Vegetative and reproductive morphology of *Botryocladia botryoides, B. occidentalis* and *B. canariensis* sp. nov. (Rhodymeniaceae, Rhodophyta) from the Canary Islands

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The type species of *Botryocladia, B. botryoides,* and *B. occidentalis* and *B. canariensis* Afonso-Carrillo & Sobrino *sp. nov.,* are described in detail from material collected in the Canary Islands. The previously incomplete and partially ambiguous information about the vegetative and reproductive morphology of *B. botryoides* is completed and clarified. *Botryocladia botryoides* exhibits as its most relevant attributes arborescent solid axes bearing near-spherical determinate lateral vesicles, vesicle walls consisting of four (to six) cell layers, outer cortical cells loosely arranged forming a near-continuous surface layer, one to four secretory cells borne both on unmodified and modified stellate medullary cells, spermatangia cut off from closely packed palisade-like spermatangial mother cells, cystocarps incompletely immersed in the vesicle, and tetrasporangia derived from an inner intercalary cortical cell remaining immersed in the subsurface cortical layer. Occurrence of *B. occidentalis* in the eastern Atlantic is confirmed. *Botryocladia occidentalis* differs from *B. botryoides* mainly by its thinner three-layered vesicle walls and by the fact that its secretory cells are borne exclusively on unmodified medullary cells. *Botryocladia canariensis,* known so far only from the Canary Islands, differs from other *Botryocladia* species by a unique combination of significant attributes, including a dimorphism in secretory cells (obovoid to pyriform when they occur in small clusters on modified medullary cells, and subspherical when solitary on unmodified medullary cells). It is postulated that the eastern Atlantic *B. guineensis,* the western Atlantic *B. ganesanii,* and the Indo-Pacific *B. skottsbergii* are the closest relatives of the new species. We analyse the features of the type species *B. botryoides* with the aim of delineating a clear boundary between *Botryocladia* and the next genus *Irvinea.* The pattern of growth of the vesicles (determinate vs indeterminate) is suggested as a potentially important diagnostic feature for genus separation.

INTRODUCTION

The red algal genus *Botryocladia* (J. Agardh) Kylin was first established as a section of *Chrysymenia* J. Agardh by Agardh (1851) and then elevated to a genus by Kylin (1931). *Botryocladia* currently includes erect species with solid axes bearing hollow mucilage-filled vesicular laterals. The structure is multiaxial and the vesicle walls consist of large inner cells grading outwards into a cortex of smaller cells that form a continuous or reticulate surface layer. The secretory cells are solitary or in groups and are borne on modified initial cells or directly on unmodified medullary cells. The carpogonial branches are four-celled and the cystocarps protrude both inwards and outwards; the spermatangia are cut off from initials on cortical cells, and the cruciately or decussately divided tetrasporangia are originated by transformation of intercalary cortical cells (Feldmann 1945; Feldmann & Bodard 1965; Brodie & Guiry 1988a; Womersley 1996).

Thirty-seven species are currently assigned to *Botryocladia,* most of them from warm temperate to tropical seas in both hemispheres, where they are generally sublittoral and usually grow in shady habitats. Brodie & Guiry (1988a) compiled information on most of the known species, and later, Aponte Díaz (1988), Norris (1989), Millar (1990), Schneider & Lane

(2000) and Ballantine & Aponte (2002) added new species. When Guiry (in Saunders *et al.* 1999) created the genus *Irvinea* to receive *B. ardreana* J. Brodie & Guiry, *Botryocladia* was noted to be a heterogeneous assemblage of species united only by the possession of hollow vesicles formed on a solid axis. Nevertheless, subdivision of the genus has been prevented by incomplete knowledge of the morphology and reproduction of various species, including the type species, *B. botryoides* (Wulfen) Feldmann [heterotypic synonym: *B. uvaria* (Wulfen) Kylin]. Although the type species has been examined in previous studies (Kuckuck 1912 and Børgesen 1929, both as *Chrysymenia uvaria*; Feldmann 1941; Coppejans 1983), essential vegetative and reproductive features remain unknown. Brodie & Guiry (1988a) and Guiry (in Saunders *et al.* 1999) have emphasized the absence of relevant reproductive information, and also the existence of contradictory published information about taxonomically important vegetative attributes, such as the number of cell layers in the vesicle walls and the position of secretory cells. Although cystocarps were described and figured by Kuckuck (1912), information on the tetrasporangia and spermatangia is largely insufficient. Consequently, before a clear definition of *Botryocladia* can be established, *B. botryoides* needs to be studied in detail.

Because knowledge of various species is largely unsatisfactory, it has been suggested that the genus needs revision in particular regions, including the eastern Atlantic (Price *et al.* 1986). During the course of our studies of the Canarian algal flora, we had an opportunity to examine the vegetative and

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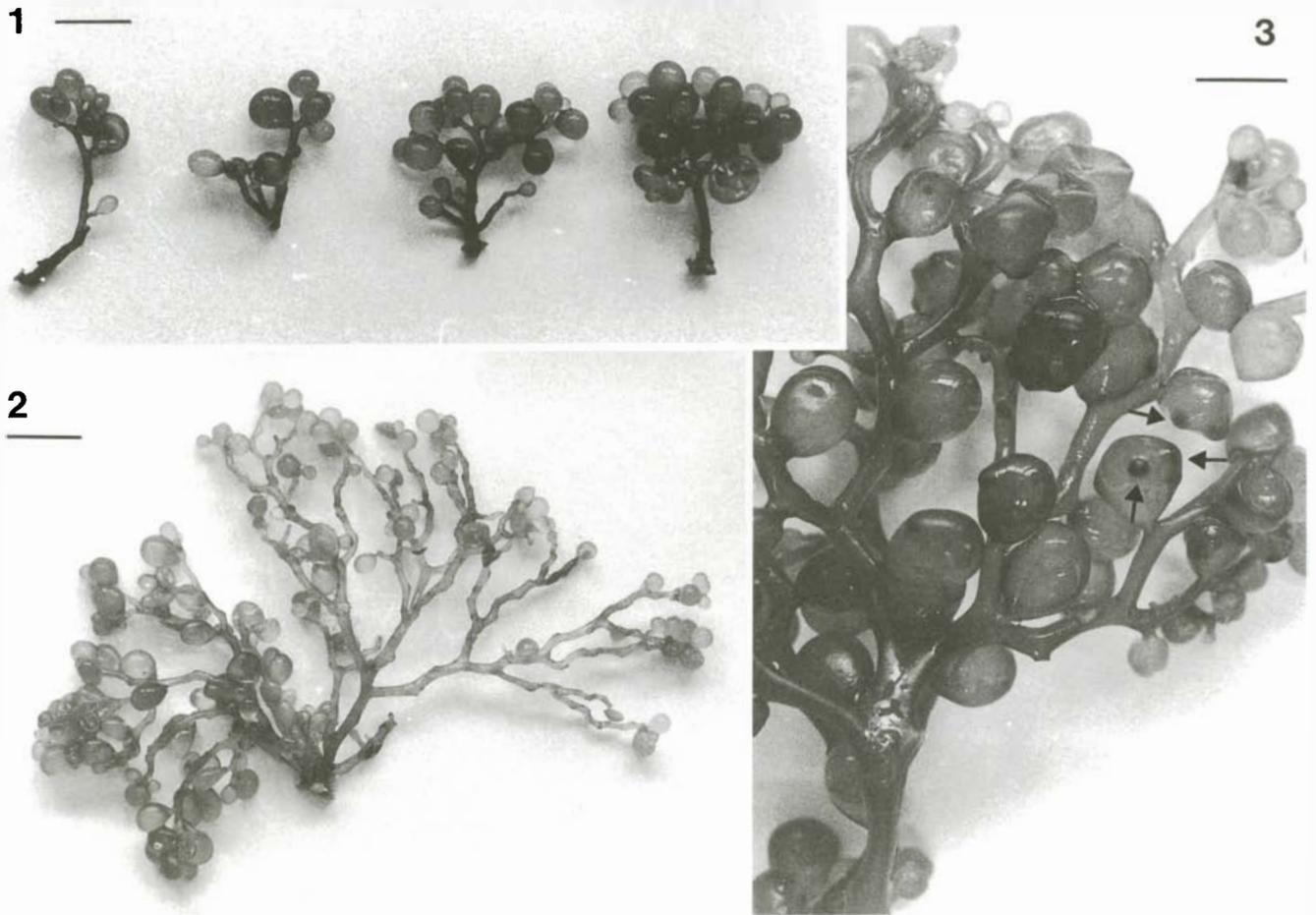
Figs 1–3. *Botryocladia botryoides.* Liquid-preserved specimens. Scale bars = 10 mm.
   Fig. 1. Habit variation in four mature tetrasporophytes (TFC Phyc 10425).
   Fig. 2. Aged tetrasporophyte showing largely denuded axes (TFC Phyc 10414).
   Fig. 3. Detail of female gametophyte showing cystocarps (arrows) (TFC Phyc 10413).

reproductive features both in the type species, *B. botryoides,* and in *B. occidentalis* (Børgesen) Kylin, a rarely reported species in the eastern Atlantic. A third widely distributed species in the Canaries, previously reported as *Botryocladia* sp. (Afonso-Carrillo & Sansón 1999), is recognized here as *B. canariensis* Afonso-Carrilo & Sobrino *sp. nov.*

MATERIAL AND METHODS

Our observations are based on fresh specimens, collected at numerous localities in the Canary Islands, preserved in 4% formalin in seawater and deposited at the University of La Laguna, Canary Islands, Spain (TFC), and also dried herbarium specimens housed at TFC. Herbarium abbreviations follow Holmgren *et al.* (1990). Western Mediterranean specimens of *B. botryoides* housed at the University of Málaga, Málaga, Spain (MGC) and the University of Valencia, Valencia, Spain (VAL), and western Atlantic specimens of *B. occidentalis* deposited at the University of Michigan, Ann Arbor, USA (MICH) were also examined for comparative purposes. 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 specimens from herbaria were rehydrated in 4% formalin in seawater. Drawings were made by using a camera lucida attached to a Zeiss Standard microscope.

OBSERVATIONS

Botryocladia botryoides (Wulfen) Feldmann

Figs 1–15

BASIONYM: *Fucus botryoides* Wulfen *in* Jacquin (1791, p. 146, pl. 13, fig. 1) [for a full list of synonyms see Kylin (1931) and Feldmann (1941)].

TYPE LOCALITY: Trieste, Adriatic Sea (western Mediterranean).

REPRESENTATIVE SPECIMENS EXAMINED: **Canary Islands.** El Hierro: Arenas Blancas (*B. Rojas & J. Afonso-Carrillo*, 21 April 1993, TFC Phyc 10420; *C. Sobrino & P. Conesa*, 3 May 1997, TFC Phyc 10421); Bahía de Naos (*J. Reyes*, 20 November 1996, TFC Phyc 10423, 10424). Tenerife: San Marcos, Icod (*E. Muñoz, M. Sansón, & J. Reyes*, 14 June 1994, TFC Phyc 9761); Puerto de la Cruz (*J. Reyes & M. Sansón*, 25 May 1990, TFC Phyc 10465; 21 June 1990, TFC Phyc 10466; *J. Afonso-Carrillo*, 12 February 1993, TFC Phyc
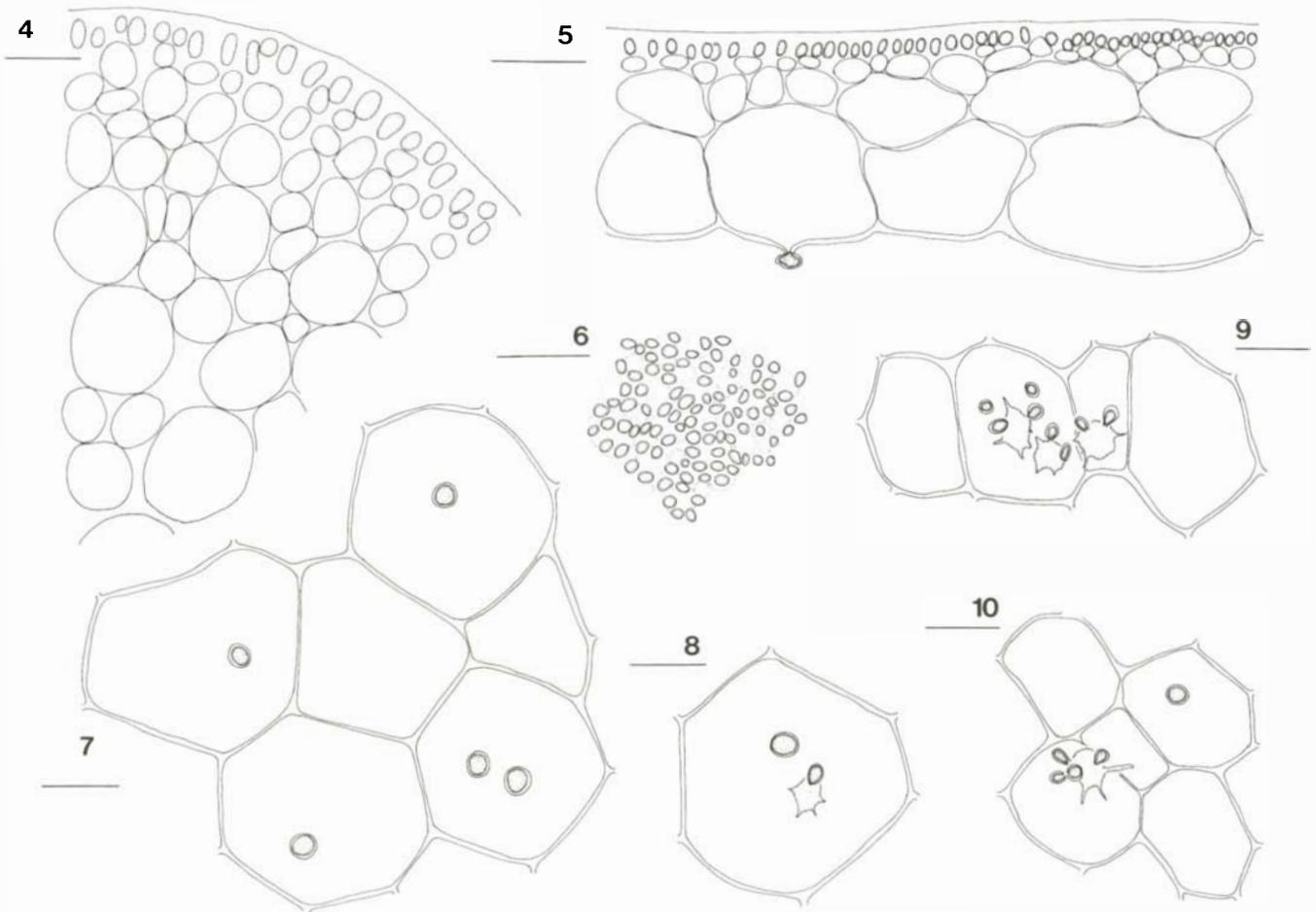
Figs 4–10. *Botryocladia botryoides.* Scale bars = 50 μm.
Fig. 4. Detail of transverse section of an axis showing inner medullary cells (large) and outer cortical cells (smaller) (TFC Phyc 10413).
Fig. 5. Transverse section of vesicle wall showing four cell layers. A secretory cell is borne by an unmodified medulary cell (TFC Phyc 9909).
Fig. 6. Surface view of cortical cells of vesicles. Subsurface cells are shown in dashed outline (TFC Phyc 9909).
Fig. 7. Inner surface of the vesicle wall showing unmodified medullary cells bearing secretory cells (TFC Phyc 8848).
Figs 8–10. Details of inner surface of the vesicle wall showing secretory cells borne both on unmodified medullary cells and on modified stellate initials (TFC Phyc 10415).

10411, 10412; 13 July 1993, TFC Phyc 10413; 15 April 1994, TFC Phyc 10416; 10 April 2001, TFC Phyc 10425; *E. Guadalupe*, 19 July 1993, TFC Phyc 10414, 10415); Punta Hidalgo (*J. Reyes & M. Sansón*, 1 April 1992, TFC Phyc 9909); El Médano (*J. Reyes & M. Sansón*, 29 October 1991, TFC Phyc 7710, 7711; *M. González*, 28 April 1997, TFC Phyc 10417); Peña María (*M.C. Gil-Rodríguez*, 6 March 1995, TFC Phyc 10418). Lanzarote: Arrecife (*E. Guadalupe*, 4 May 1992, TFC Phyc 8648; *B. Rojas & C. Ibeas*, 7 May 1993, TFC Phyc 8848, 10419); Caletón Blanco (*J. Reyes & M. Sansón*, 24 April 1990, TFC Phyc 10464). Fuerteventura: Cotillo (*M. Sansón & J. Reyes*, 21 March 1992, TFC Phyc 8284; 20 November 1992, TFC Phyc 8445, 8447).

DISTRIBUTION: Mediterranean Sea and the eastern Atlantic (Azores, Madeira, Salvage Islands, and Canary Islands). Also reported for the Indian Ocean (India, Sri Lanka, Tanzania, Kenya, and Madagascar) and south-western Pacific (Philippines), but these records need to be checked because they may be misidentified specimens of other species, such as *B. madagascariensis* G. Feldmann and *B. leptopoda* (J. Agardh) Kylin (Feldmann 1945; Silva *et al.* 1996).

HABITAT: *Botryocladia botryoides* grows epilithically or on crustose corallines in shady caves and crevices and on overhanging rocks, either in the lower eulittoral or in the shallow sublittoral to a depth of up to 17 m, usually in sheltered situations on wave-exposed shores. Other sciaphilic algae occurring in this habitat include *Cor-*

allina elongata Ellis & Solander, *Nemastoma canariensis* (Kützing) C. Agardh, and *Valonia utricularis* (Roth) C. Agardh and the nongeniculate coralline algae *Hydrolithon onkodes* (Heydrich) Penrose & Woelkerling, *Lithophyllum vickersiae* Lemoine, and *Neogoniolithon hirtum* (Lemoine) Afonso-Carrillo. Plants of *B. botryoides* are perennial and new vesicles are usually produced every year.

HABIT AND VEGETATIVE STRUCTURE: Plants are erect, red to reddish-brown, and 20–90 mm in height; they are attached by a discoid holdfast, from which arise one to several erect, terete, relatively stiff, alternately branched, arborescent axes 0.7–2 mm in diameter, which bear many (up to 500) radially arranged and closely spaced lateral vesicles (Figs 1, 2). The axes are verrucose in aged plants, as a result of vesicle loss (Fig. 2). Vesicles are subspherical to pyriform, 2.5–6 mm in diameter and 3.5–8 mm long (Figs 1–3). Solid pseudoparenchymatous axes consist of an inner medulla of ovoid and subspherical hyaline cells (38–108 μm in diameter) and an outer thick cortex of ovoid pigmented cells (5–12 μm in diameter) (Fig. 4). The vesicle walls are relatively stiff and up to 140 μm thick; they consist of four (to six) cell layers, with one or two inner layers of large, subspherical to polygonal, hyaline
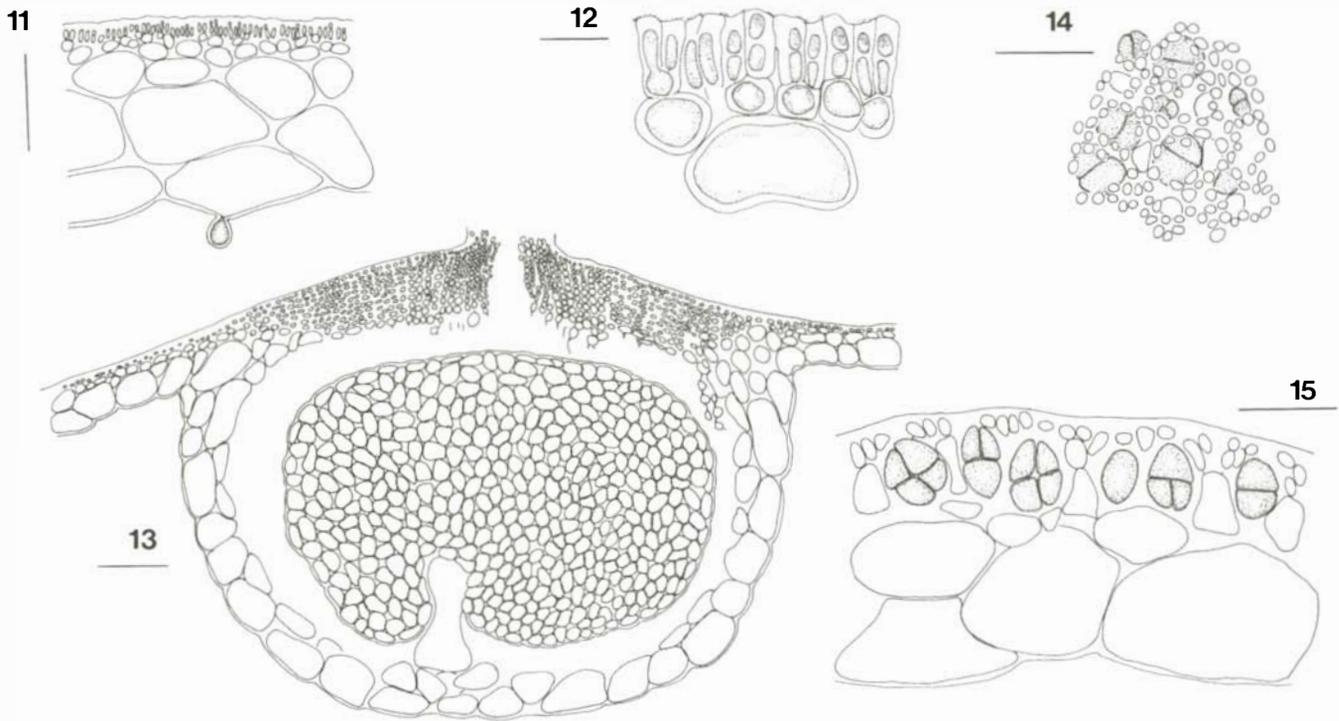
Figs 11–15. *Botryocladia botryoides.*
Fig. 11. Transverse section of vesicle wall in a fertile male gametophyte, showing spermatangial sorus (TFC Phyc 10415). Scale bar = 50 μm.
Fig. 12. Detail of transverse section of spermatangial sorus, showing elongate spermatangial mother cells cutting off spermatangia on the outer side (TFC Phyc 10415). Scale bar = 10 μm.
Fig. 13. Transverse section of a cystocarp with the medullary layers of hyaline cells invaginating and the pericarp of smaller cells protruding slightly from the vesicle wall (TFC Phyc 10413). Scale bar = 100 μm.
Fig. 14. Surface view of tetrasporangial sorus with mature tetrasporangia partially covered by outer cortical cells (TFC Phyc 10414). Scale bar = 50 μm.
Fig. 15. Transverse section of vesicle wall through a tetrasporangial sorus, showing cruciately and decussately divided tetrasporangia in the subsurface layer (TFC Phyc 10414). Scale bar = 50 μm.

medullary cells (55–190 μm in diameter in surface view), which subtend two or three layers of progressively smaller, pigmented cortical cells (Fig. 5). The outer cortical cells are ovoid (4–10 μm in diameter in surface view) and loosely arranged, forming a near-continuous layer over the subsurface layer of intermediate-sized cells (Fig. 6). The secretory cells are subspherical to pyriform, 8–20 μm in diameter, and are produced from medullary cells lying near the inner vesicle cavity (Fig. 7). Single or up to three noncontiguous secretory cells are normally borne on unmodified medullary cells. In younger vesicles and usually only in the terminal region of mature vesicles, secretory cells occur in the margins of medullary cells, whereas they are positioned centrally in mature vesicles (Fig. 7). Modified stellate cells bearing one to four, usually smaller secretory cells are relatively common (Figs 8–10).

REPRODUCTIVE STRUCTURES: The gametophytes are dioecious. Male plants form spermatangial areas in the central portions of vesicles. All outermost cortical cells (Fig. 11) form closely packed, elongate spermatangial mother cells (*c.* 2 μm in diameter and up to 7 μm long), which cut off ovoid spermatangia outwards (*c.* 2 μm in diameter and 3–4 μm long) (Fig. 12). In female plants (Figs 2, 3), early stages of carpogonial branch formation and stages of the cystocarp development were not examined. Cystocarps are very numerous (up

to 12 per vesicle) and are scattered irregularly over the vesicles; when mature, they are largely immersed in the vesicle, but with an evident subconical pericarp protruding from the vesicle wall (Fig. 3). Mature cystocarps reach up to 1000 μm in diameter and 700 μm in height (including the pericarp). In the formation of the cystocarp cavity, the medullary and cortical layers split apart, with the medulla invaginating somewhat to accommodate the gonimoblast (Fig. 13). The outer wall consists of small rounded cells (7–15 μm in diameter) arranged in vertical rows, and around the ostiole the outer wall is slightly thicker (Fig. 13). The mature gonimoblast is subspherical, up to 700 μm in diameter, and composed almost entirely of angular carposporangia (14–30 μm in diameter), and it has a basal fusion cell (Fig. 13). Some tela arachnoidea filaments remain in the cavity of mature cystocarps. Sporangial plants form tetrasporangia in extensive sori in the distal portions of the vesicles. Tetrasporangia are derived from a midcortical cell in an intercalary position (Figs 14, 15). Mature tetrasporangia persist in the subsurface cortical layer, being covered by the outer cortical cells (Fig. 14). Tetrasporangia are subspherical to ovoid, 15–36 μm in diameter and 24–43 μm long, with cruciately or decussately arranged spores (Fig. 15).

REMARKS: Although *B. botryoides* has been examined in previous studies (e.g. Kuckuck 1912; Børgesen 1929; Feldmann
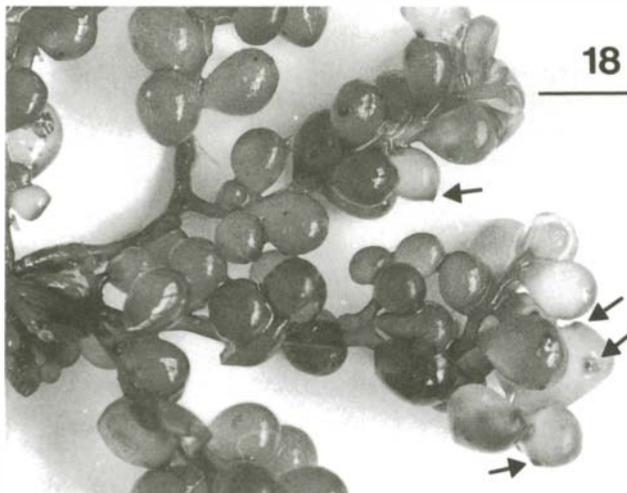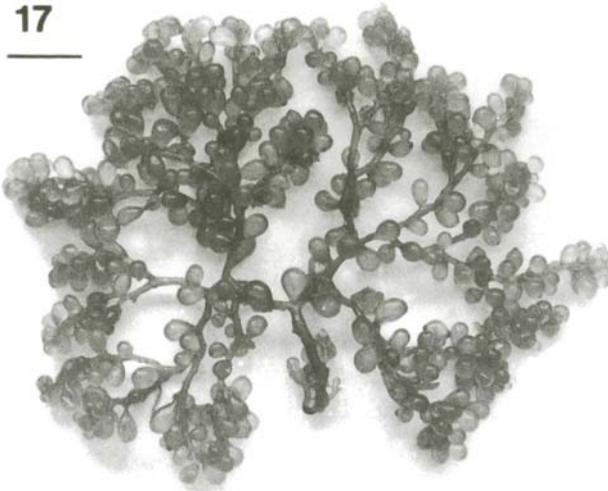
Figs 16–18. *Botryocladia occidentalis.* Liquid-preserved specimens. Scale bars = 10 mm.

1941; Coppejans 1983), our observations are presented in order to clarify ambiguities in previous accounts of the vegetative attributes and to elucidate further the reproductive morphology. Plants from the Canary Islands agree with specimens from various localities in the western Mediterranean (eastern Spain, Sicily), which is also where the type specimen comes from. *Botryocladia botryoides* can be defined by the following combination of characters: (1) arborescent solid axes bearing near-spherical lateral vesicles; (2) vesicle walls consisting of four (rarely up to six) cell layers; (3) outer cortical cells loosely arranged, forming a near-continuous surface layer; (4) one to four secretory cells borne on both unmodified and modified stellate medullary cells; (5) spermatangia cut off from closely packed palisade-like spermatangial mother cells; (6) cystocarps incompletely immersed in the vesicle; and (7) tetrasporangia arising in sori, derived from an inner intercalary cortical cell and remaining in the subsurface cortical layer.

Botryocladia occidentalis (Børgesen) Kylin

Figs 16–25

BASIONYM: *Chrysymenia uvaria* var. *occidentalis* Børgesen (1920, p. 403, fig. 388).

TYPE LOCALITY: Virgin Islands, western Atlantic.

REPRESENTATIVE SPECIMENS EXAMINED: **Canary Islands.** Fuerteventura: Corralejo (*M.C. Gil & J. Afonso-Carrillo*, 3 May 1980, TFC Phyc 2323); Cotillo (*M. Sansón & J. Reyes*, 20 November 1992, TFC Phyc 8444, 8446). Lanzarote: Orzola (*R. Haroun*, 24 June 1983, TFC Phyc 145; 7 December 1983, TFC Phyc 934; *L. Arráez*, 8 January 1984, TFC Phyc 4023; *R.M. González & J.M. Darias*, 2 March 1987, TFC Phyc 5603; *B. Rojas & C. Ibeas*, 8 May 1993, TFC Phyc 10422); Playa de la Madera (*L. Arráez*, 14 July 1987, TFC Phyc 5154).

DISTRIBUTION: Western Atlantic (from North Carolina to Brazil). Eastern Atlantic (Canary Islands).

HABITAT: Epilithic in shallow sublittoral up to 6 m depth. Cystocarpic plants and spermatangial plants were collected in November.

HABIT AND VEGETATIVE STRUCTURE: Plants are erect, rosy red, and up to 70 mm in height; they are attached by a holdfast, which gives rise to one or a few terete (up to 1 mm in diameter), pseudodichotomously branched axes, supporting many radially to distichously arranged vesicles (Figs 16, 17). Solid axes are formed by subspherical to ovoid hyaline medullary cells (25–85 μm in diameter) and ovoid pigmented cortical cells (4–10 μm in diameter) (Fig. 19). Vesicles are shortly stipitate, subspherical to obovoid, 2–4 mm in diameter, and 3–5 mm long (Figs 16–18). The vesicle walls are membranous, (two- or) three-layered, reaching up to 100 μm in thickness (Fig. 20). The inner nonpigmented medullary cells are polygonal and 60–150 μm in diameter in surface view. The outer cortex is composed of rounded cells, 4–10 μm in diameter, which are loosely arranged on a subsurface layer of intermediate-sized cells, forming a near-continuous layer (Fig.

Fig. 16. Male gametophyte with proximal portions of axes voided of lateral vesicles (TFC Phyc 8444).
Fig. 17. Female gametophyte (TFC Phyc 8446).
Fig. 18. Detail of female gametophyte showing cystocarps (arrows) (TFC Phyc 8446).
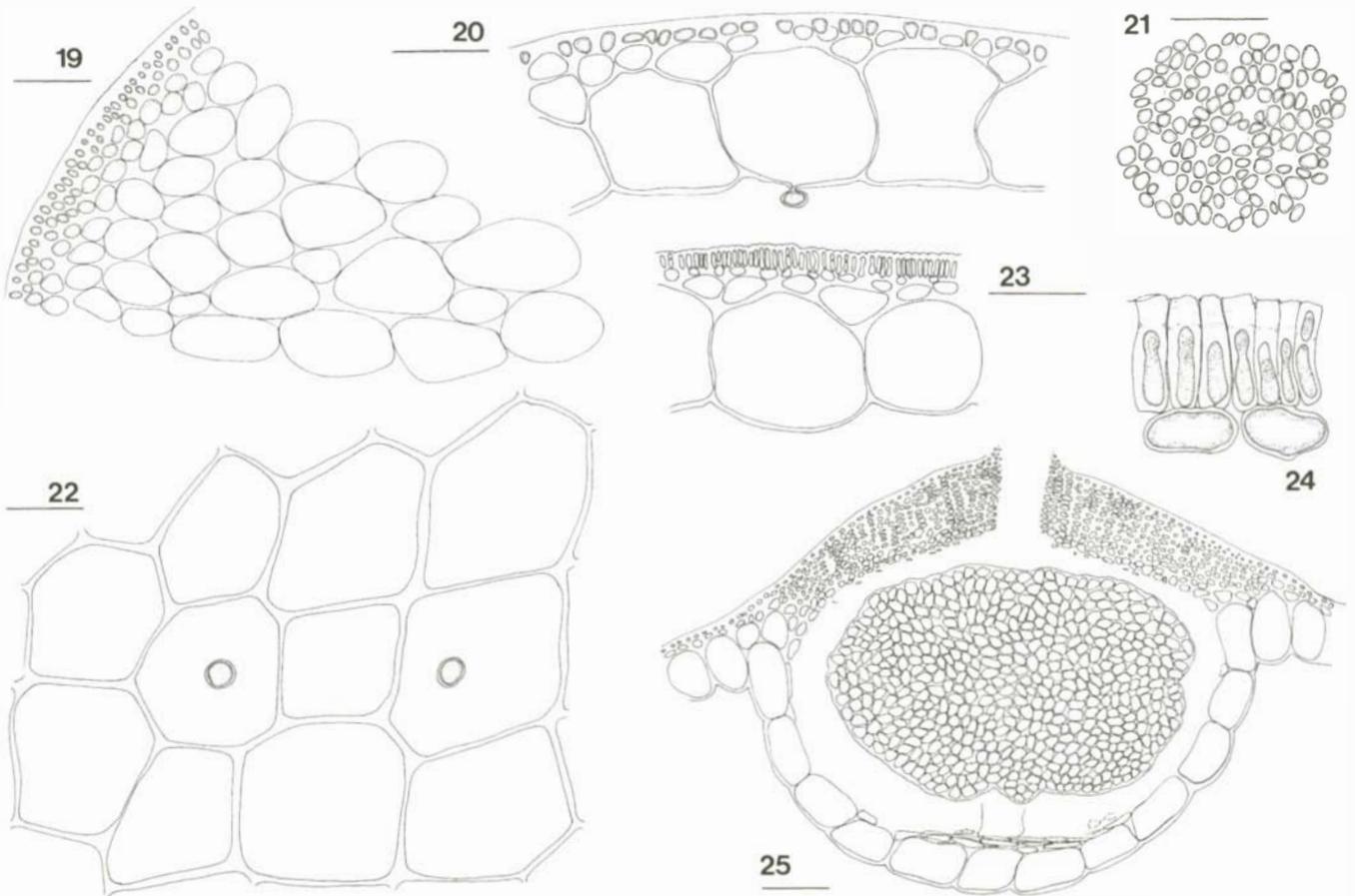
Figs 19–25. *Botryocladia occidentalis.* Scale bars = 50 μm, 10 μm (Fig. 24) or 100 μm (Fig. 25).
  Fig. 19. Detail of transverse section of an axis showing inner medullary cells and outer cortical cells (TFC Phyc 10422).
  Fig. 20. Transverse section of vesicle wall showing three cell layers (TFC Phyc 10422).
  Fig. 21. Surface view of cortical cells of vesicles. Subsurface cells are shown in dashed outline (TFC Phyc 10422).
  Fig. 22. Unmodified medullary cells bearing solitary secretory cells as viewed from the vesicle cavity (TFC Phyc 10422).
  Fig. 23. Transverse section of vesicle wall through a spermatangial sorus (TFC Phyc 8444).
  Fig. 24. Detail of transverse section of spermatangial sorus. Note the elongate spermatangial mother cells cutting off spermatangia outwards (TFC Phyc 8444).
  Fig. 25. Transverse section of a cystocarp (TFC Phyc 8446).

21). Secretory cells are subspherical, 17–27 μm diameter, single or paired on unmodified medullary cells (Fig. 22).

REPRODUCTIVE STRUCTURES: The gametophytes are dioecious. Closely packed elongate spermatangial mother cells (1.5–3 μm in diameter and up to 12 μm long) arise on outer cortical cells, cutting off ovoid spermatangia up to 3–4 μm long (Figs 23, 24). There are few cystocarps (up to four per vesicle), which are irregularly scattered (Fig. 18), reaching up to 1000 μm in diameter at maturity (including the pericarp). Mature cystocarps protrude both outwardly and into the vesicle, with the ostiolate outer wall formed by vertical rows of small rounded cells that are 8–13 μm in diameter (Fig. 25). Mature gonimoblasts are composed entirely of angular carposporangia 12–24 μm in diameter, which form a subspherical mass up to 650 μm diameter (Fig. 25). Tetrasporangia have not been seen.

REMARKS: Previous reports of *B. occidentalis* from the Canary Islands (Gil-Rodríguez *et al.* 1985) were questioned as probable misidentifications of *B. botryoides* (Price *et al.* 1986) and the species was therefore included among the algae whose presence in the Canary Islands was in need of confirmation (Afonso-Carrillo & Sansón 1999). Canarian specimens are smaller than western Atlantic plants, but the remainder of the attributes are in good agreement, both with previous descriptions (Børgesen 1920, as *Chrysymenia uvaria* var. *occidentalis*; Taylor 1960; Schneider & Searles 1991) and with the western Atlantic specimens examined from MICH. *Botryocladia occidentalis* can be separated from *B. botryoides* by its thinner, membranous vesicle walls, which consist of three (occasionally two) cell layers only, and by its secretory cells, which are borne exclusively on unmodified medullary cells. Tetrasporangia are unknown in this species and culture studies are needed to establish its life history. *Botryocladia occidentalis* belongs to a group of amphi-Atlantic marine algae (Haroun *et al.* 1993; Sansón *et al.* 2002), which are widely reported in the western Atlantic but only known from the Canary Islands in the eastern Atlantic.

Botryocladia canariensis Afonso-Carrillo & Sobrino *sp. nov.*

Figs 26–37

Plantae erectae usque 18 mm altae, axe solido simplici vel ramificato usque bis irregulariter vel dichotomo, portando 1–

4 (rare usque 14) vesiculas praesertim terminales vel subterminales. Axes rigidi, cylindrici, 350–750 μm diametro, usque 13 mm alti. Vesiculae ad initium subsphaericae, in maturitate pyriformes usque ad obovatae, 4–5 mm diametro, 5–7(–9) mm longae. Axes solidi ex cellulis medullaribus hyalinis ovoideis usque ad subsphaericis (30–98 μm diametro) et cellulis corticalibus pigmentiferis ovoideis brevioribus (6–11 μm diametro) constantes. Parietes vesicularum ex tribus stratis cellularum, interius cellulis medullosis subpolygonalibus (53–180 μm diametro), medium cellulis brevioribus (18–58 μm diametro), et exterius quasi continuum cellularum corticalium subsphaericarum, 4–12 μm diametro. Cellulae secretoriae solitariae aut congestae ita super cellulas medullosas non transmutatas sic paulo mutatas. Duae formae cellularum secretoriarum: (1) solitariae rotundatae (16–24 μm diametro) 1–3 super cellulas medullae non mutatas aut (2) congestae obovatae ad pyriformes (10–34 μm diametro et 15–48 μm longas), 3–5(–7) super cellulas medullae transmutatas. Tetrasporangia sphaerica vel ellipsoidea cruciata–decussata, 22–34 μm diametro et 26–48 μm longa, in strato subexterno sub cellulis corticalibus exterioribus. Gametophyta ignota.

Plants erect, up to 18 mm in height, with a solid axis that is simple or branched up to twice, irregularly or dichotomously, and bears 1–4 (rarely up to 14) mostly terminal and subterminal vesicles. Axes stiff, terete, 350–750 μm in diameter, and up to 13 mm in height. Vesicles initially subspherical, pyriform to obovoid at maturity, 4–5 mm in diameter, and 5–7(–9) mm long. Solid axes with ovoid to subspherical hyaline medullary cells, 30–98 μm in diameter, and smaller pigmented cortical ovoid cells, 6–11 μm in diameter. Vesicle walls of three cell layers, the innermost consisting of subpolygonal medullary cells (53–180 μm in diameter), the median of smaller cells (18–58 μm in diameter), and the near-continuous surface layer of subspherical cortical cells (4–12 μm in diameter). Secretory cells are solitary or occur in clusters on both unmodified and somewhat modified medullary cells. Two shapes of secretory cells present are (1) solitary rounded (16–24 μm in diameter) cells, one to three in number on unmodified medullary cells and (2) obovoid to pyriform (10–34 μm diameter and 15–48 μm long) cells occurring in clusters of 3–5(–7) on modified medullary cells. Tetrasporangia spherical to ellipsoidal, cruciate–decussate, 22–34 μm in diameter, and 26–48 μm long, positioned in the subsurface layer below the outer cortical cells. Gametophytes unknown.

HOLOTYPE: TFC Phyc 10490 (Fig. 26). Tetrasporophyte; in a shaded crevice in the middle intertidal, Punta Hidalgo, Tenerife, Canary Islands, 8 November 2001; leg. M. Sansón & J. Afonso-Carrillo. Isotypes in MICH, L, and TFC.

ETYMOLOGY: The specific epithet refers to the Canary Islands, which is the type locality.

REPRESENTATIVE SPECIMENS EXAMINED: **Canary Islands.** La Palma: Charco Verde (*B. Rojas*, 7 April 1993, TFC Phyc 10475); La Fajana (*M.C. Gil, J. Afonso-Carrillo & R. Haroun*, 15 June 1983, TFC Phyc 3033; *B. Rojas*, 5 July 1993, TFC Phyc 10478). Tenerife: Punta Hidalgo (*M. Acevedo*, 1 December 1974, TFC Phyc 1800; *Y. Elejabeitia*, 21 January 1991, TFC Phyc 6930; 24 April 1991, TFC Phyc 6880; 11 July 1991, TFC Phyc 6825; *J. Afonso-Carrillo & M. Sansón*, 8 January 1992, TFC Phyc 10467; 9 November 1992, TFC Phyc
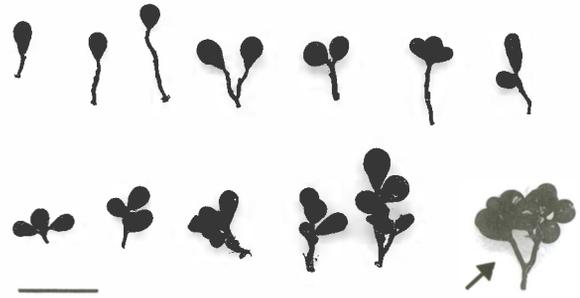

Fig. 26. *Botryocladia canariensis*. Type collection. One specimen (arrow) has been selected as the holotype; the remainder are isotypes (TFC Phyc 10490).

10468; *B. Rojas*, 11 February 1993, TFC Phyc 10469; *C. Ibeas & B. Rojas*, 4 April 1993, TFC Phyc 10473; *J. Afonso-Carrillo*, 31 May 1993, TFC Phyc 10477; 24 March 1994, TFC Phyc 10479; 27 February 1997, TFC Phyc 10483; *J. Afonso-Carrillo, J. Reyes & M. Sansón*, 18 November 1996, TFC Phyc 10481; *C. Sobrino*, 18 February 1997, TFC Phyc 10482; 18 April 1997, TFC Phyc 10488; *C. Sobrino & J. Reyes*, 15 March 1997, TFC Phyc 10486; *P. Conesa & C. Sobrino*, 16 May 1997, TFC Phyc 10487); Mesa del Mar (*B. Rojas*, 10 March 1993, TFC Phyc 10471); El Pris (*C. Ibeas & B. Rojas*, 7 April 1993, TFC Phyc 10474); La Barranquera (*M.C. Gil & R. Haroun*, 11 June 1984, TFC Phyc 4050); San Marcos, Icod (*J. Reyes & M. Sansón*, 30 September 1994, TFC Phyc 10480); Punta Arenitas, Güímar (*R. Haroun*, 13 October 1981, TFC Phyc 828); El Socorro, Güímar (*M. López*, 7 November 1979, TFC Phyc 2104); Puerto de la Cruz (*S. Pinedo*, 21 June 1991, TFC Phyc 5833; *J. Afonso-Carrillo*, 12 February 1993, TFC Phyc 10470; 26 March 1993, TFC Phyc 10472; 1 March 1997, TFC Phyc 10484; 27 May 2001, TFC Phyc 10489; *C. Sobrino*, 14 March 1997, TFC Phyc 10485); El Médano (*M. Sansón, J. Reyes & J. Afonso-Carrillo*, 11 February 1993, TFC Phyc 7803). Lanzarote: Arrecife (*C. Ibeas & B. Rojas*, 7 May 1993, TFC Phyc 10476).

DISTRIBUTION: Canary Islands (La Palma, Tenerife, and Lanzarote).

HABITAT: *B. canariensis* grows epilithically or on nongeniculate coralline algae, forming large clumps in shaded open caves and crevices in the middle eulittoral at moderately sheltered sites in wave-exposed localities. The species grows frequently with *Gymnothamnion elegans* (C. Agardh) J. Agardh, *Corallina elongata* Ellis & Solander, *Valonia utricularis* (Roth) C. Agardh, and *Neogoniolithon hirtum* (Lemoine) Afonso-Carrillo. Plants occur throughout the year and are probably perennial. Plants with tetrasporangia occur in all months but gametophytic plants were not observed.

HABIT AND VEGETATIVE STRUCTURE: Plants are brownish-red, up to 18 mm in height, attached by a discoid, occasionally confluent holdfast, which gives rise to a single short, simple or up to twice, irregularly to dichotomously branched solid axis, bearing one to four (rarely up to 14 in richly branched plants), shortly stipitate vesicles (Fig. 26). Axes are stiff, terete, 350–
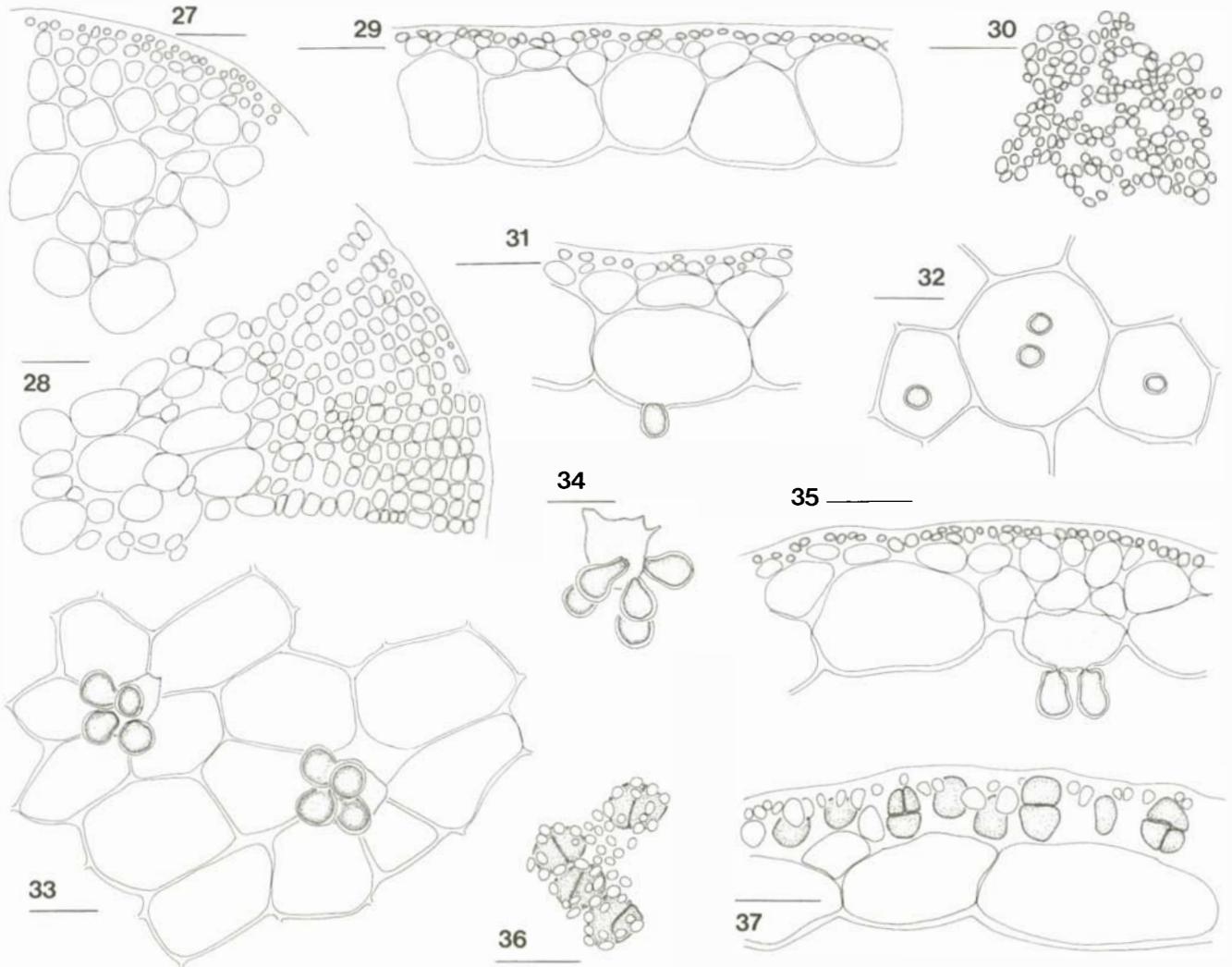
Figs 27–37. *Botryocladia canariensis.* Scale bars = 50 μm.

Fig. 27. Detail of transverse section of axis in a young specimen showing inner medullary cells and outer cortical cells (TFC Phyc 10468).

Fig. 28. Detail of transverse section of axis in an aged specimen with a thickened cortex (TFC Phyc 10480).

Fig. 29. Transverse section of vesicle wall (TFC Phyc 10468).

Fig. 30. Surface view of vesicle, showing a near-continuous cortical layer but with some cortical cells arranged in minute rosettes on the adjacent walls of subsurface cells, which are shown in dashed outline (TFC Phyc 10468).

Fig. 31. Transverse section of vesicle wall, showing a rounded secretory cell borne by an unmodified medullary cell (TFC Phyc 10468).

Fig. 32. Solitary rounded secretory cells on unmodified medullary cells as viewed from the vesicle cavity (TFC Phyc 10468).

Fig. 33. Inner surface of the vesicle wall, showing two clusters of pyriform secretory cells on modified medullary cells (TFC Phyc 10490).

Fig. 34. Detail of a detached modified medullary cell supporting a cluster of five pyriform secretory cells (TFC Phyc 10467).

Fig. 35. Transverse section of vesicle wall through a modified medullary cell with secretory cells. Smaller medullary cells occur just above the bearing secretory cell (TFC Phyc 10467).

Fig. 36. Surface view of a tetrasporangial sorus with mature tetrasporangia partially covered by outer cortical cells (TFC Phyc 10467).

Fig. 37. Transverse section of vesicle wall through a tetrasporangial sorus, showing tetrasporangia in the subsurface layer (TFC Phyc 10474).

750 μm in diameter, and up to 13 mm in height. Vesicles are initially subspherical and become pyriform to obovoid at maturity; they are 4–5 mm in diameter and 5–7(–9) mm long (Fig. 26). Usually, some vesicles are distally compressed and cup-shaped. Solid axes have a central medulla composed of ovoid to subspherical hyaline cells (30–98 μm in diameter), surrounded by a cortex of smaller pigmented ovoid cells (6–11 μm in diameter) (Fig. 27). In aged, solid axes, the cortex increases by proliferation of angular, radially arranged cortical cells (Fig. 28). Vesicle walls are relatively leathery, ranging from 53 to 120 μm in thickness, and consist of three cell layers (Fig. 29). The innermost nonpigmented medullary cells are subpolygonal, 53–180 μm in diameter in surface view, and surmounted by two layers of progressively smaller cortical cells (Fig. 29). Rounded cells, 18–58 μm in diameter, form a nearly continuous subsurface layer. On the outside are subspherical, loosely arranged cortical cells, 4–12 μm in diameter, which form a near-continuous surface layer; occasionally, they occur only on the adjacent walls of the subsurface cells and form small rosettes (Fig. 30). Solitary secretory cells or clusters of secretory cells project into the vesicle cavity and occur on both unmodified and somewhat modified medullary cells (Figs 31–35). One to three rounded secretory cells, 16–24 μm in diameter, are scattered on unmodified medullary

cells (Figs 31, 32). Clusters of three to five (rarely up to seven) obovoid to pyriform secretory cells (10–34 μm in diameter and 15–48 μm long) occur on readily stained, rounded, smaller medullary cells (36–94 μm in diameter), which stand out from the surrounding cells (Figs 33–35). Frequently, the vesicle wall above a modified medullary cell is constructed of smaller rounded medullary cells (Fig. 35). Both types of secretory cells occur simultaneously, showing a similar percentage in an individual vesicle, but solitary, rounded secretory cells can occasionally occur.

REPRODUCTIVE STRUCTURES: Gametophytes were not observed. Tetrasporangia occur in irregular sori in terminal portions of vesicles. They are derived from a midcortical cell in an intercalary position and remain in the subsurface layer below the outer cortical cells (Figs 36, 37). The tetrasporangia are spherical to ellipsoidal, of the cruciate–decussate type, 22–34 μm in diameter and 26–48 μm long (Fig. 37).

REMARKS: *Botryocladia canariensis* has no unique features, but differs from the other *Botryocladia* species by its unique combination of characters, which are consistently represented in the numerous specimens examined. Eleven species of *Botryocladia* have been reported in the eastern Atlantic (Price *et al.* 1986), with six species recorded from the Canary Islands: *B. botryoides, B. boergesenii* Feldmann, *B. chiajeana* (Meneghini) Kylin, *B. occidentalis* (Børgesen) Kylin, *B. pyriformis* (Børgesen) Kylin, and *B. wynnei* D.L. Ballantine (Afonso-Carrillo & Sansón 1999). The remaining five species – *B. bullosa* (Levring) J.N. Norris & D.L. Ballantine (Norris & Ballantine 1995) from Madeira and Azores, *B. microphysa* (Hauck) Kylin (Kylin 1931) from the Mediterranean and Madeira, *B. guineensis* D.M. John (John 1972) and *B. lawsonii* D.M. John (John 1980) from Ghana, and *B. senegalensis* G. Feldmann & Bodard (Feldmann & Bodard 1965) from Senegal – have not been reported from the Canary Islands.

Botryocladia canariensis is different from the 11 species of *Botryocladia* reported in the eastern Atlantic. It differs greatly in habit from the large arborescent *B. botryoides* and *B. occidentalis* and the elongate *B. chiajeana,* which lack clustered secretory cells. It differs from *B. boergesenii, B. bullosa, B. lawsonii, B. microphysa, B. senegalensis,* and *B. wynnei* in lacking outer cortical cells arranged in rosettes. It differs from *B. pyriformis* by its smaller habit, the number of cell layers in the vesicle wall, the arrangement of the outer cortical cells, and the shape, size and position of the secretory cells [see tables of features in Brodie & Guiry (1988a) and Schneider & Lane (2000)]. From this ensemble of eastern Atlantic species, only *B. guineensis,* a species known from the Gulf of Guinea (John 1972; Lawson & John 1982), seems related to *B. canariensis.* The new species seems also to be closely related to *B. ganesanii* Aponte Díaz and *B. skottsbergii* (Børgesen) Levring. The former is only known from the Caribbean coast of Venezuela (Aponte Díaz 1988); *B. skottsbergii* was initially described from Easter Island (Børgesen 1924, as *Chrysymenia*) and later widely reported in the Indo-Pacific Ocean (Levring 1941; Srinivasan 1962; Silva *et al.* 1996; Abbott 1999), when *B. kuckuckii* (Weber van Bosse) Yamada & Tanaka (Yamada & Tanaka 1938) was accepted as a synonym (Feldmann 1945). *Botryocladia canariensis* differs from these species by its smaller habit, slender solid axis, smaller vesicles (significantly larger in *B. ganesanii* and *B. guineensis*), and thinner vesicle walls (Table 1). It differs from *B. guineensis*

and *B. skottsbergii* by the smaller number of cell layers in the vesicle walls. Although in all four species secretory cells are attached in close clusters on medullary cells, they occur on modified medullary cells only in *B. canariensis* and apparently in *B. ganesanii* (i.e. smaller medullary cells that intrude into the vesicle cavity and stain readily with aniline). The new species differs also in having a smaller number of secretory cells in each cluster. *Botryocladia canariensis* can be mainly separated in this group of species by the dimorphism exhibited by its secretory cells. Secretory cells occurring in tight clusters are large and obovoid to pyriform, whereas they are smaller and subspherical when solitary on medullary cells (Table 1).

Although the *Polysiphonia*-type life history is almost universal in Rhodymeniales, the absence of fertile gametophytic plants in the numerous collections examined suggests that *B. canariensis* could be an exception. A repeated recycling of the tetrasporangial phase in culture has been shown in *Lomentaria orcadensis* (Harvey) W.R. Taylor (Foran & Guiry 1983). Although rarely reported in the Rhodymeniales (Brodie & Guiry 1988b), the formation of gametangia could be also related to photoperiodic responses. Further culture studies are needed in order to establish the life history of the new species.

DISCUSSION

The genus *Botryocladia,* as currently circumscribed (Norris 1989; Schneider & Lane 2000), comprises a heterogeneous group of species, which show disorderly variation with respect to prominent vegetative and reproductive features. With the recent recognition of the genus *Irvinea* (Guiry *in* Saunders *et al.* 1999), the proper defining characters of *Botryocladia* became obscured, because of insufficient knowledge of its type species. Erection of *Irvinea* was based on molecular evidence and on an apparently unusual combination of morphological characters: the outer cortex is arranged in rosettes; the secretory cells are borne on modified medullary cells; and the cystocarps protrude strongly. It was suggested that, after further studies, some of the *Botryocladia* species with this ensemble of morphological features could be moved into the new genus (Saunders *et al.* 1999). Nevertheless, Schneider & Lane (2000) found that the ensemble of attributes proposed by Guiry *in* Saunders *et al.* (1999) to separate *Irvinea* from *Botryocladia* showed an important overlap among species. Greater knowledge of potentially important morphological and reproductive characters of *B. botryoides* should enable a more reliable definition of the two genera, but a consistent definition of *Botryocladia* is difficult to assess at present because the published information is largely inadequate for most *Botryocladia* species.

The number of cell layers in the vesicle wall, the arrangement of the outer cortical cells, and the positions of the secretory cells are at present important vegetative features used in the separation of species within the genus *Botryocladia,* but they possibly lack generic importance. Most species in *Botryocladia* have vesicle walls formed by two or three cell layers (Brodie & Guiry 1988a). Only *B. beckeriana* (Holmes) Papenfuss (Norris 1989), *B. guineensis* (John 1972), *B. madagascariensis* G. Feldmann (Feldmann 1945), *B. paucivesicaria* Stegenga, Bolton, & Anderson (Stegenga *et al.* 1997), *B.*

Table 1. Comparison of *Botryocladia canariensis* and related species.

Character	B. ganesanii[1]	B. guineensis[2]	B. skottsbergii[3]	B. canariensis[4]
Maximum height of habit (mm)	35	50	30	18
Holdfast	discoid	discoid	irregular	discoid
No. of axes in holdfast	1	1	many	1
Length of axis (mm)	2–7	no data	up to 22	up to 13
Diameter of axis (mm)	1	1–1.5	1	0.35–0.75
Branching of axis	opposite, tri- or polychotomous	irregular	irregular	irregular to dichotomous
No. of vesicles in plant	7–20	2–6 (–10)	up to 15+	1–4 (–14)
Shape of vesicles	spherical to ovoid	spherical to elongate-pyriform	ovoid to pyriform	subspherical, pyriform, obovoid, cup-shaped
Size of vesicles (mm)	10–18 × 20–25	11–21 × 16–35	3–6 (–9) × 3–8 (–10)	4–5 × 5–7 (–9)
Thickness of vesicle wall (μm)	100–200	32–180	95–170	53–120
No. of cell layers in vesicle wall	3	(3–) 4 (–5)	3–5	3
Secretory bearing cells	modified and unmodified	unmodified	unmodified	modified and unmodified
No. of secretory cells in cluster	6–12 (–15)	4–8 (–12)	(1–) 2–8 (–20)	3–5 (–7)
Shape of clustered secretory cells	pyriform or ovoid	spherical to pyriform	club-shaped to elongate	obovoid to pyriform
Size (μm)	20–35 × (25–) 30–45 (–50)	10–25 × 11–33	20 × 40	10–34 × 15–48
Solitary secretory cells	absent	absent	absent	1–3
Shape of solitary secretory cells	—	—	—	subspherical
Size (μm)	—	—	—	16–24
Tetrasporangia	ovoid	ovoid	spherical to ellipsoidal	spherical to ellipsoidal
Size (μm)	20 × 24–28	16–22 × 22–33	19–22 × 22–33	22–34 × 26–48
Spermatangial mother cells	subspherical	no data	no data	no data
Cystocarp position	immersed	prominent	immersed	no data
Diameter (μm)	700–900	c. 600	no data	—
Gametophytes	monoecious	dioecious?	dioecious?	dioecious?

[1] Data on *B. ganesanii* from Aponte Díaz (1988).
[2] Data on *B. guineensis* from John (1972) and Lawson & John (1982).
[3] Data on *B. skottsbergii* from Børgesen (1924, as *Chrysymenia*), Yamada & Tanaka (1938, as *B. kuckuckii*), Levring (1941), Srinivasan (1962), and Abbott (1999).
[4] Data on *B. canariensis* from the present study.

Table 2. Comparison of selected features of the type species of the genera *Botryocladia* and *Irvinea*.

Character	*Botryocladia botryoides*	*Irvinea ardreana*
Holdfast	discoid	stoloniferous
Solid axes	arborescent	simple or branched stipe
Growth of axes	indeterminate	determinate
Shape of vesicles	subspherical to pyriform	pyriform to elongate cylindrical or compressed
Growth of vesicles	determinate	indeterminate
Branching of vesicles	absent	absent or dichotomous
Number of cell layers in vesicle walls	4 (–6)	3
Outer cortex	continuous	arranged in rosettes
Bearing secretory cells	unmodified and modified	modified
Distribution of secretory cells	solitary	groups
Number of secretory cells	1–3	1–6
Spermatangial mother cells	palisade-like	elongate
Cystocarps	partially immersed	strongly protuberant
Position of tetrasporangia	immersed in the subsurface cortical layer	exposed in the outer cortical layer
References	this article	Brodie & Guiry (1988a, as *B. ardreana*) and Guiry (1999).

skottsbergii (Srinivasan 1962), and *B. sonderi* P.C. Silva (Womersley 1996) exhibit thick vesicle walls as described in *B. botryoides.* Nevertheless, *B. occidentalis,* an unequivocal member of the genus *Botryocladia,* has only three layers of cells in vesicle walls. Cortical cells arranged in rosettes have been documented in at least 18 species presently included in *Botryocladia* (Ballantine 1985; Millar 1990; Schneider & Lane 2000; Ballantine & Aponte 2002). Nevertheless, in other genera of hollow Rhodymeniales, such as *Chrysymenia* J. Agardh (Kylin 1931) and *Lomentaria* Lyngbye (Ercegovic 1956), elaboration of cortical rosettes is a minor vegetative character useful only in species delineation. Species in *Botryocladia* exhibit a wide range of variation in the number and position of secretory cells (i.e. on unmodified medullary cells, on modified medullary cells, and on both types simultaneously), illustrated by the three species examined in this study. Development of secretory cells on both unmodified and modified medullary cells in the type species *B. botryoides* prevents the use of this unreliable character in genus delineation.

Production of spermatangia occurs via elongate initials and is very similar in the small number of species where spermatangia have been reported (Brodie & Guiry 1988a). Elongate palisade-like spermatangial mother cells that cut off spermatangia singly are formed in *B. botryoides* and *B. occidentalis,* and apparently also in *B. madagascariensis* (Norris 1989). Elongate scattered spermatangial mother cells, giving rise to spermatangia singly or in pairs, are present in the remaining *Botryocladia* species. These minor morphological differences do not correspond to any change in the formation of the spermatangia and seem useful only as a character to distinguish species.

In species presently accepted as belonging to *Botryocladia,* three morphologically distinct cystocarp types have been described. Incompletely immersed cystocarps, such as occur in *B. botryoides* and *B. occidentalis,* have also been reported in *B. sonderi* (Womersley 1996), *B. pienaari* R.E. Norris (Norris 1989), *B. bahamense* Ballantine & Aponte (Ballantine & Aponte 2002) and apparently in *B. wynnei* (Wynne 2001). Strongly protuberant cystocarps are formed in *B. beaudettei* E.Y. Dawson (Dawson 1960), *B. darwinii* C.W. Schneider & C.E. Lane (Schneider & Lane 2000), *B. fernandeziana* Levring (Levring 1941), *B. guaymasensis* E.Y. Dawson (Dawson 1963), *B. guineensis* (John 1972), *B. papenfussiana* Ganesan

& Lemus (Ganesan & Lemus 1972), and *B. senegalensis* G. Feldmann & Bodard (Feldmann & Bodard 1965). Finally, completely immersed cystocarps occur in *B. ganesanii* (Aponte Díaz 1988), *B. hancockii* E.Y. Dawson (Dawson 1944), *B. lawsonii* (John 1980), *B. madagascariensis* (Norris 1989), *B. paucivesicaria* (Stegenga *et al.* 1997), *B. pseudodichotoma* (Farlow) Kylin (Dawson 1963), and *B. skottsbergii* (Yamada & Tanaka 1938). These distinct morphologies apparently do not imply a major change in the development of the cystocarp. Within the Rhodymeniaceae, there are species with immersed cystocarps and others with protruding cystocarps within the same genus, e.g. *Coelarthrum* Børgesen (Huisman 1996). Although useful in species separation, cystocarp position does not appear to be of generic importance (Huisman 1996).

Tetrasporangia in *Botryocladia* are scattered throughout the cortex and are derived from a midcortical cell in an intercalary position (Millar 1990; Womersley 1996). There are differences in the final tetrasporangium position, which can be useful as a taxonomic character. In *B. botryoides,* mature tetrasporangia persist in the subsurface cortical layer and are covered by the outer cortical cells. In most species with networked outer cortex, and apparently also in *B. fernandeziana* Levring (1941) and *B. papenfussiana* (Ganesan & Lemus 1972), mature tetrasporangia remain exposed just below the cuticle in the outer cortical layer. A similar disposition is exhibited by *Irvinea ardreana* (J. Brodie & Guiry) Guiry *in* Saunders *et al.* (1999) (Brodie & Guiry 1988a, as *B. ardreana*). On the other hand, tetrasporangial sori with a modified cortex have been described in *B. madagascariensis* (Norris 1989), *B. paucivesicaria* (Stegenga *et al.* 1997), and *B. sonderi* (Womersley 1996). In the Rhodymeniaceae, whether the elaboration of tetrasporangia is or is not associated with a modification of the cortex is an important taxonomic character at the genus level (Huisman 1996). *Botryocladia* could probably be made a more workable taxonomic unit if species forming tetrasporangia in nemathecial sori were removed from it. Further morphological and molecular studies are needed, however, before this segregation can be made with confidence.

Although a consistent definition of *Botryocladia* seems impossible at present, the position of the boundary between *Botryocladia* and *Irvinea* can be clarified. In addition to the unquestionable molecular differences reported by Saunders *et al.* (1999), *B. botryoides* and *I. ardreana* differ significantly in

overall morphology (Table 2). Whereas *B. botryoides* consists of an arborescent solid axis supporting numerous nearly spherical vesicular laterals, in *I. ardreana* a dominant axis is not formed and only a few elongate, undivided or dichotomously lobed vesicles are produced. Although vesicle morphology is very variable within the genus *Botryocladia* and details of its shape depend on the reproductive state and apparently also on the ambient environment (Brodie & Guiry 1988a; Norris 1989), two different patterns in the growth of hollow branches can be recognized. In several species, the hollow branches consist of vesicles that remain spherical or become ovate or pyriform, but do not elongate to any extent. This determinate growth of vesicles occurs in *B. botryoides, B. occidentalis,* and *B. canariensis,* and in many other *Botryocladia* species (Brodie & Guiry 1988a; Norris 1989). On the contrary, several species [e.g. *B. chiajeana* (Meneghini) Kylin (Kylin 1931), *B. darwinii* (Schneider & Lane 2000), *B. fernandeziana* (Levring 1941), *B. lawsonii* (John 1980), *B. papenfussiana* (Ganesan & Lemus 1972), and *B. senegalensis* (Feldmann & Bodard 1965)] have in common with *Irvinea ardreana* the elaboration of elongate hollow branches with indeterminate growth in length. In these species, solid axes are relatively short and apparently have determinate growth. Bifurcate vesicles have also been reported (e.g. in *B. chiajeana, B. papenfussiana,* and *B. senegalensis*), showing a similar appearance to the indeterminate axes of *Chrysymenia* J. Agardh, a closely related genus characterized vegetatively by its hollow axes lacking solid portions (Kylin 1931). Morphological data suggest that the genus *Botryocladia* could be defined more clearly if species with indeterminate growth of vesicles were removed from it, but at present there are no characteristics that support a reasonable subdivision of the genus without an alteration of the current concept of *Irvinea.* An acceptable boundary between *Botryocladia* and *Irvinea* could be delineated on the basis of differences in the patterns in vesicle development, with simultaneous reduction in the relative importance of the arrangement of cortical cells, the positions of secretory cells, and, possibly, variation in cystocarp protrusion. However, the correct generic affiliation of *Botryocladia* species with indeterminate vesicle growth will remain equivocal until new molecular or morphological data of taxonomic relevance become available. Molecular studies are necessary to select the morphological characters with diagnostic value in the definition of closely related genera (Saunders & Necchi 2002). At present, of the 38 species (including *I. ardreana*) that are accepted in *Botryocladia,* molecular information is available for only three (Saunders *et al.* 1999). Further vegetative and reproductive information is also needed in many poorly known *Botryocladia* species, and studies now in progress on the Canarian *Botryocladia* species with indeterminate elongate vesicles may provide additional data supporting generic revision.

ACKNOWLEDGEMENTS

REFERENCES

ABBOTT I.A. 1999. *Marine red algae of the Hawaiian Islands.* Bishop Museum Press, Honolulu. 477 pp.

AFONSO-CARRILLO J. & SANSÓN M. 1999. *Algas, hongos y fanerógamas marinas de las Islas Canarias. Clave analítica.* Serie Biología 2. Materiales Didácticos Universitarios, Servicio de Publicaciones de la Universidad de la Laguna, Tenerife. 254 pp.

AGARDH J.G. 1851. *Species, genera et ordines algarum,* vol. 2. C.W.K. Gleerup, Lund. 336 pp.

APONTE DÍAZ, M. 1988. *Botryocladia ganesanii* sp. nov. (Rhodophyta, Rhodymeniales) from the Caribbean coast of Venezuela. *Cryptogamie, Algologie* 9: 43–52.

BALLANTINE D.L. 1985. *Botryocladia wynnei* sp. nov. and *B. spinulifera* (Rhodymeniales, Rhodophyta) Taylor & Abbott from Puerto Rico. *Phycologia* 24: 199–204.

BALLANTINE D.L. & APONTE N.E. 2002. *Botryocladia bahamense* sp. nov. (Rhodymeniaceae, Rhodophyta) from the Bahamas, western Atlantic. *Cryptogamie, Algologie* 23: 123–130.

BØRGESEN F. 1920. The marine algae of the Danish West Indies. Part 3. Rhodophyceae (6) with addenda to the Chlorophyceae, Phaeophyceae and Rhodophyceae. *Dansk Botanisk Arkiv* 3: 369–498.

BØRGESEN F. 1924. Marine algae from Easter Island. In: *Natural history of Juan Fernandez and Easter Island,* vol. 2 (Ed. by C. Skottsberg), pp. 247–309. Almqvist & Wiksells, Uppsala.

BØRGESEN F. 1929. Marine algae from the Canary Islands especially from Teneriffe and Gran Canaria. III. Rhodophyceae. Part II. Cryptonemiales, Gigartinales and Rhodymeniales. *Kongelige Danske Videnskabernes Selskab Biologiske Meddelelser* 8(1): 1–97.

BRODIE J. & GUIRY M.D. 1988a. Life history and reproduction of *Botryocladia ardreana* sp. nov. (Rhodymeniales, Rhodophyta) from Portugal. *Phycologia* 27: 109–130.

BRODIE J. & GUIRY M.D. 1988b. Life history and reproduction of *Cordylecladia erecta* (Rhodymeniaceae, Rhodophyta). *British Phycological Journal* 23: 347–364.

COPPEJANS E. 1983. Iconographie d'algues Méditerranées. Chlorophyta, Phaeophyta, Rhodophyta. *Bibliotheca Phycologica* 63: 1–28, 317 pl.

DAWSON E.Y. 1944. The marine algae of the Gulf of California. *Allan Hancock Pacific Expeditions* 3: 189–432.

DAWSON E.Y. 1960. New records of marine algae from Pacific Mexico and Central America. *Pacific Naturalist* 1: 31–52.

DAWSON E.Y. 1963. Marine red algae of Pacific Mexico. Part 6. Rhodymeniales. *Nova Hedwigia* 5: 437–476.

ERCEGOVIC A. 1956. Famille des Champiacées (Champiaceae) dans l'Adriatique moyenne. *Acta Adriatica* 8: 1–63.

FELDMANN G. 1945. Révision du genre *Botryocladia* Kylin (Rhodophycées–Rhodyméniacées). *Bulletin de la Société de l'Histoire Naturelle de l'Afrique du Nord* 35: 49–61.

FELDMANN G. & BODARD M. 1965. Une nouvelle espèce de *Botryocladia* des côtes du Sénégal. *Bulletin de l'Institut Océanographyque de Monaco* 65: 1–14.

FELDMANN J. 1941. Algues marines de la côte des Alberes. IV. Rhodophycées (suite). *Revue Algologique* 12: 77–100.

FORAN C.F. & GUIRY M.D. 1983. The life history in culture of isolates of *Lomentaria orcadensis* (Rhodophyta) from Ireland and Scotland. *British Phycological Journal* 18: 204.

GANESAN E.K. & LEMUS A.J. 1972. Studies on the marine algal flora of Venezuela. IV. *Botryocladia papenfussiana* sp. nov. (Rhodophyceae, Rhodymeniales). *Phycologia* 11: 25–31.

GIL-RODRÍGUEZ M.C., HAROUN TABRAUE R., AFONSO-CARRILLO J. &

WILDPRET W. 1985. Adiciones al catálogo de algas marinas bentónicas para el Archipiélago Canario. II. *Vieraea* 15: 101–112.

HAROUN R.J., PRUD'HOMME VAN REINE W.F., MÜLLER D.G., SERRÃO E. & HERRERA R. 1993. Deep-water macroalgae from the Canary Islands: new records and biogeographical relationships. *Helgoländer Meeresuntersuchungen* 47: 125–143.

HOLMGREN P.K., HOLMGREN N.H. & BARNETT I.C. 1990. Index herbariorum part I: the herbaria of the world, ed. 8. *Regnum Vegetabile* 120: 1–693.

HUISMAN J.M. 1996. The red algal genus *Coelarthrum* Børgesen (Rhodymeniaceae, Rhodymeniales) in Australian seas, including the description of *Chamaebotrys* gen. nov. *Phycologia* 35: 95–112.

JACQUIN N.J. 1791. *Collectanea ad botanicam, chemiam, et historiam naturalem spectantia, cum figuris,* vol. 3. Vindobonae [Vienna]. 306 pp.

JOHN D.M. 1972. A new species of *Botryocladia* (Rhodophyceae, Rhodymeniales) from the Gulf of Guinea. *Phycologia* 11: 33–36.

JOHN D.M. 1980. A new species of *Botryocladia* (Rhodophyceae, Rhodymeniales) from Ghana (tropical West Africa). *Phycologia* 19: 91–95.

KUCKUCK P. 1912. Beiträge zur Kenntnis der Meeresalgen. 13. Untersuchungen über *Chrysymenia*. *Wissenschaftliche Meeresuntersuchungen Helgoland, neue Folge* 5: 211–225.

KYLIN H. 1931. Die Florideenordnung Rhodymeniales. *Lunds Universitets rsskrift,* Ny Följd, Andra Afdelningen 27(11): 1–48.

LAWSON G.W. & JOHN D.M. 1982. The marine algae and coastal environment of tropical west Africa. *Nova Hedwigia, Beiheft* 70: 1–455.

LEVRING T. 1941. Die Meeresalgen der Juan Fernandez-Inseln. In: *Natural history of Juan Fernandez and Easter Island,* vol. 2 (Ed. by C. Skottsberg), pp 601–670. Almqvist & Wiksells, Uppsala.

MILLAR A.J.K. 1990. Marine red algae of the coffs harbour region, northern New South Wales. *Australian Systematic Botany* 3: 293–593.

NORRIS R.E. 1989. Natalian *Botryocladia* (Rhodymeniales, Rhodophyceae), including description of a new, long axis-forming species. *Botanica Marina* 32: 131–148.

NORRIS J.N. & BALLANTINE D.L. 1995. Two new species of the red alga *Chrysymenia* J. Agardh (Rhodymeniales: Rhodymeniaceae) from the tropical western Atlantic. *Proceedings of the Biological Society of Washington* 108: 153–165.

PRICE J.H., JOHN D.M. & LAWSON G.W. 1986. Seaweeds of the western coast of tropical Africa and adjacent islands: a critical assessment. III. Rhodophyta (Florideae). 1. Genera A–F. *Bulletin of the British Museum (Natural History), Botany* 15: 1–122.

SANSÓN M., REYES J., AFONSO-CARRILLO J. & MUÑOZ E. 2002. Sublittoral and deep-water red and brown algae new from the Canary Islands. *Botanica Marina* 45: 35–49.

SAUNDERS G.W. & NECCHI O. JR. 2002. Nuclear rDNA sequences from *Ballia prieurii* support recognition of *Balliopsis* gen. nov. in the Batrachospermales (Florideophyceae, Rhodophyta). *Phycologia* 41: 61–67.

SAUNDERS G.W., STRACHAN I.M. & KRAFT G.T. 1999. The families of the order Rhodymeniales (Rhodophyta): a molecular-systematic investigation with a description of Faucheaceae fam. nov. *Phycologia* 38: 23–40.

SCHNEIDER C.W. & LANE C.E. 2000. A new species of *Botryocladia* (Rhodymeniales, Rhodophyta) from the Galapagos Islands. *Cryptogamie, Algologie* 21: 167–175.

SCHNEIDER C.W. & SEARLES R.B. 1991. *Seaweeds of the southeastern United States. Cape Hatteras to Cape Canaveral*. Duke University Press, Durham. 533 pp.

SILVA P.C., BASSON P.W. & MOE R.L. 1996. Catalogue of the benthic marine algae of the Indian Ocean. *University of California Publications in Botany* 79: 1–1259.

SRINIVASAN K.S. 1962. On *Botryocladia skottsbergii* (Boergs.) Levr., a red alga new to Indian region. *Phytomorphology* 12: 49–53.

STEGENGA H., BOLTON J.J. & ANDERSON R.J. 1997. Seaweeds of the South African west coast. *Contributions from the Bolus Herbarium* 18: 1–655.

TAYLOR W.R. 1960. *Marine algae of the eastern tropical and subtropical coasts of the Americas*. The University of Michigan Press, Ann Arbor. 870 pp.

WYNNE M.J. 2001. New records of benthic marine algae from the Sultanate of Oman, northern Arabian Sea. II. *Nova Hedwigia* 72: 347–374.

WOMERSLEY H.B.S. 1996. *The marine benthic flora of Southern Australia. Part IIIB. Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales*. Australian Biological Resources Study and the State Herbarium of South Australia, Canberra. 392 pp.

YAMADA Y. & TANAKA T. 1938. The marine algae from the Island of Yonakuni. *Scientific Papers of the Institute of Algological Research, Hokkaido University* 2: 53–86.