

***Botryocladia chiajeana* and *Botryocladia macaronesica* sp. nov.
(Rhodymeniaceae, Rhodophyta) from the Mediterranean and the eastern
Atlantic, with a discussion on the closely related genus *Irvinea***

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Specimens from the eastern Atlantic, Mediterranean and Adriatic seas previously reported as *Botryocladia chiajeana* showed differences in morphology, and re-examination of Meneghini's original collection of *Chrysomenia chiajeana* (basonym *B. chiajeana*) revealed that only the Mediterranean and Adriatic specimens are in agreement with the original protologue, whereas plants reported from the eastern Atlantic are recognised here as *Botryocladia macaronesica* Afonso-Carrillo, Sobrino, Tittle & Neto *sp. nov.* The vegetative and reproductive morphology of western Mediterranean plants is examined in detail for the first time, and *B. chiajeana* is characterised by the following combination of features: solid axes bearing frequently dichotomously branched vesicles, vesicle walls three layered, outer cortical cells arranged in rosettes, secretory cells borne on modified medullary cells, spermatangia cut off from scattered spermatangial mother cells, cystocarps strongly protuberant and tetrasporangia cruciately divided and exposed on the outer cortical layer at maturity. From the Meneghini collection, a lectotype specimen of *C. chiajeana* was selected. *Botryocladia macaronesica*, known so far only from the islands of Azores, Madeira, Canaries and Cape Verde, differs from other *Botryocladia* species by a unique combination of significant attributes including elongate saccate vesicles, near-continuous cortication of vesicle walls, secretory cells on unmodified medullary cells and completely immersed cystocarps. An analysis of the morphological characters currently used for separating *Botryocladia* from related genera (i.e. *Chrysomenia*, *Gloiosaccion* and *Irvinea*), showed that there is considerable overlap between *Botryocladia* and *Irvinea*. These genera are presently discriminated mostly by molecular evidence as the supposed morphological characters are shown here to vary considerably within the genus *Botryocladia*.

KEY WORDS: *Botryocladia*, *Botryocladia chiajeana*, *Botryocladia macaronesica*, *Irvinea*, Rhodophyta, Rhodymeniaceae, Rhodymeniales

INTRODUCTION

The Rhodymeniaceae with solid axes bearing hollow, mucilage-filled, vesicular laterals are presently placed in the genera *Botryocladia* (J. Agardh) Kylin (1931), *Gloiosaccion* Harvey (1859) and *Irvinea* Guiry in Saunders *et al.* (1999). *Gloiosaccion* and *Irvinea* are at present monospecific, but *Botryocladia* possesses approximately 40 species (Ballantine & Aponte 2002; Gavio & Fredericq 2003). Species of *Gloiosaccion* and *Irvinea* exhibit short axes with large, elongate, cylindrical or saccate vesicles; however, *Botryocladia* is more heterogeneous morphologically, including species with greater developed arborescent solid axes with numerous vesicles, and species with short axes that bear small, near-spherical vesicles or large, elongate, cylindrical vesicles (Feldmann 1945). Boundaries among these genera are presently a matter of discussion because morphological characters used to define them

have been obscured by recent molecular evidence (Saunders *et al.* 1999). The subset of *Botryocladia* that includes species with large elongate vesicles is with difficulty distinguished from related genera (Schneider & Lane 2000; Afonso-Carrillo & Sobrino 2003).

Most of the 14 *Botryocladia* species reported in the Mediterranean Sea and the eastern Atlantic are known only from their type locality, but the large-vesicled species, until now known as *Botryocladia chiajeana* (Meneghini) Kylin, has been more widely reported geographically (Afonso-Carrillo & Sobrino 2004). *Botryocladia chiajeana* was originally described as *Chrysomenia chiajeana* by Meneghini (1844) from plants collected along the Dalmatian coast, Adriatic Sea. The proposal of Kützing (1849) to transfer the species to *Gastroclonium* Kützing did not receive acceptance, and Zanardini (1860) and Funk (1927) retained the species in *Chrysomenia*. Børgesen (1929) documented two taxonomic vegetative features (cortical cells forming a dense, near-complete covering and secretory cells borne singly or in groups of two to four on unmodified medullary cells) when examining plants from

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the Canary Islands, and Kylin (1931) ultimately transferred *C. chiajeana* to *Botryocladia*.

Although *B. chiajeana* has been reported in the Adriatic Sea and the western Mediterranean (Feldmann 1941; Augier & Boudouresque 1976; Boudouresque & Perret 1977; Giaccone 1978; Boudouresque *et al.* 1984; Gallardo *et al.* 1985; Boisset & García Carrascosa 1987; Perret-Boudouresque & Seridi 1989; Ballesteros 1990, 1992, 1994; Furnari *et al.* 2003) and Madeira, the Canary Islands and Mauritania in the eastern Atlantic (Levring 1974; Afonso-Carrillo & Sansón 1999; John *et al.* 2004), the present knowledge of the diagnostic characters of this species is unsatisfactory. According to Brodie & Guiry (1988), *B. chiajeana* is characterised by: (1) elongate-bifurcate vesicles; (2) complete outer cortex; (3) two to three layers of cells in the vesicle wall and (4) secretory cells ovoid-pyriform, simple or in groups of two to four on unmodified medullary cells. Although fertile plants have occasionally been reported (i.e. Codomier *et al.* 1988; Ballesteros 1992), information on the morphology of reproductive structures has not been published. Therefore, a detailed study on the vegetative and reproductive structures of *B. chiajeana* was undertaken.

In recent studies conducted on the genus *Botryocladia* from the eastern Atlantic (Afonso-Carrillo & Sobrino 2003, 2004) and the Rhodymeniales from the western Mediterranean (Sánchez 2003; Sánchez & Rodríguez-Prieto 2005), we had an opportunity to examine abundant material that allowed us to detect significant differences in morphological characters between plants from the western Mediterranean and the Adriatic seas and plants from the islands of Madeira, Canaries and Cape Verde, all of which have been attributed to *B. chiajeana*. In this article, we present a detailed description of the Mediterranean and Adriatic plants based on fresh material, the original material of *C. chiajeana* and other herbarium collections. Examination of Meneghini's collection allowed us to select a lectotype specimen of *C. chiajeana*. Plants from the Atlantic islands previously reported as *C. chiajeana* (= *B. chiajeana*) were in agreement with the account provided by Børgesen (1929) and are recognised here as *Botryocladia macaronesia* Afonso-Carrillo, Sobrino, Tittley & Neto *sp. nov.*

MATERIAL AND METHODS

Specimens were preserved in 4% formalin in seawater or dried as herbarium specimens deposited at BM, FI, HGI, L, TFC, UA and VAL. Selected fragments from formalin-preserved material were stained in 1% aniline blue and mounted in 20% aqueous Karo syrup (Bestfoods, Englewood Cliffs, NJ, USA). Sections were made by hand with a razor blade. Dried specimens from herbaria were rehydrated in 4% formalin in seawater. Drawings were obtained by using a camera lucida attached to a Zeiss microscope (Carl Zeiss, Berlin, Germany). Photomicrograph was taken with a Spot Insight digital camera (Diagnostic Instruments, Sterling Heights, MI, USA) attached to an Axioskop 2 plus microscope (Carl Zeiss, Berlin, Germany). Herbarium abbreviations follow Holmgren *et al.* (1990).

OBSERVATIONS

Botryocladia chiajeana (Meneghini) Kylin

Figs 1–7, 9–11, 13–29

BASIONYM: *Chrysymenia chiajeana* Meneghini (1844, p. 296).

TYPE LOCALITY: Dalmatian coast, Croatia, Adriatic Sea (Silva *et al.* 1996).

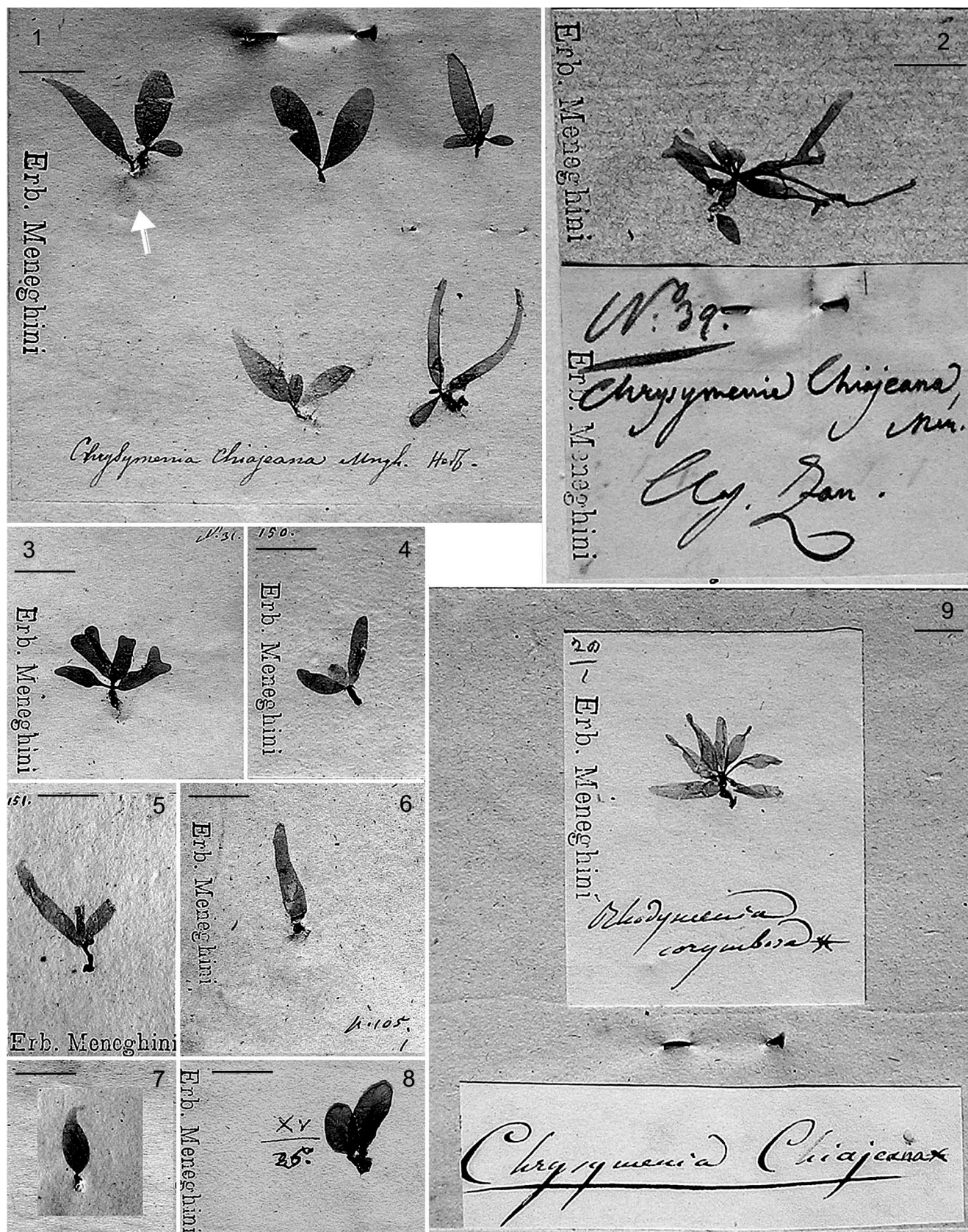
HOMOTYPIC SYNONYMS: *Gastroclonium chiajeanum* (Meneghini) Kützing (1849, p. 866).

MENEGHINI COLLECTION AND OTHER HISTORICAL SPECIMENS: FI contains four sheets with the stamp 'Erb. Meneghini' which include non-numbered collections labelled *Chrysymenia chiajeana* (Figs 1–9). The locality and the date are not indicated for any of the collections. Only on sheet #2 has the name of the collector been conserved (Fig. 2). The specimens are completely adhered to the paper except one included on sheet #3 (Fig. 8). On sheet #1 there are five specimens on the same card labelled '*Chrysymenia chiajeana* Menegh. Herb.' (Fig. 1). Sheet #2 contains a single specimen and a label: 'N° 39.- *Chrysymenia chiajeana* Men. Leg. Zan.' (Fig. 2). Sheet #3 includes six specimens, all on an individual card (Figs 3–8). And, on sheet #4 there is a single specimen initially labelled '*Rhodymenia corymbosa*', to which an annotation label '*Chrysymenia chiajeana*' has been added (Fig. 9). On the basis of the handwriting, Meneghini likely did not write these labels. With the exception of one specimen on sheet #3 (Fig. 8) that possesses a foliose habit, all specimens from the Meneghini's collections have morphological characters (i.e. habit morphology, arrangement of outer cortical cells and shape and position of secretory cells) that fit the original diagnosis of Meneghini and which are in accordance with the observations presented here.

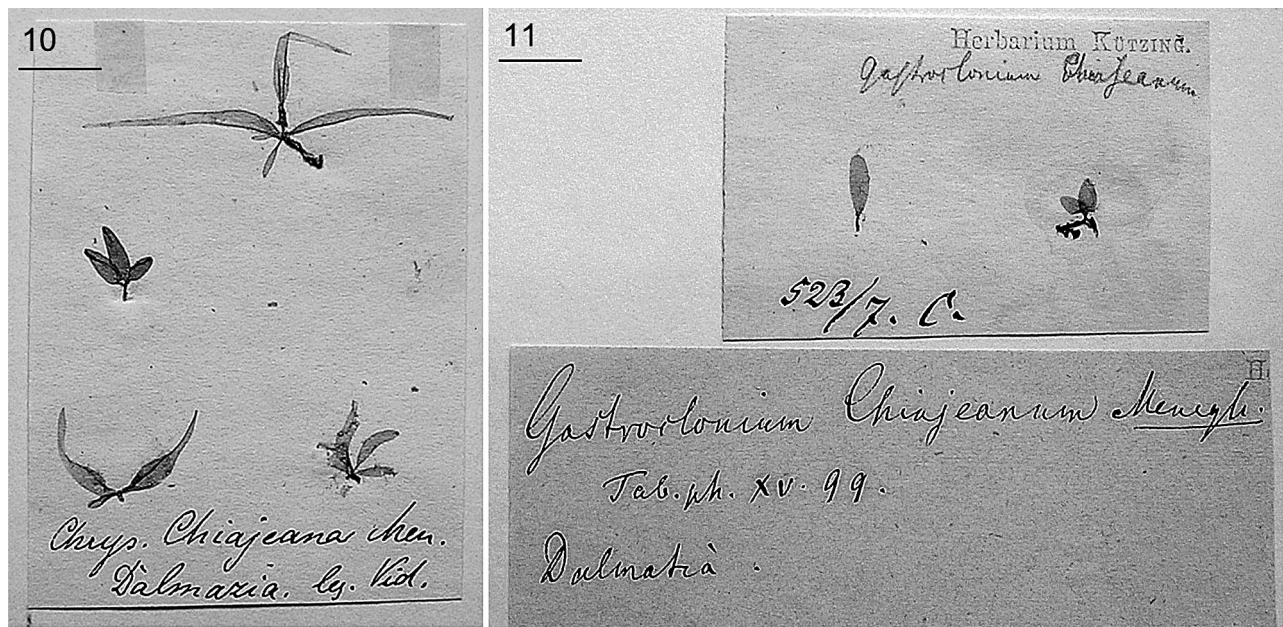
Two collections housed at L are also in agreement with the plants assigned to *B. chiajeana*. These include a sheet from the Weber-van Bosse herbarium containing four specimens adhered to the same card with the following label: '*Chrys. Chiajeana* Men., Dalmazia, leg. Vid.' (Fig. 10). The other sheet belongs to the Kützing herbarium; it contains a single card with two specimens, the number 523/7 and the label '*Gastroclonium Chiajeanum*' (Fig. 11). An additional label also includes 'Tab Ph. XV, 99. Dalmazia' (Fig. 11).

LECTOTYPIFICATION: To select the lectotype specimen of *C. chiajeana*, we examined the materials deposited in FI and L housing the collections of Meneghini (Koster 1969). Meneghini (1844, p. 296) based *C. chiajeana* on plants that possessed simple short axes, frequently ovate-lanceoid and umbellate large vesicles, collected along the Dalmatian coast by Vidovich. Meneghini also indicated that the plants were almost 25 mm in height, with a solid axis up to 5 mm long, crowned by up to 8 vesicles up to 5 mm wide, and with solitary 'flavellidia' (cystocarps) in the middle of the branches. The original material of Meneghini was examined by Zanardini (1860), who did not find cystocarps and indicated 'Capocesto' (the Italian name of Primosten, Croatia) as the locality of origin of the material collected by Vidovich. Although the collections of *C. chiajeana* in the herbaria of Weber-van Bosse and Kützing housed at L come from the Dalmatian coast (Figs 10, 11), and one of them was collected by Vidovich (Fig. 10), there is no evidence that these were used by Meneghini in his original description. Kützing (1865, as *Gastroclonium chiajeanum*) illustrated the specimens from his own herbarium (Fig. 11).

Because the Meneghini herbarium contains 15 specimens, the name *C. chiajeana* must, in accordance with ICBN Art. 9.2 (see Greuter 2000), remain attached to the specimen that corresponds most closely with the original description. The specimen on sheet #2, collected by Zanardini, exhibits dichotomously branched vesicles (Fig. 2) that are not mentioned in the protologue and, therefore, cannot be considered. Among specimens in sheet #3, one of them (Fig. 3) possesses dichotomous vesicles and another lacks vesicles altogether and belongs to a different taxon (Fig. 8). Sheet #4 contains a single specimen with an axis of about 5 mm in length and eight vesicles, which is in agreement with the protologue, but its initial identifi-



Figs 1–9. *Botryocladia chiajeana* (= *Chrysymenia chiajeana*). The four sheets of the Meneghini collection housed in FI. Scale bars = 10 mm.
Fig. 1. Sheet #1: Lectotype collection. Above left specimen is the lectotype (arrow).
Fig. 2. Sheet #2: Specimen with dichotomously branched vesicles collected by Zanardini.
Figs 3–8. Sheet #3: Six specimens on individual cards. Specimen in Fig. 8 is laminar in habit and it is not in accordance with the protologue.
Fig. 9. Sheet #4: Single specimen initially labelled as *Rhodymenia corymbosa*.



Figs 10, 11. *Botryocladia chiajeana* (= *Chrysomenia chiajeana*). Specimens housed in L. Scale bars = 10 mm.

Fig. 10. Specimens from the Webber-van Bosse herbarium collected along the Dalmatian coast by Vidovich.

Fig. 11. Specimens from the Kützing herbarium illustrated by him as *Gastroclonium chiajeanum* in *Tabulae Phycologicae* 15.

cation as *Rhodymenia corymbosa* is not mentioned in the original description (Fig. 9). Sheet #1 contains five specimens and all of them are in accordance with the protologue with respect to vesicle morphology (Fig. 1), although indication concerning locality, the date and the collector is lacking. Fourteen (of the 15) specimens of the Meneghini herbarium are in accordance with the recently collected plants that we described above. There are five specimens from sheet #1. The upper left specimen (Fig. 1) has been selected as the lectotype of *C. chiajeana*.

REPRESENTATIVE SPECIMENS EXAMINED: Dalmatian coast, Croatia: (locality, collector and date lacking, as *C. chiajeana*, Herbarium Meneghini, four sheets unnumbered, FI); (Vidovich, undated, as *C. chiajeana*, Herbarium Weber-van Bosse, unnumbered, L; no collector, undated, as *Gastroclonium chiajeanum*, Herbarium Kützing n. 523/7, L). **France:** Corsica, Calvi, Pointe de la Revellata (W.F. Prud'homme van Reine, 05 July 1983, 1–8 m depth, L 2040; 10 July 1983, 20 m depth, L 2139); Banyuls-sur-Mer, Cap L'Abeille (G.M. Lokhorst et W.F. Prud'homme van Reine, 03 May 1976, 20–25 m depth, L 202, L 206, L 214); Banyuls-sur-Mer, Ille Grosse (C. Rodríguez-Prieto, 26 July 1988, 6 m depth, HGI-A 1365). **Italy:** Miramar, Trieste (Vogel, 01 February 1870, as *Gastroclonium chia-*

jeanum, Herbarium Weber-van Bosse unnumbered, L; no collector, 03 March 1875, as *C. chiajeana*, Herbarium Hauck, unnumbered, L); Gulf of Naples, Grotta di Misseno (E. Brunner-de Vries, 28 May 1913, as *C. chiajeana*, unnumbered, L); Sicily, Capo Murro di Porco (G. Furnari, 07 October 1996, 15 m depth, Furnari 1600). **Spain:** Illes Balears, Cabrera, Cova Blava (C. Rodríguez-Prieto, 23 May 1996, 10 m depth, HGI-A 1709); Illes Balears, Cabrera, Cap Falcó (C. Rodríguez-Prieto, 24 May 1996, 50 m depth, HGI-A 1737); Catalunya: Girona, Palamós, Illes Formigues (C. Rodríguez-Prieto, 03 May 1996, 26–29 m depth, HGI-A 1790); Girona, Palamós, Llosa (C. Rodríguez-Prieto, 14 May 1997, 36 m depth, HGI-A 2608); Girona, Palamós, Mont de Fora (C. Rodríguez-Prieto, 19 March 1997, 35 m depth, HGI-A 2610); Girona, Begur, Sa Tuna (C. Rodríguez-Prieto, 18 October 1996, 16 m depth, HGI-A 2127); Girona, Llafranch, Quart Ullastre (C. Rodríguez-Prieto, 23 March 1997, 40 m depth, HGI-A 2606); Girona, Platja d'Aro, El Marge (C. Rodríguez-Prieto, 07 May 1997, 30 m depth, HGI-A 2618); Girona, Platja d'Aro, Tinent de Ridaura (C. Rodríguez-Prieto, 30 March 1997, 30–35 m depth, HGI-A 2611); Girona, Platja d'Aro, Els Canyers (C. Rodríguez-Prieto, 12 March 1997, 35 m depth, HGI-A 2616); Girona, Begur, Canons d'Aigua Gelida (C. Rodríguez-Prieto, 21 February 1998, 40 m depth, HGI-A 4353); Girona, Palamós, Roca del Pedro Lázaro (C. Rodríguez-Prieto, 28 March 2004, 27 m depth, HGI-A 6523); Tarragona, Hospitalet de l'Infant, Freu de Terra (A. Manghisi, N. Salvador & J. Rull, 7 July 2004, 20 m depth, VAL-Algae 2162); Valencia: Alicante, Jávea, El Portitxol (F. Boisset, 18 March 1984, 8 m depth, VAL-Algae 2163); Alicante, Calpe, La Fosa (F. Boisset, 29 May 1984, 0.3 m depth, VAL-Algae 2164); Alicante, La Granadella (F. Boisset, 11 June 1983, 1 m depth, VAL-Algae 2165); Alicante, Denia, Les Rotes (F. Boisset, 26 April 1984, 4 m depth, VAL-Algae 2166).

DISTRIBUTION: The distribution of *B. chiajeana* (= *C. chiajeana*) is now known to be only the western Mediterranean (Spain, France and western Italy) and the Adriatic Sea (Croatia and eastern Italy) (Fig. 12). Records from Mediterranean Egypt (Aleem 1993) and the Red Sea (Papenfuss 1968) require re-examination. Previous extra-Mediterranean records from the eastern Atlantic [i.e. Madeira, Canary Islands, Mauritania (Børjesen 1929; Levring 1974; John et al. 2004)] are probably misidentifications of the species described below as *B. macaronesica*. The reports from Kenya and Tanzania in the Indian Ocean (see Silva et al. 1996) have been considered as doubtful records.

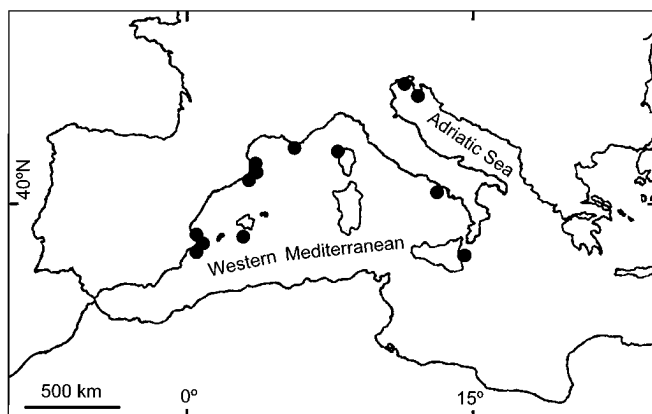
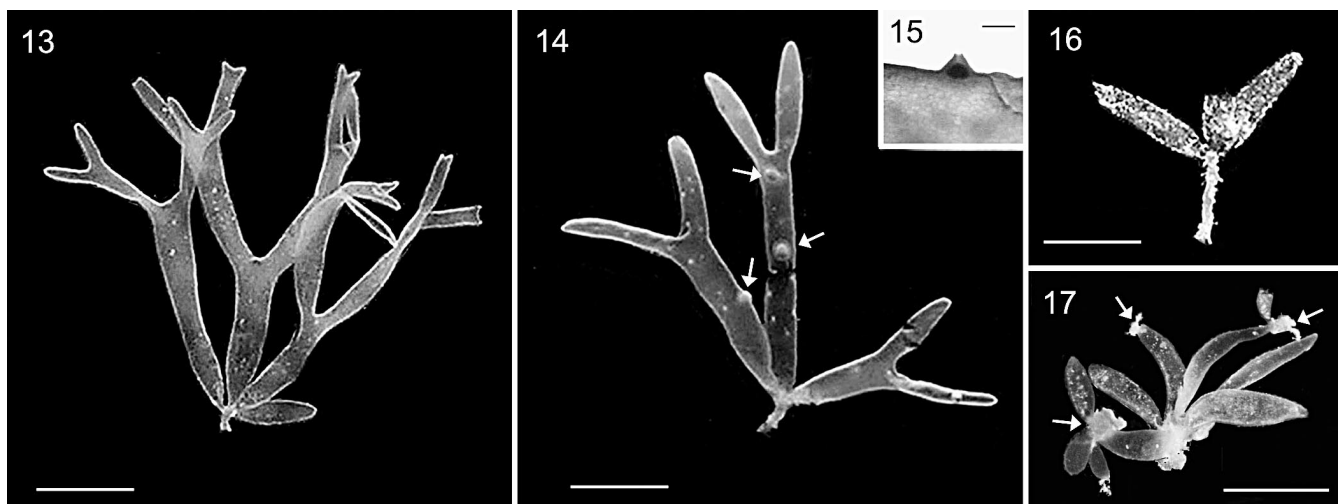


Fig. 12. Map showing localities with confirmed occurrence of *B. chiajeana*.



Figs 13–17. *Botryocladia chiajeana*. Liquid-preserved specimens.

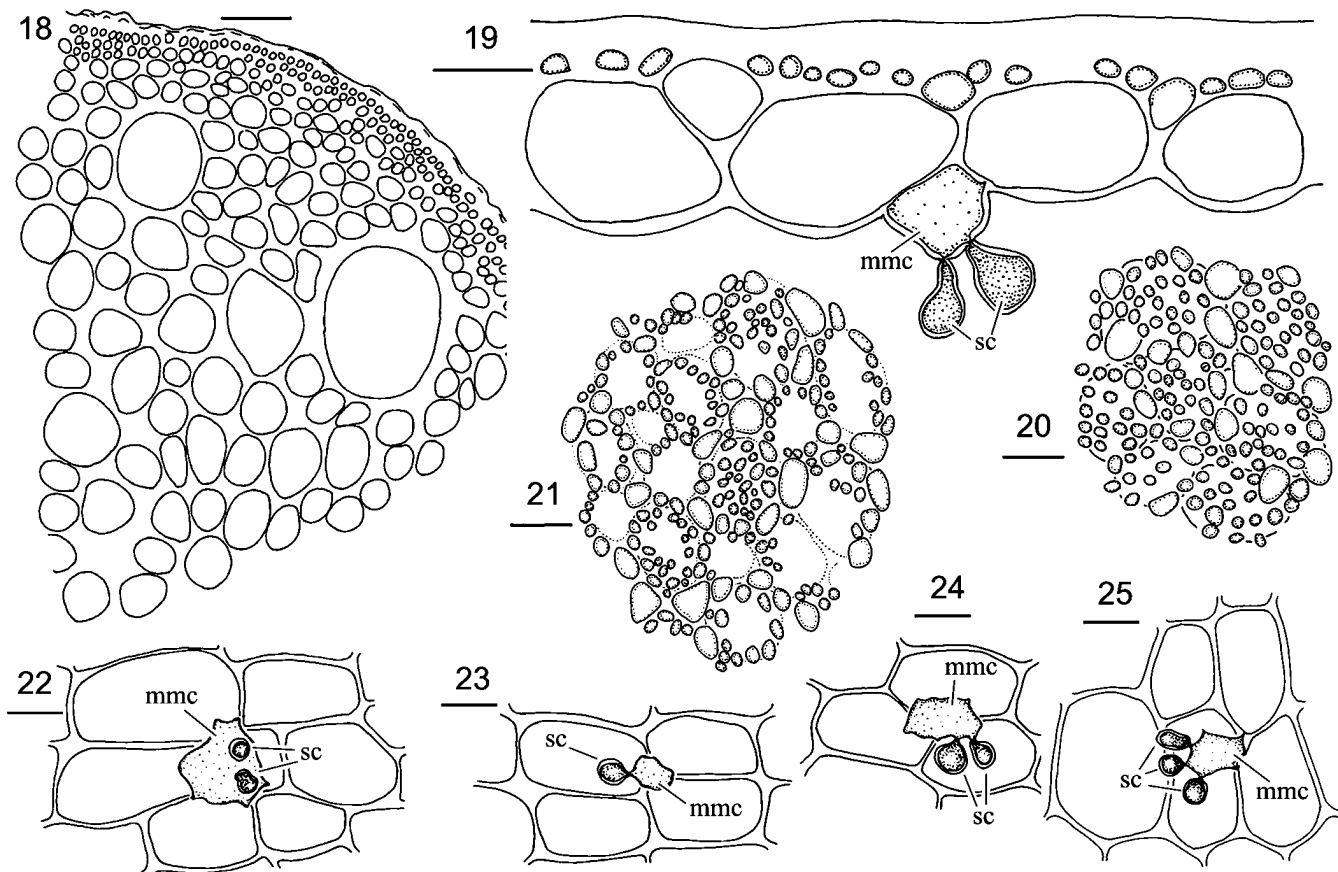
Fig. 13. Habit of a mature tetrasporophyte (HGI-A 2611). Scale bar = 10 mm.

Fig. 14. Female gametophyte showing cystocarps (arrows) (HGI-A 2616). Scale bar = 10 mm.

Fig. 15. Detail of a cystocarp (HGI-A 6523). Scale bar = 1 mm.

Fig. 16. Aged male gametophyte (HGI-A 4353). Scale bar = 10 mm.

Fig. 17. Stoloniiferous female gametophyte showing reflexed fusiform vesicles forming rhizoids near the apex (arrows) (VAL Algae 2164). Scale bar = 10 mm.



Figs 18–25. *Botryocladia chiajeana*. Scale bars = 50 µm.

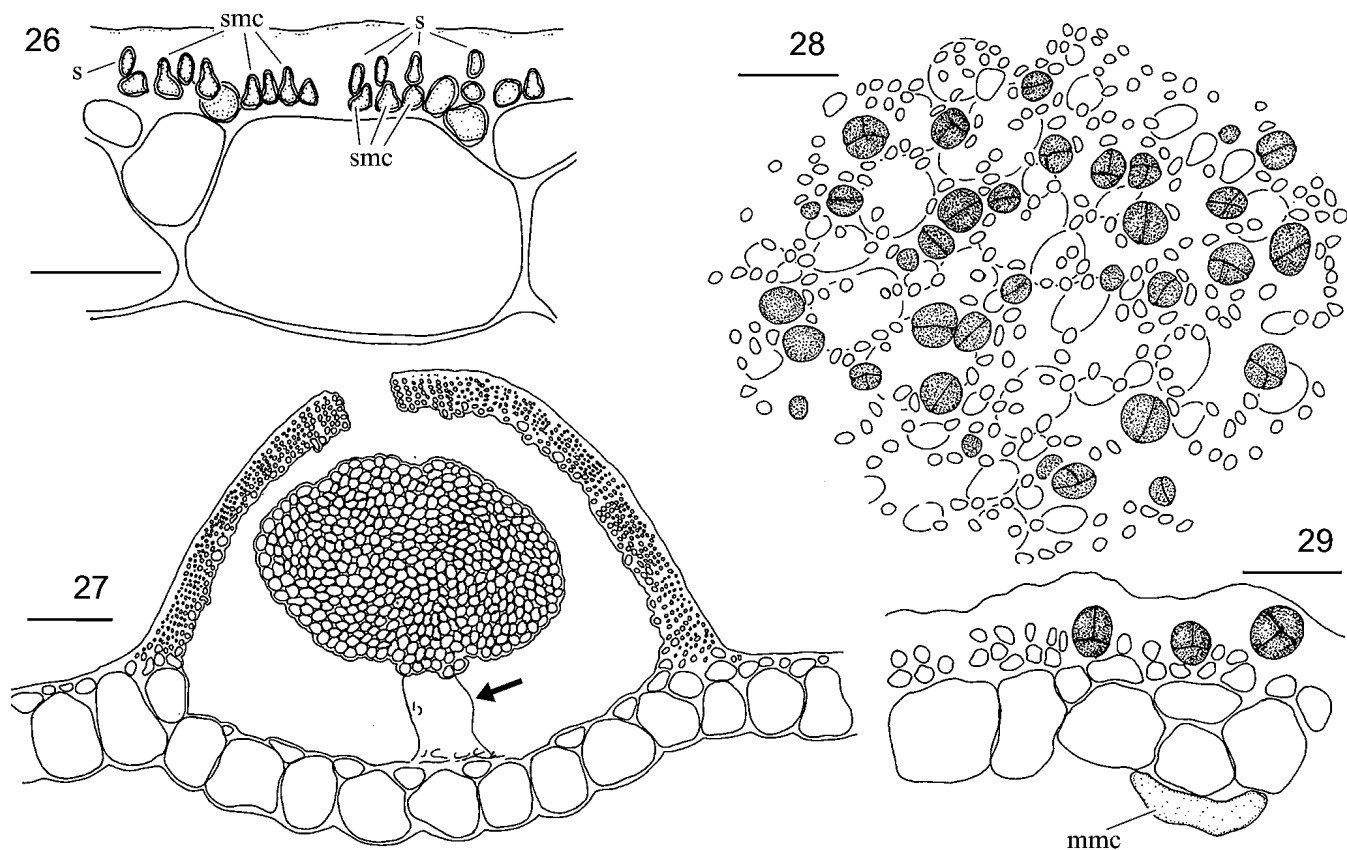
Fig. 18. Detail of a transverse section of an axis showing inner medullary cells (large) and outer cortical cells (smaller) (HGI-A 2610).

Fig. 19. Transverse section of a vesicle wall showing three cell layers. Secretory cells (sc) are born on a modified medullary cell (mmc) (HGI-A 2618).

Fig. 20. Surface view of a vesicle showing outer cortical cells arranged in rosettes (HGI-A 1709).

Fig. 21. Surface view of a distal portion of vesicle showing a discontinuous cortex where arrangement in rosettes is obscured (HGI-A 1709).

Figs 22–25. Details of the inner surface of the vesicle wall showing secretory cells (sc) on modified medullary cells (mmc) (HGI-A 1365).



Figs 26–29. *Botryocladia chiajeana*.

Fig. 26. Transverse section of vesicle wall through a spermatangial sorus, showing elongate spermatangial mother cells (smc) cutting off spermatangia (s) on the outer side (HGI-A 4353). Scale bar = 20 μm .

Fig. 27. Transverse section of a conical cystocarp with the fusion cell (arrow) giving rise to a subspherical mass of carposporangia (VAL Algae 2164). Scale bar = 100 μm .

Fig. 28. Surface view of tetrasporangial sorus with mature tetrasporangia surrounded by outer cortical cells (HGI-A 1365). Scale bar = 50 μm .

Fig. 29. Transverse section of vesicle wall through a tetrasporangial sorus showing cruciately divided tetrasporangia completely exposed on the outer cortical layer of cells. A modified medullary (mmc) cell lacking secretory cells protrudes into the vesicle cavity (HGI-A 1365). Scale bar = 50 μm .

HABITAT AND SEASONALITY: *Botryocladia chiajeana* grows epilithically or on crustose corallines in a wide bathymetric range in the sublittoral. In the shallow sublittoral, it occurs from 0.5 m below the surface mainly in shady crevices and on overhanging rocks. In the deep sublittoral and coralligenous bottoms, it occupies habitats with a high water circulation to a depth of up to 50 m. *Botryocladia chiajeana* was observed to be perennial because, in late autumn and winter, the plants are reduced to axes and fragments of senescent vesicles and subsequently develop new vesicles in late winter (see Codomier *et al.* 1988). Spermatangia have only been observed in February, cystocarps occur from March to May, and tetrasporangia from March to October.

HABIT AND VEGETATIVE STRUCTURE: Plants are erect, rosy red to reddish-brown, up to 50 mm in height, attached by a small discoid holdfast that gives rise to a single, usually short, simple (rarely distally branched) solid axis, bearing distally 1–12 (–20) vesicles. Axes are flexuous to slightly stiff, terete, 0.3–2 mm in diameter, and up to 5 (–10) mm in height. Vesicles are initially simple, ovate or pyriform, and become rounded-cylindrical or fusiform at maturity; they are 1.5–4 mm in di-

ameter and 4–30 mm long. Some vesicles become compressed and regularly dichotomously branched up to three times, reaching up to 50 mm in length (Figs 13, 14, 16). In plants with short axes, fusiform vesicles can become reflexed and form thick rhizoids near the apex (Fig. 17). From this secondary holdfast, new solid axes and vesicles arise, resulting in the appearance of a stoloniferous plant (Fig. 17). Solid pseudoparenchymatous axes consist of an inner medulla of thin-walled ovoid and subspherical hyaline cells [21–60 (–120) μm in diameter], and an outer cortex of rounded pigmented cells (4–10 μm in diameter). The vesicle walls are membranous, three layered, ranging from (50–) 80 to 115 μm in thickness (Fig. 19). The inner nonpigmented medullary cells are subpolygonal, isodiametric or longer than wide (40–100 μm wide and 75–170 μm long in surface view). The outer cortex is composed of rounded cells, 5–15 μm in diameter, which are arranged forming rosettes on a subsurface layer of intermediate-sized cells (Fig. 20). Arrangement of cortical cells in rosettes is unclear in distal portions of vesicles (Fig. 21). Secretory cells are pyriform (15–34 μm in diameter and 18–43 μm long), and occur 1–2 (–4) on modified medullary

cells (20–75 μm in diameter), which protude into the vesicle cavity (Figs 19, 22–25). Modified medullary cells lacking secretory cells are common (Fig. 29).

REPRODUCTIVE STRUCTURES: Gametophytes are dioecious. Male plants have flaccid vesicles with a thick mucilaginous surface layer as a result of the extension of the spermatangial sori (Fig. 16). Loosely arranged spermatangial mother cells are formed radially from outer cortical cells of vesicles and each cut off one or two hyaline spermatangia, 1.5–2.5 μm in diameter and 2.5–4.0 μm long (Fig. 26). Carpogonial branches were not observed. Up to four cystocarps occur per vesicle and are irregularly scattered over the middle region of the vesicles (Fig. 14). Gonimoblasts are compact, subspherical, up to 400 μm in diameter, consisting of a basal elongated fusion cell that gives rise to a spherical mass of rounded carposporangia, 12–25 μm in diameter (Fig. 27). The gonimoblast is surrounded by a relatively thin pericarp resulting in a conical cystocarp, up to 900 μm in diameter and 650 μm in height (Figs 14, 15, 27). The pericarp, up to 40–70 μm thick, consists of small rounded hyaline cells (7–18 μm in diameter), with an ostiole up to 100 μm in diameter. No tela arachnoidea were observed in cystocarp cavities. Tetrasporangia are formed in extensive sori in the middle and distal portions of the vesicles. Tetrasporangia are derived from midcortical cells in an intercalary position. Pit connections of tetrasporangia to cortical cell are lost early and thus they appear as terminal. Mature tetrasporangia are subspherical to ovoid, 17–26 μm in diameter and 21–29 μm long, with cruciately or irregularly arranged sporangia (figs 28, 29) and are completely exposed on the outer cortical layer (Figs 28, 29).

REMARKS: In the absence of the reproductive features that have remained unknown until now, plants previously reported as *C. chiajeana* or *B. chiajeana* have been characterised by an unsatisfactory suite of vegetative characters obtained from the descriptions of specimens collected in the Adriatic Sea, the western Mediterranean and the Canary Islands (Zanardini 1860; Børgesen 1929; Feldmann 1945). Presence of occasionally dichotomously branched elongate vesicles, a continuous outer cortex in vesicle wall and secretory cells originating from unmodified medullary cells have been the principal attributes used to distinguish *B. chiajeana* from other species of *Botryocladia* (Brodie & Guiry 1988). However, both the arrangement of the cortical cells and the disposition of the secretory cells have been apparently misinterpreted in the Mediterranean plants. A discontinuous outer cortex with cells frequently arranged in rosettes and secretory cells occurring on modified medullary cells characterised all plants examined in this study.

The confusion with respect to the arrangement of cortical cells and the disposition of the secretory cells is related to the observations made by Børgesen (1929) in plants from the Canary Islands (recognised here as the new species *Botryocladia macaronesica*), where this author described cortical cells forming a nearly complete covering, whereas secretory cells occurred singly or in groups of two to four on unmodified medullary cells. Apparently, these features have been erroneously attributed to Mediterranean plants (Feldmann 1941, fig. 29c), although Børgesen (1929) pointed out that no original specimens from the Mediterranean Sea had been used for comparative purposes in his identification of the Canarian

plants. Some of the characters described here had been previously observed in the Mediterranean plants. Feldmann (1945) reported a loose arrangement of cortical cells in young plants, and Codomier *et al.* (1988, fig. 20) illustrated secretory cells originated on modified medullary cells. However, these observations have been overlooked.

Plants from Meneghini's collection and the other materials examined here display a suite of morphological features and belong to a single species, and the name *C. chiajeana* Meneghini (1844) was first validly published to designate it. However, vegetative characters exhibited by these plants are not in accordance with *Chrysymenia* Agardh (1842: 105), a genus that, as currently circumscribed (Kylin 1956), possesses entirely hollow fronds, and the solid portion is tiny and restricted to the basal attachment structure. Plants examined have solid terete axes up to 2 mm in diameter and up to 10 mm in height, and must therefore be attributed to *Botryocladia*, *Gloiosaccion* (Harvey 1859) or *Irvinea* that possess one, few or many vesicles arranged on solid terete axes (Womersley 1996; Saunders *et al.* 1999). *Gloiosaccion brownii* Harvey, the type and only species of *Gloiosaccion*, possesses a filamentous cortex and tetrasporangia arranged in nemathecium (Womersley 1996), thus differing from *C. chiajeana*. Both *Botryocladia* and the recently erected *Irvinea* (Saunders *et al.* 1999) include species with an apparently similar ensemble of morphological attributes to those observed in *C. chiajeana*.

Among the species with cylindrical or fusiform vesicles that are presently attributed to *Botryocladia* (Table 1), *B. chiajeana* shows similarities to *Botryocladia beaudettei* E.Y. Dawson, *Botryocladia darwinii* Schneider & Lane, *Botryocladia fernandeziana* Levring, *Botryocladia papenfussiana* Ganesan & Lemus, *Botryocladia senegalensis* G. Feldmann & Bodard and *Botryocladia wynnei* Ballantine by nature of their outer cortex arranged in rosettes and cystocarps, which are protuberant (Table 1). However, *B. darwinii*, *B. fernandeziana*, *B. senegalensis* and *B. papenfussiana* differ in producing more numerous secretory cells borne exclusively on unmodified medullary cells (Levring 1941; Feldmann & Bodard 1965; Ganesan & Lemus 1972; Schneider & Lane 2000). *Botryocladia wynnei* differs by its secretory cells borne both on modified and unmodified medullary cells (Ballantine 1985), and *B. beaudettei* by its unbranched vesicles and secretory cells consistently in groups of three (Dawson 1960).

Botryocladia chiajeana exhibits also the diagnostic characters used by Guiry in Saunders *et al.* (1999) in the description of the genus *Irvinea* and it appears to be closely related to *I. ardreana*, the type and single species of *Irvinea*, differing from it by relatively minor details as smaller habit, discoid holdfast, simple axis (rarely ramified), smaller number of secretory cells per bearing cell, absence of filaments arising from clusters of secretory cells, smaller size of reproductive structures, and absence of tela arachnoidea (Table 2). The taxonomic value of some of these distinguishing characters is limited (see Discussion) because knowledge of *I. ardreana* (Brodie & Guiry 1988, as *B. ardreana*) is based on cultured plants originating in Portugal. Because morphological differences between cultured specimens and field specimens have been observed in species of *Botryocladia* (Norris 1989), morphological studies on specimens from natural populations of the Portuguese coasts are needed. Data on these plants are limited to a field collection identified by Ardré (1970) as *Bo-*

Table 1. Comparison of *Botryocladia chiajeana*, *B. macaronesica*, species of *Botryocladia* with one of few elongate, cylindrical or fusiform vesicles, which are more than two diameters long, *Gloiosaccion brownii* and *Irvinea ardreana* (n.d. = no data).

Species	Branching of vesicles	Cell layers in vesicle wall	Outer cortex of vesicles	Bearing secretory cells	Number of secretory cells	Position and size (μm) of tetrasporangia	Position and size (μm) of spermatangia	Position and size (μm) of cystocarps	Monoecious/dioecious	Type locality	References
<i>Botryocladia adhaerens</i> E. Y. Dawson	absent or radial	3	continuous	modified	3	n.d.	n.d.	n.d.	n.d.	Baja California, eastern Pacific	Dawson (1963)
<i>B. beaudettei</i> E. Y. Dawson	absent	3	arranged in rosettes	modified	3	n.d.	n.d.	strongly protuberant 750–900	dioecious?	Costa Rica, eastern Pacific	Dawson (1960)
<i>B. bullosa</i> (Levring) J. N. Norris & Ballantine	absent	2	arranged in rosettes	unmodified	2–3	scattered among cortical cells n.d.	n.d.	n.d.	n.d.	Madeira, eastern Atlantic	Levring (1974), Norris & Ballantine (1995)
<i>B. chiajeana</i> (Meneghini) Kylin	absent or dichotomous	3	arranged in rosettes	modified	1–2 (–4)	sori 21–29 \times 17–26	clusters on outer cortical cells 2.5–4 \times 1.5–2.5	strongly protuberant 650–900	dioecious	Adriatic Sea	this paper
<i>B. connexa</i> Chanh & Xia	absent	4–5	continuous	modified	10–20	n.d.	n.d.	n.d.	n.d.	Guangdong, China, western Pacific	Chang & Xia (1978)
<i>B. darwinii</i> Schneider & Lane	absent	2 (–3)	arranged in rosettes	unmodified	1–17	n.d.	clusters on outer cortical cells 1–2	strongly protuberant 400–700	dioecious	Galapagos Is., eastern Pacific	Schneider & Lane (2000)
<i>B. fernandeziana</i> Levring	absent	2	arranged in rosettes	unmodified	3–7	scattered among cortical cells n.d.	n.d.	strongly protuberant n.d.	dioecious	Juan Fernandez Is., eastern Pacific	Levring (1941), John (1980)
<i>B. hancockii</i> E. Y. Dawson	absent or radial	3	arranged in rosettes	unmodified and modified	4–8	n.d.	n.d.	completely immersed 300–600	dioecious?	Baja California, eastern Pacific	Dawson (1944), Abbott & Hollenberg (1976)
<i>B. lawsonii</i> John	absent	2–3	arranged in rosettes	unmodified	(1–) 2–8 (–10)	scattered among cortical cells 21–28 (–32)	clusters on outer cortical cells 2–4 (–6)	completely immersed 450–500	dioecious	Ghana, eastern Atlantic	John (1980)
<i>B. macaronesica</i> sp. nov.	absent or radial	3 (–4)	nearly continuous	unmodified	(1–) 2–4 (–8)	shallow nemathecia 17–30	clusters on outer cortical cells 3–4 \times 2	completely immersed 825–1050	monoecious	Canary Islands, eastern Atlantic	this paper
<i>B. papenfussiana</i> Ganesan & Lemus	absent or dichotomous	2–3	arranged in rosettes	unmodified	2–8	scattered among cortical cells 20–33	clusters on outer cortical cells 2–3 (–4)	strongly protuberant 500–660	dioecious	Venezuela, western Atlantic	Ganesan & Lemus (1972)
<i>B. paucivesicaria</i> Stegenga, Bolton & Anderson	absent	5	continuous	modified	up to 10	nemathecia 45 \times 22	n.d.	completely immersed n.d.	dioecious?	South Africa	Stegenga <i>et al.</i> (1997)
<i>B. senegalensis</i> G. Feldmann & Bodard	absent or dichotomous	3	arranged in rosettes	unmodified	1–12	n.d.	n.d.	strongly protuberant 100	dioecious?	Senegal, eastern Atlantic	Feldmann & Bodard (1965)

Table 1. Continued.

Species	Branching of vesicles	Cell layers in vesicle wall	Outer cortex of vesicles	Bearing secretory cells	Number of secretory cells	Position and size (μm) of tetrasporangia	Position and size (μm) of spermatangia	Position and size (μm) of cystocarps	Monoeocious/dioecious	Type locality	References
<i>B. wynnei</i> Ballantine	absent	2	arranged in rosettes	unmodified and modified	2–6	scattered among cortical cells 18–24	clusters on outer cortical cells 2–3	incompletely immersed 440–670	monoeocious	Puerto Rico, western Atlantic	Ballantine (1985), Schneider & Searles (1991), Wynne (2001), Womersley (1996)
<i>Glotosaccion brownii</i> Harvey	absent or dichotomous	4–10	antichinal filaments	unmodified	1–12	nemathecia 40–55 \times 10–22	scattered sori 1.5–2	incompletely immersed 500–1000	dioecious	Tasmania	
<i>Irvinea ardreana</i> (Brodie & Guiry) Guiry	absent or dichotomous	3	arranged in rosettes	modified	1–6	sori 21–40 \times 21–28	clusters on outer cortical cells 4.5–6 \times 3.5–5	strongly protuberant 500–950	dioecious	Portugal, eastern Atlantic	Brodie & Guiry (1988, as <i>Botryocladia ardreana</i>)

tryocladia boergesenii that, according to Brodie & Guiry (1988), could belong to *Irvinea ardreana*. Presently, there is no information on the degree of variation of morphological characters in field plants from Portugal, and the possibility that these plants belong to a single species cannot be rejected. Despite the considerable overlap between *Irvinea* and *Botryocladia* with respect to all taxonomic characters, we retain *B. chiajeana* in the genus *Botryocladia*.

***Botryocladia macaronesica* Afonso-Carrillo, Sobrino, Tittley & Neto sp. nov.**

Figs 31–48

Plantae erectae usque 45 mm altae, axe solido simplici usque 4 mm altae, portando 1–12 (rare usque 19) vesiculas terminales et subterminales. Vesiculae ab obovovatis ad fusiformes, saccatae, grandilongatae in maturitate, usque 7 mm diametro et usque 40 mm longae, simplici vel radiatim ramificatae formando plantas saccatas compositas. Parietes vesicularum ex tribus stratis cellularum (rare usque 4), interius cellulis medullosis subpolygonalibus (84–175 μm longis et 67–115 μm largis), uno vel duobus stratis medium cellulis brevioribus ab angularibus ad subsphaericas (14–24 μm diametro), et exterius quasi continuum cellulis corticalibus a sphaericis ad ovoideas (5–12 μm diametro). Cellulae secretoriae congestae duo vel quattuor (rare usque octo) super cellulas medullosas non transmunitas. Gametophyta monoica. Spermatangia simplicia vel paria super cellulas matriciales spermatangiales subsphaericas in cortice exterius. Cystocarpia, 825–1050 μm diametro, immersa in cavitate, cum tetrasporangia subsphaerica, cruciata, decussata vel irregulariter divisa 17–30 μm diametro, in extensos nemathecial soros et in maturitate mixta inter filamenta antichinalia corticalia tricelularia.

Plants erect, up to 45 mm in height, with a simple solid axis, up to 4 mm in height, which bears 1–12 (rarely up to 19) terminal and subterminal vesicles. Vesicles obovoid to fusiform, saccate, greatly elongate at maturity, up to 7 mm in diameter and up to 40 mm long, simple or radially branched forming compound saccate plants. Vesicle walls of three (rarely four) cell layers, the innermost consisting of subpolygonal medullary cells (84–175 μm long and 67–115 μm broad), one or two median layers of angular to subspherical smaller cells (14–24 μm in diameter) and the near-continuous surface layer of spherical to ovoid cortical cells (5–12 μm diameter). Secretory cells occur in groups of two to four (rarely one to eight) on unmodified medullary cells. Gametophytes monoecious. Spermatangia borne singly or in pairs on subspherical spermatangial mother cells in outer cortex. Cystocarps, 825–1050 μm in diameter, immersed into the cavity, with a distinctive ostiole and ovoid carposporangia, 9–15 μm in diameter. Tetrasporangia subspherical, cruciately, decussately or irregularly divided, 17–30 μm in diameter, in extensive nemathecial sori and interspersed between three-celled antichinal cortical filaments when mature.

HOLOTYPE: TFC Phyc 3502 (Fig. 31). Gametophyte; Montaña Clara, north of Lanzarote, Canary Islands, 31 March 1983, leg. Gramonal.

ISOTYPES: TFC Phyc 13056, tetrasporophyte (Fig. 32); and TFC Phyc 5641, one gametophyte and four tetrasporophytes; Montaña Clara, north of Lanzarote, Canary Islands, 31 March 1983, leg. Gramonal. Isotypes in L and TFC.

ETYMOLOGY: The specific epithet refers to the Macaronesia, biogeographical region constituted by the islands of Azores, Madeira, Canaries and Cape Verde, which included the localities where this species has been identified.

REPRESENTATIVE SPECIMENS EXAMINED: **Azores:** São Miguel, São Vicente (*A.I. Neto*, 15 July 1997, UA SMG-97-123). Caloura (*A.I. Neto*, 20 February 2000, UA SMG-00-45). Mosteiros (*A.I. Neto*, 17 July 1997, BM SMG-97-155/BM000619722). **Madeira:** Porto Santo, SW coast Baixo (Cancap, 9 June 1980, L 4068). **Canary Islands:** La Palma, Punta Garafia (*T. Cruz*, 12 July 1983, TFC Phyc 3095). El Hierro, Arenas Blancas (*J. Afonso-Carrillo & B. Rojas-*

Table 2. Morphological differences between *Botryocladia chiajeana* and *Irvinea ardreana*.

Characters	<i>Botryocladia chiajeana</i>	<i>Irvinea ardreana</i>
Maximum height habit (mm)	50	77
Holdfast	discoid	rhizoidal, dichotomously branched
Fusiform stoloniferous vesicles	present	absent
No. secretory cells in clusters	1–2 (4)	1–6
Secretory cells (μm)	pyriform	rounded, ovate or pyriform
Size	16–34 \times 24–43	20–55
Three-celled filaments in clusters of secretory cells	absent	present
Tetrasporangia	subspherical to ovoid	ovoid
Size (μm)	17–26 \times 21–19	21–28 \times 21–40
Spermatangia size (μm)	2.5–4 \times 1.5–2.5	4.5–6 \times 3.5–5
Carposporangia size (μm)	12–25	(10) 16–34 (60)
Tela arachnoidea	absent	present

González, 21 April 1993, TFC Phyc 10440). Tenerife: Punta Hidalgo (*J. Reyes & M. Sansón*, 4 April 1992, TFC Phyc 9842; *J. Afonso-Carrillo & Y. Elejabeitia*, 1 March 1991, TFC Phyc 6952; *C. Ibeas & B. Rojas-González*, 4 April 1993, TFC Phyc 9843; *P. Conesa & C. Sobrino*, 16 May 1997, TFC Phyc 10441). San Marcos, Icod (*E. Muñoz, J. Reyes & M. Sansón*, 16 June 1994, TFC Phyc 9754, 9755, 9756, 9758; *J. Reyes & M. Sansón*, 30 September 1994, TFC Phyc 9844). Playa de Los Troches (*Cancap*, 31 May 1982, L 6317). Lanzarote: La Madera (*L. Arráez*, 17 July 1987, TFC Phyc 5153). Orzola (*R. Haroun*, 7 December 1983, TFC Phyc 924; *C. Ibeas & B. Rojas-González*, 8 May 1993, TFC Phyc 9845). Caletón Blanco (*J. Reyes & M. Sansón*, 24 April 1990, TFC Phyc 10442). Fuerteventura: Cotillo (*J. Reyes & M. Sansón*, 20 November 1992, TFC Phyc 8448). **Cape Verde Islands:** W coast Island of Fogo (*Cancap*, 9 June 1982, L 6646).

DISTRIBUTION: Azores, Madeira, Canary Islands and Cape Verde Islands (Fig. 30).

HABITAT: *Botryocladia macaronensis* is an occasional element in the lower eulittoral and shallow sublittoral marine flora of the Macaronesian Islands. In lower tidepools, the species

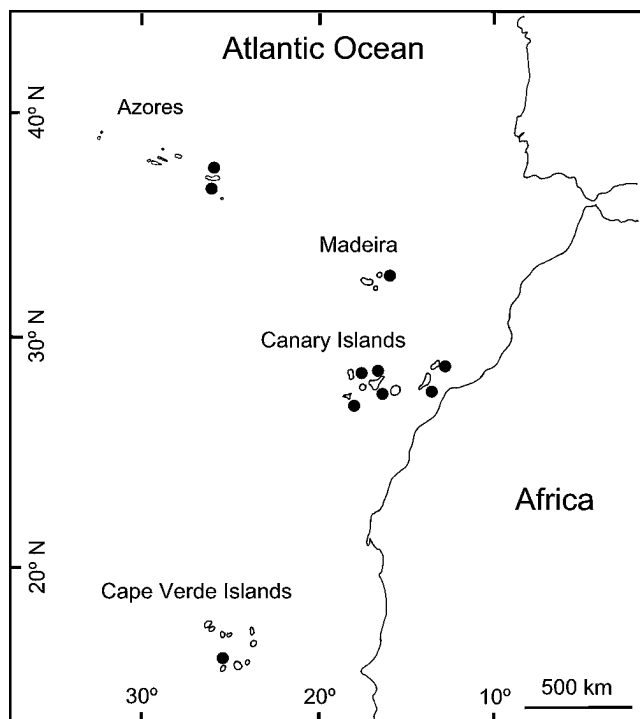
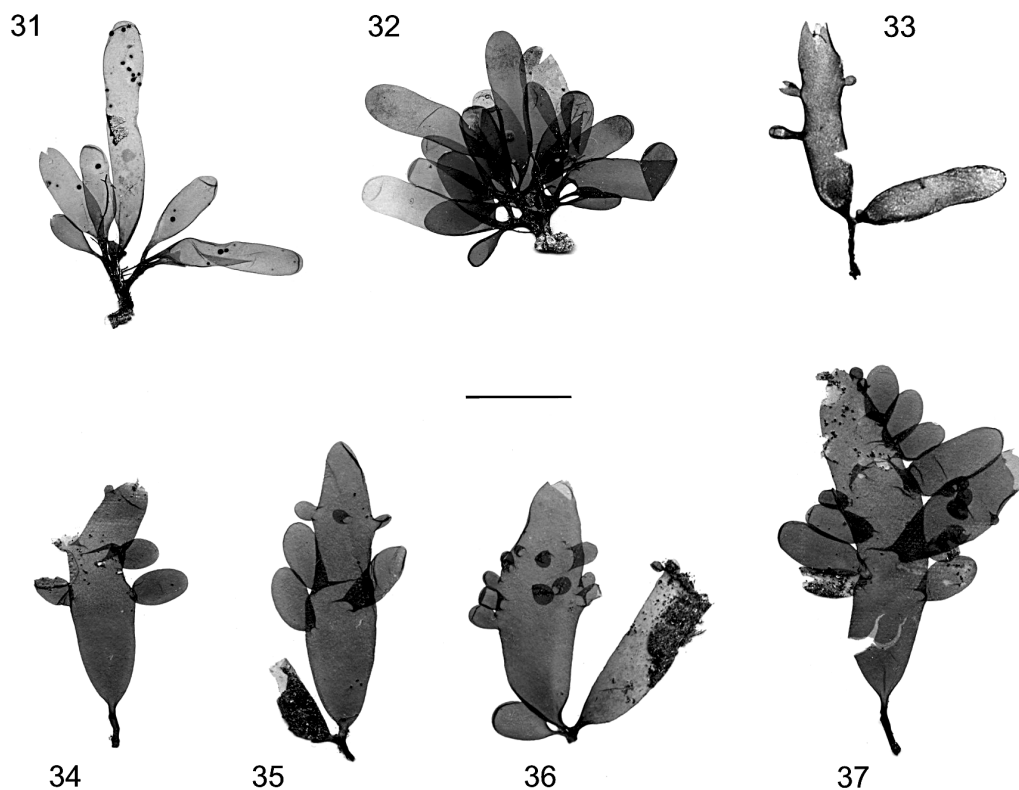


Fig. 30. Map showing localities with confirmed occurrence of *Botryocladia macaronensis*.

grows epilithically in shady habitats (caves, overhanging and under macrophytes). In the sublittoral, it colonises rock and cobbles in sand-influenced areas up to 15 m depth. This species grows in areas of moderate water movement and plants occur mainly from spring to summer, although also rarely collected in autumn and winter. Plants from tidepools usually have vesicles undivided, whereas plants from the sublittoral exhibit frequently radially branched vesicles.

HABIT AND VEGETATIVE STRUCTURE: Plants are rosy-red to rosy-green in colour, erect up to 45 mm in height, consisting in a single discoid holdfast, which gives rise to one to four short, usually simple solid axes, bearing distally 1–12 (–19) shortly stipitate gelatinous vesicles (Figs 31–37). Axes are terete, 1–1.5 mm diameter, and up to 4 mm in height. Vesicles are flexuous, saccate, obovoid to fusiform, and becoming greatly elongate at maturity, up to 7 mm diameter and up to 40 mm long. Mature vesicles are simple or branch radially with up to 10 secondary vesicles forming compound saccate plants (Figs 33–37). Vesicles are usually undivided in plants bearing numerous vesicles, but they are often branched in plants with one or two initial vesicles. Secondary vesicles are up to 5 mm in diameter and up to 16 mm long, basally attenuate, and, occasionally bear short tertiary protuberances (Fig. 37). Solid axes consist of subspherical to ovoid hyaline medullary cells, 25–50 μm diameter, surrounded by smaller pigmented ovoid cortical cells, 3–5 μm diameter (Fig. 38). Pit connections are common between medullary cells. Globose secretory cells, 15–18 μm in diameter, are borne occasionally from unmodified medullary cells (Fig. 38). Vesicle walls are soft, mucilaginous, 70–115 μm thick, consisting of three (occasionally four) cell layers (Fig. 39). The innermost nonpigmented medullary cells are subpolygonal, 84–175 μm long and 67–115 μm broad in surface view, surmounted by one or two layers of angular to subspherical smaller cells, 14–24 μm broad, and an outer cortex of spherical to ovoid cells, 5–12 μm diameter, forming a nearly continuous surface layer (Fig. 40). Two to four (rarely one–eight) secretory cells are scattered on unmodified medullary cells and project into the vesicle cavity (Figs 41–43). Secretory cells are pyriform to obovoid, greater, 18–33 μm diameter and 25–38 μm long when occur few (Figs 41, 42), and smaller, 10–24 μm diameter and 13–26 μm in larger groups (Fig. 43).

REPRODUCTIVE STRUCTURES: Gametophytes are monoecious. Ovoid spermatangia, c. 2 μm broad and 3–4 μm long, are borne singly or in pairs from subspherical spermatangial



Figs 31–37. *Botryocladia macaronesica*. Scale bar = 10 mm.

Fig. 31. Holotype (gametophyte, TFC Phyc 3502).

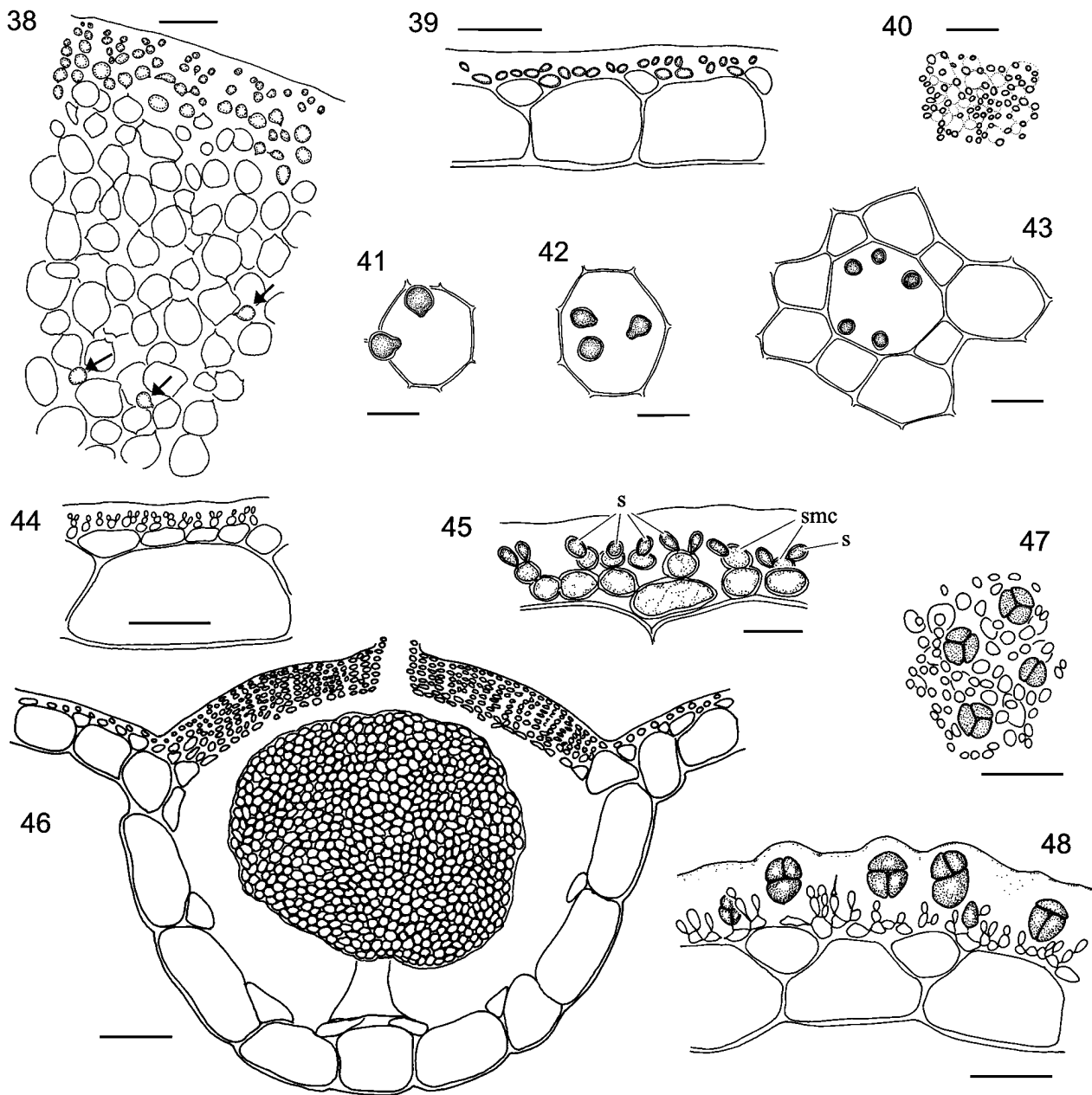
Fig. 32. Isotype (tetrasporophyte, TFC Phyc 13056).

Figs 33–37. Specimens showing radially branched vesicles (Fig. 33: L 6317, the remainder TFC Phyc 9754).

mother cells (4–7 μm diameter) on outer cortical cells in mid- portions of mature vesicles (Figs 44, 45). Carpogonial branches were not observed. Cystocarps are irregularly scattered (up to 30 per vesicle), and are immersed into the cavity, with a thickened ostiolate pericarp projecting only slightly above the level of the outer cortex (Fig. 46). Mature cystocarps are 825–1050 μm in diameter (including the pericarp) with the subspherical mature gonimoblast composed entirely of ovoid carposporangia, 9–15 μm in diameter, supported by a basal fusion cell (Fig. 46). No tela arachnoidea was observed in the cavity of the cystocarp. The outer wall of the pericarp consists of small rounded or flattened cells (6–12 μm in diameter) arranged in vertical rows. Subspherical, cruciately, decussately or rarely irregularly divided tetrasporangia, 17–30 μm diameter (Figs 47, 48), are borne in extensive shallow nemathecia that are initiated in the distal portions and progressively extend to proximal portions of mature vesicles. Sporangia are derived intercalary from a midcortical cell and, when mature, are interspersed between short (up to three cells long) anticlinal cortical filaments (Fig. 48).

REMARKS: By its solid axes, hollow portions lacking diaphragms and constrictions, near-continuous cortication of vesicles, secretory cells on unmodified medullary cells and completely immersed cystocarps, this species is a member of *Botryocladia* as currently circumscribed (Afonso-Carrillo & Sobrino 2003). *Botryocladia macaronesica* has no single unique feature, but differs from the other species of the genus previously reported from the eastern Atlantic (see Afonso-Car-

rillo & Sobrino 2004), by a distinctive combination of attributes. Most of the species [i.e. *Botryocladia boergesenii* J. Feldmann, *B. botryoides* (Wulfen) J. Feldmann, *B. canariensis* Afonso-Carrillo & Sobrino, *B. guineensis* John, *B. madagascariensis* G. Feldmann, *B. microphysa* (Hauck) Kylin, *B. occidentalis* (Børgesen) Kylin, *B. pyriformis* (Børgesen) Kylin, and *B. shanksii* E.Y. Dawson] differ clearly in habit by their hollow branches that remain spherical or become pyriform, but do not elongate to any extent. Only *Botryocladia bullosa* (Levring) Norris & Ballantine (1995), *B. chiajeana*, *B. lawsonii* John (1980), *B. senegalensis* Feldmann & Bodard (1965) and *B. wynnei* Ballantine (1985) have elongate hollow saccate branches with indeterminate growth in length, exhibiting some likeness in external appearance with *B. macaronesica*. Other *Botryocladia* species also possess elongate-saccate vesicles: *B. adhaerens* Dawson (1963), *B. beaudettei* Dawson (1960) and *D. hancockii* Dawson (1944) from the Pacific coast of Central America, *B. connexa* Chang & Xia (1978) from China, *B. darwinii* Schneider & Lane (2000) from Galapagos Islands, *B. fernandeziana* Levring (1941) from Juan Fernández Islands and Baja California, *B. papenfussiana* Ganesan & Lemus (1972) from Venezuela and Colombia, and *B. paucivesicaria* Stegenga, Bolton & Anderson (1997) from South Africa (Table 1). The new species resembles *B. bullosa*, *B. darwinii*, *B. fernandeziana*, *B. hancockii*, *B. lawsonii*, *B. papenfussiana*, *B. senegalensis* and *B. wynnei* with respect to secretory cells borne on unmodified medullary cells. However, in all these species, outer cortical cells are arranged in rosettes that are lacking in *B. macaronesica* (Table 1).



Figs 38–48. *Botryocladia macaronesica*. Scale bars = 50 μm , unless stated.

- Fig. 38.** Detail of a transverse section of an axis showing inner medullary cells (large) and outer cortical cells (smaller). Note small secretory cells on inner medullary cells (arrows) (TFC Phyc 9758).
Fig. 39. Transverse section of vesicle wall showing three cell layers (TFC Phyc 9842).
Fig. 40. Surface view of cortical cells of vesicles. Subsurface cells are shown in dashed outline (TFC Phyc 8448).
Figs 41–43. Details of inner surface of the vesicle wall showing secretory cells borne on unmodified medullary cells (TFC Phyc 6952).
Fig. 44. Transverse section of vesicle wall in a fertile gametophyte showing spermatangial sorus (TFC Phyc 6952).
Fig. 45. Detail of transverse section of spermatangial sorus, showing subspherical spermatangial mother cells (smc) cutting off spermatangia (s) on the outer side (TFC Phyc 6952).
Fig. 46. Transverse section of a cystocarp with the fusion cell giving rise to a subspherical mass of carposporangia (TFC Phyc 6952). Scale bar = 100 μm .
Fig. 47. Surface view of tetrasporangial nemathecium with mature tetrasporangia surrounded by sterile cells (TFC Phyc 8448).
Fig. 48. Transverse section of vesicle wall through a shallow nemathecium showing cruciately divided tetrasporangia interspersed between three-celled anticlinal cortical filaments (TFC Phyc 8448).

Branching of vesicles to form compound saccate plants is quite unusual among species of *Botryocladia*, and until now it was an exclusive character of *B. hancockii* (Dawson 1944, 1963). However, in addition to the arrangement of outer cor-

tical cells, *B. macaronesica* can be separated from the latter species by (1) the secretory cells borne exclusively on unmodified medullary cells; (2) the greater size of cystocarps and (3) its assumed monoecious condition (Table 1).

DISCUSSION

The problems inherent in identifying plants with elongate-saccate vesicles became apparent in material from the Mediterranean and the eastern Atlantic that was previously referred to *C. chiajeana*. These difficulties are related to the unsatisfactory ensemble of morphological attributes used in the segregation of the genera of hollow Rhodymeniaceae lacking regular constrictions or diaphragms. Plants with these features were first included in the genus *Chrysymenia* Agardh (1842: 105). Later, Kylin (1931) subdivided *Chrysymenia*, transferring to *Cryptarachne* (Harvey) Kylin the flattened species with 'internal rhizoids' in the medullary cavities, and to *Botryocladia* the species with solid axes in different extension. He only retained in *Chrysymenia* the species with entirely hollow fronds. Although distinction of *Cryptarachne* as different from *Chrysymenia* has been later rejected (Abbott & Littler 1969), Ben Maïz *et al.* (1987) regarded it as probably valid.

Kylin (1956) discussed two additional genera with solid axes that had been previously overlooked, *Myrioglossa* Holmes (1894) and *Gloiosaccion* Harvey (1859), and along with *Botryocladia* included them in his '*Botryocladia* group'. *Myrioglossa* and *Gloiosaccion* are monospecific, and later, both genera were accepted as synonyms of *Botryocladia*, and their species transferred to it (Papenfuss 1958; Feldmann & Bodard 1965). However, Womersley (1996) retained *Gloiosaccion* as a distinct genus on the basis of its habit, cortical construction, tetrasporangia arrangement and cystocarp protrusion. Finally, Saunders *et al.* (1999) removed *B. ardreana* to the segregate genus *Irvinea*.

It is assumed *Botryocladia* still constitutes a heterogeneous group of species (Brodie & Guiry 1988; Norris 1989; Schneider & Lane 2000; Afonso-Carrillo & Sobrino 2003). This morphological heterogeneity was observed by Feldmann (1945) that, based mainly in the habit features, divided the genus *Botryocladia* into two sections: Sect. Microphysae, which includes small-sized species with little-branched solid axes bearing a small number of vesicles; and Sect. Botryoideae, which includes species with greater developed arborescent solid axes with numerous spherical, ovate or pyriform vesicles. Species from Botryoideae, including the type species *Botryocladia botryoides*, constitute apparently a homogeneous group and they are easily recognisable by their habit like clusters of grapes (Schneider & Lane 2000). By contrast, the Microphysae seem to be a more heterogeneous group and its habit differences have allowed differentiating two subsets of species (Feldmann 1945; Feldmann & Bodard 1965), one for those that bear elongate, cylindrical or saccate vesicles, and another one for those that produce near subspherical vesicles. For comparative purposes, current species of *Botryocladia* are listed in Table 3 following the sections proposed by Feldmann (1945). It is precisely in the subset that includes the species with elongate, cylindrical or fusiform vesicles where are seemingly located the greater difficulties in establishing a clear distinction between *Botryocladia* and related genera *Chrysymenia*, *Gloiosaccion* and, specially, *Irvinea*. Both *B. chiajeana* and *B. macaronesica* belong to this controversial group of species.

In this context, the erection of the genus *Irvinea* by Saunders *et al.* (1999) has blurred the morphological features that

supported distinction between *Botryocladia*, *Chrysymenia* and *Gloiosaccion*. *Irvinea* was mainly supported by molecular data and by an ensemble of morphological features (i.e. rosetted cortex, modified cells bearing the secretory cells, and strongly protuberant cystocarps) which, according to Saunders *et al.* (1999), had made *Botryocladia ardreana* a morphologically anomalous species in the genus *Botryocladia*. Although Saunders *et al.* (1999) suggested that some of the *Botryocladia* species with this ensemble of features might be moved to *Irvinea*, Schneider & Lane (2000) and Afonso-Carrillo & Sobrino (2003) observed a considerable overlap between both genera. Therefore, the morphological characters used in delineation of *Irvinea* need to be reviewed.

The pattern of cell arrangement in the vesicle walls is a character often used to separate *Botryocladia* and some *Chrysymenia* species, and therefore its potentiality as a diagnostic feature of *Irvinea* needs to be checked. Among the 41 species currently accepted in *Botryocladia*, vesicles in which cortical cells are arranged forming open rosettes have been reported in 17 species (Table 3). Rosetted cortices occur in species with two-layered vesicle walls, where cortical cells form open rosettes or rings around the underlying larger non-pigmented medullary cells, and in species with three-layered vesicle walls, where outer cortical cells are arranged around the intermediate layer of cells that form partial rosettes around medullary cells. Most of the species with rosetted cortex belong to the Microphysae, excepting *Botryocladia ebriosa* and *B. leptopoda* (Millar 1990), both from Botryoideae. It is also a relatively common characteristic in the large-vesicled subgroup (Table 3). However, this feature has been considered inconsistent in some species (Ballantine & Aponte 2002). In *Botryocladia bahamense*, portions of older vesicles may become completely or nearly completely corticated (Ballantine & Aponte 2002). Although the variation in cortication of the vesicles is generally not included in species descriptions, at least *I. ardreana* (Brodie & Guiry 1988, as *B. ardreana*) and *B. chiajeana* display a near-continuous cortex becoming denser in some portions of the vesicles. The diagnostic value of rosetted cortex has not been confirmed by the molecular data, as shown by *B. ebriosa*, which exhibits this arrangement in cortical cells (Millar 1990); this species is probably not related to *Irvinea* but to *Botryocladia* (Saunders *et al.* 1999).

Formation of secretory cells on anatomically distinct initials seems to be also a doubtful diagnostic feature of *Irvinea* because the type species *B. botryoides* form secretory cells both on unmodified and modified medullary cells (Afonso-Carrillo & Sobrino 2003). A similar positioning of secretory cells was also reported in *B. bahamense* (Ballantine & Aponte 2002), *B. canariensis* (Afonso-Carrillo & Sobrino 2003), *B. ebriosa* (Millar 1990), *B. hancockii* (Dawson 1944), *B. madagascanensis* (Norris 1989), *B. pianaari* (Norris 1989) and *B. wynnei* (Ballantine 1985).

Additionally, cystocarp protrusion does not appear to be of generic importance. The three morphologically distinct cystocarp types described in *Botryocladia* (i.e. completely immersed, incompletely immersed and strongly protuberant) do not imply a major change in the development of the cystocarp, and it seems a useful character to separate species only (Afonso-Carrillo & Sobrino 2003). In addition, species with incompletely immersed cystocarps [e.g. *Botryocladia sonderi* Silva (Womersley 1996)] and species with strongly protuberant cys-

Table 3. Comparison of species of *Botryocladia* based on morphological features used as prominent in characterization of the genus *Irvinea* (n.d. = no data).

Species	Cortex arranged in rosettes	Secretory cells on modified medullary cells	Cystocarp strongly protuberant
Sect. Botryoideae G. Feldmann (1945)			
<i>B. beckeriana</i> (Holmes) Papenfuss	–	+	+
<i>B. botryooides</i> (Wulfen) J. Feldmann	–	–	–
<i>B. ebriosa</i> Millar	+	+–	n.d.
<i>B. guaymasensis</i> E. Y. Dawson	–	–	+
<i>B. leptopoda</i> (J. Agardh) Kylin	+	–	+
<i>B. madagascariensis</i> G. Feldmann	–	+–	–
<i>B. neushulii</i> E. Y. Dawson	–	–	+
<i>B. occidentalis</i> (Børgesen) Kylin	–	–	–
<i>B. pienaarri</i> R. E. Norris	–	+–	–
<i>B. pseudodichotoma</i> (Farlow) Kylin	–	–	+
<i>B. pyriformis</i> (Børgesen) Kylin	–	–	–
<i>B. shanksii</i> E. Y. Dawson	–	+	n.d.
<i>B. sonderi</i> Silva	–	–	–
<i>B. uvarioides</i> E. Y. Dawson	–	–	n.d.
Sect. Microphysae G. Feldmann (1945)			
With vesicles spherical, ovate or pyriform			
<i>B. bahamense</i> Ballantine & Aponte	+	+–	–
<i>B. boergesenii</i> J. Feldmann	+	+	n.d.
<i>B. canariensis</i> Afonso-Carrillo & Sobrino	–	+–	n.d.
<i>B. caraibica</i> Gavio & Fredericq	–	+	n.d.
<i>B. feldmannii</i> Pham-HoangHo	–	–	n.d.
<i>B. ganesanii</i> Aponte Díaz	–	–	–
<i>B. guineensis</i> John	–	–	+
<i>B. kuckuckii</i> (Weber-van Bosse) Yamada & Tanaka	–	–	–
<i>B. microphysa</i> (Hauck) Kylin	+	n.d.	n.d.
<i>B. monoica</i> Schnetter	+	+	+
<i>B. skottsbergii</i> (Børgesen) Levring	–	–	–
<i>B. spinulifera</i> Taylor & Abbott	–	–	n.d.
<i>B. tenuissima</i> Taylor	+	–	n.d.
With vesicles elongate, cylindrical or fusiform			
<i>B. adhaerens</i> E. Y. Dawson	–	+	n.d.
<i>B. beaudetti</i> E. Y. Dawson	+	+	+
<i>B. bullosa</i> (Levring) J. Norris & Ballantine	+	–	n.d.
<i>B. connexa</i> Chanh & Xia	–	+	n.d.
<i>B. chiajeana</i> (Meneghini) Kylin	+	+	+
<i>B. darwinii</i> Schneider & Lane	+	–	+
<i>B. fernandeziana</i> Levring	+	–	+
<i>B. hancockii</i> E. Y. Dawson	+	+–	–
<i>B. lawsonii</i> John	+	–	–
<i>B. macaronesica</i> Afonso-Carrillo, Sobrino, Tittley & Neto	–	–	–
<i>B. paperfussiana</i> Ganesan & Lemus	+	–	+
<i>B. paucivesicaria</i> Stegenga, Bolton & Anderson	–	+	–
<i>B. senegalensis</i> G. Feldmann & Bodard	+	–	+
<i>B. wynnei</i> Ballantine	+	+–	–

tocarps, e.g. *Chrysymenia wrightii* (Harvey) Yamada (Ben Maiz *et al.* 1987), are related closely using molecular evidence (Saunders *et al.* 1999).

Finally, other characters proposed to define *Botryocladia* do not clarify the boundary with *Irvinea*. Kylin (1956) characterised *Botryocladia* as being sympodially constructed, a character later emphasised by Norris (1989), Millar (1990) and Abbott (1999). However, the genus *Irvinea* has been also characterised by its sympodial construction (Saunders *et al.* 1999). The pattern of ramification can be helpful to discriminate *Botryocladia* and *Irvinea* from *Chrysymenia*, although it is not useful to distinguish between the former genera. The determinate growth of the vesicles suggested by Afonso-Carrillo & Sobrino (2003) as a potentially important feature of *Botryocladia* is in discord with the molecular evidence although

elaboration of elongate dichotomously branched vesicles is an exclusive feature of *Irvinea*.

Initial molecular data obtained from a limited number of species from this group of Rhodomeniaceae (Saunders *et al.* 1999) show a complex scene, in which in addition to *Irvinea*, at least two different assemblages of species can be differentiated. These assemblages are not in agreement with the current generic segregation. Therefore, although the vegetative and reproductive characters of *Irvinea* are seemingly different from the type species of *Botryocladia*, there is an extensive overlap between both genera, which prevents a morphological definition of *Irvinea*. Presently the genus *Irvinea* exists only at the molecular level, and in this provisional situation, the generic assignation of the species here examined is a debatable matter.

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