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Two amphi-Atlantic species of *Botryocladia* (Rhodymeniales, Rhodophyta) in the Canary Islands (Eastern Atlantic)

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Abstract — The morphology of the western Atlantic *Botryocladia shanksii* E. Y. Dawson and *B. pyriformis* (Børgesen) Kylin are examined in material collected in the Canary Islands, confirming the amphi-Atlantic distribution of both species. *Botryocladia shanksii*, which was found growing in the lower eulittoral, is reported for the first time in the eastern Atlantic, and the origin and disposition of tetrasporangia is documented. Tetrasporangia are derived from inner intercalary cortical cells and are scattered throughout the cortex in the subsurface cortical layer. The occurrence of *B. pyriformis* in the eastern Atlantic is confirmed by an examination of deep-water plants from the Canaries that are in agreement with the original description of *Chrysymenia pyriformis* Børgesen. Cystocarp structure is described in detail for the first time. Cystocarps are largely immersed in the vesicle with compact lobed gonimoblasts composed entirely of angular carposporangia. The distribution of *Botryocladia* species in the Atlantic Ocean is given.

***Botryocladia pyriformis* / *Botryocladia shanksii* / Canary Islands / marine algae / morphology / Rhodophyta / Rhodymeniales**

Résumé — Deux espèces amphi-atlantiques de *Botryocladia* (Rhodymeniales, Rhodophyta) aux îles Canaries (Atlantique Est). La morphologie de deux algues de l'Atlantique occidental *Botryocladia shanksii* E. Y. Dawson et *B. pyriformis* (Børgesen) Kylin est examinée sur des échantillons collectés aux îles Canaries, confirmant leur distribution des deux côtés de l'Atlantique. Le *B. shanksii*, qui a été trouvé dans l'étage littoral inférieur, est signalé pour la première fois dans l'Océan Atlantique oriental ; l'origine et la disposition des tétrasporocystes sont décrites. Les tétrasporocystes dérivent de cellules corticales intercalaires internes et sont dispersés dans tout le cortex sous la couche corticale la plus externe. La présence du *B. pyriformis* est confirmée dans l'Océan Atlantique oriental avec des échantillons trouvés en profondeur aux Canaries ; sa description concorde avec celle, originale, du *Chrysymenia pyriformis* Børgesen. Le développement des cystocarpes est décrit en détail pour la première fois. Les cystocarpes sont en grande partie immergés dans la vésicule avec des gonimoblastes lobés et compacts, composés entièrement de carposporocystes anguleux. La distribution de ces espèces de *Botryocladia* dans l'Océan Atlantique est donnée.

Algues marines / *Botryocladia pyriformis* / *Botryocladia shanksii* / Iles Canaries / morphologie / Rhodophyta / Rhodymeniales

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INTRODUCTION

The red algal genus *Botryocladia* (J. Agardh) Kylin (1931) includes erect species with solid axes bearing hollow, mucilage-filled, vesicular laterals, the plants usually growing in shady habitats in warm temperate and tropical seas (Schneider & Lane, 2000; Afonso-Carrillo & Sobrino, 2003). Of the approximately forty species currently assigned to *Botryocladia*, twenty are present in the Atlantic Ocean (Ballantine & Aponte, 2002; Afonso-Carrillo & Sobrino, 2003; Gavio & Fredericq, 2003). Most species have been exclusively reported from one side of the Atlantic Ocean: nine species are considered endemic to the eastern Atlantic (Afonso-Carrillo & Sobrino, 2003), and seven species endemic to the western Atlantic (Gavio & Fredericq, 2003). The existence of vicarious pairs of species occurring on the two sides of the warm waters of the Atlantic has been suggested by Aponte-Díaz (1988) to explain this pattern in species distribution. However, based on occasional reports from the Canary Islands (eastern Atlantic), amphi-Atlantic distributions were suggested for three species widely distributed in the western Atlantic [*Botryocladia occidentalis* (Børgesen) Kylin, *B. pyriformis* (Børgesen) Kylin and *B. wynnei* D.L. Ballantine]. Although some of these reports were questioned as probable misidentifications (Price *et al*., 1986), the occurrence of *B. occidentalis* in the eastern Atlantic was recently demonstrated and its amphi-Atlantic distribution confirmed (Afonso-Carrillo & Sobrino, 2003).

During the course of our studies of the Canarian representatives of *Botryocladia* (Afonso-Carrillo & Sobrino, 2003), we had an opportunity to examine numerous collections, including several of unreported or rarely reported species in the eastern Atlantic, and to make observations on reproductive morphology in a genus in dire need of studies of this nature (Brodie & Guiry, 1988). In the present account, morphological data are presented for Canarian plants belonging to two species of *Botryocladia* originally described from the western Atlantic. *Botryocladia shanksii* Dawson (1962) is reported for the first time in the eastern Atlantic and tetrasporangia are documented in a species only known from sporophytic plants. The second species, *Botryocladia pyriformis*, had been previously reported in the Canary Islands (Gil-Rodríguez & Afonso-Carrillo, 1980), but since Gavio & Fredericq (2003) showed that under the name *B. pyriformis* at least two different taxonomic entities were involved [*B. pyriformis sensu* Børgesen (1910, 1920) and *B. pyriformis sensu* Taylor (1960) (= *B. caraibica* Gavio *et* Fredericq)] the identity of the eastern Atlantic plants was in need of clarification. Although *B. pyriformis* had been examined in previous studies (Børgesen (1920), as *Chrysymenia pyriformis*; Gavio & Fredericq, 2003), some details of its reproductive morphology, potentially important in species delineation, remained unknown. Cystocarp development of *B. pyriformis* is herein described in detail for the first time.

MATERIAL AND METHODS

Observations are based on specimens freshly collected in the Canary Islands, preserved in 4% formalin in sea water and deposited at TFC; as well as on dried herbarium specimens housed at TFC. Selected fragments from formalin-preserved material were stained in 1% aniline blue and mounted in a 20% Karo® corn syrup solution. Sections were made by hand with a razor blade. Dried spec-

imens from herbaria were rehydrated in 4% formalin in sea water. Drawings were made by using a camera lucida attached to a Zeiss standard microscope. Herbarium abbreviations follow Holmgren *et al*. (1990).

OBSERVATIONS AND DISCUSSION

Botryocladia shanksii E. Y. Dawson (Figs 1-10)

E.Y. Dawson (1962: 385; pl. 1, fig. a; pl. 2, figs a, b; pl. 5, fig. b).

Type locality: Puerto Limon, Atlantic Costa Rica.

Distribution: Western Atlantic: Bahamas, Belize, Colombia, Costa Rica, Pelican Cays and Puerto Rico (Littler & Littler, 1997, 2000). Eastern Atlantic: Canary Islands.

Material examined: TFC Phyc 10429 and 10430 (08 Nov. 1991, San Sebastián, La Gomera, leg. *J. Reyes* and *M. Sansón*, lower eulittoral).

Plants were growing epilithically and forming large clumps alongside *Corallina elongata* Ellis *et* Solander in a shady crevice in the lower eulittoral. Plants are red in colour, to 26 mm in height, and attached by a discoid holdfast

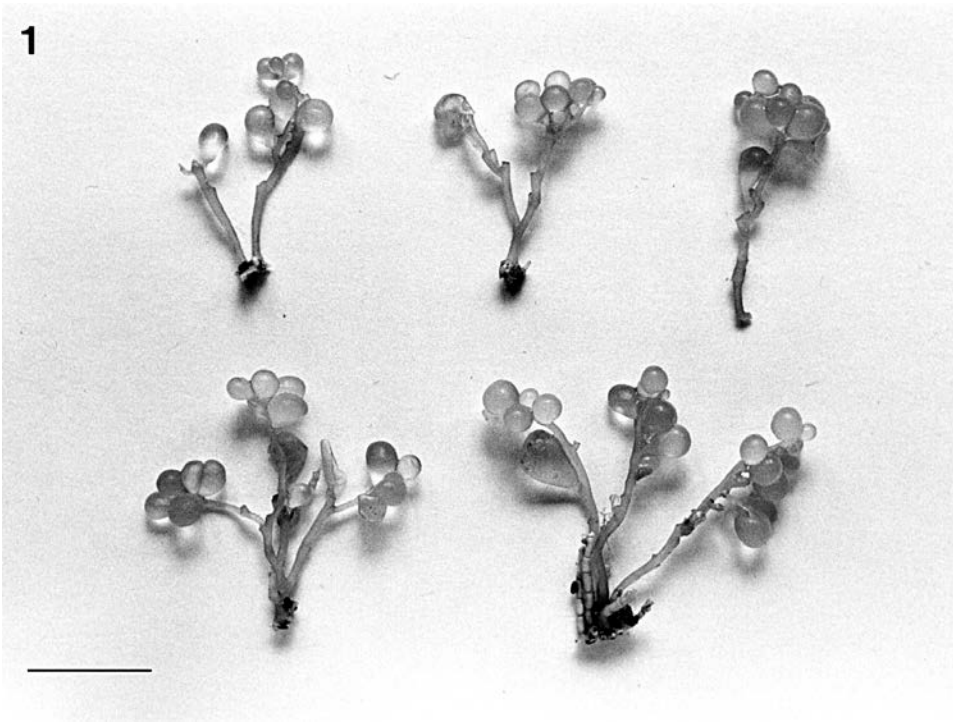
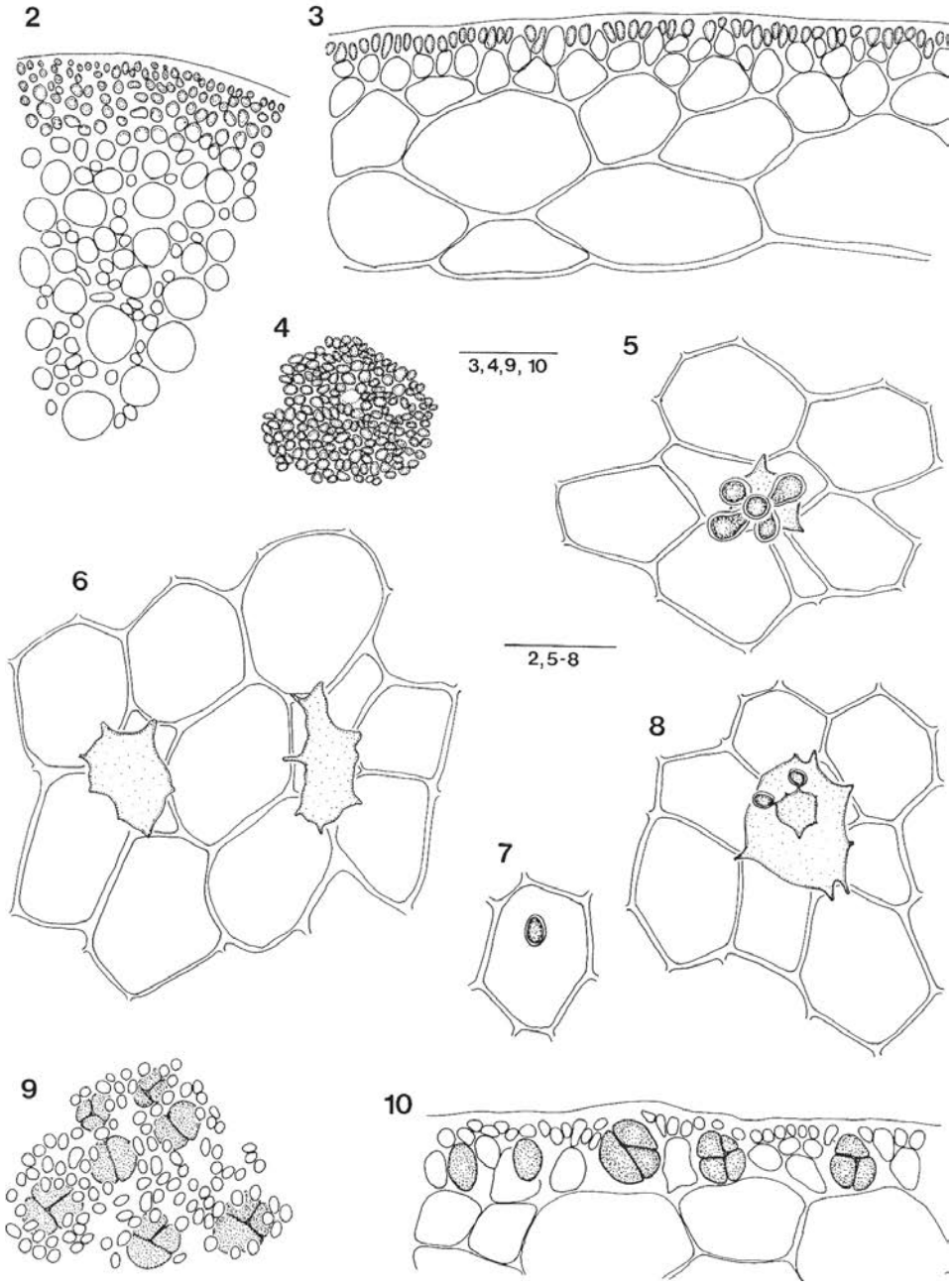


Fig. 1. *Botryocladia shanksii*. Habit variation of five liquid-preserved mature tetrasporophytes (TFC Phyc 10430). Scale bar = 1 cm.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that gives rise to one or two stiff, solid terete axes (nearly 0.5 mm in diam.). Axes are 1-2 times dichotomously branched, somewhat divaricately disposed, each axis bearing up to ten lateral vesicles restricted to distal portions (Fig. 1). Vesicles are subspherical to pyriform, shortly stipitate, and range from 3-4 mm diam. and 4-6 mm long (Fig. 1). Solid axes consist of an inner medulla of large spherical hyaline cells, 28-50 µm diam. mixed with smaller cells 10-17 µm diam., and an outer cortex of spherical to ovoid pigmented cells, 5-10 µm diam. (Fig. 2). The vesicle walls are relatively leathery, 90-130 µm thick, and consist of three to five cell layers (Fig. 3). The innermost nonpigmented medullary cells are subpolygonal (90-205 µm diam. in surface view), and surmounted by two to four layers of progressive smaller cells (Fig. 3). A continuous cortical layer is present and is composed of rounded cells, 6-10 µm diam. (Fig. 4). Secretory cells are subspherical to pyriform (18-30 µm diam. and 25-54 µm long), and occur in clusters of 2-5 on modified medullary cells (Fig. 5). Modified medullary cells lacking secretory cells are common (Fig. 6), and occasionally a single secretory cell is formed directly from a normal medullary cell (Fig. 7), or smaller secretory cells occur on a modified cell borne on another modified medullary cell (Fig. 8).

Only tetrasporangial plants were collected. Tetrasporangia are formed in extensive sori in the distal portions of the vesicles and are cruciately divided, subspherical to ovoid, 20-30 µm diam. and 25-50 µm long (Figs 9, 10). Tetrasporangia are derived from a midcortical cell in an intercalary position, and when mature persist below the outer cortical cells in the subsurface cortical layer (Fig. 10).

The examined plants are in agreement in all relevant diagnostic features with both the original description of *Botryocladia shanksii* given by Dawson (1962) for plants from Costa Rica, and the observations of the species made by Schnetter (1977) based on collections from Colombia. Plants from the Canary Islands are somewhat smaller in habit than plants from the western Atlantic; Dawson (1962) described plants up to 7 cm high, and those of Schnetter (1977) were up to 14 cm high. However, the stiff and forked axes with vesicles restricted to the upper parts, the small vesicles with walls composed of 3-5 cell layers, and the disposition of the secretory cells are sufficiently characteristic to allow identification of this species with confidence. We did not find plants consisting of a single vesicle or showing lateral fusions between vesicles, features described by Littler & Littler (1997) for plants from Belize.

Our observations on reproductive morphology show that *Botryocladia shanksii* exhibits the same pattern of tetrasporangial development as the type species, *B. botryoides* (Wulfen) J. Feldmann. Tetrasporangia are derived from an inner intercalary cortical cell and are scattered throughout the cortex in the subsurface cortical layer (Afonso-Carrillo & Sobrino, 2003). In others species of

Figs 2-10. *Botryocladia shanksii* (TFC Phyc 10430, unless stated). Fig. 2. Detail of transverse section of an axis showing inner medullary cells and outer cortical cells (TFC Phyc 10429). Fig. 3. Transverse section of vesicle wall. Fig. 4. Surface view of cortical cells of vesicles. Fig. 5. Inner surface of the vesicle wall showing a cluster of secretory cells on a modified medullary cell. Figs 6-8. Details of inner surface of the vesicle wall showing modified medullary cells lacking secretory cells, and secretory cells borne both on an unmodified medullary cells and on a modified cell placed on also modified medullary cell. Fig. 9. Surface view of tetrasporangial sorus with mature tetrasporangia partially covered by outer cortical cells (TFC Phyc 10429). Fig. 10. Transverse section of vesicle wall through a tetrasporangial sorus, showing tetrasporangia in the subsurface layer. Scale bar for figures 3, 4, 9 and 10 = 50 µm; scale bar for figures 2, 5-8 = 100 µm.

Botryocladia [e.g., *B. monoica* Schnetter (1978) and *B. wynnei* Ballantine (1985)], mature tetrasporangia are exposed just below the cuticle in the outer cortical layer, a reproductive morphological feature with high taxonomic value, potentially useful for future segregation of species from the heterogeneous assemblage that is presently included in *Botryocladia*.

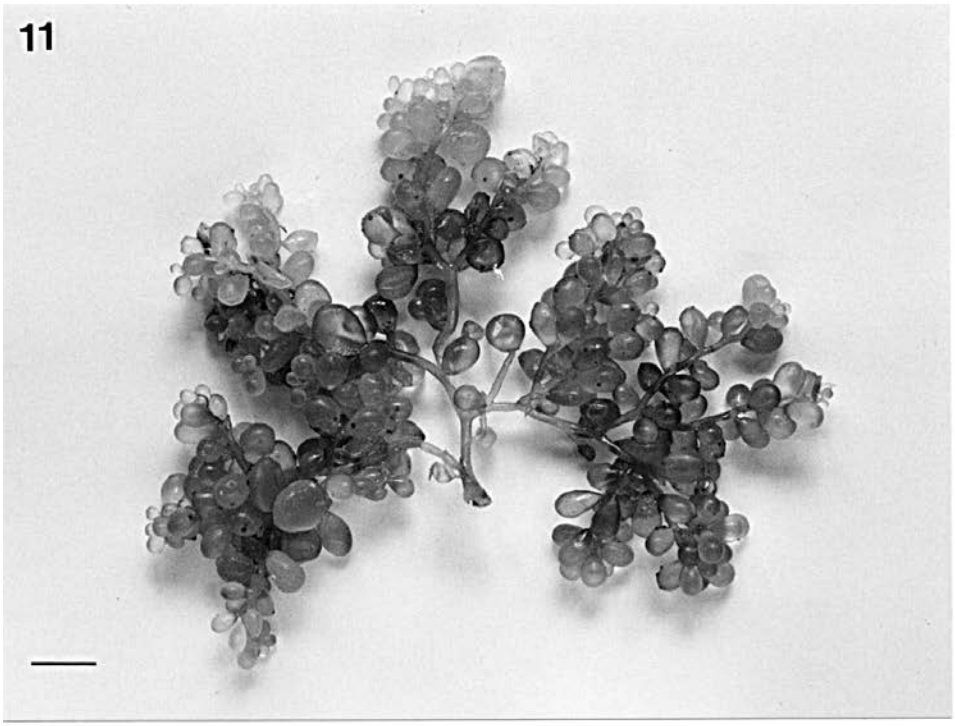
Botryocladia shanksii and *B. botryoides* are the only *Botryocladia* species reported from the Canary Islands exhibiting thick vesicle walls composed of more than three cell layers. Although both species can show a similar habit, they differ mainly in the morphology and position of secretory cells. In *B. botryoides* secretory cells are smaller, occurring singly or up to three on unmodified medullary cells or 1-4 on smaller modified stellate cells (Afonso-Carrillo & Sobrino, 2003). *Botryocladia madagascariensis* G. Feldmann also belongs to this group of species with thicker vesicle walls. Initially described from Madagascar (G. Feldmann, 1945), this species has been reported recently from the Mediterranean Sea (Cormaci *et al*., 1992; Turna *et al*., 2000). *Botryocladia madagascariensis* present similarities with *B. shanksii*, both in habit and position of secretory cells. However, *B. madagascariensis* can be distinguished by its vesicles being distichously arranged in distal parts of the plants, and by its tetrasporangia arising in nemathecial sori (Norris, 1989).

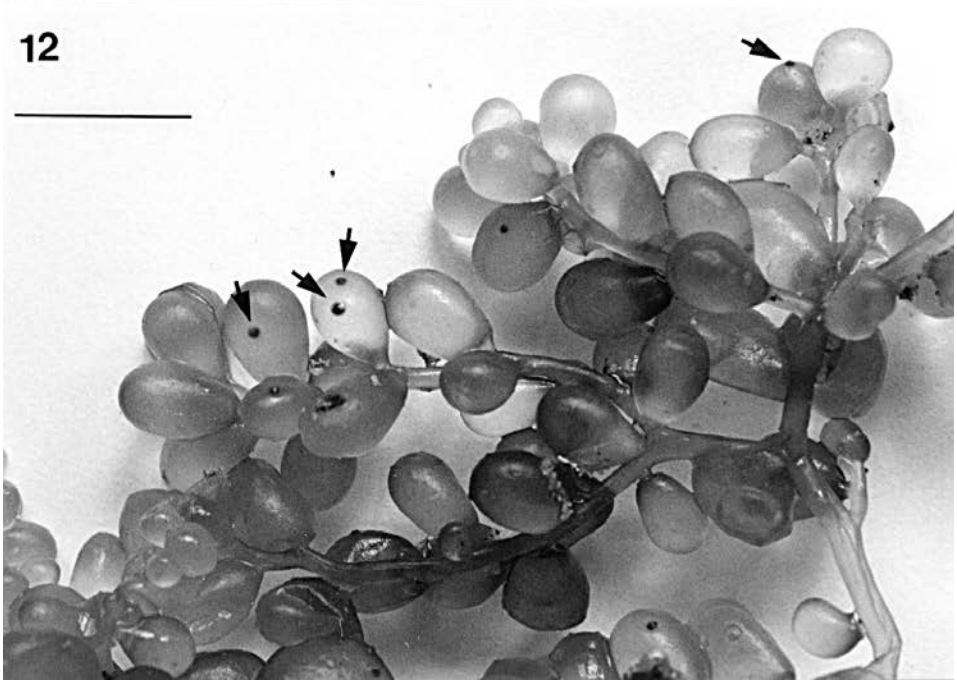
Botryocladia pyriformis (Børgesen) Kylin (1931: 18) (Figs 11-17)

Basionym: *Chrysymenia pyriformis* Børgesen (1910: 187; figs 8, 9).
Type locality: North of St. John, Virgin Islands.
Distribution: Western Atlantic: North Carolina, South Carolina, Bermuda, Florida, Gulf of Mexico, Netherlands Antilles, Barbados, Virgin Islands, Jamaica, Brazil (Taylor, 1960; Schneider & Searles, 1991; Gavio & Fredericq, 2003). Eastern Atlantic: Canary Islands.
Material examined: TFC Phyc 00899 (08 Nov. 1983, Candelaria, Tenerife, leg. *Hernández*; 50 m depth), TFC Phyc 10426 (02 Aug. 1996, Roque de Naos, El Hierro, leg. *J. Reyes*, 45 m depth), TFC Phyc 10427 (20 Nov. 1996, Bahía de Naos, El Hierro, leg. *J. Reyes*, 17 m depth), TFC Phyc 10428 (20 Nov. 1996, Bahía de Naos, El Hierro, leg. *J. Reyes*, 54 m depth), TFC Phyc 11468 (16 June 2003, La Herradura, La Restinga, El Hierro, leg. *R. Hernández Díaz*, 15 m depth).

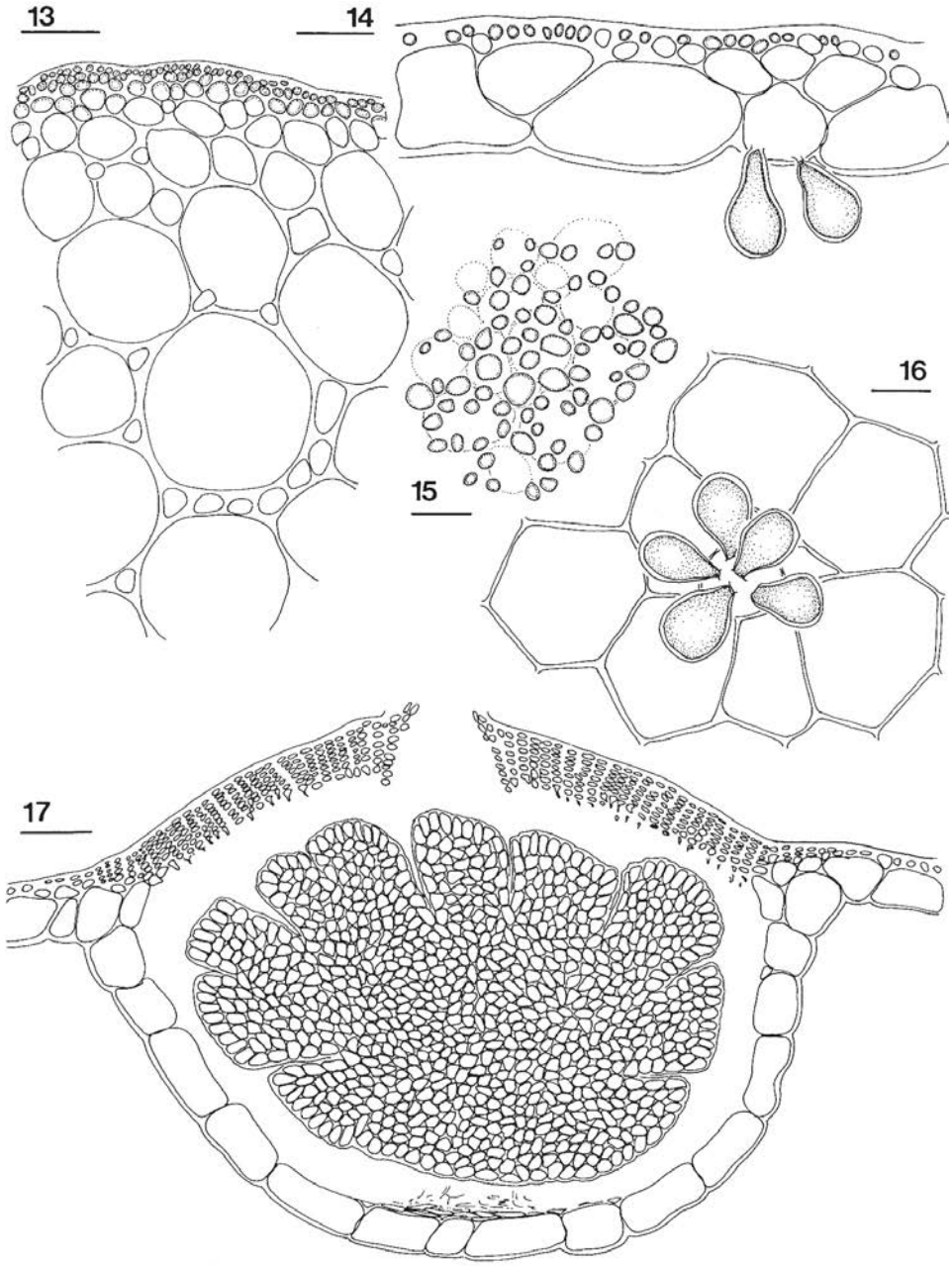
Previous reports of this species in the Canary Islands, including the first report by Gil-Rodríguez & Afonso-Carrillo (1980), have been limited to short references in floristic lists, lacking information on the vegetative and reproductive morphology of the Canarian plants. Close examination of herbarium specimens has shown that all eulittoral specimens previously collected in the Canary Islands and referred to *Botryocladia pyriformis* are misidentifications of the recently described *B. canariensis* Afonso-Carrillo *et* Sobrino (2003). However, several specimens collected offshore, growing epilithically between 15 and 54 m depths, are in agreement with the current concept of *B. pyriformis*.

Plants examined are erect, rosy red, up to 10 cm in height, arising from a small holdfast, and consisting of one to several terete axes (up to 2.4 mm in diameter and 2-9 times pseudodichotomously branched), bearing many (up to 200) radially arranged lateral vesicles (Figs 11, 12). Vesicles are pyriform, oblong or subspherical, shortly stipitate, and 4-8 mm diam. and 6-12 mm long. Solid axes consist of an inner medulla of large rounded hyaline cells (80-220 μm diam.), intermingled with a few small cells (20-50 μm diam.), decreasing in size towards the periphery and an outer thick cortex of rounded pigmented cells, 8-20 μm diam.





Figs 11-12. *Botryocladia pyriformis* (TFC Phyc 11468). Fig. 11. Habit of female gametophyte. Scale bar = 1 cm. Fig. 12. Detail of female gametophyte showing cystocarps (arrows). Scale bar = 1 cm.



Figs 13-17. *Botryocladia pyriformis*. Fig. 13. Detail of transverse section of an axis (TFC Phyc 11468). Fig. 14. Transverse section of vesicle wall showing three cell layers and two secretory cells borne on a smaller medullary cell (TFC Phyc 10426). Fig. 15. Surface view of vesicle showing cortical cells loosely arranged in a discontinuous layer (TFC Phyc 10426). Fig. 16. Inner surface of the vesicle wall showing a cluster of five pyriform secretory cells (TFC Phyc 10426). Fig. 17. Transverse section of a cystocarp (TFC Phyc 11468). Scale bar for figures 13 and 17 = 100 μm; scale bar for figures 14-16 = 50 μm.

(Fig. 13). The vesicle walls are slimy and soft, 55-105 μm thick, consisting of two or three cell layers, with an inner layer of large subpolygonal hyaline medullary cells (50-180 μm diam. in surface view) that subtend one or two layers of progressively smaller, pigmented cortical cells (Fig. 14). The outer cortical cells are subspherical (5-12 μm diam. in surface view) loosely arranged in a discontinuous (not arranged in rosettes) layer (Fig. 15). The secretory cells occur in clusters of 2-7 on smaller (34-72 μm diam.) medullary cells (Figs 14, 16). Secretory cells are obovoid to pyriform, 19-55 μm diam. and 30-77 μm long.

Gametophytes are dioecious and only cystocarpic plants were observed. Cystocarps are numerous (up to five per vesicle) and are scattered irregularly over the distal region of the vesicles (Fig. 12). Mature cystocarps are ca 1000 μm diam. and largely immersed in the vesicle, with only the slightly subconical pericarp protruding from the vesicle wall (Fig. 17). The outer wall of the cystocarp consists of vertical rows of small rounded cells (8-12 μm diam.), with an ostiole up to 150 μm diam. Mature gonimoblasts are compact, with a subspherical lobed mass up to 800 μm diam. composed entirely of angular carposporangia (25-50 μm diam.) (Fig. 17).

The examined plants are in full agreement with *Botryocladia pyriformis* as it was described by Børgesen (1910, 1920, as *Chrysymenia pyriformis*) and recent plants collected in the Gulf of Mexico (Gavio & Fredericq, 2003). This species was originally described from vegetative plants and reproductive stages have remained unknown. Although Ballantine (1989) reviewed herbarium specimens from the Caribbean for the presence of reproductive structures, only information on the size of cystocarps and tetrasporangia was given for the several female, male, and tetrasporic individuals examined. Schneider & Searles (1991) also reported spermatangia and cystocarps in a large-vesicled form from North Carolina referred by them to *B. pyriformis*. But, as Gavio & Fredericq (2003) have recently speculated, perhaps several species reside under the name *B. pyriformis*, thus the current taxonomic placement of the fertile North Carolina plants is uncertain. In genuine *B. pyriformis*, Gavio & Fredericq (2003) documented tetrasporangia and referred to the cystocarps as 'unknown', overlooking the observations previously made by Ballantine (1989) which noted 'cystocarps large and spherical, reached 1 mm diam.'. Tetrasporangia are subspherical (Gavio & Fredericq, 2003, fig. 13) and apparently persist in the subsurface cortical layer, being covered by the outer cortical cells as showed in the type species *B. botryoides* by Afonso-Carrillo & Sobrino (2003). The cystocarps documented here are also in agreement with the type species, differing only in smaller details as the size and shape of gonimoblasts and carposporangia.

The soft and slimy consistency of the vesicles, which adhere strongly to paper, is a useful feature that permits us to distinguish *B. pyriformis* from the others species of *Botryocladia* with spherical or near spherical lateral vesicles growing in the Canary Islands. *Botryocladia boergesenii*, *B. botryoides*, *B. canariensis, B. occidentalis* and *B. shanksii* exhibit relatively leathery vesicles that do not adhere easily to herbarium paper.

CONCLUSIONS

The finding of *Botryocladia shanksii* in the Canary Islands significantly increases the range of distribution of this species (see Littler & Littler, 2000), and it is shown that at least some Canarian plants referred to *Botryocladia pyriformis*

Table 1. Distribution of the Atlantic species of *Botryocladia*.

Species	*Western Atlantic*	*Eastern Atlantic*	*References*
B. bahamense D.L. Ballant *et* Aponte	Bahamas	–	Ballantine & Aponte (2002)
B. boergesenii J. Feldmann	–	Portugal, Salvage Islands, Canary Islands, Mediterranean	Afonso-Carrillo & Sobrino (2003), Audiffred & Weisscher (1984), Gallardo *et al.* (1985)
B. botryoides (Wulfen) J. Feldmann	–	Azores, Madeira, Salvage Islands, Canary Islands, Mediterranean	Afonso-Carrillo & Sobrino (2003)
B. bullosa (Levring) J.N. Norris *et* Ballant	–	Madeira, Azores	Norris & Ballantine (1995)
B. canariensis Afonso-Carrillo *et* Sobrino	–	Canary Islands	Afonso-Carrillo & Sobrino (2003), Gil-Rodríguez & Afonso-Carrillo, 1980, as *B. pyriformis*)
B. caraibica Gavio et Fredericq	Caribbean Panamá, Martinique, Florida	–	Gavio & Fredericq (2003)
B. chiajeana (Menegh.) Kylin	–	Madeira, Canary Islands, Mediterranean	Afonso-Carrillo & Sansón (1999), Gallardo *et al.* (1985), Levring (1974)
B. ganesanii Aponte Díaz	Venezuela	–	Aponte Díaz (1988)
B. guineensis D.M. John	–	Ghana	John (1972)
B. lawsonii D.M. John	–	Ghana	John (1980)
B. madagascariensis G. Feldmann	–	Mediterranean	Cormaci *et al.* (1992), Turna *et al.* (2000)
B. microphysa (Hauck) Kylin	–	Madeira, Mediterranean	Kylin (1931), Levring (1974)
B. monoica Schnetter	Colombia, Gulf of Mexico	–	Gavio & Fredericq (2003), Schnetter (1978)
B. occidentalis (Børgesen) Kylin	from North Carolina to Brazil	Canary Islands	Afonso-Carrillo & Sobrino (2003), Schneider & Searles (1991)
B. papenfussiana Ganesan *et* Lemus	Venezuela, Colombia	–	Ganesan & Lemus (1972), Schnetter (1977)
B. pyriformis (Børgesen) Kylin	from North Carolina to Brazil	Canary Islands	Schneider & Searles (1991), this paper
B. senegalensis G. Feldmann *et* Bodard	–	Senegal	Feldmann & Bodard (1965)
B. shanksii E.Y. Dawson	Caribbean, Costa Rica, Belize, Colombia	Canary Islands	Dawson (1962), Littler & Littler (1997, 2000), Schnetter (1977), this paper
B. spinulifera W.R. Taylor *et* I.A. Abbott	Virgin Islands, Belize, Bahamas, Puerto Rico, Venezuela	–	Ballantine (1985), Littler & Littler (2000) Taylor & Abbott (1973)
B. wynnei D.L. Ballant.	North Carolina, Georgia, Puerto Rico	Canary Islands	Afonso-Carrillo & Sansón (1999), Ballantine (1985), Schneider & Searles (1991)

agree with the protologue of the species (Børgesen, 1910, as *Chrysymenia pyriformis*), despite the exclusion of earlier records now attributed to *B. canariensis*. Thus it is confirmed that *B. pyriformis* is present in the eastern Atlantic. The known distribution of the Atlantic species of *Botryocladia* has been compiled in Table 1. Of the twenty species documented until now, only four (*B. occidentalis*, *B. pyriformis*, *B. shanksii* and *B. wynnei*) have been reported as amphi-Atlantic. Each of these species is widely distributed in the western Atlantic, but known only from the Canary Islands in the eastern Atlantic. The position of the Canary Islands in relation to the North Atlantic surface water movement can explain, at least in part, the present distribution of these species in both sides of the Atlantic Ocean. Several other species of red algae with similar distributions have been recently found in the Canaries, adding to the amphi-Atlantic biogeographical group (Sansón *et al*., 2002; Afonso-Carrillo *et al*., 2003; Afonso-Carrillo & Rojas-González, 2004). This group seems to constitute one of the most distinctive biogeographical entities known in the benthic marine flora of the Canary Islands (Sansón *et al*., 2001).

Most of the Atlantic species of *Botryocladia* have been rarely reported and are considered endemic to a few localities on only one side of the Atlantic. Species with subspherical vesicles and determinate growth are dominant in the western Atlantic (e.g., *B. bahamense*, *B. caraibica*, *B. ganesanii, B. monoica* and *B. spinulifera*); whereas species with elongate vesicles and indeterminate growth are better represented in the eastern Atlantic (e.g., *B. bullosa*, *B. chiajeana*, *B. lawsonii* and *B. senegalensis*) (Table 1). Molecular studies on the phylogenetic relationships of those species will allow a better evaluation of this pattern of distribution in the Atlantic, which could be a consequence both of the evolutionary history of the genus *Botryocladia* and of the formation and expansion of the Atlantic Ocean.

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