ML searches were performed using the Branch-and-Bound algorithm and evolutionary model derived with Modeltest. ML bootstrap analyses consisted of 463 replications of Branch-and-Bound searches with the Modeltest model. Distance analyses consisted of neighbor-joining (NJ) tree building, using distances corrected with the same model used in the ML analyses. NJ bootstrap analyses were based on 5,000 replications of NJ tree building with the same distance correction. Parsimony searches were performed using the Branch-and-Bound algorithm and parsimony bootstrap analyses consisted of 2,000 replications of Branch-and-Bound searches.

Observations

Gloiocladia repens (C. Agardh) Sánchez et Rodríguez-Prieto comb. nov. (Figs 1–36)

BASIONYM: *Sphaerococcus repens* C. Agardh, 1823: 244.

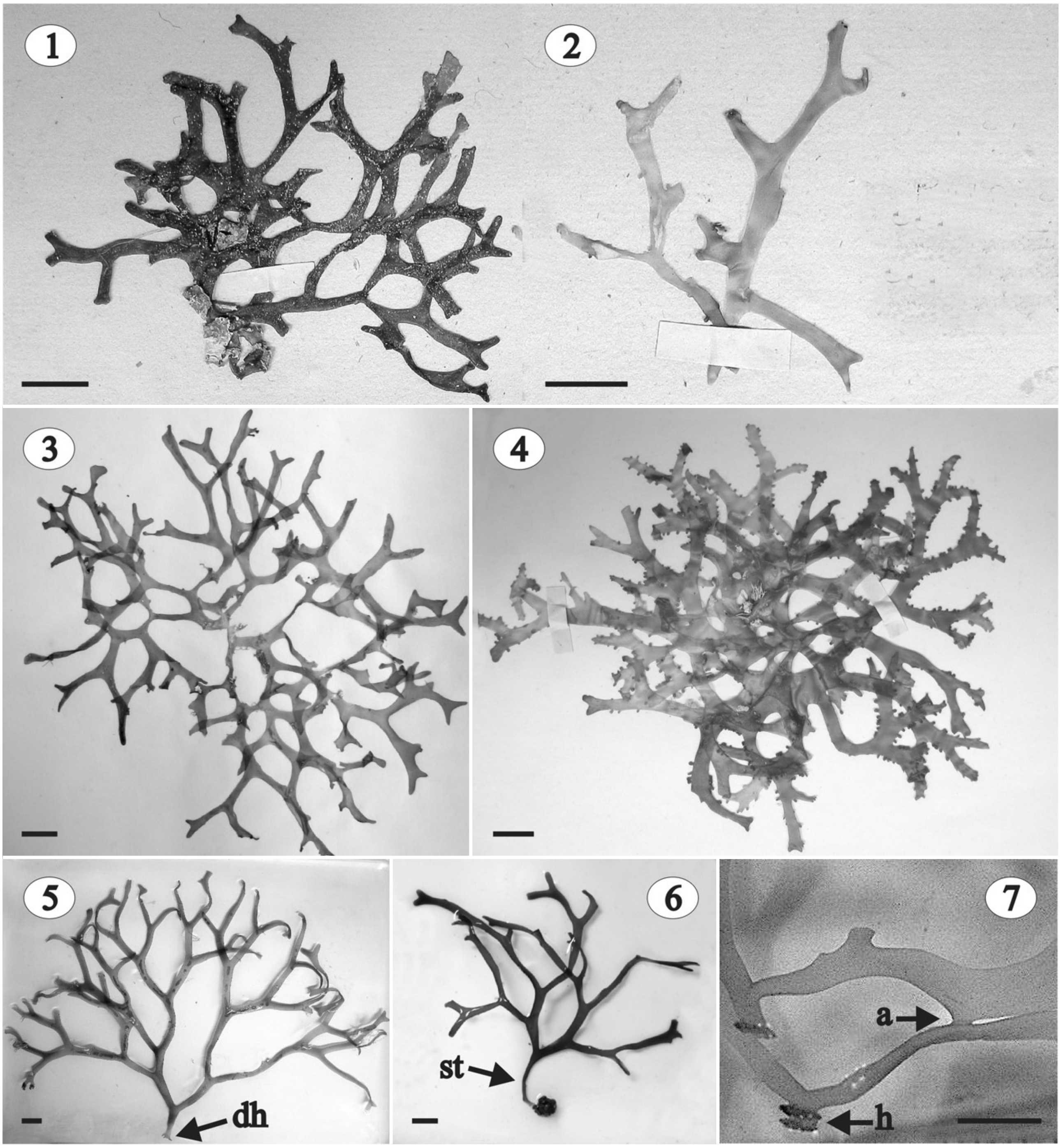
NOMENCLATURAL SYNONYMS: *Gracilaria repens* (C. Agardh) J. Agardh, 1842: 152.
Dichophycus repens (C. Agardh) Zanardini, 1847: 16, pl. 6, figs a–i.
Fauchea repens (C. Agardh) Montagne et Bory, nom illeg. *in* Montagne, 1846: 64.

LECTOTYPE: Agardh herbarium, LD 25705. There are four specimens in the Agardh herbarium (LD 25705, Fig. 1; LD 25704, Fig. 2; LD 25702, Fig. 3; LD 25703, Fig. 4), all of which agree with our recently collected material. Specimens LD 25704 and LD 25705 were identified as *Sphaerococcus repens* by C. Agardh. We chose LD 25705 as the lectotype because it shows the diagnostic features of the species most clearly.

TYPE LOCALITY: Atlantic coast near Cadiz, Spain.

DISTRIBUTION: Mediterranean Sea and East Atlantic (Iberian Peninsula, Morocco and Canary Islands). In our opinion, records from the Maldives (Hackett, 1977) need to be verified.

HABITAT: In the Mediterranean Sea, *G. repens* grows in the sublittoral on rocky bottoms, on



Figs 1–7. *Gloiocladia repens*. Habit. Fig. 1. Habit of the lectotype (LD 25705). Fig. 2. Habit of a fertile male and female gametophyte in the original collection (LD 25704). Fig. 3. Habit of a sterile specimen in the original collection (LD 25702). Fig. 4. Habit of a fertile female gametophyte in the original collection (LD 25703). Fig. 5. Habit of a tetrasporophyte (HGI-A 6320). Fig. 6. Habit of a sterile stipitate specimen (HGI-A 6746). Fig. 7. Detail of the thallus showing marginal haptera and thalli anastomoses (HGI-A 5463). Abbreviations: a: anastomosis; dh: discoid holdfast; h: hapterum; st: stipe. Scale bars: 1 cm (Figs 1–6); 0.5 cm (Fig. 7).

crustose corallines or on maërl, usually between 25 and 50 m deep (Feldmann, 1941; Gautier & Picard, 1957; Ballesteros i Sagarra, 1984). In 1889, J.J. Rodríguez y Femenías reported a specimen from 200 m, but recent studies with a Johnson-Sea-Link submersible have shown that, at present, photosynthetic macroalgae are only found down to 108 m in the Mediterranean Sea (E. Ballesteros, personal communication). In Mediterranean waters under Atlantic influence (e.g. Alboran Sea, Algeria or Sicily), *G. repens* has been found at 10 m depth, usually in communities of Laminariales or Fucales [Feldmann, 1943; Giaccone, 1969; Rindi & Cinelli, 1995]. On the Atlantic coast of the Iberian Peninsula, the species has been found between 6 and 14 m deep on rocky bottoms or with *Laminaria ochroleuca* De La Pylaie (López Varela *et al*., 2002). Finally, in the Canary Islands, it has been

Table 1. *Gloiocladia repens*. Examined specimens. Locality, legit, date and depth of collection, herbarium identification number and phenology are indicated. All the specimens come from the coasts of Spain

Catalonia	
Blanes	L. Polo: 23 May 1976 (HGI-A 2615)
Lloret de Mar	E. Ballesteros: 8 August 2003, 30 m (HGI-A 6623)
Balearic Islands	
Cabrera	*Ansiola*. E. Ballesteros: 23 July 2003, 60 m (HGI-A 6040). *Cap Falcó*. C. Rodr.-Prieto: 24 May 1996, 50 m (HGI-A 1710). *Cova Blava*. C. Rodr.-Prieto: 23 May 1996, 30 m (HGI-A 1716). *L'Imperial*. C. Rodr.-Prieto: 1 May 1996, 50 m (HGI-A 1563). E. Ballesteros: 30 January 1999, 65 m (HGI-A 5759)
Eivissa	*Espartar*. E. Ballesteros: 14 September 2004, 55 m (HGI-A 6622)
Formentera	E. Ballesteros: 9 May 2004, 59 m (HGI-A 6621, 6334 ♀); 10 May 2004, 55 m (HGI-A 6671)
Mallorca	*Cap Catalunya*. E. Ballesteros: 18 July 2001, 45 m (HGI-A 5404)
Minorca	*Addaia*. J.J. Rodr. y Fem.: 25 March 1897, 105 m (RyF 1653 ⊕); 24 October 1899, 90 m (RyF 1654 ♀); 9 November 1899, 90 m (RyF 1656 ⊕); 10 November 1899, 90 m (RyF 1657 ♀, 1658 ♀). *Alaior*. J.J. Rodr. y Fem.: 29 December 1887, 95 m (RyF 1639 ⊕). *Binidalí*. J.J. Rodr. y Fem.: 28 May 1897, 95 m (RyF 1661 ⊕). *Binisafuller*. J.J. Rodr. y Fem.: 3 January 1888, 100 m (RyF 1641 ⊕, 1640 ♀). *Cala Coves*. J.J. Rodr. y Fem.: 28 September 1893, 75 m (RyF 1630). *Canutells*. J.J. Rodr. y Fem.: 3 January 1888, 110 m (RyF 1632); 19 January 1888, 110 m (RyF 1633); 4 February 1888, 95 m (RyF 1634 ⊕); 15 September 1890, 95 m (RyF 1635 ⊕); 15 December 1895, 40 m (RyF 1637); 7 January 1896, 55 m (RyF 1638 ⊕). *Cap Font*. J.J. Rodr. y Fem.: 11 October 1887, 95 m (MA-A 3916); 18 October 1888, 95 m (RyF 1642, MA-A 3915); 21 September 1891, 85/95 m (RyF 1643 ♀); 4 February 1897 (RyF 1644 ⊕); 22 October 1897, 70/80 m (RyF 1645 ⊕). *Cap Negre*. J.J. Rodr. y Fem.: 29 October 1889, 95 m (RyF 1648); 9 November 1897, 80 m (RyF 1649 ♀). *Northern coast*. 26 October 1889 (RyF 1646, 1647). *Canal de Menorca*. C. Rodr.-Prieto: 28 July 1994, 50 m (HGI-A 3242). S. Mallol: 30 August 2003, 84 m (HGI-A 5939). *Els Freus*. J.J. Rodr. y Fem.: 22 March 1897, 80 m (RyF 1659 ♀). *Enderrosay*. J.J. Rodr. y Fem.: 18 September 1891, 100 m (RyF 1650 ♀). *La Mola*. 24 November 1897, 95 m (RyF 1662 ⊕, 1663 ⊕). *Maó*. J.J. Rodr. y Fem.: 3 September 1887, 90 m (RyF 1624 ⊕); 9 April 1888, 120 m (RyF 1627 ⊕); 19 May 1890 (RyF 1626 ⊕); 26 May 1898, 10 m (RyF 1628 ⊕). *Montjofre*. J.J. Rodr. y Fem.: 26 March 1897, 80 m (RyF 1660 ⊕). *Rafalet*. J.J. Rodr. y Fem.: 29 September 1891, 100 m (RyF 1651 ♀)
?	E. Ballesteros: 20 May 2004, 62/67 m (HGI-A 6320, 6625 ⊕)
Columbretes Islands	
Escala d'en Rossi	C. Rodr.-Prieto: 11 May 2002, 42 m (HGI-A 5460, 5462 ⊕, 5463 ⊕, 5470 ⊕); 4 June 2005, 42 m (HGI-A 6746, 6752, 6753, 6754, 6755, 6756, 6757, 6745 ♀). C. Rodr.-Prieto and N. Sánchez: 14 September 2002, 40 m (HGI-A 5627, 5628, 5629, 5633, 5634, 5636, 5812); 17 September 2002, 42 m (HGI-A 6170)
La Foradada	C. Rodr.-Prieto: 12 May 2002, 42 m (HGI-A 5476 ⊕)
Manco Libre	C. Rodr.-Prieto and N. Sánchez: 15 September 2002, 40 m (HGI-A 5637, HGI-A 5638 ⊕); 16 September 2002, 43 m (HGI-A 5632, 5631 ⊕). F. Boisset: 16 September 2002, 45 m (HGI-A 6300)
Mascarat	F. Boisset: 15 September 2002, 35 m (HGI-A 6301, 6302 ⊕, 6303 ♀/♂). C. Rodr.-Prieto: 11 May 2002, 35 m (HGI-A 5542 ♀)
Piedra Joaquín	E. Ballesteros: 22 June 1996, 45 m (HGI-A 1793)
?	J.C. Lino: 7 March 2002, 50 m (VAL-A 2135); 7 March 2002, 60 m (VAL-A 2159). F. Boisset: 17 May 2002, 60 m (HGI-A 6299, 6297 ⊕, 6298 ⊕)
Alboran I. sland	I. E. O.: July 1996 (MGC-A 3549). Fauna IV: July 1996 (MGC-A 3564, 3565, 3566)
Andalusia	*Cadis*. Cabrera (LD 25702, 25703 ♀); (LD 25704 ♀/♂, 25705 ♀) [as *Sphaerococcus repens*]
Galicia	
A Coruña	*Mugardos*. C. López Varela: 1 September 1998, 12 m (SANT-A 11760 ⊕). M. Domínguez: 17 July 2003, 14 m (SANT-A 14962 ♀)
Lugo	*San Ciprián*. I. Bárbara, P. Díaz and J. Cremades, 13 July 2005: 6 m (SANT-A 16072); 11 m (SANT-A 16063)

Abbreviation: RyF = Herbarium of J.J. Rodríguez y Femenías.

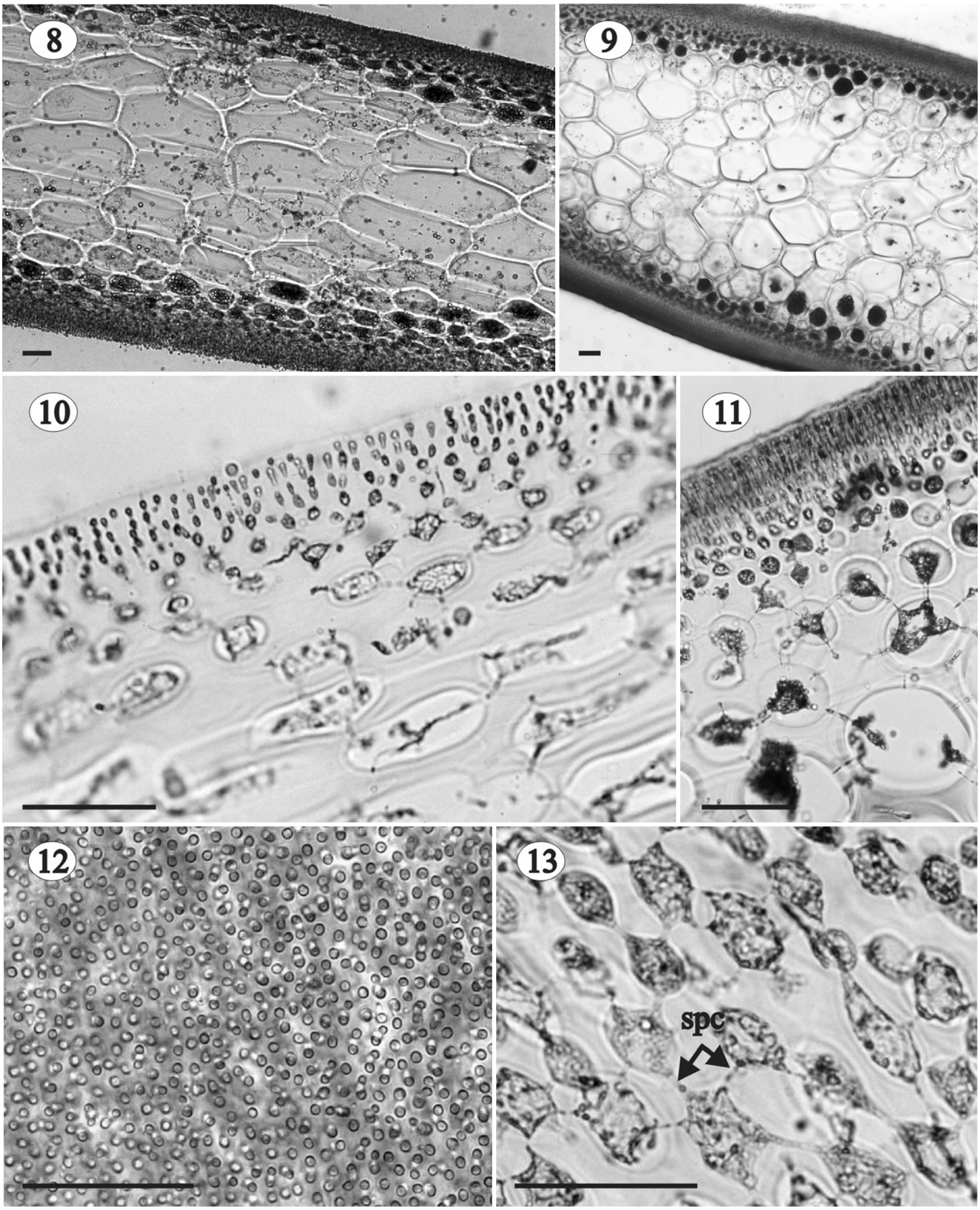
found epilithic on small rhodoliths or on organic sandy bottoms at 60 m depth (Sansón *et al*., 2002).

SEASONALITY: Spermatangia were observed in September; cystocarps occur throughout the year, and tetrasporangia were found from September to May (C. Agardh, 1823; Berthold, 1882; Hauck, 1885; Rodríguez y Femenías, 1889; Feldmann, 1937; Cormaci *et al*., 1985; López Varela *et al*., 2002; Sansón *et al*., 2002; this work).

SPECIMENS EXAMINED: see Table 1.

Habit and vegetative structure

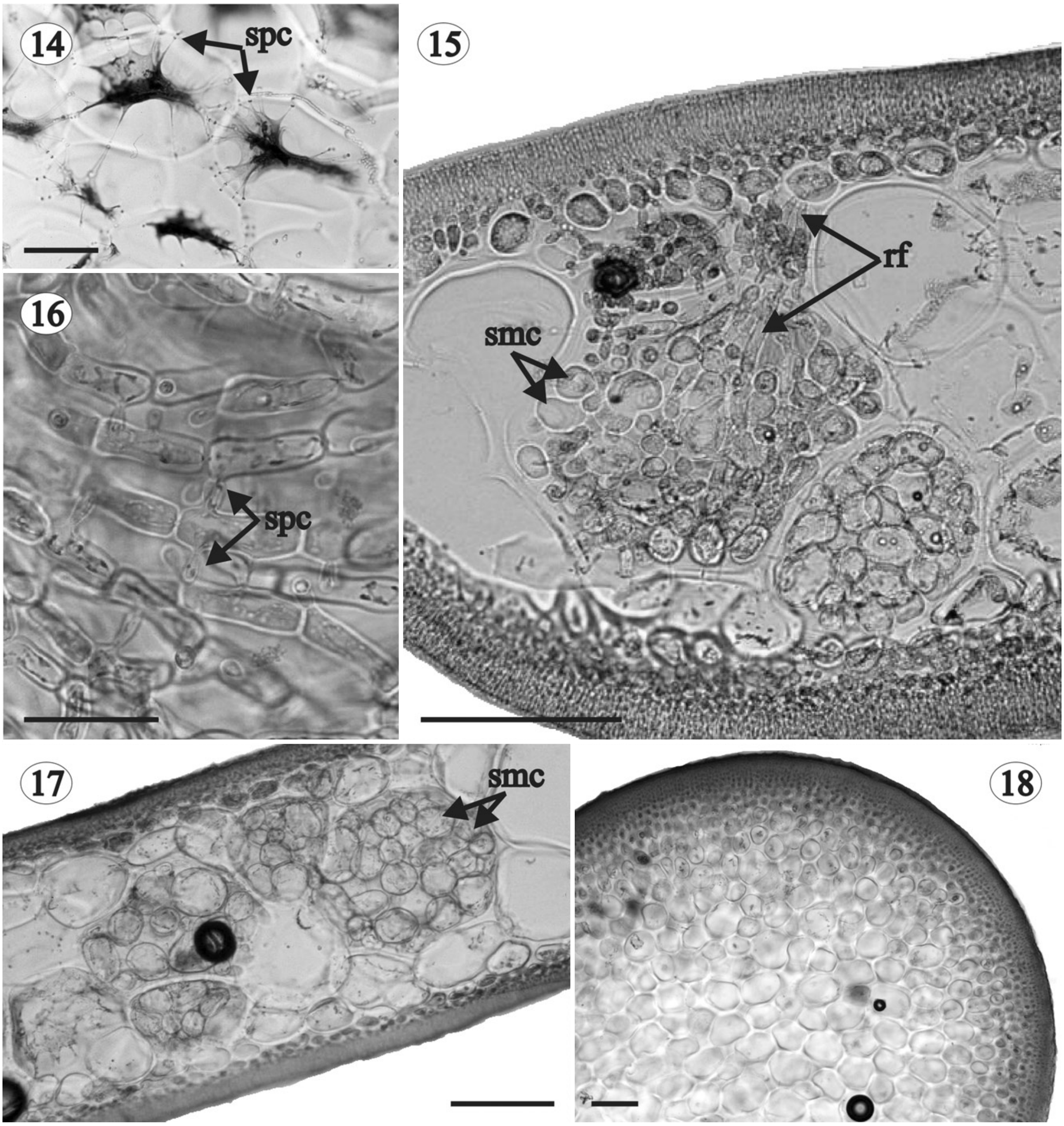
Thalli decumbent, to 25 cm high and 18 cm wide (Figs 1–6), primarily attached to the substratum by a discoid holdfast (Fig. 5). Plants sessile or occasionally stipitate (Fig. 6). The stipe, when present, cartilaginous, cylindrical, up to 13.0 mm long and 3.0 mm in diameter (Fig. 6). Fronds much branched, complanate and somewhat dichotomous, with dorsiventrally compressed branches, 2–6 mm wide at the base and 1–6 mm wide near the apex. Branch tips rounded and furcate with smooth margins (Figs 1–6). Thallus 560–1,500 μm thick at the base of the plant and 500–1,000 μm at the apex. Texture cartilaginous and slippery to the touch, and the appearance shiny. Colour bright rose or reddish, but some old individuals nearly white. Fronds usually secondarily fixed to the substratum



Figs 8–13. *Gloiocladia repens*. Vegetative structure. Aniline blue staining. Figs 8, 9. Longitudinal (8) and transverse (9) sections of a sterile individual in the middle part of the plant (HGI-A 5631, 5637). Figs 10, 11. Cortex and subcortex in longitudinal (10) and transverse (11) section (HGI-A 5631, 5637). Fig. 12. Outer cortical cells in a surface view (HGI-A 5629). Fig. 13. Network of subcortical cells showing frequent secondary pit-connections between cells (HGI-A 5637). Abbreviation: spc: secondary pit-connection. Scale bars: 50 μm.

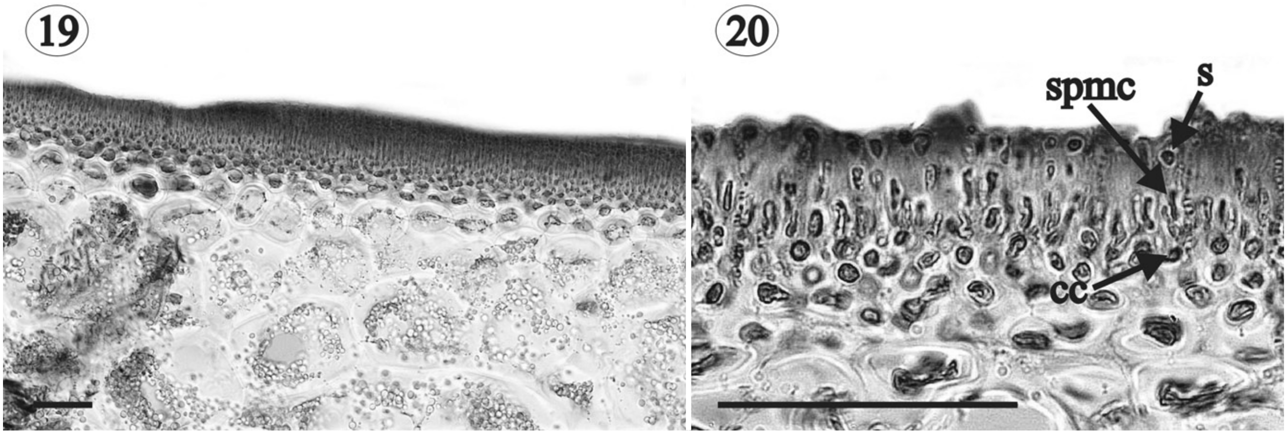
by marginal haptera and axes often anastomosing (Fig. 7).

Axes multiaxial and solid (Figs 8, 9, 15, 17, 18), the outer cortex composed of compact anticlinal, simple or pseudodichotomously branched filaments arising from the subcortex (Figs 10, 11). Cortical filaments 5–7 cells long at the base of the plant and 3–5 cells long at the apex, with ovoid to



Figs 14–18. *Gloiocladia repens*. Vegetative structure. Aniline blue staining. Fig. 14. Medullary cells in transverse section showing several secondary pit-connections between them (HGI-A 5463). Fig. 15. Transverse section of the basal part of the thallus showing the development of rhizoidal filaments and secondary medullary cells (HGI-A 5632). Fig. 16. Detail of the rhizoidal filaments connected by secondary pit-connections (HGI-A 5632). Fig. 17. Transverse section of the basal part of the thallus with many secondary medullary cells (HGI-A 5632). Fig. 18. Transverse section of the stipe (HGI-A 1793). Abbreviations: rf: rhizoidal filament; smc: secondary medullary cell; spc: secondary pit-connection. Scale bars: 50 μm (Fig. 14); 100 μm (Figs 15, 17, 18); 25 μm (Fig. 16).

rounded cells diminishing in size outwardly (inner cells 6–10 × 2–8 μm; outer cells 2–6 × 2–4 μm), and without lateral secondary pit-connections (Figs 10–12). Subcortex consisting of ovoid to angular cells, 6–30 μm long, 6–20 μm wide and 6–28 μm thick, interconnected by secondary pit-connections, thus forming a network parallel to the thallus surface (Fig. 13). Medulla cellular and compact, composed of large hyaline cells diminishing in size in an outward direction. Medullary cells elongated in longitudinal section, 20–500 μm long, 14–240 μm wide and 16–192 μm thick (Fig. 8), rounded or ovoid in transversal section (Fig. 9), and developing numerous secondary pit-connections (up to 36 from a single cell, Fig. 14). Multicellular rhizoidal filaments



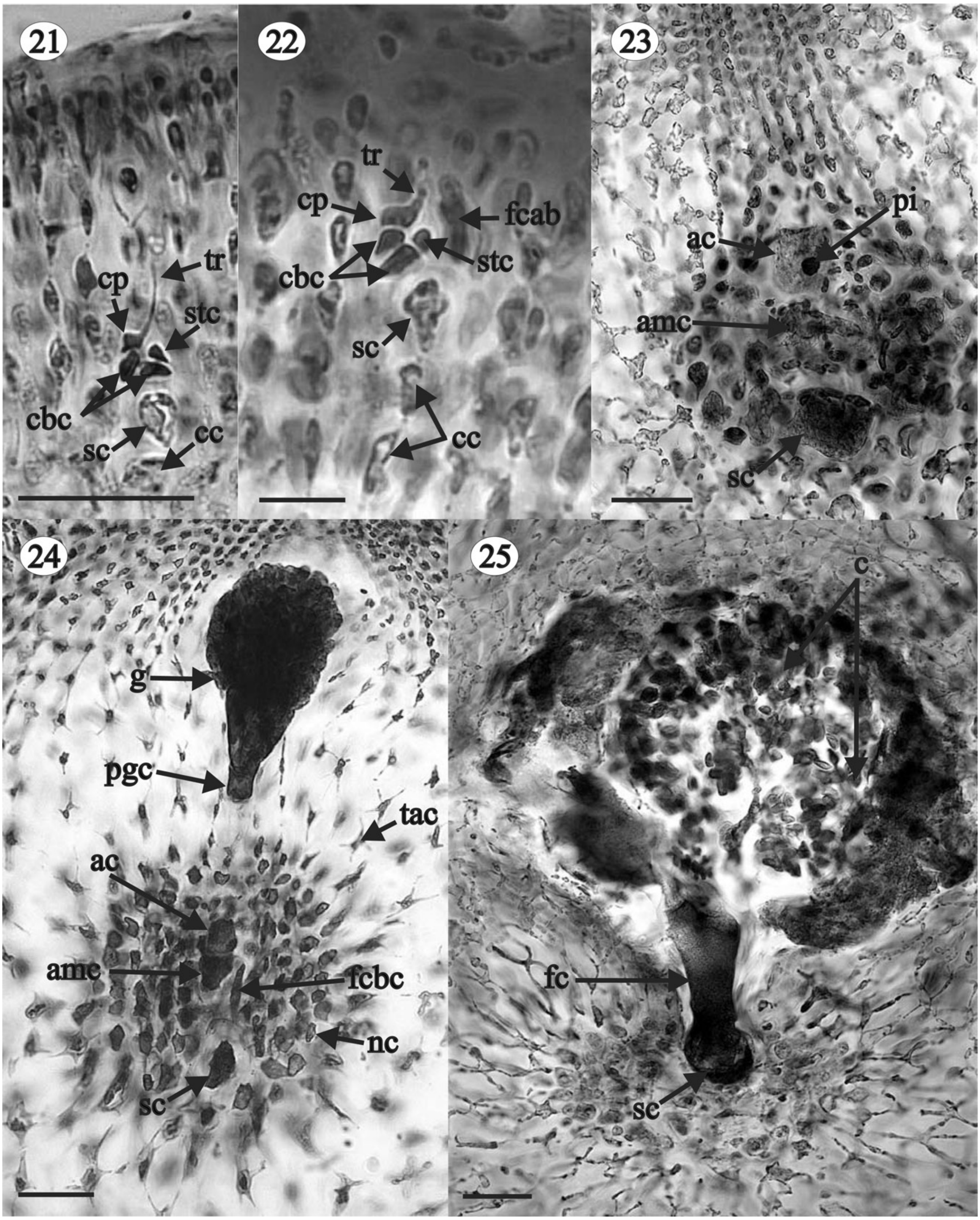
Figs 19, 20. *Gloiocladia repens*. Light photomicrographs of male reproductive structures. Aniline blue staining. Fig. 19. Transverse section of a fertile area of the thallus showing a spermatangial sorus (HGI-A 6303). Fig. 20. Transverse section of a fertile area of the thallus showing spermatia borne on spermatangial mother cells (LD 25704). Abbreviations: cc: cortical cell, s: spermatium; spmc: spermatangial mother cell. Scale bars: 50 µm.

usually present in the basal parts of adult plants, developing from inner cortical cells or outer medullary cells, and growing between the medullary cells throughout the thallus (Fig. 15). Cells of rhizoidal filaments rectangular to ovoid, up to 32 × 20 µm, connected to each other and to the nearby medullary cells by secondary pit-connections (Fig. 16). Secondary medullary cells occasionally present in the basal parts of adult specimens, sometimes mixed with rhizoidal filaments (Fig. 15). Secondary medullary cells rounded, 15–40 µm in diameter, and interspersed among the large medullary cells (Figs 15, 17). Within the stipe, medullary cells rounded or slightly angular, not elongated in longitudinal section, and smaller than in the rest of the frond (up to 100 µm) (Fig. 18).

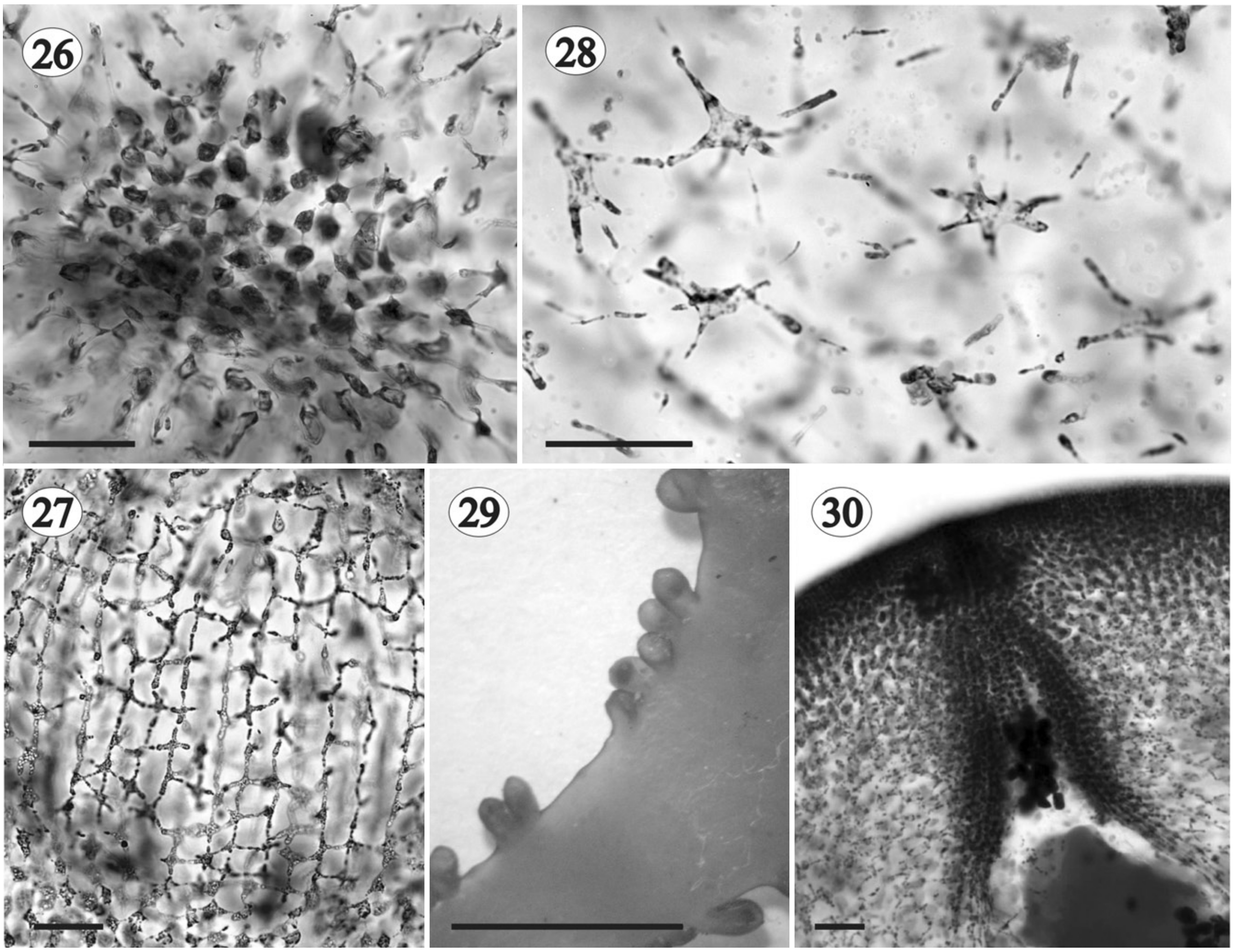
Reproductive structures

Plants monoecious. Spermatangia 1–2 µm in diameter, grouped in surface sori (Fig. 19) and cut off singly or in pairs from ovoid spermatangial mother cells that develop from the outer cortical cells (Fig. 20). Female gametophytes procarpic. The carpogonial branch curved and outwardly directed, arising from a mid cortical cell (= supporting cell), and composed of three cells plus a lateral sterile cell that arises from the basal cell of the carpogonial branch (Fig. 21). Auxiliary cell branch situated on the supporting cell and only one cell long before fertilization (Fig. 22). Mature auxiliary cell branch two-celled, composed of an auxiliary mother cell and a terminal auxiliary cell containing a conspicuous globular proteinaceous inclusion (Fig. 23). Carpogonial branch cells fusing after fertilization and connecting to the auxiliary cell, which divides transversely to cut off a primary gonimoblast cell (= gonimoblast initial) (Fig. 24). Area adjacent to the supporting cell developing a subspherical mass of highly pigmented nutritive cells (Fig. 24) connected to each other and to the supporting cell by secondary pit-connections (Fig. 26). These cells somewhat stellate, with the main cell body up to 23 µm in diameter and lobes up to 8 µm long (Fig. 26). Basal nutritive tissue developing a network of persistent filaments (= *tela arachnoidea*) that surrounds the fertilized procarp (Figs 24, 27), and is composed of stellate cells up to 23 µm in diameter with lobes up to 37 µm long (Fig. 28). A fusion cell is formed through enlargement of the pit-connection between the auxiliary cell and the auxiliary mother cell, which later coalesces with the fused cells of the carpogonial branch and the surrounding cells, ultimately incorporating the supporting cell. Components of the fusion cell, except the supporting cell, becoming indiscernible when the structure is mature (Fig. 25). The gonimoblast (120–750 µm in diameter) arising from the distal end of the primary gonimoblast cell and composed of several elongated lobes of ovoid carposporangia surrounded by the cells of the tela arachnoidea (Figs 24, 25). Carposporangia 20–40 µm in diameter. Cystocarps (400–1,500 µm in diameter) situated on the branch margins (Fig. 29), substipitate, globose, and ostiolate (Figs 29, 30).

Tetrasporangia developing in extensive (<6 mm long × 2 mm wide), ovoid to elongate and prominent nemathecia situated in the middle part of the branch tips (Fig. 31), not produced simultaneously but with different developmental phases adjacent to one another (Fig. 32). Nemathecial cortical filaments longer (10–15 cells long) and their basal cells larger (10–23 × 2–6 µm) than in sterile parts of the plant (Fig. 32). Tetrasporangia fusiform or



Figs 21–25. *Gloiocladia repens*. Light photomicrographs of female reproductive structures and postfertilization stages. Aniline blue staining. Fig. 21. Carpogonial branch (HGI-A 6303). Fig. 22. Procarp at a stage in which the first cell of the auxiliary branch can just be distinguished (HGI-A 6303). Fig. 23. Auxiliary cell branch composed of an auxiliary mother cell and an auxiliary cell with a proteinaceous inclusion (HGI-A 6334). Fig. 24. Young gonimoblast arising from the primary gonimoblast cell. The fusion cell between the carpogonial branch cells can also been seen (LD 25703). Fig. 25. Detail of the fusion cell (HGI-A 6303). Abbreviations: ac: auxiliary cell; amc: auxiliary mother cell; c: carposporangia; cbc: cells of the carpogonial branch; cc: cortical cell; cp: carpogonium; fc: fusion cell; fcab: first cell of the auxiliary branch; fcbc: fused cells of the carpogonial branch; g: gonimoblast; nc: nutritive cell; pgc: primary gonimoblast cell; pi: proteinaceous inclusion; sc: supporting cell; tr: trichogyne; stc: sterile cell; tac: cell of the tela arachnoidea. Scale bars: 25 μm (Figs 21, 22); 50 μm (Figs 23–25).



Figs 26–30. *Gloiocladia repens*. Light photomicrographs of the female reproductive structures with aniline blue staining. Fig. 26. Detail of stellate nutritive cells (HGI-A 5542). Figs 27, 28. Details of stellate cells of the tela arachnoidea (HGI-A 5542). Fig. 29. Cystocarps (LD 25703). Fig. 30. Detail of the carposporangia going out through the ostiole (HGI-A 5542). Scale bars: 50 µm (Figs 26–28, 30); 5 mm (Fig. 29).

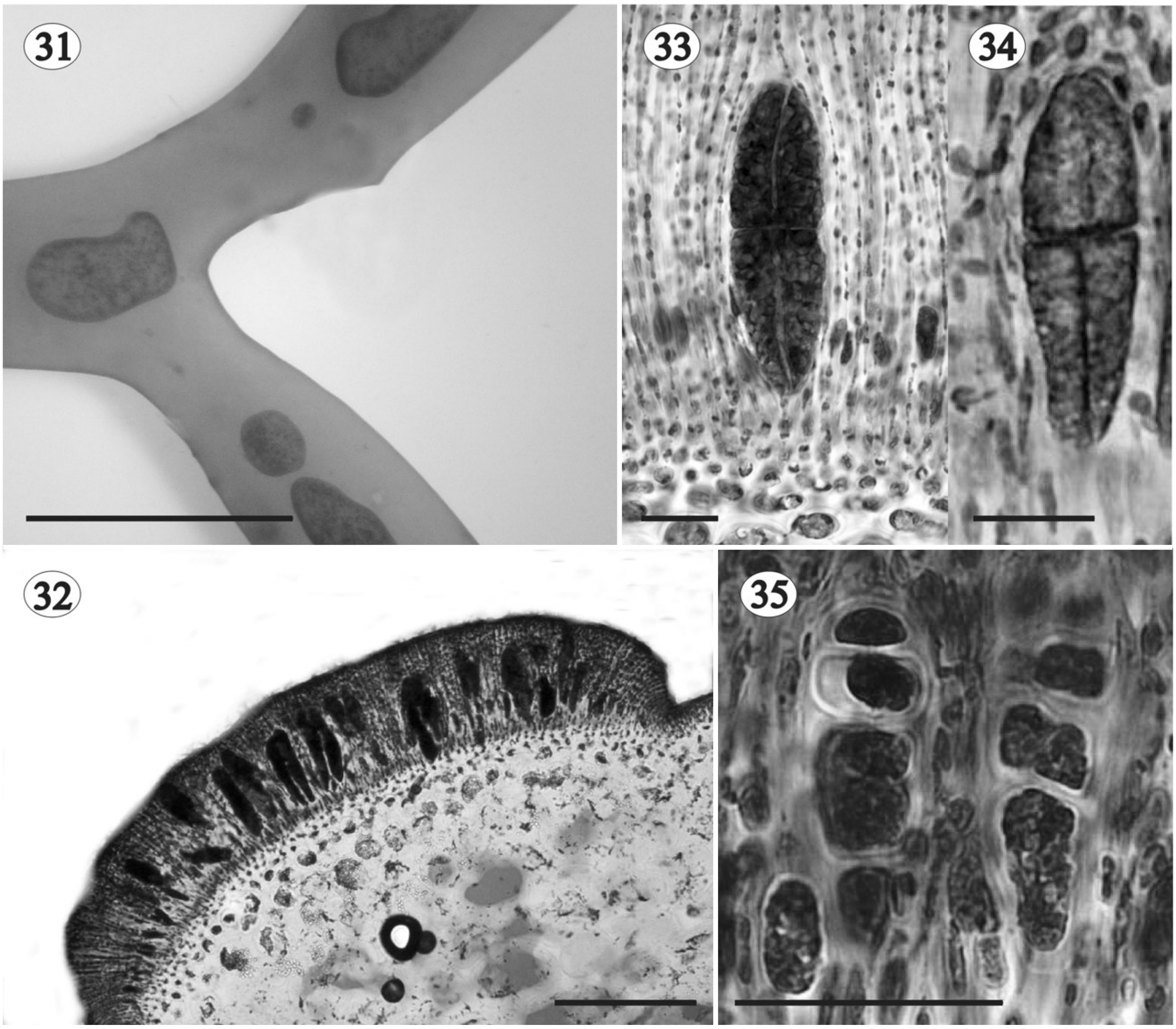
ovoid, up to 30–136 µm × 10–48 µm, and cruciate (Fig. 33), decussately cruciate (Fig. 34) or irregularly divided (Fig. 35). Tetrasporangia subapical, arising from one of the first dichotomies of an outer cortical filament with the pit-connection between the tetrasporangium and the filament situated proximally, at the basal part of the tetrasporangium (Fig. 36).

Notes

The white colour of some adult specimens of *G. repens* was previously reported by López Varela *et al.* (2001, 2002). It could be due to the accumulation of floridean starch, as seen in other Rhodophyta such as *Kallymenia feldmannii* Codomier and *K. requienii* (J. Agardh) J. Agardh (Rodríguez-Prieto & Vergés, 2001). Rhizoidal filaments and secondary medullary cells are correlated with injury to the thallus (Sparling, 1957; Irvine & Guiry, 1980; Sánchez, 2005; Sánchez & Rodríguez-Prieto, 2005) and could be involved in increasing the thallus toughness (Sánchez, 2005; Sánchez & Rodríguez-Prieto, 2005). Although this feature was not recorded for the type species, *F. repens*, the presence of rhizoidal filaments within the medulla was considered to be a key feature of Group 1 Rhodymeniales (Irvine & Guiry, 1980; Guiry & Irvine, 1981), which included *Fauchea*. Finally, López Varela *et al.* (2001, 2002) described the tetrasporangia as either zonate or cruciate, and aligned in groups of fours. However, we observed only cruciate, decussately cruciate or irregularly divided tetrasporangia, even in the specimen examined by these authors (SANT-A 11760).

Molecular analyses

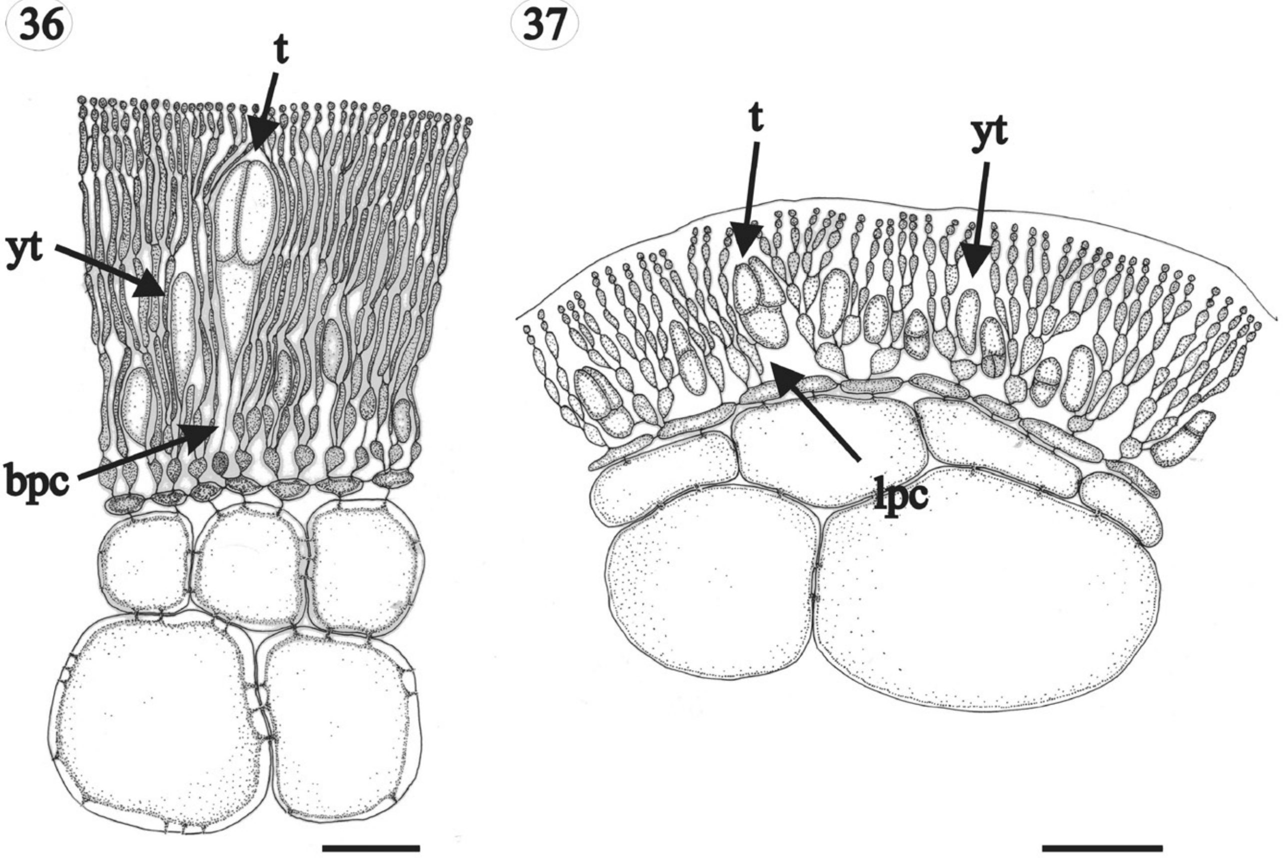
The 18S data set included 139 variable (8.3%) and 36 parsimony informative (2.2%) sites. A Tamura-Nei correction with invariant sites and gamma distribution was determined to be the best-fit model of sequence evolution for this data set.



Figs 31–35. *Gloiocladia repens*. Tetrasporangial development. Fig. 31. Nemathecia in branch surface (HGI-A 6320). Fig. 32. Transverse section of a well-developed nemathecium (HGI-A 5463). Fig. 33. Transverse section of nemathecium with cruciately dividing tetrasporangia (HGI-A 6298). Fig. 34. Transverse section of nemathecium with decussately cruciate dividing tetrasporangia (HGI-A 6302) (aniline blue staining). Fig. 35. Transverse section of nemathecium with irregularly dividing tetrasporangia (HGI-A 6302) (aniline blue staining). Scale bars: 5 mm (Fig. 31); 100 μm (Fig. 32); 25 μm (Figs 33–35).

Maximum likelihood, distance and parsimony analyses of these data did not result in identical trees, but the major relationships were congruent (Fig. 38) All analyses resolved a clade containing *Fauchea* spp. and *Gloiocladia furcata*, and three additional lineages leading to *Faucheopsis coronata* (Harvey) Kylin, *Gloioderma fruticulosum* and *Webervanbossea splachnoides* (Harvey) De Toni fil. The *Fauchea*/*Gloiocladia* clade received strong to moderate bootstrap support (maximum likelihood [M] = 78%, distance [D] = 79%, parsimony [P] = 97%), but the relationships among the four lineages vary in topology and bootstrap support among the three types of analyses. A sister relationship between the *Fauchea*/*Gloiocladia* clade and *Faucheopsis* was resolved with good support in parsimony and distance analyses (P = 84%, D = 85%) but was only weakly supported in the maximum likelihood analysis (M = 57%). *Gloioderma* and *Webervanbossea* De Toni were resolved as sister taxa with weak support in the maximum likelihood analysis (M = 63%), but *Gloioderma* was resolved as sister to the *Faucheopsis*/*Fauchea*/*Gloiocladia* clade with weak support in the parsimony and distance analyses (P = 62%, D = 59%).

Relationships among the four specimens in the *Fauchea*/*Gloiocladia* clade are not resolved and the three specimens identified as *Fauchea* species do not form a separate clade. Pairwise sequence divergences for the four sequences vary from eight (0.48%) between the Spanish



Figs 36, 37. *Gloiocladia repens* and *Gloiocladia furcata*. Tetrasporangial pit-connections with aniline blue staining. Fig. 36. Tetrasporangia of *G. repens* showing basal pit-connection with cortical filaments (HGI-A 5631). Fig. 37. Tetrasporangia of *G. furcata* showing lateral pit-connection with cortical filaments (HGI-A 5769). Abbreviations: bpc: basal pit-connection; lpc: lateral pit-connection; t: tetrasporangium; yt: young tetrasporangium. Scale bars: 50 µm.

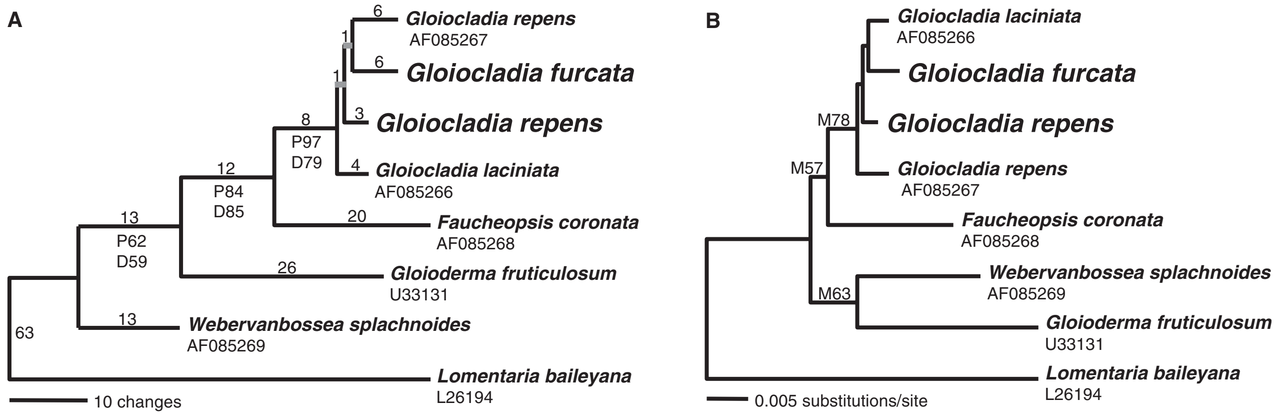


Fig. 38. Phylogenetic trees resulting from analyses of 18S rRNA gene sequences of Faucheacean species. Accession numbers for previously published sequences are given below species names. Sequences generated in this study are shown in larger font. (A) One of four most parsimonious trees (length = 176; CI = 0.687; RI = 0.580). Inferred branch lengths are shown above branches, parsimony (P) and distance (D) bootstrap proportions are shown below branches. (B) Maximum-likelihood tree (lnL = −3340.58416) with likelihood bootstrap proportions shown above branches.

G. repens and California *G. laciniata* (J. Agardh) Sánchez et Rodríguez-Prieto comb. nov. (= *Fauchea laciniata* J. Agardh) specimens, to twelve (0.72%) between two specimen pairs, the Italian *G. repens* and Californian *G. lacinata*, and the Italian *G. repens* and Spanish *G. furcata*. The *G. repens* specimen from the Spanish Mediterranean islands of Columbretes is different from the Italian specimen identified as *G. repens* at 10 sites (0.60%).

Discussion

Studies of the generitype of *Gloiocladia*, *G. furcata* by Sánchez (2005) and Sánchez & Rodríguez-Prieto (2005), and our present observations on *F. repens*, the generitype of *Fauchea* (= *G. repens*), show that the main qualitative differences (Table 2) between the two species are: (i) the shape of the outer cortical filaments, (ii) the location of the supporting cell, (iii) the presence or absence of a small lateral cell on the basal cell of the carpogonial branch, (iv) the inclusion of the supporting cell in the fusion cell, (v) the morphology of the fusion cell, (vi) the existence of substipitate or sessile cystocarps, (vii) the arrangement of tetrasporangia, and (viii) the location of the pit-connection between the tetrasporangium and the cortical cell (Figs 36, 37). The presence of coronate cystocarps, highlighted by Kylin (1931) and Sparling (1957), cannot be included because such coronate cystocarps are only occasionally present in *G. furcata* (Sánchez, 2005, Sánchez & Rodríguez-Prieto, 2005).

Traditionally, the genera *Fauchea* and *Gloiocladia* have been separated morphologically using some of the differences between *G. furcata* and *G. repens* which we have highlighted here, although the lack of detailed information on the reproductive structures of the type species has prevented a clear concept of *Fauchea* and its relationship with *Gloiocladia* (Irvine & Guiry, 1980; Norris, 1991). The shape of the outer cortical filaments (compact or lax) was used by Sparling (1957) and the arrangement of tetrasporangia (conspicuously raised nemathecia in *Fauchea* and in slightly raised nemathecia or scattered in *Gloiocladia*), was used by De Toni (1900) and Irvine & Guiry (1980). Moreover, Norris (1991) transferred all species of *Fauchea*, *Gloiocladia* or *Gloioderma* with strongly raised nemathecia to *Fauchea*, and those with tetrasporangia scattered or in only slightly raised nemathecia to *Gloiocladia*.

Information about the taxonomic characters that differentiate *G. furcata* and *G. repens* is lacking for most other species of *Fauchea* (Table 2) and *Gloiocladia* (Sánchez & Rodríguez Prieto, 2005). *Gloiocladia laciniata* (as *F. laciniata*) is by far the best known species (Sparling, 1957; Dawson, 1963) and is closer to *G. furcata* than to *G. repens* (Table 2), having a lax outer cortex, a simple three-celled carpogonial branch and a supporting cell that does not become part of the fusion cell. It is also characterized by coronate cystocarps and cruciately divided tetrasporangia.

The utility of 18S sequence analyses in taxonomic studies of the Rhodymeniales has been demonstrated previously (Millar *et al.*, 1996; Saunders *et al.*, 1999; Freshwater *et al.*, 2005). Representative specimens of *G. repens* and *G. furcata*, the type species of *Fauchea* and *Gloiocladia*, respectively, were sequenced and analysed in this study together with other available Faucheaceae 18S sequences. Results of these sequence analyses support a close relationship between these species and suggest that a generic distinction is unwarranted. In contrast, *G. furcata* and *Gloioderma fruticulosum* are not more closely related in the 18S trees than either is to species from *Faucheopsis* Kylin or *Webervanbossea*, indicating that the transfer of at least some *Gloioderma* species into *Gloiocladia* by Norris (1991) was unwarranted.

Pairwise 18S sequence divergences between specimens representing different species within the same Rhodymeniales genera range from 0.17% to 0.97% (Saunders *et al.*, 1999; Freshwater *et al.*, 2005). The pairwise sequence divergence of 0.60% between specimens identified as *G. repens* from the Mediterranean coastal area of Spain and *G. repens* from Italy is within this range, and greater than the divergence between the Spanish *G. repens* and a Californian specimen of *G. lacinata*. The type locality for *G. repens* is the Atlantic coast of Spain near the mouth of the Mediterranean and characters of the sequenced Spanish specimen match typical *G. repens*, suggesting that the Italian specimen could represent a different, cryptic species.

In the light of these observations, we reassess the genus *Gloiocladia* and formally propose transfer of the species of *Fauchea* to the earlier described genus *Gloiocladia* (Table 3). Although *Gloioderma fruticulosum* is not the generitype of *Gloioderma*, the distance between this and the *Gloiocladia* species in sequence analyses (Fig. 38), suggest that *Gloioderma* should be reinstated, at least for some species, especially those recorded from southern Australia and New Zealand.

Emended description of *Gloiocladia* J. Agardh

Fronds much branched, complanate and somewhat dichotomous. Axes multiaxial and solid, the outer cortex composed of compact anticlinal, simple or pseudodichotomously branched filaments arising from the subcortex. Cortical filaments diminishing in size outwardly, without lateral secondary pit-connections. Subcortex consisting of ovoid to angular cells interconnected by secondary pit-connections, thus forming a network parallel to the thallus surface. Medulla cellular and compact, composed of large hyaline cells elongated in longitudinal section. Spermatangia grouped in surface sori. Plant procarpic. Carpogonial branch three-celled, with or without a lateral sterile cell arising from the first

Table 2. Comparison of the main features of species currently placed in the genus *Fauchea* and transferred here to *Gloiocladia*

	G. fryeana (Setchell) Sánchez et Rodríguez-Prieto comb. nov.	***G. furcellata*** (Baardseth) Sánchez et Rodríguez-Prieto comb. nov.	***G. furcata*** (C. Agardh) J. Agardh	***G. galapagensis*** (W.R. Taylor) Sánchez et Rodríguez-Prieto comb. nov.	***G. hassleri*** (M. Howe et W.R. Taylor) Sánchez et Rodríguez-Prieto comb. nov.	***G. laciniata*** (J. Agardh) Sánchez et Rodríguez-Prieto) comb. nov.	***G. leptophylla*** (Segawa) Sánchez et Rodríguez-Prieto comb. nov.
Branch pattern	Dichotomous*	Dichotomous	Dichotomous	Dichotomous	Dichotomous	Dichotomous or subdichotomous	Dichotomous
Outer cortical filaments	Compact	Straight*	Lax, curled at the base	–	–	Lax*	–
Subcortex	–	Present*	Present	Present	Present	Present	Present
Rhizoidal medullary filaments	Present	–	Present	–	–	Present	–
Secondary medullary cells	–	–	Present	–	–	–	–
Spermatangia	–	–	–	Ill-defined areas	–	Sori	–
Plant procarpic	Yes	–	Yes	–	–	Yes	–
Supporting cell	Subcortical cell	–	Subcortical cell	Cortical cell	–	Subcortical cell	–
Cells in carpogonial branch	3	–	3	2 (3?)	–	3	–
Fusion of carpogonial branch cells	Present*	–	Present	–	–	Present	–
Cells in auxiliary cell branch	2	–	2	–	–	2	–
Connecting cell between fused carpogonial branch cells and auxiliary cell	Absent	–	Absent	–	–	Present	–
Nutritive cells	Present	–	Present	Present	–	–	–
Tela arachnoidea	Present	–	Present	Present	–	Present	Present*
Components of the fusion cell	Auxiliary mother cell, auxiliary cell, surrounding cells	–	Auxiliary mother cell, lower auxiliary cell, fused cells of carpogonial branch, surrounding cells	–	–	Auxiliary mother cell, auxiliary cell, fused cells of carpogonial branch	–
Fusion cell shape	–	–	Globose	–	–	–	–
Gonimoblast origin	Primary gonimoblast cell*	–	Primary gonimoblast cell	Erect, big and ovoid cell	–	Primary gonimoblast cell*	–
Cystocarp locating	Marginal	–	Marginal	Marginal	Marginal	Marginal, scattered	Marginal
Cystocarp sessile or stipitate	–	–	Sessile	–	Sessile	–	–
Cystocarp coronate	Occasionally	–	Occasionally	Yes	–	Yes	No
Ostiole	Present	–	Present	Present	–	Present	Present*
Tetrasporangia arrangement	Sori/nemathecia	Swollen sori	Slightly raised nemathecia or scattered	Sori	–	Sori (nemathecia*)	–
Situation of tetrasporangia	Subapical	–	Subapical	–	–	–	–
Situation of the pit-connection	–	–	Lateral	–	–	–	–
Division of tetrasporangia	Cruciate or decussate*	Cruciate or decussate*	Cruciate or decussate	–	–	Cruciate	–
References	Sjöstedt, 1926; Sparling, 1957; Abbott & Hollenberg, 1976	Baardseth, 1941	Sánchez, 2005; Sánchez & Rodríguez-Prieto, 2005	Taylor, 1945; Abbott & Hollenberg, 1976	Taylor, 1960	Sparling, 1957; Dawson, 1963	Segawa, 1941

(*continued*)

Table 2. Continued

	G. microspora (Bornet ex Rodríguez y Femenías) Sánchez et Rodríguez-Prieto comb. nov.	***G. procumbens*** (Weber-van Bosse) Sánchez et Rodríguez-Prieto comb. nov.	***G. profunda*** (Børgesen) Sánchez et Rodríguez-Prieto comb. nov.	***Gloiocladia repens*** (C. Agardh) Sánchez et Rodríguez-Prieto comb. nov.	***G. spinulosa*** (Okamura et Segawa in Segawa) Sánchez et Rodríguez-Prieto comb. nov.	***G. stipitata*** (Yamada et Segawa) Sánchez et Rodríguez-Prieto comb. nov.	***G. xishaensis*** (B.M. Xia et Y.Q. Wang) Sánchez et Rodríguez-Prieto comb. nov.
Branch pattern	Dichotomous	Distichous	Irregular	Subdichotomous	Dichotomous*	Di- or polichotomous	–
Outer cortical filaments	Lax	–	–	Compact/straight	–	–	–
Subcortex	Present	–	Present	Present	Present	–	Present
Rhizoidal medullary filaments	–	–	–	Present	–	–	–
Secondary medullary cells	–	–	–	Present	–	–	–
Spermatangia	–	–	–	Sori	–	–	Sori
Plant procarpic	–	–	–	Yes	–	–	–
Supporting cell	–	–	–	Mid outer cortical cell	–	–	–
Cells in carpogonial branch	–	–	–	3 + 1 lateral cell	–	–	–
Fusion of carpogonial branch cells	–	–	–	Present	–	–	–
Cells in auxiliary cell branch	–	–	–	2	–	–	–
Connecting cell between fused carpogonial branch cells and auxiliary cell	–	–	–	Absent	–	–	–
Nutritive cells	–	–	–	Present	–	–	Present

Tela arachnoidea	–	–	Present	–	Present	Present*	
Components of the fusion cell	–	–	–	Auxiliary mother cell, lower auxiliary cell, fused cells of the carpogonial branch, supporting cell, surrounding cells	–	–	–
Fusion cell shape	–	–	–	Elongated	–	–	–
Gonimoblast origin	–	–	–	Primary gonimoblast cell	–	–	–
Cystocarp locating	Marginal	–	–	Marginal	–	Marginal	Scattered
Cystocarp sessile or stipitate	Sessile	–	–	Stipitate	–	Stipitate	–
Cystocarp coronate	–	–	–	No	Yes	No	–
Ostiole	–	–	–	Present	–	–	Present
Tetrasporangia arrangement	Nemathecia	–	Sori (Very raised nemathecia*)	Very raised nemathecia	–	–	–
Situation of tetrasporangia	–	–	–	Subapical	–	–	–
Situation of the pit-connection	–	–	–	Basal	–	–	–
Division of tetrasporangia	Cruciate or decussate*	–	Cruciate or decussate	Cruciate, decussate or irregular	–	–	–
References	Bornet, 1890	Weber-van Bosse, 1928	Børgesen, 1944	This work	Norris & Aken, 1985	Yamada, 1941	Xia & Zhang, 1999

Key: *: from the illustrations; –: unknown.

Table 3. Formal transfers to the genus *Gloiocladia*

Gloiocladia fryeana (Setchell) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Fauchea fryeana* Setchell, *Univ. Calif. Publ. Bot.*, 4: 239, pl. 31, figs 13, 14. 1912.

Gloiocladia furcellata (Baardseth) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Fauchea furcellata* Baardseth, *Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937–1938*, 9: 80–81, figs 41, 42. 1941.

Gloiocladia laciniata (J. Agardh) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Fauchea laciniata* J. Agardh, Acta Univ. Lund 21: 40. 1885.
Synonyms: *Fauchea laciniata* f. *pygmaea* Setchell et N.L. Gardner *in* Setchell, *Univ. Calif. Publ. Bot.*, 4: 238. 1912.
Fauchea pygmaea (Setchell et N.L. Gardner *in* Setchell) Kylin, Acta Univ. Lund, 37(2): 27. 1941.
Fauchea media Kylin, *Lunds Universitets Årsskrift, Ny Foljd, Andra Afdelningen*, 37(2): 27, pl. 10, fig. 24. 1941.

Gloiocladia galapagensis (W.R. Taylor) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Fauchea galapagensis* W.R. Taylor, *Allan Hancock Pacif. Exped.*, 12: 246–247, pl. 82, figs 1, 2. 1945.

Gloiocladia hassleri (M. Howe et W.R. Taylor) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Fauchea hassleri* M. Howe et W.R. Taylor, *Brittonia*, 1: 13, fig. 6, pl. 2, figs 2, 3. 1931.

Gloiocladia leptophylla (Segawa) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Fauchea leptophylla* S. Segawa, *Sci. Pap. Inst. Algol. Res., Fac. Sci. Hokkaido. Univ.*, 2: 264–265, fig. 10, pl. 58, fig. 1. 1941.

Gloiocladia microspora (Bornet ex Rodríguez y Femenías) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Fauchea microspora* Bornet ex Rodríguez y Femenías, *Bull. Soc. Bot. Fr.*, 37: 142, figs 1–4. 1890.

Gloiocladia procumbens (Weber-van Bosse) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Fauchea procumbens* Weber-van Bosse, *Siboga Exped. Monogr.*, 59: 459, pl. 11, figs 2, 3. 1928.

Gloiocladia profunda (Børgesen) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Fauchea profunda* Børgesen, *Det Kgl. Danske Vid. Selsk. Biol. Medd.*, 19: 11, figs 6–8. 1944.

Gloiocladia repens (C. Agardh) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Sphaerococcus repens* C. Agardh, *Species Algarum rite cognitae*. Vol. 1, part 2: 244–245. 1823.
Synonyms: *Gracilaria repens* (C. Agardh) J. Agardh, *Algae maris Mediterranei et Adriatici*, 152. 1842.
Dichophycus repens (C. Agardh) Zanardini, *Atti del Reale Istituto Veneto di Scienze, Lettere ed Arti,* 6: 16, pl. 6, figs a–i. 1847.
Fauchea repens (C. Agardh) Montagne et Bory *in* Montagne, *Exploration scientifique de l'Algérie pendant 1840–42, Sciences naturelles, Botanique, 1, Cryptogamie*: 64–67. 1846.

Gloiocladia spinulosa (Okamura et Segawa *in* Segawa) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Fauchea spinulosa* Okamura et Segawa *in* Segawa, *Sci. Pap. Inst. Algol. Res., Fac. Sci., Hokkaido Univ.,* 1: 84–85, figs 4, 5, pl. 20, fig. 2. 1935.

Gloiocladia stipitata (Yamada et Segawa) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Fauchea stipitata* Yamada et Segawa *in* Yamada, *Sci. Pap. Inst. Algol. Res. Fac. Sci., Hokkaido Univ.*, 2: 200, pl. 44. 1941.

Gloiocladia xishaensis (B.M. Xia et Y.Q. Wang) Sánchez et Rodríguez-Prieto comb. nov.
Basionym: *Fauchea xishaensis* B.M. Xia et Y.Q. Wang, *Acta Phytotaxon. Sin.*, 38: 38, figs 3, 6. 2000.

cell of the carpogonial branch. Auxiliary cell branch two-celled, composed of an auxiliary mother cell and an auxiliary cell, and situated on the supporting cell. Carpogonial branch cells fusing after fertilization and connecting to the auxiliary cell, which divides transversely to form a primary gonimoblast cell. Nutritive cells and tela arachnoidea present. Fusion cell formed through coalescence of the auxiliary and auxiliary mother cells, the fused cells of the carpogonial branch and the surrounding cells, with the supporting cell sometimes participating in the fusion process. Constituents of the fusion cell (except the supporting cell) are indiscernible when the structure is mature. Gonimoblast arising from the distal end of the primary gonimoblast cell consisting of several elongated lobes of ovoid carposporangia, and surrounded by the cells of the tela arachnoidea. Cystocarps situated on the branch margins or on the thallus surface, sessile or substipitate, prominent, globose, and ostiolated. Tetrasporangia developed in nemathecia or scattered, subapical, cruciately, decussately cruciate or irregularly divided.

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