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Vegetative and reproductive morphology of *Helminthocladia calvadosii*, *H. agardhiana* and *H. reyesii* sp. nov. (Liagoraceae, Rhodophyta) from the eastern Atlantic

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The type species of *Helminthocladia, Helminthocladia calvadosii,* and two species known from the eastern Atlantic and Mediterranean, *H. agardhiana* and *H. reyesii* O'Dwyer & Afonso-Carrillo *sp. nov.*, are described in detail. The species are mainly distinguishable by their habit, the morphology of the cortical fascicles, and the type of carposporangium (undivided single terminal, quadripartite single terminal, and undivided in short chains). The previously controversial reproductive morphology in *H. calvadosii* has been clarified from observations of plants from northern Spain. In *H. calvadosii,* simultaneously with gonimoblast development, sterile postfertilization filaments are produced from the suprasupporting cell and some other cortical cells adjacent to the carpogonial branch. The development of these sterile filaments is highly variable within the same area of the plant. Sterile filaments can be absent, presenting an entirely naked carpogonial branch below the mature carposporophyte. *H. reyesii,* known so far only from the Canary Islands, has a unique feature: the elaboration from the suprasupporting cells of sterile moniliform postfertilization filaments that partially or completely surround the carpogonial branch. Additionally, *H. reyesii* differs from other *Helminthocladia* species by a unique combination of significant attributes. We analyse the features used at present to delineate the genus *Helminthocladia* in the Liagoraceae and give a comparative table of the morphological attributes of the species currently accepted in *Helminthocladia.*

INTRODUCTION

The genus *Helminthocladia* was established by J. Agardh (1852) and includes multiaxial, variously branched species with a medulla of slender filaments; a cortex of subdichotomously divided filaments with terminal cells that are usually enlarged; lateral carpogonial branches with a short conical carpogonium; an initial median division of fertilized carpogonium, the division usually being oblique, with both products dividing to form the carposporophyte; compact gonimoblasts of densely aggregated filaments and sterile postfertilization filaments produced from various cells adjacent to the carpogonial branch; and the absence of descending rhizoidal filaments. Its distinctive features within the family Liagoraceae are a matter of controversy. Delineation of genera in the Liagoraceae is largely based on reproductive features (Huisman & Kraft 1994), and the nature of the sterile filaments associated with the carposporophyte has figured prominently in definitions of various genera in the Liagoraceae. In *Helminthocladia,* this is a controversial character, owing to the contradictory information published on postfertilization development in European plants of *H. calvadosii* (Lamouroux *ex* Duby) Setchell, the type species of the genus. Rosenvinge [1909, referring to *H. calvadosii* as *H. purpurea* (Harvey) J. Agardh] described the carposporophyte as being surrounded by sterile filaments, while Kylin (1930) observed gonimoblasts lacking sterile filaments. Papenfuss (1946) suggested that two different taxonomic entities might be involved. Consequently, before a consistent definition of *Helminthocladia* can be developed, *H. calvadosii* needs to be studied with respect to the presence or absence of sterile filaments (Womersley 1965).

Species of *Helminthocladia* have been defined by a combination of features: (1) external ones, such as habit and branching pattern; (2) internal vegetative features, such as the length of the cortical fascicles and the size and shape of the outer cortical cells; and (3) reproductive characters, such as the plane of the first division of the fertilized carpogonium, the presence or absence of postfertilization fusion between the carpogonial branch cells, the origin and degree of development of sterile postfertilization filaments, the size of the gonimoblast, the type of carposporangium (undivided or quadripartite, single or in short chains), the anatomy of spermatangial axes, and the monoecious or dioecious nature of the gametophytes (Womersley 1965, 1994; Searles & Lewis 1983; Afaq-Husain & Shameel 1991). As it is currently circumscribed, the genus *Helminthocladia* contains 12 species, most of them from warm temperate seas in both hemispheres, where they are generally sublittoral and grow as ephemeral spring–summer annuals. Various authors have credited some 19 species, but Womersley (1965) has reduced many to synonymy under *H. australis* Harvey. *H. calvadosii* has been reported from both the eastern and western Atlantic, and India (Dixon & Irvine 1977; Guimarães *et al.* 1990; Silva *et al.* 1996; Wynne 1998). *H. australis* has been widely reported from Australia and New Zealand (Womersley 1965, 1994), China (Tseng 1983), Japan (Umezaki 1960, as *H. macrocephala* Yamada), South Africa (Martin 1939, as *H. papenfussii* Kylin) and California [Abbott 1965, as *H. californica* (J. Agardh) Kylin]. *H. densa* (Harvey) Schmitz & Hauptfleisch is recorded from Australia, New Zealand and Tasmania (Womersley 1965, 1994), and *H. agardhiana* Dixon is known

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from the eastern Atlantic and the Mediterranean Sea (Dixon 1962a, 1962b; Sansón *et al.* 1991; Aleem 1993). The remaining species have been only reported infrequently and appear to have very restricted distributions. *H. dotyi* Womersley (1965) from Australia and Tasmania; *H. beaugleholei* Womersley (1965) from Australia; *H. rhizoidea* Doty & Abbott (1961) and *H. simplex* Doty & Abbott (1961) from Hawaii; *H. senegalensis* Bodard (1971) from Senegal; *H. andersonii* Searles & Lewis (1983) from North Carolina (USA); *H. nizamuddinii* Afaq-Husain & Shameel (1991) from Pakistan; and *H. sreeramului* Umamaheswara Rao (1991) from India. As well as *H. calvadosii,* several species, including the eastern Atlantic *H. agardhiana* and *H. senegalensis,* are in need of investigation, owing to the limited number of specimens on which descriptions were based and to the poor knowledge of the limits of morphological variability within species.

During recent taxonomic studies of the Liagoraceae of the Canary Islands (Kvaternik & Afonso-Carrillo 1995; Kvaternik *et al.* 1996; Afonso-Carrillo *et al.* 1998), some specimens of *Helminthocladia* were examined and two species were identified: *H. calvadosii* and *H. agardhiana* (Afonso-Carrillo & Sansón 1999). New observations carried out on plants of *H. calvadosii* from Europe and numerous specimens collected recently in the Canaries showed obvious differences among these plants. In the present report we examine in detail the postfertilization changes in European plants of the controversial features found in the type species, *H. calvadosii,* and compare them with those observed in *H. agardhiana* and the newly described species *H. reyesii.*

MATERIAL AND METHODS

Observations are based on (1) fresh specimens collected at Lastras de Pachón, Santander (northern Spain) and Tenerife (Canary Islands), preserved in 4% formalin in seawater and deposited at TFC; and (2) dried herbarium specimens housed at L and TFC (herbarium abbreviations follow Holmgren *et al.* 1990). Selected fragments from formalin-preserved material were stained in 1% aniline blue, mounted in a 50% Karo® corn syrup solution, and slightly squashed to separate the filaments. Dried specimens from herbaria were rehydrated in 4% formalin in seawater. Drawings were obtained by using a camera lucida attached to a Zeiss microscope. Cell measurements are given as diameter × length.

OBSERVATIONS

Helminthocladia calvadosii (Lamouroux *ex* Duby) Setchell

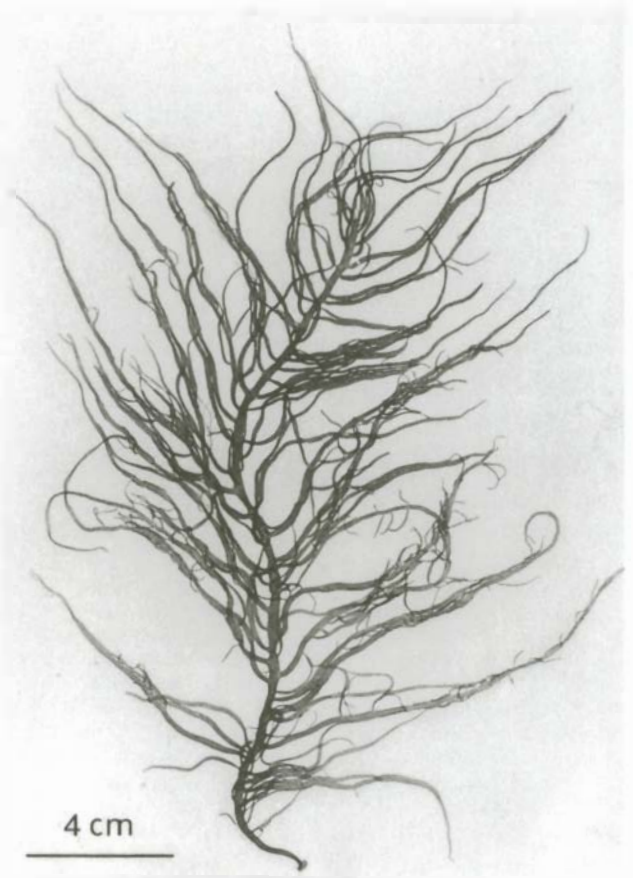
Figs 1–18

BASIONYM: *Dumontia calvadosii* Lamouroux *ex* Duby (1830) p. 941. [For a full list of synonyms see Hamel (1930) and Dixon & Irvine (1977)].

LECTOTYPE: in CN ('provisional' designation by Dixon & Irvine 1977).

TYPE LOCALITY: Calvados (France).

REPRESENTATIVE SPECIMENS EXAMINED: Germany: Helgoland (*P. Kuckuck,* 01 September 1895, L919.335338; *P. Kuckuck,* 28 August 1897, L963.58476; *W. Sonder,* without date, L941.95205). United Kingdom: Torquay (*M. Wyatt,* without date, L910.1841308). France: Calvados (*J.F. Chauvin,* without date, L. 941.95209), Herm (*C. den Hartog,* 07 September 1960, L961.26281), Roscoff (*A.A. Weber-van Bosse,* 1894, L941.95204), Cap de la Chêvre (*T. C. Kemperman & H. Stegenga,* 28 September 1981, L5477), Belle Ile (*A.A. Weber-van Bosse,* July 1851, L941.156179). Spain: Lastras de Pachón, Santander (*J. Cremades,* 09 August 1989, 4 m depth, TFC Phyc 10034), Punta Insua, La Coruña (*J. Otero,* 26 May 1990, 2 m depth, TFC Phyc 10032 *ex* SANT), Playa San Francisco, La Coruña (*J. Cremades,* 20 August 1989, 3 m depth, TFC Phyc 10033 *ex* SANT).

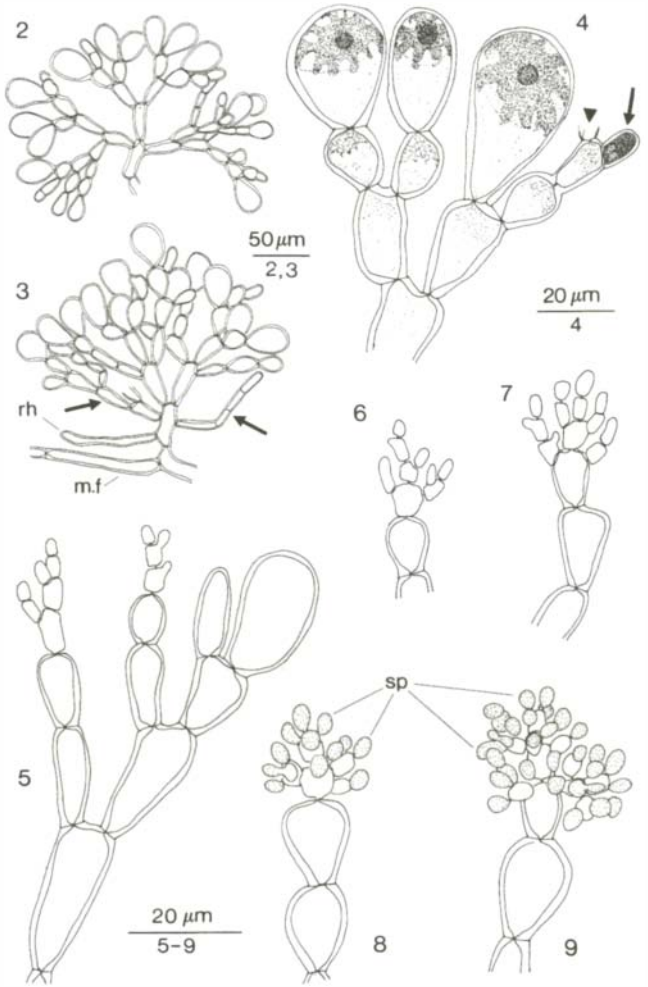


Abbreviations for Figs 1–47. ca = carposporangium; c.br = carpogonial branch; cp = carpogonium; g.f = gonimoblastic filament; is = infrasupporting cell; m.f = medullary filament; rh = rhizoid; s = supporting cell; sp = spermatangium; ss = suprasupporting cell; st.f_1 = sterile filament produced from the suprasupporting cells; st.f_2 = sterile filament produced from the infrasupporting cell and adjacent cells; tr = trichogyne.

Fig. 1. *H. calvadosii:* habit (TFC Phyc 10032).

DISTRIBUTION: *H. calvadosii* forma *calvadosii* has been reported in the eastern Atlantic Ocean from Denmark to the Canaries and Cape Verde Islands and in the western Atlantic Ocean from Florida to Brazil. The remainder *formae* are only known from the Indian Ocean: *H. calvadosii* f. *indica* Desikachary (1957) and *H. calvadosii* f. *comorinensis* Krishnamurthy & Sundararajan (1985) are both reported from India.

HABITAT AND SEASONALITY: *H. calvadosii* is a late spring–summer annual (May–September), occurring in the upper sublittoral, usually on rocks next to the sand, at depths of 1–5 m.



Figs 2–9. *H. calvadosii* (TFC Phyc 10034).
Fig. 2. Little-developed cortical fascicle.
Fig. 3. Well-developed cortical fascicle. Note the origin of a rhizoid and adventitious cortical filaments (arrows) from the basal cell of the cortical fascicle.
Fig. 4. Detail of terminal cells of cortical filaments showing large and clavate cells with an irregularly stellate chloroplast and a central pyrenoid. Note a presumed secretory cell (arrow) and remnant cell walls (arrowhead).
Figs 5–7. Early developmental stages of spermatangial clusters arising from nonenlarged terminal cortical cells.
Figs 8, 9. Mature spermatangial clusters showing terminal spermatangia.

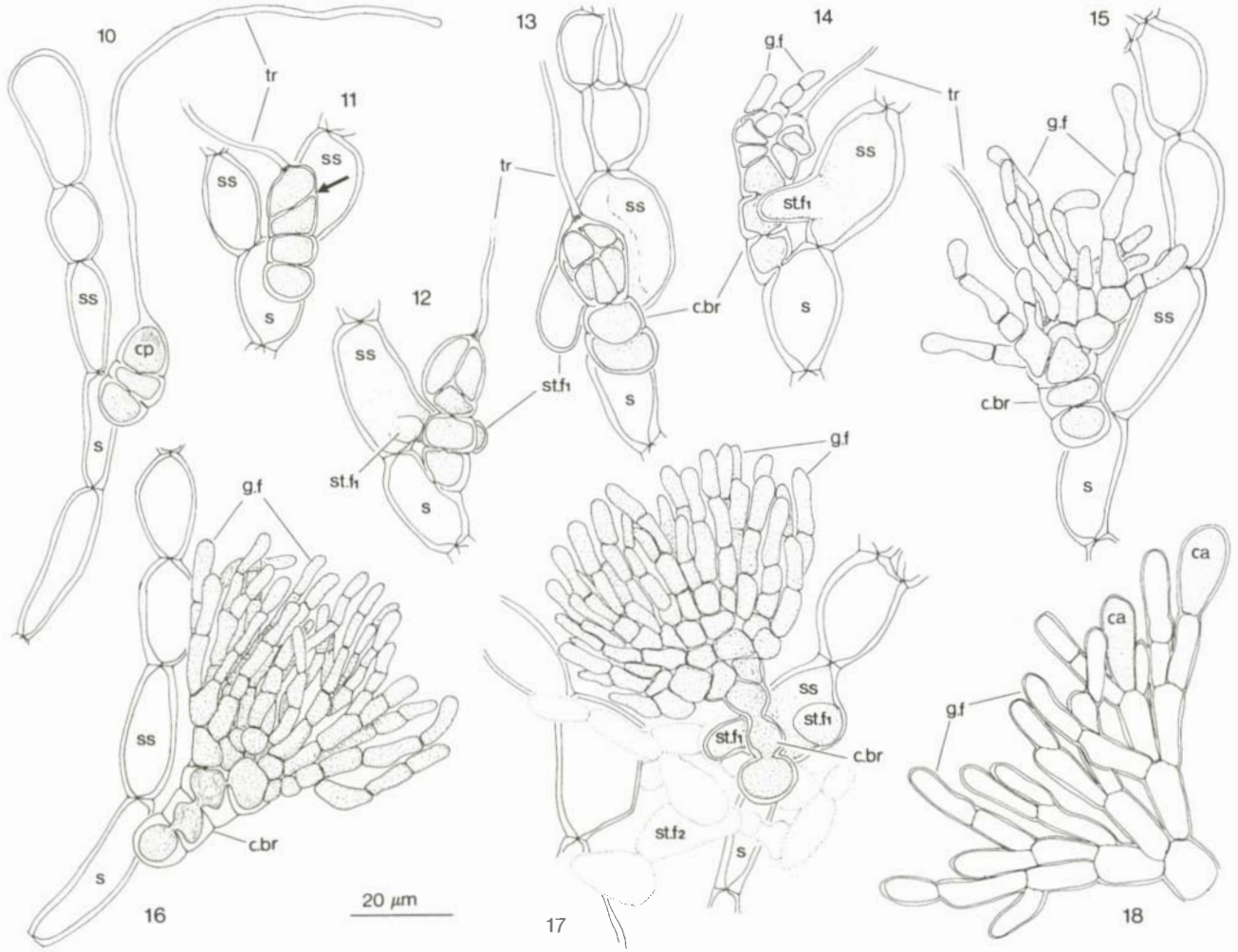
HABIT: Plants are erect, arising from a single discoid holdfast, to 60 cm in height, red to brown in colour, mucilaginous, smooth and slippery but firm, and radial to irregularly branched (Fig. 1). Main axes are terete or slightly compressed, 2–15 mm in diameter below, 0.4–2 mm above. Lateral and adventitious branches vary from few to numerous; they are long, simple or little branched, and gradually decrease in diameter towards the apex and base.

VEGETATIVE STRUCTURE: Axes are multiaxial, with a central medulla composed of loose filaments composed of subcylindrical cells measuring 3–6 × 80–150 μm in the apical 2 mm of axes to 12 × 160 μm at 15 mm from the apex. Each cell of each external medullary filament branches distally to form a cortical fascicle orientated at right angles to the medullary axis (Figs 2, 3). The medulla becomes surrounded by numerous rhizoids that arise from the basal one to three cells of the cortical fascicles (Fig. 3). Cortical filaments are four to six cells long, up to 180 μm in length, and are branched three or four times, pseudodichotomously to trichotomously (Figs 2, 3). Much of the branching arises from adventitious initials that develop distally on cells of the filaments. Adventitious cortical filaments and rhizoids are common, arising from basal cells. Rhizoids produce perpendicularly adventitious cortical filaments and cortical fascicles. The one to three basal cells of the cortical fascicles are subcylindrical, 7.5–9 × 20–30 μm; subterminal cells are shorter, 13–17.5 × 15–20 μm; and terminal cells are large, clavate, (15–)20–26(–32) × 27–36(–50) μm (Figs 2, 3), showing a conspicuous, irregularly stellate chloroplast and a central pyrenoid (Fig. 4). In young axes, small terminal cortical cells often bear two subcylindrical darkly stained cells, 7.5 × 10 μm, assumed to be secretory cells or remnant cell walls (Fig. 4). Hairs were not observed.

REPRODUCTION: Gametophytes are monoecious. Spermatangial clusters are densely paniculate and borne on nonenlarged terminal cells of cortical fascicles (Figs 5–7). Spermatangial axes are three-celled, bearing three to six radially positioned spermatangial mother cells, which in turn cut off two to three ovoid spermatangia 3–5 μm in diameter (Figs 8, 9).

Carpogonial branches arise on the basal two to three cells of cortical fascicles and are straight to slightly curved, 8–10 × 21–23 μm (Fig. 10). They consist of (2–)3(–4) cells, with the conical carpogonium prolonged by a trichogyne that often has several spermatia attached to it. After presumed fertilization, the base of the trichogyne is plugged and the carpogonial branch cells and the suprasupporting cell appear darkly stained. The first division of the carpogonium is longitudinally oblique (Fig. 11) and later the basal daughter cell itself divides obliquely (Fig. 12); both cells take part in the formation of the gonimoblast. Young gonimoblasts are formed by densely compacted isodiametric cells (Fig. 13), which later form outwardly growing, relatively loose gonimoblastic filaments which are up to five cells long, subdichotomous and composed of subcylindrical cells, 4–8 × 12–15 μm (Figs 14–17). Mature gonimoblasts are slightly penicillate in shape, 100–150 μm in diameter, and bear single ovoid terminal carposporangia, 7–9 μm × 15–20 μm (Fig. 18), and residual carposporangial walls.

During gonimoblast development, cells of the carpogonial branch fuse and often the proximal cells of the gonimoblast also (Figs 16, 17). Sterile postfertilization filaments (a few cells long), produced from cortical cells adjacent to the carpogonial branch, are common, but sterile filaments can be absent in numerous gonimoblasts within the same area of the gametophyte (Figs 15, 16). Sterile filaments arise only from the suprasupporting cell, from some cells of the adjacent cortical filaments, and occasionally from the infrasupporting cell. Two short filaments, one or two cells long, arise laterally from the suprasupporting cell (Figs 12–14), and curve and grow towards the carpogonial branch, which is partially embraced (Fig. 17). Other sterile filaments, arising from the adjacent cortical filaments or from the infrasupporting cell often produce laterally pigmented filaments of cells like those of the cortex.



Figs 10–18. *H. calvadosii* (TFC Phyc 10034).
Fig. 10. Carpogonial branch.
Fig. 11. First longitudinally oblique division of the fertilized carpogonium (arrow).
Fig. 12. Second division of the fertilized carpogonium showing both products of the carpogonium taking part in gonimoblast production. Sterile filaments arise from the suprasupporting cell.
Figs. 13, 14. Early developmental stages of carposporophytes with young gonimoblasts composed of densely compacted isodiametric cells. Note sterile filaments arising from the suprasupporting cell.
Figs 15–17. Young gonimoblasts consisting of relatively loose outwardly orientated gonimoblastic filaments. Note the absence of sterile filaments in Figs 15 and 16.
Fig. 18. A fragment of a mature gonimoblast showing terminal carposporangia.

REMARKS: Although *H. calvadosii* has been examined in numerous previous studies (e.g. Rosenvinge 1909; Hamel 1930; Kylin 1930; Dixon & Irvine 1977), our findings are presented in order to clarify its controversial reproductive morphology and to facilitate comparisons between the type species and taxa from the Canary Islands. In *H. calvadosii,* contradictory descriptions of postfertilization development have been published. Rosenvinge (1909, as *H. purpurea*) found that the gonimoblast was surrounded by sterile postfertilization filaments. Kylin (1930), however, observed a gonimoblast without sterile filaments. This feature was therefore assumed to vary between individuals of *H. calvadosii* (Papenfuss 1946; Doty & Abbott 1961; Womersley 1965), suggesting perhaps that two different species were involved (Papenfuss 1946). The apparent inconsistency of Rosenvinge's and Kylin's observations prevented the full characterization of the type species and compromised the delineation of *Helminthocladia.* However, our postfertilization observations, carried out mainly on liquid-preserved specimens from northern Spain (TFC Phyc 10034), have shown that *H. calvadosii* exhibits a wide range of variation in the sterile postfertilization filaments. In the same part of the plant, there may be short, sterile filaments that partially encircle a portion of the carpogonial branch, or sterile filaments may be entirely absent. Thus, the observations of Rosenvinge (1909) and Kylin (1930) are not contradictory: the type species is variable with respect to this feature and there is no indication, from this source at least, that *H. calvadosii* is heterogeneous.

H. calvadosii exhibits two vegetative attributes useful for species delineation: (1) the irregular to radially branched main axes of the habit; and (2) the short cortical fascicles (less than 180 μm in length). Both features were known from previous

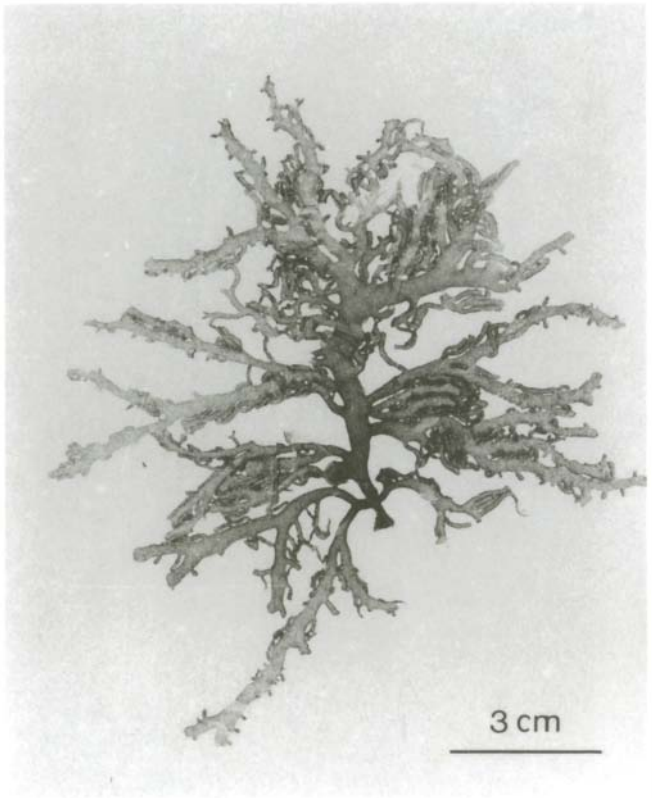


Fig. 19. *H. agardhiana:* habit (TFC Phyc 10031).

descriptions (Hamel 1930; Feldmann 1939; Dixon & Irvine 1977) and were prominent in all specimens examined.

Helminthocladia agardhiana Dixon

Figs 19–30

SYNONYM: *Helminthocladia hudsonii* J.G. Agardh *auct. nonn.* (see Dixon 1962a, pp. 245–249)

HOLOTYPE: LD, Herb. alg. Agardh 31937 (Dixon 1962a).

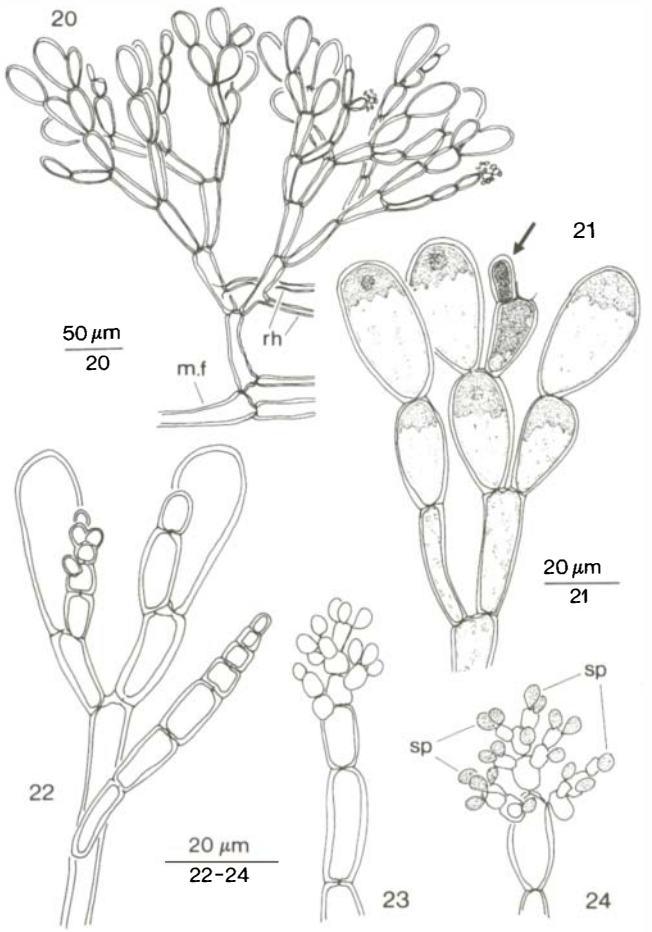
TYPE LOCALITY: Tangier (Morocco).

REPRESENTATIVE SPECIMENS EXAMINED: Canary Islands, Tenerife: El Médano (*M. Sansón & J. Reyes,* 14 May 1990, TFC Phyc 5708, and 10 July 1991, TFC Phyc 7677; *J. Reyes,* 08 May 1992, TFC Phyc 7849; *M. Sansón, J. Reyes & J. Afonso-Carrillo,* 18 July 1998, TFC Phyc 10016–10024; *M. Sansón, J. Afonso-Carrillo & J.A. O'Dwyer,* 21 April 1999, TFC Phyc 10031).

DISTRIBUTION: Eastern Atlantic: Spain, Morocco, Canary Islands, Mediterranean Sea.

HABITAT AND SEASONALITY: Plants grow at 1–3 m depth on rocks next to beds of sand, occasionally as an epiphyte on *Cymodocea nodosa* (Ucria) Ascherson, and occur seasonally from spring (April) to early summer (July).

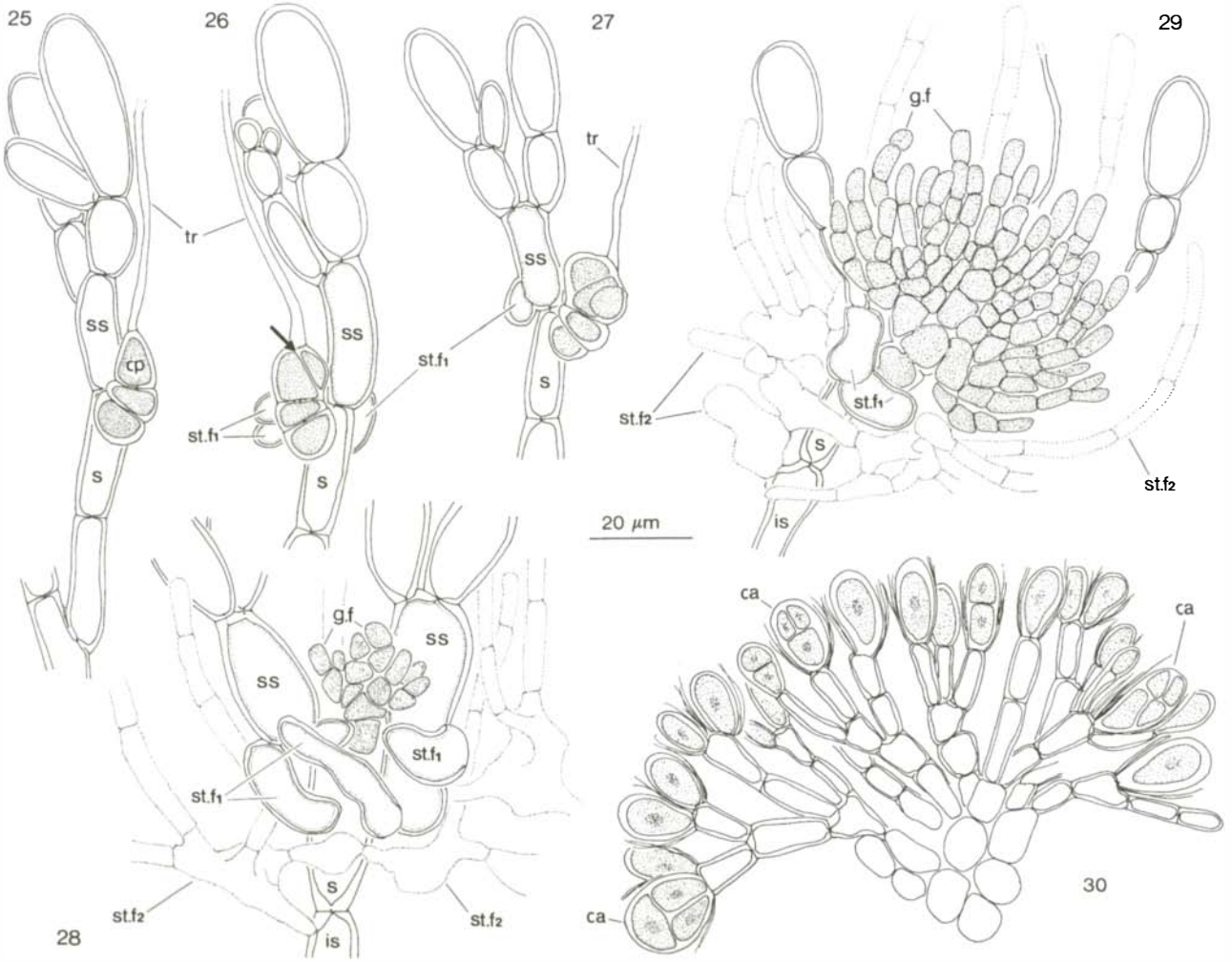
HABIT: Plants are erect, up to 23 cm high, reddish-brown to yellowish-green, mucilaginous, smooth and slippery but firm, with one to five main axes arising from a small discoid holdfast (Fig. 19). Main axes branch close to the holdfast and are densely irregularly branched below, with some subdichotomies above. They are terete or slightly compressed, up to 10



Figs 20–24. *H. agardhiana.*
Fig. 20. Well-developed cortical fascicle (TFC Phyc 10018).
Fig. 21. Detail of a cortical fascicle, showing enlarged outer cortical cells and a secretory cell (arrow) (TFC Phyc 5708).
Fig. 22. Early developmental stage of spermatangial clusters (TFC Phyc 10018).
Fig. 23. Immature spermatangial cluster (TFC Phyc 10022).
Fig. 24. Mature spermatangial cluster (TFC Phyc 10017).

mm in diameter, with branch tips 0.5 mm in diameter; they usually bear numerous simple or furcate lateral adventitious branches, *c.* 1 mm in diameter. Senescent plants are verrucose, as a result of branch loss.

VEGETATIVE STRUCTURE: Medullary filaments are composed of subcylindrical cells, which are 6–15 × 60–200 µm in the apical 2 mm of axes to 10–40 × 200–350 µm 15 mm from the apex. Rhizoidal filaments arise from the basal one to three cells of cortical fascicles (Fig. 20). Mature cortical filaments are 6–8 cells long, up to 350 µm long, and five to six times branched, the branching being pseudodichotomous to trichotomous (Fig. 20). The one to four basal cells of the cortical fascicles are subcylindrical, 8–20 × 40–60(–80) µm; the subterminal cells are shorter and ovoid to pyriform, and the terminal cells are larger and clavate, up to 30 × 60 µm (Fig. 20). A stellate chloroplast with a conspicuous pyrenoid is present in each cell (Fig. 21). Some terminal nonenlarged cortical cells on young axes often bear two darkly stained subcylindrical secretory cells (or remnant cell walls), 7.5 × 50 µm (Fig. 21). Hairs were not observed.

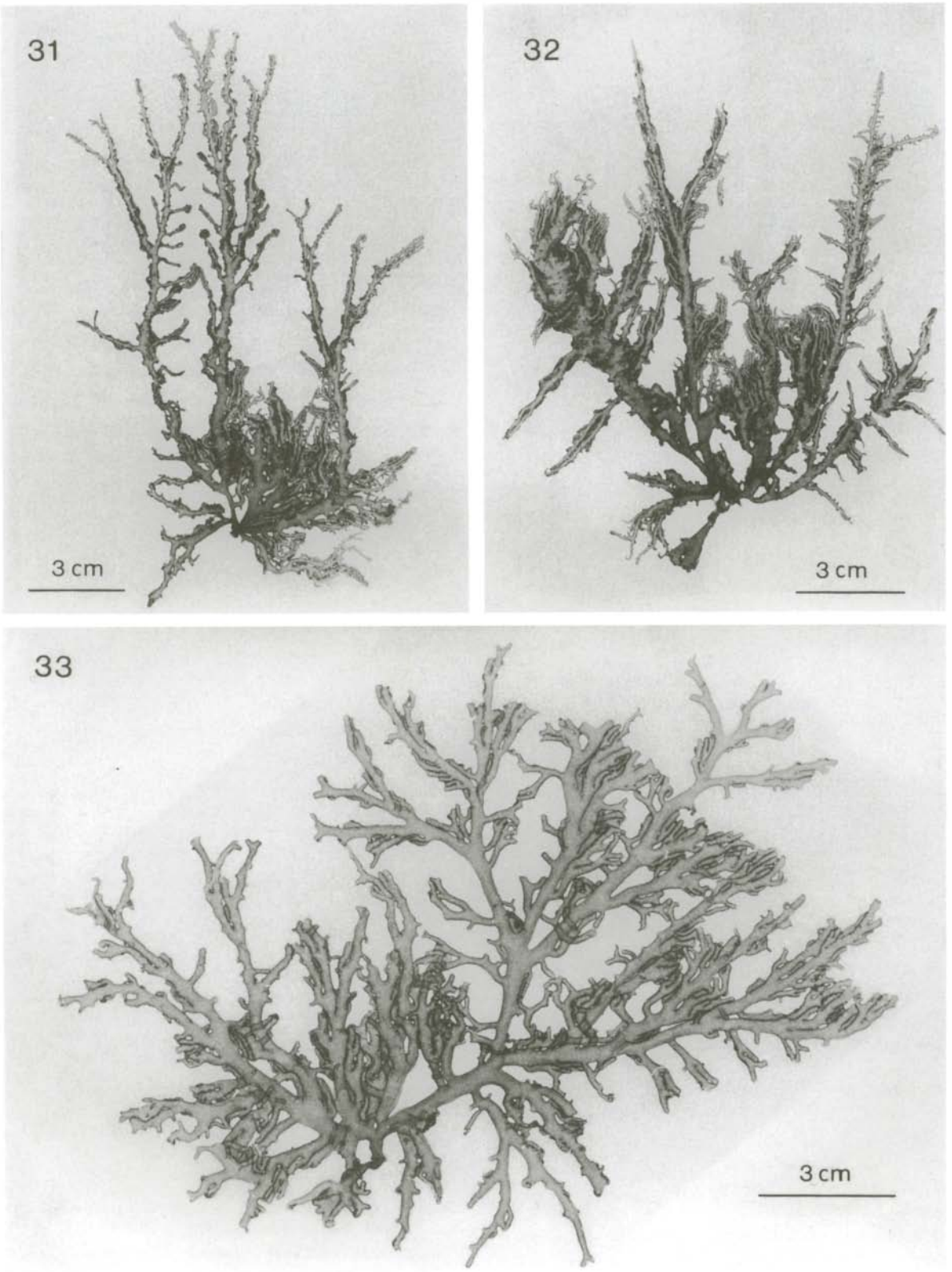


Figs 25–30. *H. agardhiana.*
Fig. 25. Cortical filament bearing a carpogonial branch (TFC Phyc 5708).
Fig. 26. First longitudinally oblique division of the carpogonium (arrow) (TFC Phyc 7677).
Fig. 27. Second division of the fertilized carpogonium (TFC Phyc 10022).
Fig. 28. Early developmental stage of the carposporophyte, showing both products of the carpogonium taking part in gonimoblast production. Note numerous sterile filaments arising from the suprasupporting cells and the infrasupporting cell (TFC Phyc 5708).
Fig. 29. Young carposporophyte with extensive development of sterile filaments around cells of the carpogonial branch, some of them producing cortical-type filaments laterally (TFC Phyc 10018).
Fig. 30. A fragment of a mature gonimoblast with immature undivided and mature quadripartite terminal carposporangia (TFC Phyc 10018).

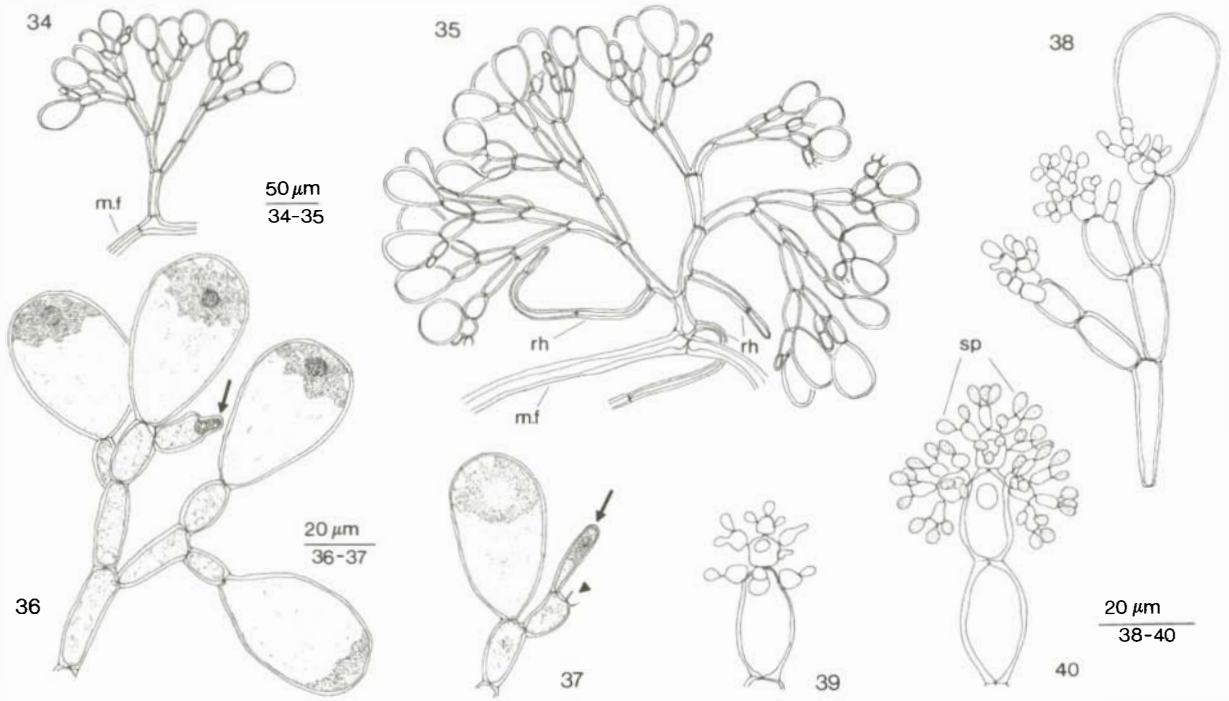
REPRODUCTION: Gametophytes are monoecious. Spermatangial paniculate clusters arise on nonenlarged terminal cells of cortical fascicles (Fig. 22). Three to four spermatangial mother cells are borne on each cell of the three-celled spermatangial axis, each forming two to three subspherical spermatangia, 2–3 μm in diameter (Figs 23, 24).

Carpogonial branches are slightly curved, 7–9(–12) × 19–22(–28) μm, and are borne on the basal three to four cells of the cortical fascicles (Fig. 25). They consist of 3(–4) cells, with a conical carpogonium (Fig. 25). After presumed fertilization, the cells of the carpogonial branch, the supporting cell and both suprasupporting cells become darkly stained. The first division of the carpogonium is longitudinally oblique (Fig. 26) and both products divide (Fig. 27), producing short and densely compact gonimoblast filaments (Fig. 28). Distally, this young gonimoblast forms subdichotomous or trichotomous relatively loose gonimoblastic filaments up to five cells in length (Fig. 29), with subcylindrical cells 10 × 20 μm. The filaments develop single terminal carposporangia, which are irregularly quadripartite and ovoid, 7–15 × 12–21 μm (Fig. 30). Residual carposporangial walls are retained (Fig. 30). Mature gonimoblasts are subhemispherical and up to 350 μm in diameter (in surface view).

Simultaneously, cells of the carpogonial branch fuse and sterile postfertilization filaments are formed from the suprasupporting cells, the infrasupporting cell and some other cells of adjacent cortical filaments (Fig. 28). Both suprasupporting cells enlarge towards the carpogonial branch and form short simple filaments containing up to four subcylindrical cells; the filaments gradually increase in size and finally encircle the carpogonial branch completely (Fig. 28). The remaining sterile filaments consist of slender cells, several of which become



Figs 31–33. *H. reyesii.*
Fig. 31. Holotype specimen, female (TFC Phyc 9982).
Fig. 32. Male isotype specimen (TFC Phyc 9984).
Fig. 33. Female specimen (TFC Phyc 9985).



Figs 34–40. *H. reyesii* (holotype TFC Phyc 9982, unless stated).
Fig. 34. Little-developed cortical fascicle obtained from the apical branch.
Fig. 35. Well-developed cortical fascicle.
Fig. 36. Detail of cortical filaments showing enlarged terminal cells. Note a secretory cell (arrow) on an nonenlarged outer cortical cell.
Fig. 37. Detail of cortical filament with deciduous terminal hair (arrow) and remnant cell walls (arrowhead).
Figs 38, 39. Early developmental stages of spermatangial clusters (TFC Phyc 9984).
Fig. 40. Mature spermatangial cluster (TFC Phyc 9984).

inflated and form pigmented filaments of cortex-type cells (Figs 28, 29).

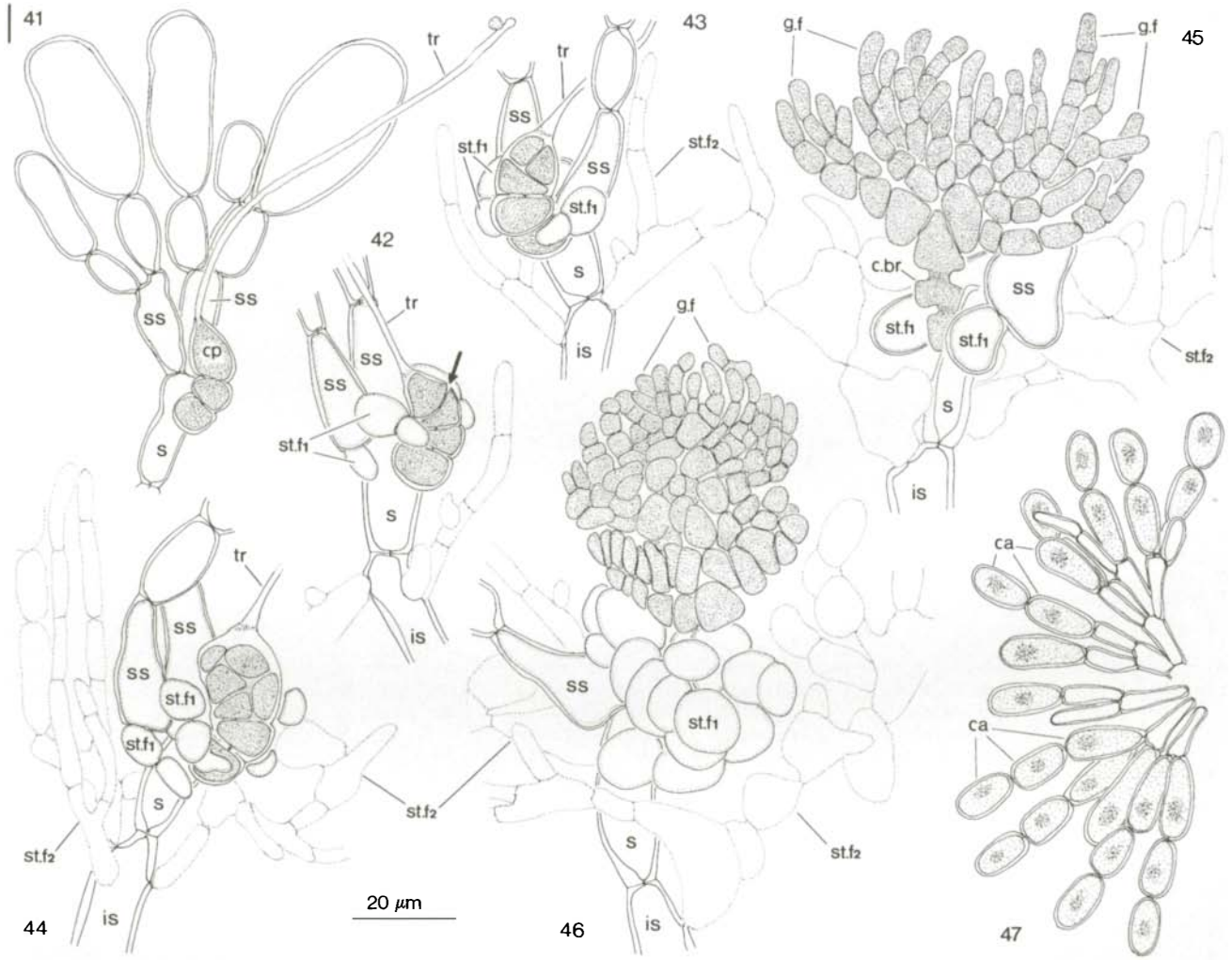
REMARKS: Dixon (1962a) proposed the name *H. agardhiana* as a substitute for *H. hudsonii* (C. Agardh) J. Agardh (1852) because the specimen examined by J. Agardh from Tangier was not conspecific with that to which the basionym *Mesogloia hudsonii* C. Agardh was applied, which is a specimen of *Halarachnion ligulatum* (Woodward) Kützing. *H. agardhiana* has been characterized by Feldmann (1939, as *H. hudsonii*) as having the following features: (1) plants that grow up to 30 cm high, with subdichotomously branched main axes; (2) cortical fascicles and proximal cortical cells that are longer than in *H. calvadosii*; (3) an absence of sterile postfertilization filaments; and (4) quadripartite carposporangia. Plants collected in the Canary Islands agree with previous accounts of the species, except in the presence of sterile filaments. However, in *H. calvadosii,* the presence or absence of sterile postfertilization filaments is a variable feature and it is likely that in *H. agardhiana* too this character is without diagnostic value for species delineation. *H. agardhiana* is closely related to *H. senegalensis* (Bodard 1971), which also forms quadripartite carposporangia but differs by the transversely oblique first division of the carpogonium and the lack of fusion in the carpogonial branch. Both features appear to have limited taxonomic value (Womersley 1965). A review of fresh material of *H. senegalensis* is needed before the status of this taxon can be evaluated.

Helminthocladia reyesii O'Dwyer & Afonso-Carrillo, *sp. nov.*

Figs 31–47

Plantae saxicolae, erectae usque 26 cm altae, axes lubrici, cylindrici vel leviter compressi, usque 10 mm diametro. Axes principales subdichotome ramificati paucis vel numerosis ramis adventitiis. Rami multiaxiales, medulla multis filamentis medullosis, cortex in fasciculos usque 400 μm longos. Cellulae corticales exteriores claviformes, 20–35 × 36–60 μm. Plantae monoicae vel dioicae. Spermatangia racemos paniculatim densos in cellulis corticalibus terminalibus vel subterminalibus non amplificatis formantia. Rami carpogoniales 3(–4) cellulis lateraliter in cellula sustinente in cortice interno portati. Post fecundationem carpogonium conicum dividens transversaliter oblique et utraque mediana oriuntur massam compactam initialem filamentorum gonimoblasticorum, quae filamenti gonimoblastici relative soluti cum catenis brevibus distalibus 1–3 carposporangiorum indivisorum, 5–7 × 11–20 μm. Carposporophytum maturum 140–250 μm diametro. Cellulae ramorum carpogonialium conjugant. Filamenta sterilia moniliformia orientia ab utraque cellula suprasustinente circumdant partialiter aut omnino ramum carpogoniale, et possunt formare massam compactam sub gonimoblasto. Tetrasporophytum tetrasporangiaque ignota.

Plants saxicolous, erect, to 26 cm in height, the axes smooth and slippery, terete or slightly compressed, up to 10 mm in diameter. Main axes subdichotomously branched with several to numerous adventitious branches. Branches multiaxial, the medulla consisting of many medullary filaments, the cortex consisting of fascicles up to 400 μm in length. Outer cortical cells clavate, 20–35 × by 36–60 μm. Plants monoecious or dioecious. Spermatangia forming dense paniculate clusters on terminal or subterminal nonenlarged cortical cells. Carpogonial branches 3(–4)-celled, borne laterally on inner cortical supporting cell. Following fertilization the conical car-



Figs 41–47. *H. reyesii* (holotype TFC Phyc 9982, unless otherwise stated).
Fig. 41. Carpogonial branch.
Fig. 42. First transversely oblique division of the fertilized carpogonium (arrow). Note sterile filaments arising from both suprasupporting cells and the infrasupporting cell.
Figs 43, 44. Early developmental stages of the carposporophyte, with both products of the carpogonium taking part in gonimoblast production. Note sterile filaments arising from the suprasupporting cells and the infrasupporting cell.
Fig. 45. Young gonimoblast with short sterile filaments that arise from the suprasupporting cells and grow towards the carpogonial branch. Note cellular fusion in carpogonial branch (TFC Phyc 10028).
Fig. 46. Young gonimoblast, showing sterile filaments around the carpogonial branch, which form a compact mass of moniliform cells below the gonimoblast.
Fig. 47. A fragment of a mature gonimoblast showing undivided chains of carposporangia containing up to three cells apiece.

pogonium divides obliquely transverse and both halves give rise to an initial compact mass of gonimoblast filaments, which forms relatively loose gonimoblast filaments with short distal chains of 1–3 undivided carposporangia, 5–7 × 11–20 μm. Mature carposporophytes 140–250 μm in diameter. Cells of the carpogonial branch fuse. Moniliform sterile filaments arise from both suprasupporting cells and partially or completely surround the carpogonial branch; they may form a compact mass below the gonimoblast. Tetrasporophyte and tetrasporangia unknown.

HOLOTYPE: TFC Phyc 9982 (Fig. 31). Female gametophyte; on rock at 9–10 m depth, San Marcos, Icod, Tenerife, Canary Islands. 01 May 1999; leg. *J. Reyes & M. Sansón.*

ETYMOLOGY: The specific epithet *reyesii* honours Dr Javier Reyes for his contributions to the marine botany of the Canaries; he collected most specimens of the present species.

REPRESENTATIVE SPECIMENS EXAMINED: Canary Islands, Tenerife: Los Cristianos (*H. Fernández,* 23 July 1972, female: TFC Phyc 1161; *M.C. Gil,* 1974, female, TFC Phyc 1137). El Médano (*J. Reyes,* 22 June 1989, female: TFC Phyc 7703, 7704, 7705, 7755; *J. Reyes & M. Sansón,* 14 May 1991, female, TFC Phyc 7608; *J. Reyes,* 21 April 1992, female, TFC Phyc 7754; *F.D. Melián,* 11 April 1999, female, TFC Phyc 9987; *M. Sansón, J. Reyes & J. Afonso-Carrillo,* 18 July 1998, monoecious, TFC Phyc 10028; female, TFC Phyc 10029). Playa de San Marcos, Icod (*J. Reyes, M. Sansón & E. Muñoz,* 19 May 1994, female, TFC Phyc 9491; *J. Reyes, M. Sansón & E. Muñoz,* 13 June 1994, monoecious, TFC Phyc 9619, 9620; *J. Reyes, M. Sansón & E. Muñoz,* 14 June 1994, female, TFC Phyc 9492; *J. Reyes, M. Sansón & E. Muñoz,* 16 June 1995, monoecious, TFC Phyc 9656; *J. Reyes,* 18 May 1998, monoecious, TFC Phyc 9988; *J. Reyes & M. Sansón,* 01 May 1999, female, TFC Phyc 9983, 10030; male, TFC Phyc 9984; monoecious, TFC Phyc 9989–9992, 10027; *J. Reyes & M. Sansón,* 07 August 1999, monoecious, TFC Phyc 9993–10015). Puertito de Güímar (*E. Moreno,* 22 May 1972, monoecious, TFC Phyc 1153; *M.C. Gil,* March 1975, monoecious, TFC Phyc 1151). Las Eras (*M. Sansón, J. Afonso-Carrillo & J.A.*

Table 1. Comparison of species of *Helminthocladia.*

Character	*H. agardhiana*[1]	*H. andersonii*[2]	*H. australis*[3]	*H. beaugleholei*[4]	*H. calvadosii*[5]	*H. densa*[6]
Habit	one to five irregularly branched to subdichotomous axes covered with short laterals	single subdichotomous axis with several short laterals	one to many irregularly to profusely branched axes	one to several axes densely covered with short simple laterals	one to several simple to little branched axes covered with short and long laterals	one to several subdichotomous axes densely beset with subdichotomous laterals
Maximum height (cm)	30	5	40	30	60	25
Maximum diameter of axes (cm)	1	0.1	1	0.6	1.5	0.4
Length of cortical fascicles (μm)	up to 350	no data	100–200(–300)	160–210	up to 180	100–200
Maximum size of outer cortical cells (μm)	30 × 60	5 × 13[14]	30 × 60	15 × 40	32 × 50	12 × 25
Cells in carpogonial branch	3(–4)	(1–)3(–5)	3	3(–4)	(2–)3(–4)	(2–)3
First carpogonium division	longitudinally oblique	transversely oblique	longitudinally oblique	transverse of partly oblique	longitudinally oblique	oblique or transverse
Daughter cells from the first carpogonium division that develop the gonimoblast	both cells	both cells	both cells	upper cell	both cells	upper cell or both cells
Postfertilization fusion	absent or present	absent	present	only pit-connections enlarged	present	present
Sterile postfertilization filaments	absent to very numerous, entangled below the gonimoblast	numerous and loosely surrounding the gonimoblast	inconspicuous to very numerous, entangled below the gonimoblast	inconspicuous mass below the gonimoblast	absent to inconspicuous, adjacent to the carpogonial branch	absent or inconspicuous, adjacent to the carpogonial branch
Site of derivation of sterile postfertilization filaments	supra- and infrasupporting cell and cells of adjacent filaments	supra- and infrasupporting cells	suprasupporting cell and cells of adjacent filaments	suprasupporting cells and cells of adjacent filaments	supra- and infrasupporting cells and cells of adjacent filaments	suprasupporting cells[14]
Diameter of carposporophyte (μm)	up to 350	up to 140	150–250	100–200	100–270	60–140
Carposporangia	quadripartite and single	undivided and single or in two-celled chains	undivided and single	undivided and single	undivided and single	undivided and single
Size (μm)	7–15 × 12–21	10 × 22	6–11 × 15–25	4–8 × 15–20	7–9 × 15–20	6–10 × 12–18
Spermatangial clusters	paniculate	digitate	paniculate	digitate	paniculate	digitate
Gametophyte	monoecious	monoecious	dioecious	monoecious	monoecious	dioecious

[1] Data on *H. agardhiana* Dixon from Feldmann [1939, as *H. hudsonii* (C. Agardh) J. Agardh] and the present study.
[2] Data on *H. andersonii* Searles & Lewis from Searles & Lewis (1983).
[3] Data on *H. australis* Harvey from Womersley (1965, 1994).
[4] Data on *H. beaugleholei* Womersley from Womersley (1965, 1994).
[5] Data on *H. calvadosii* (Lamouroux *ex* Duby) Setchell from Rosenvinge [1909, as *H. purpurea* (Harvey) J. Agardh], Kylin (1930) and the present study.
[6] Data on *H. densa* (Harvey) Schmitz & Hauptfleisch from Womersley (1965, 1994).
[7] Data on *H. dotyi* Womersley from Womersley (1965, 1994).
[8] Data on *H. nizamuddinii* Afaq-Husain & Shameel from Afaq-Husain & Shameel (1991).
[9] Data on *H. reyesii* O'Dwyer & Afonso-Carrillo from the present study.
[10] Data on *H. rhizoidea* Doty & Abbott from Doty & Abbott (1961).
[11] Data on *H. senegalensis* Bodard from Bodard (1971).
[12] Data on *H. simplex* Doty & Abbott from Doty & Abbott (1961).
[13] Data on *H. sreeramului* Umamaheswara Rao from Umameheswara Rao (1991).
[14] Based on published illustrations.

O'Dwyer, 13 April 1999, female, TFC Phyc 9985). Barranco Hondo (*J.J. Ubach,* 16 May 1999, female, TFC Phyc 9986). Punta de Barbero, Playa de La Arena (*Cancap,* 29 May 1982, female, L 0099675).

DISTRIBUTION: Tenerife, Canary Islands.

HABITAT AND SEASONALITY: *H. reyesii* grows on bare rocks, usually at the sand–rock interface, at depths of 3–10 m. It is a spring–early summer annual in areas of moderate to relatively high water movement and is probably subject to sand abrasion during storm periods. Other ephemeral red algae occurring in this habitat include species of the genera *Acrosymphyton* Sjöstedt, *Dudresnaya* P. Crouan & H. Crouan, *Thuretella* Schmitz, *Scinaia* Bivona, *Naccaria* Endlicher and *Predaea* De Toni.

HABIT: Plants are erect, arising from a single small discoid holdfast, up to 26 cm in height, mucilaginous, smooth and

Table 1. Extended.

H. dotyi[7]	*H. nizamuddinii*[8]	*H. reyesii*[9]	*H. rhizoidea*[10]	*H. senegalensis*[11]	*H. simplex*[12]	*H. sreeramului*[13]
one to several much-branched subdichotomous axes	three to seven irregularly to radially branched axes with several palmate branches	one to three subdichotomous axes covered with short laterals	strongly mucosoid, radially branched axis with short laterals	single axis radially branched below, subdichotomous above and covered with short laterals	simple or subsimple axes with few laterals	irregularly to densely branched slightly calcified axes
7	70	26	9	30	9.5	25
0.3	2	1	0.4	0.4	0.4	0.2
200–400	200–300	up to 400	up to 350	no data	*c.* 150[14]	250–300
8 × 24	40 × 82	35 × 60	26 × 45	30 × 45	16 × 33[14]	8 × 12
3–4	2(–3)–4	3(–4)	3	3–4	3	3–4
oblique	transverse, oblique or longitudinal	transversely oblique	longitudinal	transversely oblique	oblique or longitudinal	oblique
both cells	both cells	both cells	both cells?	both cells	both cells	both cells
present	absent	present	absent	absent	only pit-connections slightly enlarged	present
inconspicuous, entangled mass below the gonimoblast	numerous, entangled below the gonimoblast	few or forming a compact mass of moniliform cells below the gonimoblast	few and loosely surrounding the gonimoblast	inconspicuous below the gonimoblast	inconspicuous below the gonimoblast	very numerous, entangled below the gonimoblast
supra- and infra-supporting cells and supporting cells	supra- and infra-supporting cells and cells of adjacent filaments	supra- and infra-supporting cells and cell of adjacent filaments	supra- and infra-supporting cells	supra-supporting cells	supra- and infra-supporting cells	supra- and infra-supporting cells
150–200	100–220	up to 250	no data	no data	no data	up to 140
undivided and single	undivided and up to four-celled chains	undivided and up to three-celled chains	undivided and single	quadripartite and single	undivided in two-celled chains	undivided and single
4–8 × 8–10	7–9 × 10–15	5–7 × 11–20	no data	10–12 × 20–30[14]	12 × 16[14]	6 × 8
digitate	paniculate	paniculate	no data	paniculate	paniculate	digitate
dioecious (rare monoecious)	monoecious or dioecious	monoecious or dioecious	dioecious	monoecious	dioecious	dioecious

slippery (Figs 31–33). Mature plants are reddish-brown to greenish-brown when alive. One to three main axes, each terete or slightly compressed at furcations and up to 10 mm in diameter, arise from the holdfast. The main axes are initially subdichotomously branched, with up to five furcations in well-developed plants (Figs 31–33). Several to very numerous adventitious laterals are borne perpendicular to the main axes. They are usually short, up to 8 mm long, terete, up to 1 mm in diameter, and simple or furcate. Some senescent plants become progressively verrucose by branch denudation.

VEGETATIVE STRUCTURE: The central medulla is composed of 11–13 filaments, with subcylindrical cells ranging from 5–22 × 60–200 μm in the apical 2 mm of axes to 20–50 × 200–350 μm 15 mm from the apex. Cortical fascicles arise from the distal ends of medullary cells (Figs 34, 35). The basal one to three cells of the cortical fascicles produce rhizoidal filaments that surround the medulla (Fig. 35). The rhizoids increase in diameter, reaching 50 μm in older parts, and produce adventitious cortical filaments that extend out at right angles.

Mature cortical filaments are six- to eight-celled and up to 400 μm in length (Fig. 35). Filaments of the fascicles are five or six times branched, usually pseudodichotomously and only occasionally trichotomously. Cells of the fascicles are elongate and subcylindrical near the base, 7.5–20 × 52–100 μm, becoming shorter upwards, where they are no more than 13 μm in length (Fig. 35). The outer cortical cells are mostly large and clavate, 20–35 × 36–60 μm (Fig. 35), with a stellate chloroplast and a conspicuous central pyrenoid (Fig. 36). Near the tips, nonenlarged terminal cortical cells often bear short unicellular hairs, 3–5 × 20–30 μm (Fig. 37), which are easily shed, or one or two darkly stained secretory cells, 5 × 10 μm (Fig. 36), surrounded by numerous remnant cell walls.

REPRODUCTION: Gametophytes are monoecious or dioecious and both types of plants occur in the same population. Male, female and monoecious plants are similar in habit, but male plants (Fig. 32) are slightly smaller, up to 13 cm in height. Spermatangial initials arise on subterminal or terminal nonenlarged cells of the cortex (Fig. 38) and grow to three cells in length. Each cell of the spermatangial branch produces three to six spermatangial mother cells, which in turn cut off two

to three subspherical spermatangia, 2–3 μm in diameter (Figs 39, 40). At maturity, spermatangial clusters are densely paniculate and subhemispherical and measure up to 30 μm in diameter (Fig. 40). In male plants, the spermatangial clusters are densely arranged in cortical fascicles; in monoecious gametophytes, they are often inconspicuously arranged in cortical fascicles.

Carpogonial branches are common at the tips of axes and arise from the cortical fascicles at the distal end of the basal three or four cells (Fig. 41). Supporting cells normally bears a single carpogonial branch, but supporting cells with two branches also occur. Carpogonial branches consist of 3(–4) cells, measure 10–13 × 24–43 μm, and recurve slightly towards the intercellular space between the suprasupporting cells (Fig. 41). The conical carpogonium is prolonged into a long trichogyne, which often has several spermatia attached to its distal end (Fig. 41).

After fertilization, the first division of the carpogonium is obliquely transverse (Fig. 42), with both cells giving rise to the initial compact mass of gonimoblast filaments (Figs 43, 44). From this mass of cells, relatively loose gonimoblastic filaments grow out and these branch several times subdichotomously. They are up to six cells in length (Figs 45, 46), consist of subcylindrical cells (3–5 × 10–16 μm), and distally form short chains of one to three undivided carposporangia (5–7 × 11–20 μm) (Fig. 47). Mature carposporophytes are subhemispherical and 140–250 μm in diameter in surface view.

After fertilization, the cells of the carpogonial branch, the supporting cell, and the basal ends of both suprasupporting cells become slightly inflated and stain darkly. Cells of the carpogonial branch fuse (Fig. 45) and sterile postfertilization filaments are produced from the suprasupporting cells, from the infrasupporting cells, and occasionally from cells of neighbouring cortical filaments (Figs 42–44). Two sterile filaments arise laterally from opposite sides of the basal end of each suprasupporting cell (Figs 42–44), curving and growing towards the carpogonial branch. The development of these sterile filaments is highly variable within the same area of the plant. They can be short, only partially surrounding the carpogonial branch (Fig. 45), or they can become three- to four-celled, dividing pseudodichotomously from the basal cell; in this case they may entirely surround the carpogonial branch (Fig. 46). Sterile filaments consist of moniliform cells, which enlarge progressively to 15 μm in diameter; at maturity, they can form a compact mass below the gonimoblast (Fig. 46). Some sterile filaments are formed from the infrasupporting cell or from cells of neighbouring cortical filaments. They are composed of slender cells and some produce distally orientated filaments of cortical-type cells (Fig. 44).

REMARKS: *H. reyesii* has no single unique feature, except the relatively frequent development of its sterile moniliform postfertilization filaments into a compact mass surrounding the carpogonial branch below the carposporophyte. In species of *Helminthocladia* sterile postfertilization filaments usually vary from very few to numerous, forming an inconspicuous or more obvious mass of loosely entangled filaments below the gonimoblast (Table 1); some specimens lack postfertilization filaments altogether.

H. reyesii differs from the other twelve *Helminthocladia* species by a combination of seemingly significant attributes (Table 1). It differs greatly in habit from the relatively simple *H. beaugleholei* and *H. simplex,* the subdichotomous densely bushy *H. densa,* the palmate *H. nizamuddinii* and the small *H. dotyi.* It differs from *H. calvadosii, H. australis* and *H. rhizoidea* by its subdichotomous (rather than radial or irregular) branching of the main axes, and from *H. sreeramului* by its slight calcification. From *H. australis, H. beaugleholei, H. calvadosii, H. densa, H. nizamuddinii* and *H. simplex,* it differs in cortex thickness. The new species can be separated vegetatively and reproductively from *H. andersonii, H. beaugleholei, H. densa, H. dotyi* and *H. sreeramului* by its more distinctly swollen outer cortical cells, and by its paniculate rather than digitate spermatangial clusters. It differs from *H. agardhiana* and *H. senegalensis* in lacking single terminal quadripartite carposporangia, and from the remaining species, except *H. nizamuddinii* and *H. simplex,* in lacking exclusively single terminal carposporangia.

H. reyesii and *H. agardhiana* grow together at El Médano (Tenerife, Canary Islands) and can be similar in external appearance. *H. reyesii* can readily be distinguished from *H. agardhiana,* however, by its more regular subdichotomous branching, obliquely transverse division of the carpogonium, relatively small gonimoblasts, undivided carposporangia in short chains, and moniliform sterile postfertilization filaments placed below the gonimoblasts (Table 1).

DISCUSSION

The genus *Helminthocladia,* as currently circumscribed (Searles & Lewis 1983; Kraft 1989; Umamaheswara Rao 1991; Womersley 1994), comprises an apparently heterogeneous group of species, which show disorderly variation with respect to several prominent features used in generic diagnosis in the Liagoraceae. The variability observed in the type species *H. calvadosii* with respect to the presence or absence of sterile postfertilization filaments prevents *Helminthocladia* from being subdivided on this basis and also argues against the use of this unreliable character for separating species within the genus. Although sterile postfertilization filaments are usually few in number and placed below the gonimoblast, the degree of development and the site of derivation may have value as diagnostic features at the species level (Table 1).

Helminthocladia has mostly been characterized by: (1) the presence of enlarged terminal cells in the cortical filaments; and (2) oblique or longitudinal division of the zygote, with the development of gonimoblast filaments from both daughter cells (Papenfuss 1946; Kylin 1956; Desikachary 1957). But some of these attributes are lacking in several species. In *H. andersonii* and *H. sreeramului,* cells of the cortical fascicles become progressively smaller outwards, and in *H. beaugleholei, H. densa* and *H. dotyi,* the outer cortical cells are only slightly enlarged (Table 1). In all species of *Helminthocladia* the fertilized carpogonium divides obliquely, but there is some variation in the degree of inclination in the plane of division (from transversely oblique to longitudinally oblique): several species, viz. *H. nizamuddinii, H. beaugleholei* and *H. densa* (Table 1) are described as exhibiting transverse division. In *H. beaugleholei* it seems that only the upper daughter cell takes part in the elaboration of the gonimoblast (Womersley 1965, 1994). No other genus in the Liagoraceae exhibits these

characteristics; all remaining genera with an initial median division of the fertilized carpogonium exhibit transverse division and the upper daughter cell alone forms gonimoblast filaments (Kraft 1989).

Helminthocladia has generally been characterized as forming compact gonimoblasts (Kraft 1989). In all species of *Helminthocladia* we have examined, cells of the young gonimoblast are initially more or less isodiametric and the loose, parallel gonimoblast filaments (which radiate outwards and contain subcylindrical cells) form a dense, regular to lobed mass. A similar arrangement of gonimoblast filaments is apparently displayed by all the remaining species for which postfertilization development is well documented or can reasonably be inferred from published illustrations (see Doty & Abbott 1961; Womersley 1965; Afaq-Husain & Shameel 1991). The brush-like appearance of the gonimoblasts, as a consequence of the somewhat diffuse outward disposition of the gonimoblast filaments, is apparently unreported for other genera in Liagoraceae and may be of taxonomic interest. Huisman & Wynne (1999) recognized three gonimoblast morphologies in the Liagoraceae: diffuse, moderately diffuse, and compact. As seen in the present study, the species of *Helminthocladia* exhibit a fourth gonimoblast morphology, intermediate between the strictly compact and the moderately diffuse types of gonimoblast and this could be useful as a diagnostic character at genus level.

Within the genus *Helminthocladia* there are three distinct types of carposporangia, which are very useful for species delineation. Single terminal undivided carposporangia are formed by most species, including the type species *H. calvadosii* (Table 1). Single terminal quadripartite carposporangia are known in *H. agardhiana* (Feldmann 1939, as *H. hudsonii*) and *H. senegalensis* (Bodard 1971). Finally, two- to four-celled chains of undivided carposporangia are characteristic of *H. andersonii* (Searles & Lewis 1983), *H. simplex* (Doty & Abbott 1961), *H. nizamuddinii* (Afaq-Husain & Shameel 1991) and *H. reyesii.*

Although *Helminthocladia* has been described as a heterogeneous assemblage of species (Searles & Lewis 1983), at present there are no characteristics that support a subdivision of the genus. Among genera of Liagoraceae, *Helminthocladia* is close to *Helminthora* J. Agardh and *Liagora* Lamouroux, which also exhibit carpogonial branches arising laterally on mid-cortical supporting cells and relatively compact gonimoblasts. Differences between *Helminthocladia* and *Helminthora* were emphasized by Searles & Lewis (1983). With respect to *Liagora, Helminthocladia* presents a less distinct boundary after the description by Umamaheswara Rao (1991) of *H. sreeramului* with its unusual liagoroid habit. Postfertilization studies of the less well known species of *Helminthocladia* and on the many vaguely-described species of *Liagora* are needed to delineate this boundary.

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