

The red algal genus *Liagora* (Liagoraceae, Rhodophyta) from the Canary Islands

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Eight species of the genus *Liagora* (Liagoraceae, Rhodophyta) are reported from the Canary Islands. Six of these (*L. viscida* (Forsskål) C. Agardh, *L. distenta* (Mertens) Lamouroux, *L. gymnarthron* Børgesen, *L. canariensis* Børgesen, *L. maderensis* Kützinger and *L. tetrasporifera* Børgesen) are endemic to the NE Atlantic and Mediterranean and two (*L. valida* Harvey and *L. ceranoides* Lamouroux) have a wide distribution. *L. maderensis*, known only from the type collection and often cited as a synonym for *L. ceranoides* or *L. valida*, has a reproductive and vegetative morphology that supports its recognition as an independent species. Evidence suggests that *L. gymnarthron* has often been erroneously identified as *L. distenta* (Mertens) Lamouroux and that the latter species has thus been characterized by a combination of features from two different taxonomic entities. Although closely related, the two species show distinctive differences in the morphology of their cystocarps: in *L. distenta* sterile filaments persist under the gonimoblast and do not surround the mature carposporophyte, while in *L. gymnarthron* mature carposporophytes are surrounded by a conspicuous involucre. Habit, vegetative and reproductive development have been examined in the eight species. The previously controversial reproductive development in *L. viscida*, the lectotype species of the genus, has been clarified. Gametophytes of *L. viscida* are monoecious and, after presumed fertilization, cells adjacent to the supporting cell form sterile colourless filaments that grow and branch towards the thallus surface; simultaneously gonimoblast initials produce outwardly radiating lax gonimoblast filaments that form terminal carposporangia, resulting in a mature carposporophyte with sterile filaments intermingled with the gonimoblast filaments. The features used at present to delineate the genus *Liagora* in the Liagoraceae are analysed and the potential use of post-fertilization characters to subdivide the genus is discussed.

INTRODUCTION

The red algal genus *Liagora* Lamouroux (1812) includes multiaxial, calcified, dichotomously to irregularly branched species with carpogonial branches borne laterally on a cortical supporting cell, compact gonimoblasts of densely aggregated filaments and sterile involucre filaments produced from various cells adjacent to the carpogonial branch. Its distinctive features within the family Liagoraceae were considered to be inconsistent by Kraft (1989), partly due to the limited and contradictory information on post-fertilization development in *L. viscida* (Forsskål) C. Agardh, the lectotype species of the genus (Abbott 1945). Delineation of genera in the Liagoraceae is largely based on features of the carpogonial branch, gonimoblast, and the sterile filaments associated with the carposporophyte (Huisman & Kraft 1994). In *L. viscida* these features are poorly known and published reports are conflicting. Kylin (1930) described the carposporophyte as having lax gonimoblasts lacking sterile filaments, while Desikachary & Balakrishnan (1957) observed compact gonimoblasts surrounded by sterile filaments. Moreover, Kraft (1989) showed that, among the genera of Liagoraceae, *Liagora* has been too broadly defined. Recently Huisman & Kraft (1994) proposed the reinstatement of an emended genus *Ganonema* Fan et Wang (1974) for (in addition to *L. farinosa* Lamouroux and related species) the species previously placed in the section Mucosae (see Abbott 1990b) of *Liagora*.

Since the description of *Liagora* at least 94 specific taxa have been placed in the genus. Studies by Abbott (1990a, b) on numerous type specimens have shown that there was a

great duplication of names, mainly due to the limited number of specimens on which original descriptions were based and to the poor knowledge of what constitutes the limits of species. Eight species of *Liagora* have been recorded from the Canary Islands: *Liagora albicans* Lamouroux, *L. canariensis* Børgesen, *L. ceranoides* Lamouroux, *L. distenta* (Mertens) Lamouroux, *L. gymnarthron* Børgesen, *L. tetrasporifera* Børgesen, *L. valida* Harvey and *L. viscida* (Forsskål) C. Agardh (Børgesen 1927; Gil-Rodríguez & Afonso-Carrillo 1980; Afonso-Carrillo & Sansón 1989; John *et al.* 1994). One additional species, *L. maderensis* Kützinger, previously known only from the Madeira Islands, was collected during this investigation. Although some species are relatively common in the Atlantic islands of the Canaries and Madeira, *Liagora* species have rarely been reported from the north-eastern Atlantic (Gallardo *et al.* 1985; South & Tittley 1986). The present knowledge of many species is largely unsatisfactory because of the small number of specimens examined. In addition, the lack of information on relevant reproductive features has prevented adequate species characterization. The study of numerous fresh and herbarium specimens collected in the Canary Islands has allowed us to examine in detail the post-fertilization changes in the controversial *L. viscida* and to describe the vegetative and reproductive features of each species, evaluating the range of species variation and selecting the characters more useful for species delineation.

MATERIALS AND METHODS

Observations are based on (1) fresh specimens collected between 1990 and 1994 at numerous localities in the Canary

Islands, preserved in 4% Formalin in sea water and deposited at TFC; (2) dried herbarium specimens housed at TFC; and (3) selected type specimens housed at BM, C and L. Selected fragments from Formalin-preserved material were decalcified in 1–5% HCl, washed in sea water, stained in 1% aniline blue, washed again in sea water, then mounted in a 50% Karo® corn syrup solution and slightly squashed to separate the filaments. Dried specimens from herbaria were rehydrated in 4% Formalin in sea water before decalcification. Camera lucida drawings were obtained using a Zeiss microscope. Herbarium abbreviations follow Holmgren *et al.* (1990). Cell dimensions are given as breadth by length.

SPECIES ACCOUNTS

Liagora viscida (Forsskål) C. Agardh 1822: 395

Hamel 1930: 75, figs 47, 48c; Kylin 1930: 8, figs 3a–e; Miranda 1931: 42, figs 4–5; Desikachary & Balakrishnan 1957: 457, figs 1–14; Coppejans 1983: pl. 307; Athanasiadis 1987: 27; Abbott 1990b: 310.

BASIONYM: *Fucus viscidus* Forsskål 1795: 193.

NEOTYPE: According to Børgesen (1932) the type specimen of *Fucus viscidus* is absent in the herbarium of Forsskål (C). Christensen No. 6107 (C), June 1954, was selected as neotype by Abbott (1990b).

TYPE LOCALITY: According to Børgesen (1932) the lost type specimen of *Fucus viscidus* was collected in Constantinople. The neotype was collected at Anse du Troc, east of Banyuls-sur-Mer, France.

DISTRIBUTION: Warm temperate NE Atlantic: From Brittany to Morocco; Mediterranean, Azores, Madeira and Canary Islands (Tenerife, Lanzarote and Fuerteventura).

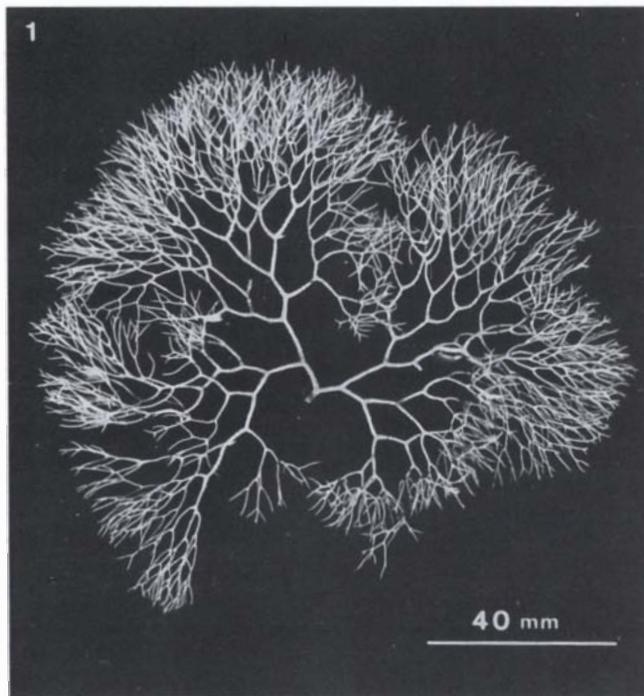


Fig. 1. *Liagora viscida* (Forsskål) C. Agardh. Habit of a recently collected specimen in the Canary Islands (TFC Phyc. 8502).

REPRESENTATIVE SPECIMENS: TENERIFE: Puertito de Güimar (Haroun, 19.viii.1982; TFC Phyc. 4137). Poris de Abona (Gil-Rodríguez, v.1972; TFC Phyc. 1248, 1363). El Médano (Sansón & Reyes, 14.v.1991; TFC Phyc. 8469), (Reyes & Afonso-Carrillo, 08.v.1992; TFC Phyc. 8459), (Reyes, 16.v.1992; TFC Phyc. 7826). El Confital (Gil-Rodríguez, viii.1972; TFC Phyc. 1243). Playa de Las Américas (Gil-Rodríguez, vii.1972; TFC Phyc. 1252). LANZAROTE: Orzola (Rojas & Ibeas, 08.v.1993; TFC Phyc. 8476, 8494). Punta del Bajío, La Graciosa (Wildpret *et al.*, 28.viii.1984; TFC Phyc. 4969, 4970). Caleta del Sebo, La Graciosa (Gramonal, 28.iii.1983; TFC Phyc. 4971). FUERTEVENTURA: El Cotillo (Sansón & Reyes, 14.vii.1991; TFC Phyc. 8467, 03.vii.92; TFC Phyc. 8342, 8502). Corralejo (Gil-Rodríguez & Alfonso-Carrillo, 03.v.1980; TFC Phyc. 2361, 2388). Gran Tarajal (Gil-Rodríguez & Alfonso-Carrillo, 02.v.1980; TFC Phyc. 2439). Puerto de la Cruz (Gil-Rodríguez & Alfonso-Carrillo, 01.v.1980; TFC Phyc. 2472).

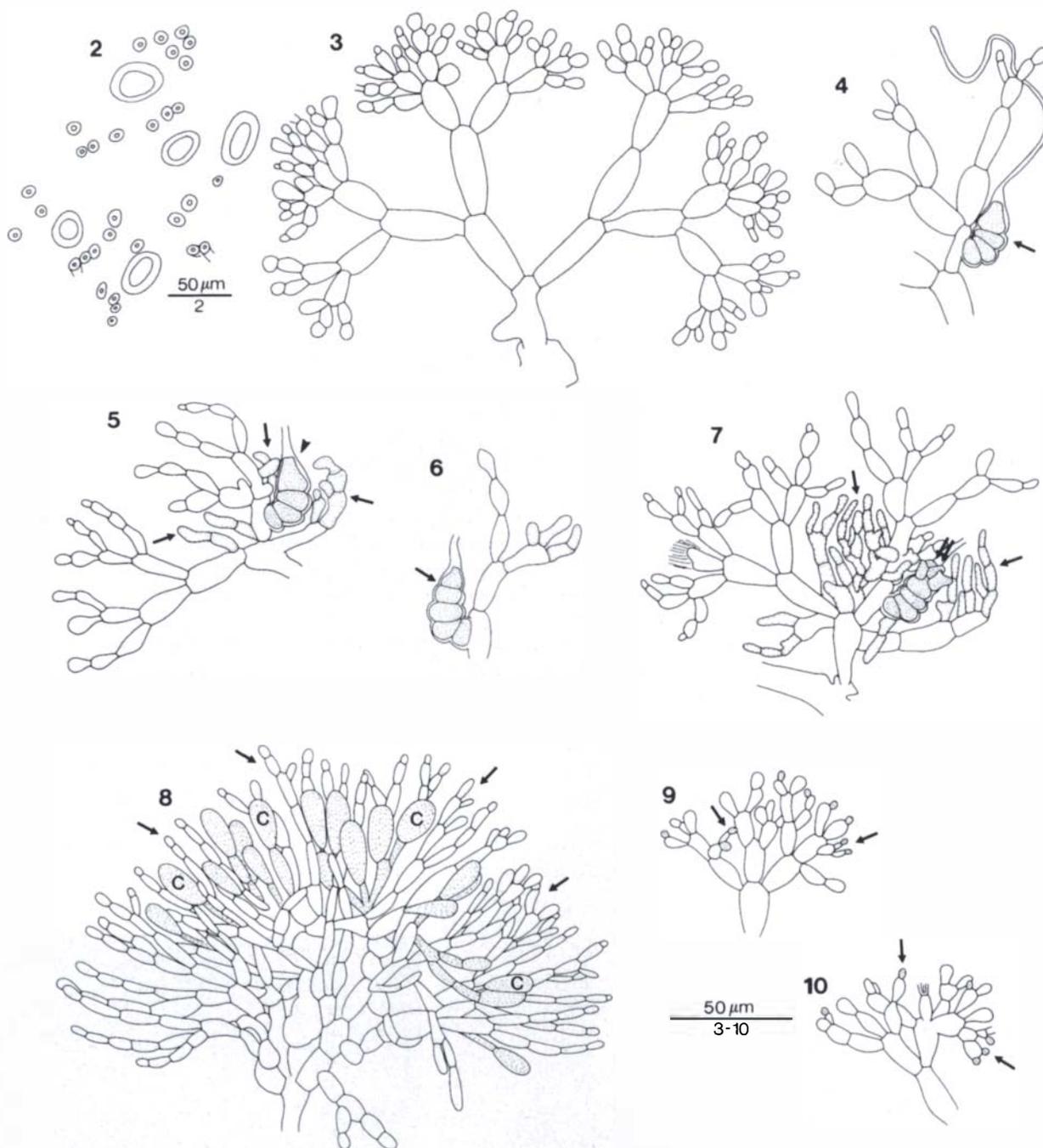
HABITAT: *Liagora viscida* always grows on rock, occasionally with its base lightly covered with sand. Specimens have been collected from the lower intertidal to 3 m depth, usually in areas of moderate water movement.

HABIT AND VEGETATIVE STRUCTURE: Plants erect, yellowish-white, to 80 mm high heavily calcified, except for tips and furcations, surface slightly mucosoid; axes terete, 1–2 mm broad, progressively thinner upwards, 7–14 times dichotomously branched in a fairly regular manner, 2–9 mm between dichotomies, angles of dichotomies wide; adventitious branches not observed (Fig. 1). Medullary filaments 16–39 μm broad, intermingled with rhizoidal filaments 7–12 μm broad (Fig. 2). Cortical assimilatory filaments 96–144 μm long, up to 5 times dichotomously branched, with trichotomies common in terminal parts (Fig. 3); cells of the assimilatory filaments cylindrical-oval, 7–11 \times 24–40 μm at the base of the filaments, becoming shorter and thinner upwards, the terminal cells pyriform or oval, 5–7 \times 7–12 μm (Fig. 3); rhizoidal filaments common, arising from the basal cells of the assimilatory filaments.

CARPOGONIAL BRANCH AND CARPOSPOROPHYTE: Plants monoecious. Carpogonial branch four-celled, slightly curved, 9–12 μm broad, attached laterally on the mid-line of the supporting cell, at the middle or inner portion of the assimilatory filaments (Fig. 4). After presumed fertilization the cells above, below and adjacent to the supporting cell form sterile colourless filaments that grow and branch almost exclusively outwards (Figs 5–7). Simultaneously the carpogonium divides transversely forming two cells (Fig. 6), the upper one continues dividing (Fig. 7) to produce outwardly radiating lax gonimoblast filaments that form terminal carposporangia, 9–12 \times 21–36 μm (Fig. 8). The mature carposporophyte measures 225–270 μm in diameter in surface view, and shows sterile filaments intermingled with gonimoblast filaments (Fig. 8). The cells of the carpogonial branch fuse after fertilization.

SPERMATANGIA: Spermatangia spherical, 2–3 μm in diameter, borne singly or in pairs on spermatangial mother cells, 2–3 μm broad and 5–6 μm long, which arise from the terminal cells of the assimilatory filaments (Figs 9, 10).

REMARKS: *Liagora viscida* is a relatively common species in some localities of the Canary Islands during spring and summer (being collected from March to August). *L. viscida* is the lectotype species of the genus (Abbott 1945), and



Figs 2–10. *Liagora viscida* (Forsskål) C. Agardh.

Fig. 2. Detail of transverse section of medulla, showing thick medullary cells intermingled with thin rhizoidal cells (TFC Phyc. 7826).

Fig. 3. Assimilatory filament (TFC Phyc. 7826).

Fig. 4. Detail of assimilatory filament with curved 4-celled carpogonial branch (arrow), borne laterally on the middle of the supporting cell (TFC Phyc. 8459).

Fig. 5. Detail of assimilatory filament with a carpogonial branch (arrowhead) and sterile filaments (arrows) growing from adjacent cells (TFC Phyc. 8459).

Fig. 6. Carpogonial branch showing the first transverse division of the carpogonium (arrow) (TFC Phyc. 8459).

Fig. 7. Early stage in the growth of the gonimoblast (double arrow). Note profuse formation of sterile filaments (arrows) (TFC Phyc. 8459).

Fig. 8. Mature carposporophyte showing lax gonimoblast filaments intermingled with sterile filaments (arrows). Note terminal carposporangia (C) (TFC Phyc. 8459).

Figs 9, 10. Portions of outer cortical filaments bearing spermatangia (arrows) (TFC Phyc. 8459).

contradictory descriptions of the carposporophyte development have been published. Kylin (1930) found that the carposporophyte was composed of lax gonimoblast filaments

intermingled with cortical filaments and without an involucre. Desikachary & Balakrishnan (1957), however, observed a compact carposporophyte surrounded by a conspicuous invo-

lucre. This inconsistency is probably due to the species being poorly defined, and as a result it is often misidentified. Abbott (1990a, 1990b) found little to distinguish between herbarium specimens of *Liagora viscida* and *L. distenta*. Abbott (1990b) differentiated *L. viscida* and *L. distenta* on the basis of external morphological features and suggested that the two taxa could be combined in some future study (Abbott 1990a). In the present study it is shown that specimens belonging to *L. gymnarthron* have been erroneously identified as *L. distenta* and the latter species has been characterized by a combination of features from two different taxonomic entities. Although *L. viscida*, *L. distenta* and *L. gymnarthron* all have relatively short cortical assimilatory filaments, some morphological differences in the assimilatory filaments occur (see Figs 3, 14, 23). The position of sterile filaments formed after fertilization appears to be a diagnostic feature useful for species differentiation. In *L. viscida* sterile filaments are intermingled with the gonimoblast filaments (Fig. 8), while in *L. distenta* sterile filaments persist under the gonimoblast and do not surround it (Fig. 18), and in *L. gymnarthron* sterile filaments surround the gonimoblast (Fig. 29).

***Liagora distenta* (Mertens) Lamouroux 1816: 240**

Hamel 1930: 78; Couté 1976: 273; Abbott 1990a: 114, figs 1–11.

BASIONYM: *Fucus distentus* Mertens in Roth 1806: 103.

LECTOTYPE: BM, leg. Mertens (lectotypified by Abbott 1990a) (Fig. 11).

TYPE LOCALITY: Cádiz, Spain.

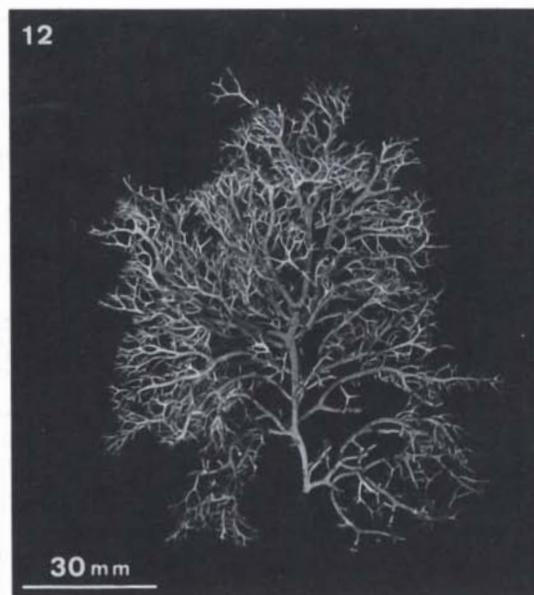
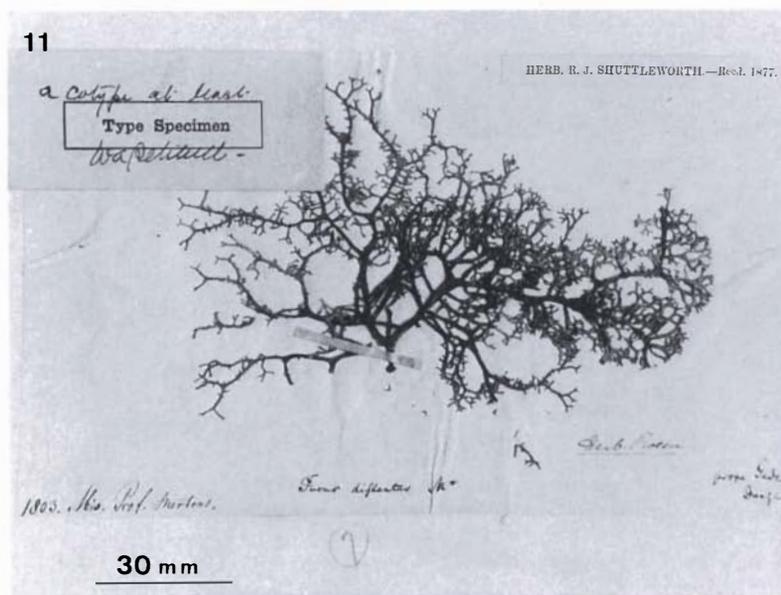
DISTRIBUTION: Warm temperate NE Atlantic: Southern Spain, Western Mediterranean, Morocco, Madeira, Salvage Islands and Canary Islands (La Palma, El Hierro, Tenerife, Gran Canaria, Lanzarote and Fuerteventura).

REPRESENTATIVE SPECIMENS: LA PALMA: Puerto Naos (*Cancap*, 30.v.1980; L 9847471). EL HIERRO: Roque de Bonanza

(*Rojas & Afonso-Carrillo*, 22.iv.1993; TFC Phyc. 8470). TENERIFE: Bajamar (*Gil-Rodríguez*, viii.1980; TFC Phyc. 366). Punta Hidalgo (*Gil-Rodríguez*, vi.1973; TFC Phyc. 1246). Playa S. Roque, Taganana (*Gil-Rodríguez et al.*, 12.viii.1982; TFC Phyc. 466). Puertito de Güimar (*Gil-Rodríguez*, iv.1972; TFC Phyc. 193). El Médano (*Sansón & Reyes*, 22.vi.1989; TFC Phyc. 8461; *Reyes & Afonso-Carrillo*, 08.v.1992; TFC Phyc. 8457, 8458, 8460). Los Abrigos (*Davara*, v.1974; TFC Phyc. 1247). Los Cristianos (*Cancap*, 30.v.1982; L 9848089). Playa de Los Troches (*Cancap*, 31.v.1982; L 9847944). Teno (*Gil-Rodríguez*, ii.1974; TFC Phyc. 1208). GRAN CANARIA: Las Canteras (*Kvaternik & Lanzadera*, 06.iv.1993; TFC Phyc. 8474, 8492). LANZAROTE: Las Caletas (*Gil-Rodríguez & Afonso-Carrillo*, 08.iii.1980; TFC Phyc. 2289). Punta Papagayo (*Cancap*, 19.v.1980; L 9847497). La Graciosa (*Cruz*, x.1981; TFC Phyc. 342). FUERTEVENTURA: El Cutillo (*Sansón & Reyes*, 03.vi.1992; TFC Phyc. 8430). Puerto de la Cruz (*Gil-Rodríguez & Afonso-Carrillo*, 01.v.1980; TFC Phyc. 2470). Punta Morro Jable (*Cancap* 2, 30.viii.1977; L 494512).

HABITAT: *Liagora distenta* is always epilithic, its base occasionally covered with sand. Plants are usually found in areas of moderate water movement and have been collected from lower intertidal pools to depths of up to 15 m.

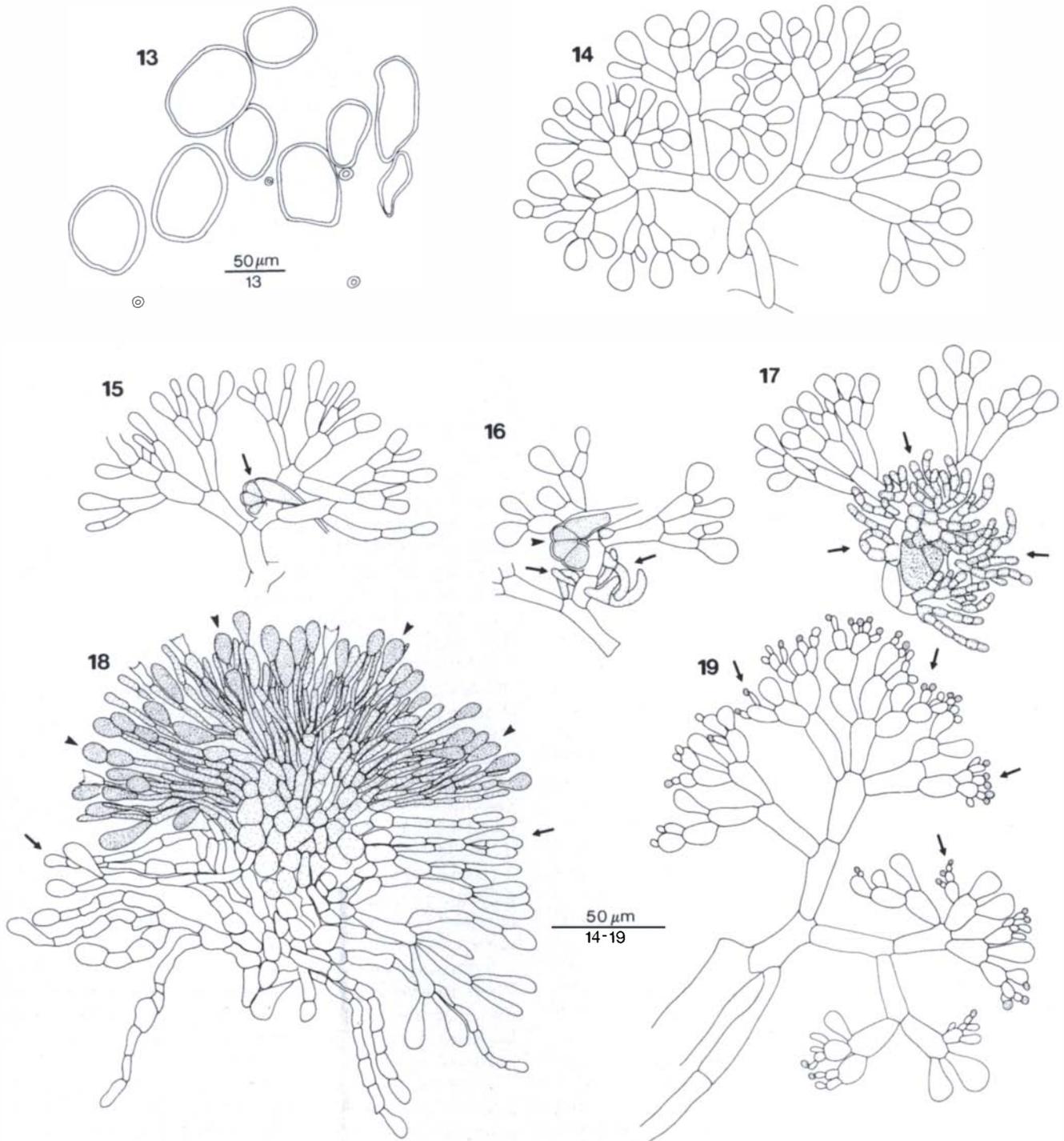
HABIT AND VEGETATIVE STRUCTURE: Plants erect, reddish-brown to whitish-green, to 160 mm high, consisting of a single main terete axis, 1–2 mm broad, dichotomously or subdichotomously branched, bearing simple or furcate terete lateral branches, 0.5–1 mm broad (Fig. 12); adventitious branches common; plants moderately calcified except at tips, lateral branchlets slightly mucosoid. Medullary filaments 36–88 (150) μm broad, intermingled with rhizoidal filaments 9–17 μm broad (Fig. 13). Cortical assimilatory filaments 84–120 μm long, 4–5 times dichotomously branched, terminating in clusters (Fig. 14). Cells of the assimilatory filaments



Figs 11, 12. *Liagora distenta* (Mertens) Lamouroux.

Fig. 11. Lectotype (BM).

Fig. 12. Habit of a recently collected specimen in the Canary Islands (TFC Phyc. 8470).



Figs 13–19. *Liagora distenta* (Mertens) Lamouroux.

Fig. 13. Detail of transverse section of medulla, showing thick medullary cells intermingled with thin rhizoidal cells (TFC Phyc. 8470).

Fig. 14. Assimilatory filament. Note the wide pyriform terminal cells (TFC Phyc. 8470).

Fig. 15. Detail of assimilatory filament with a curved 4-celled carpogonial branch (arrow), borne laterally on the middle of the supporting cell (TFC Phyc. 8470).

Fig. 16. Detail of assimilatory filament with carpogonial branch (arrowhead) and sterile filaments growing from adjacent cells (arrows) (TFC Phyc. 8470).

Fig. 17. Early stage in the growth of the gonimoblast with profuse formation of sterile filaments (arrows) (TFC Phyc. 8470).

Fig. 18. Mature carposporophyte showing carposporangia (arrowheads) ending gonimoblast filaments. Note sterile filaments (arrows) placed only under the gonimoblast (TFC Phyc. 8470).

Fig. 19. Assimilatory filament bearing terminal spermatangia (arrows) (TFC Phyc. 8457).

subcylindrical, 9–17 × 21–24 μm at the proximal portion of the filaments, becoming broader upwards, the uppermost pyriform, 7–17 × 9–24 μm (Fig. 14); rhizoidal filaments common, produced from the innermost cells of the assimilatory filaments.

CARPOGONIAL BRANCH AND CARPOSPOROPHYTE: Plants usually dioecious. Carpogonial branches four- to five-celled, strongly curved, 10–12 μm broad, laterally attached to the middle of the supporting cell, at the inner portion of the assimilatory filaments (Fig. 15). After presumed fertilization the cells above, below and adjacent to the supporting cell branch irregularly to form colourless sterile filaments (Figs 16, 17). At the same time the carpogonium divides transversely, forming radiating, compact gonimoblast filaments (Fig. 17) that develop terminal carposporangia, single or in short chains, 7–10 × 12–19 μm (Fig. 18). Sterile filaments persist under the gonimoblast and do not surround the mature carposporophyte, which is 156–240 μm in diameter in surface view. Fusions between the cells of the carpogonial branch after fertilization were not observed.

SPERMATANGIA: Spermataegia ovoid, 2–3 μm broad, 1–3 occurring on small spermatangial mother cells formed on the terminal cells of the assimilatory filaments (Fig. 19).

REMARKS: *Liagora distenta* has been characterized by Abbott (1990a) with the following features: (1) medullary filaments less than 20 μm diameter; (2) assimilatory filaments rarely more than 100 μm long; and (3) carposporophytes with a well-developed involucre of filaments, and very large carposporangia, c. 13 μm broad and 26–30 μm long. The lectotype specimen of *L. distenta* (Fig. 11) is a male plant that shows medullary filaments 40–60 μm in diameter and short cortical assimilatory filaments up to 120 μm long ending in pyriform apical cells, 12–17 μm broad and 16–24 μm long. Ovoid spermataegia, 2–3 μm broad, occur in digitate clusters on terminal cells of assimilatory filaments. The recent collections agree in most respects with the type specimen. From the numerous collections it is obvious that the species presents an extremely wide morphological range, from small plants with few lateral branches to larger and densely branched ones. But the morphology of the assimilatory filaments (short and ending in broad cells) was a consistent feature in all plants examined. Female plants collected in the Canary Islands with identical assimilatory filaments bore carposporophytes differing from those reported by Abbott (1990a), as they lack a true involucre (sterile filaments are placed only below the gonimoblast) and form smaller carposporangia. However, carposporophytes as described by Abbott (1990a) are present in *L. gymnarthron*, a species similar in habit to *L. distenta* but with longer assimilatory filaments without broad apical cells. Some non-Canarian herbarium specimens [collected in Madeira, the Salvage Islands and Marseille, S France (Mediterranean)] identified as *L. distenta* are misidentifications of *L. gymnarthron* (Afonso-Carrillo, unpublished observations). *L. distenta* is also closely related to *L. albicans* Lamouroux, but the latter has much longer and thinner assimilatory filaments and shorter carposporangia. *L. distenta* is a common species in the Canary Islands during late winter to summer.

Liagora gymnarthron Børgesen 1927: 54, figs 30–31

TYPE MATERIAL: Housed at B and probably lost. Fragments of the type material in C (Fig. 20).

TYPE LOCALITY: Near Las Palmas, Gran Canaria, Canary Islands.

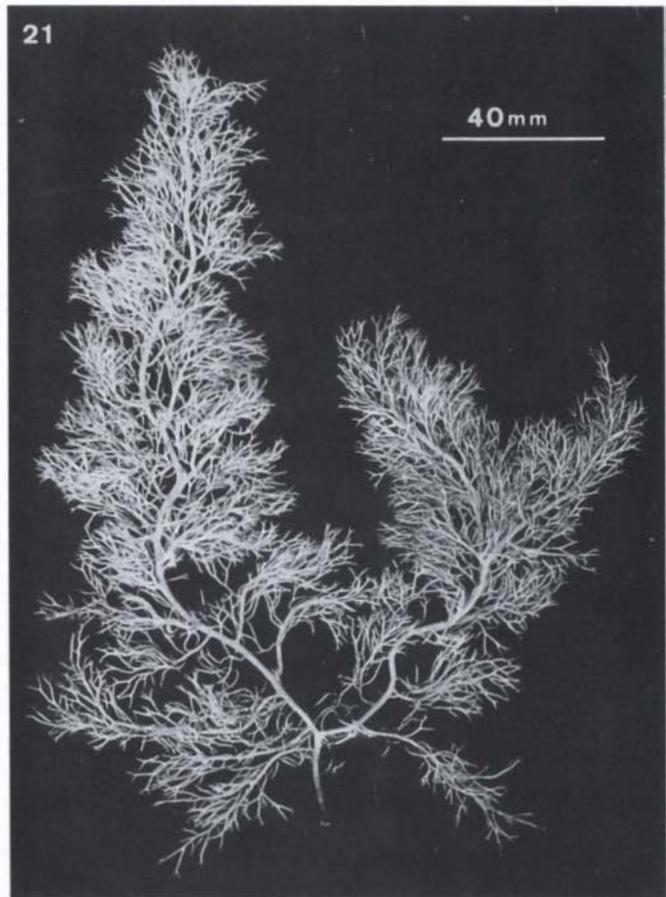
DISTRIBUTION: Warm temperate NE Atlantic: Western Mediterranean, Madeira, Salvage Islands and Canary Islands (La Palma, El Hierro, Tenerife, Gran Canaria, Lanzarote and Fuerteventura).

REPRESENTATIVE SPECIMENS: LA PALMA: Tijarafe (*Cancap*, 5.vi.1980; L 9847139). Fajana de Barlovento (*Gil-Rodríguez et al.*, 15.vi.1983; TFC Phyc. 3018). Charco Verde (*Rojas & Ibeas*, 04.vii.1993; TFC Phyc. 8524). EL HIERRO: El Verodal (*Rojas & Afonso-Carrillo*, 16.vi.1992; TFC Phyc. 8491, 8501). TENERIFE: Bajamar (*Gil-Rodríguez*, v.1974; TFC Phyc. 1302). Punta Hidalgo (*Gil-Rodríguez*, x.1978; TFC Phyc. 473). Igueste (*Kvaternik & Lanzadera*, 07.vii.1991; TFC Phyc. 8480). Poris de Abona (*Gil-Rodríguez*, v.1972; TFC Phyc. 1273; *Gil-Rodríguez*, vi.1972; TFC Phyc. 77). El Médano (*Sansón & Reyes*, 14.iv.1991; TFC Phyc. 7713). Agua Dulce, Los Abrigos (*Cruz*, 27.v.1979; TFC Phyc. 2239). Playa de Las Américas (*Gil-Rodríguez*, vi.1972; TFC Phyc. 1252). Playa de la Arena (*Acuña*, 1969; TFC Phyc. 1250). Playa de Los Troches (*Cancap*, 31.v.1982; L 9848098). GRAN CANARIA: Near Las Palmas (1856, fragments of type material; C). LANZAROTE: Playa del Paso, P.N. Timanfaya (*Arráez*, 13.vii.1987; TFC Phyc. 5230; *Arráez*, 16.vii.1987; TFC Phyc. 5228). Laja del Cochino, P.N. Timanfaya (*Arráez*, 11.viii.1987; TFC Phyc. 5176, 5229). Playa de la Madera, P.N. Timanfaya (*Arráez*, 14.vii.1987; TFC Phyc. 5136, 5250). Norte P.N. Timanfaya (*Arráez*, 28.vii.1987; TFC Phyc. 5224). Orzola (*Haroun*, 20.iv.1984; TFC Phyc. 913), (*Darias & Rodríguez*, 01.iii.1987; TFC Phyc. 5605), (*Rojas & Ibeas*, 08.v.1993; TFC Phyc. 8505). Caletón Blanco (*Haroun*, 27.vi.1983; TFC Phyc. 106). Caleta del Sebo, La Graciosa (*Gramonal*, 28.iii.1983; TFC Phyc. 4972). Punta Gorda, La Graciosa (*Wildpret et al.*, 03.vi.1985; TFC Phyc. 5049). Rada de Arrieta (*Cancap*, 22.v.1980; L 9847487). FUERTEVENTURA: Corralejo (*Gil-Rodríguez & Afonso-Carrillo*, 03.v.1980; TFC Phyc. 2360). Costa de Jandia (*Gil-Rodríguez & Afonso-Carrillo*, 01.v.1980; TFC Phyc. 2380, 2423).

HABITAT: *Liagora gymnarthron* has been always found growing on rocks. Plants were collected from the lower intertidal pools to 9 m depth, usually in areas of moderate water movement.

HABIT AND VEGETATIVE STRUCTURE: Plants erect, reddish-brown to whitish-green, to 280 mm high, consisting of one to several terete main axes, 1–2 mm broad, dichotomously branched, bearing dichotomously divided terete lateral branches, up to 20 mm long and 0.5–1 mm broad (Fig. 21); adventitious branches very common; main axes moderately calcified, lateral and adventitious branches little calcified and mucosoid. Medullary filaments 20–78 μm broad, intermingled with rhizoidal filaments 7–12 μm broad (Fig. 22). Cortical assimilatory filaments 132–192 μm long, 4–6 times dichotomously divided, with trichotomies common at the end of the filaments (Fig. 23). Cells of the assimilatory filaments cylindrical, 7–12 × 24–36 μm , becoming oval upwards, terminating in pyriform or subspherical cells, 5–12 × 9–15 μm (Fig. 23); rhizoidal filaments arise from the basal cells of the assimilatory filaments.

CARPOGONIAL BRANCH AND CARPOSPOROPHYTE: Plants as a rule dioecious. Carpogonial branches four-celled, strongly curved, 11–13 μm broad, borne laterally on the middle of the supporting cell, at the basal portion of the assimilatory



Figs 20, 21. *Liagora gymmarthron* Børgesen.

Fig. 20. Holotype material retained at C.

Fig. 21. Habit of a recently collected specimen in the Canary Islands (TFC Phyc. 8491).

filaments (Fig. 24). After presumed fertilization the cells adjacent to the supporting cell form colourless filaments that grow and divide, producing a very conspicuous involucre (Figs 25–28). Simultaneously, the carpogonium divides producing short and densely compact gonimoblast filaments (Figs 26–28) that develop terminal carposporangia $10\text{--}12 \times 21\text{--}30 \mu\text{m}$ (Fig. 29). Mature carposporophytes surrounded by the well developed involucre, measure $125\text{--}250 \mu\text{m}$ in diameter in surface view. Fusions between the cells of the carpogonial branch after fertilization were not observed.

SPERMATANGIA: Spermataegia spherical, $c. 2.5 \mu\text{m}$ in diameter, 1–2 borne on elongate spermataegia mother cells $2.5 \mu\text{m}$ broad and $4 \mu\text{m}$ long, arising on the terminal cells of the assimilatory filaments (Figs 30, 31).

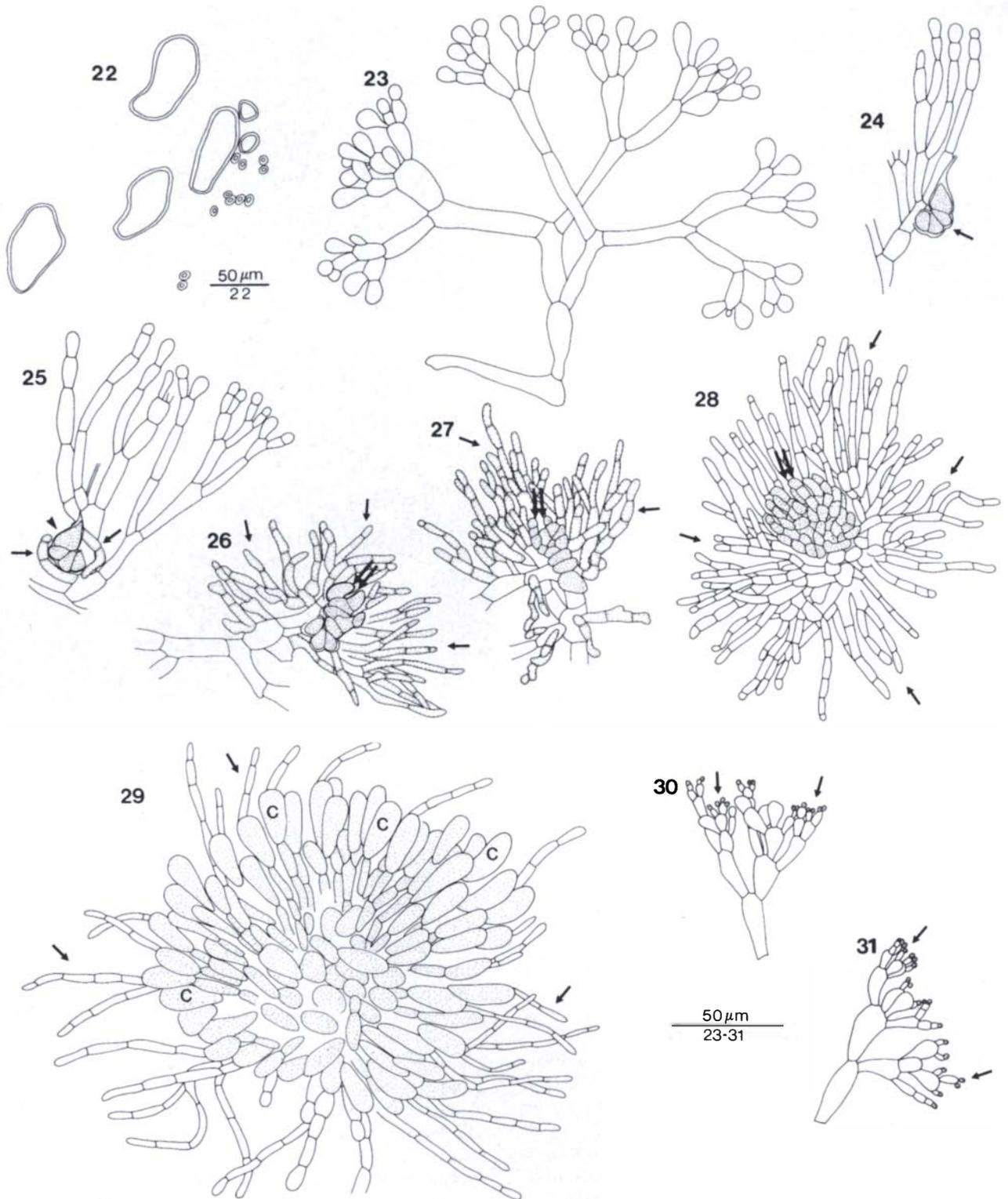
REMARKS: *Liagora gymmarthron* was described by Børgesen (1927) on a herbarium specimen, housed at B, previously identified as *L. decussata* Montagne. The type material is probably lost, but fragments of the type material (Fig. 20) were retained at C. These fragments belong to a female specimen and showed medullary filaments $25\text{--}60 \mu\text{m}$ broad and cortical assimilatory filaments up to $180 \mu\text{m}$ long, 4–5 times dichotomously divided, with some terminal trichotomies. Cells of cortical filaments were cylindrical, $8\text{--}12 \mu\text{m}$ broad and $24\text{--}30 \mu\text{m}$ long, ending in oval or pyriform cells $6\text{--}12 \mu\text{m}$ broad and $9\text{--}13 \mu\text{m}$ long. Strongly curved four-celled carpo-

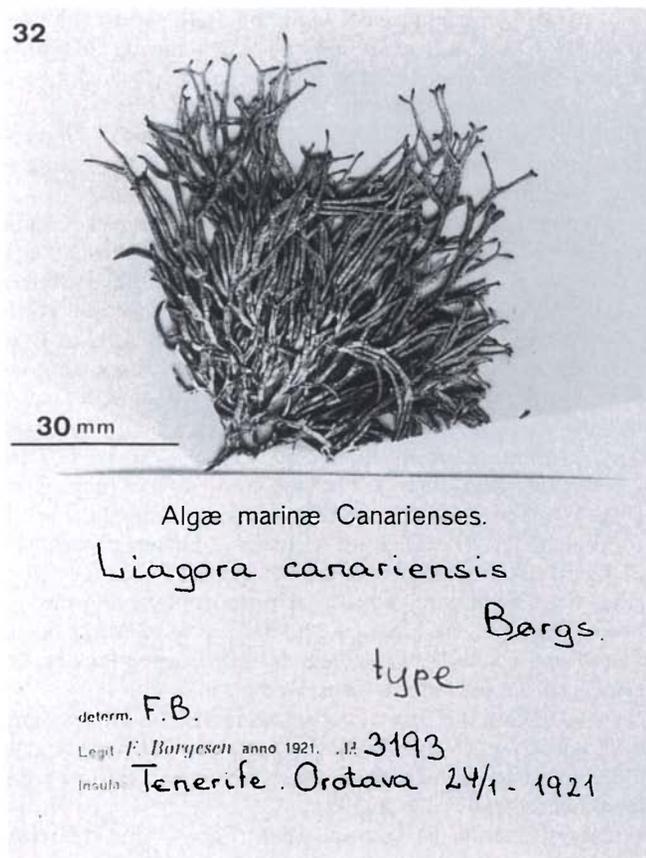
gonial branches, $c. 12 \mu\text{m}$ broad were present, borne laterally on the supporting cell. A mature carposporophyte, $180 \mu\text{m}$ in diameter, with carposporangia $c. 12 \mu\text{m}$ broad and $25\text{--}30 \mu\text{m}$ long, and surrounded by a well developed involucre was observed.

The Canarian plants examined during this study and other non-Canarian herbarium specimens (Afonso-Carrillo, unpublished observations) are in good agreement with the features observed in the fragments of the type material. *L. gymmarthron* has not been newly reported since its description, but is easily confused with *L. distenta*, which has a similar habit (see comments on *L. distenta*). Records of this last species should be checked for possible misidentification. The type material of other taxa considered as synonyms of *L. distenta* [*L. phycioides* Lamouroux and *L. complanata* C. Agardh (Abbott 1990a) and *L. ramellosa* Kützinger (Børgesen 1927)] should be re-examined and their relationships to *L. gymmarthron* investigated. *L. gymmarthron* is a common species in the Canary Islands during late winter to summer.

Liagora canariensis Børgesen 1927: 48, figs 25–29

HOLOTYPE: C Herb. Børgesen, Algae marinae Canarienses, No. 3193 (F. Børgesen, 24.01.1921; Fig. 32).





Figs 32, 33. *Liagora canariensis* Børgesen.

Fig. 32. Holotype (C).

Fig. 33. Habit of a recently collected specimen in the Canary Islands (TFC Phyc. 8489).

TYPE LOCALITY: Orotava (=Puerto de la Cruz), Tenerife, Canary Islands.

DISTRIBUTION: Warm temperate NE Atlantic: Madeira, Salvage Islands and Canary Islands (La Palma, La Gomera, El Hierro, Tenerife, Gran Canaria and Lanzarote).

REPRESENTATIVE SPECIMENS: LA PALMA: Fajana de Barlovento (*Gil-Rodríguez et al.*, 15.vi.1983; TFC Phyc. 3018, 3059). Puerto Naos (*Kvaternik & Lanzadera*, 31.x.1993; TFC Phyc. 8508). LA GOMERA: Valle Gran Rey (*Sansón & Reyes*, 24.iv.1992; TFC Phyc. 8473. 13.vi.1992; TFC Phyc. 8475, 8510. 14.xi.1992; TFC Phyc. 8509, 8511. 24.iv.1993; TFC Phyc. 8507). EL HIERRO: La Caleta (*Afonso-Carrillo*, 01.v.1979; TFC Phyc. 2236). El Verodal (*Rojas & Afonso-Carrillo*, 16.vi.1992; TFC Phyc. 8490, 8493). Pozo de Las Calcosas (*Rojas & Afonso-Carrillo*, 16.vi.1992; TFC Phyc. 8489, 8498).

Roque de Bonanza (*Rojas & Afonso-Carrillo*, 22.iv.1993; TFC Phyc. 8482). TENERIFE: Teno (*Gil-Rodríguez*, x.1975; TFC Phyc. 1339, 2153). Puerto de la Cruz (*Børgesen*, 24.i.1921; C Herb. Børgesen No. 3193, holotype). Bajamar (*Kvaternik & Lanzadera*, 20.vi.1993; TFC Phyc. 8493). Punta Hidalgo (*Gil-Rodríguez*, ii.1991; TFC Phyc. 1245), (*Elejabeitia*, 20.v.1981; TFC Phyc. 6859). Las Caletillas (*Gil-Rodríguez & Afonso-Carrillo*, vii. 1979; TFC Phyc. 2116). El Socorro, Güímar (*López*, 26.vii.1979; TFC Phyc. 2129. 11.viii.1979; TFC Phyc. 2128). Puertito de Güímar (*Gil-Rodríguez*, ii.1972; TFC Phyc. 2155), (*Haroun*, 19.viii.1982; TFC Phyc. 4138). Porís de Abona (*Gil-Rodríguez*, iv.1972; TFC Phyc. 76. vi.1972; TFC Phyc. 1253). Las Galletas (*Moreno*, 04.iv.1972; TFC Phyc. 1256), Palm Beach (*Haroun*, 14.vii.1984; TFC Phyc. 4123). Playa de La Arena (*Acuña*, 1969; TFC Phyc. 1251). GRAN CANARIA:

Figs 22–31. *Liagora gymnarthron* Børgesen.

Fig. 22. Detail of transverse section of medulla, showing thick medullary cells intermingled with thin rhizoidal cells (TFC Phyc. 8491).

Fig. 23. Assimilatory filament (TFC Phyc. 8491).

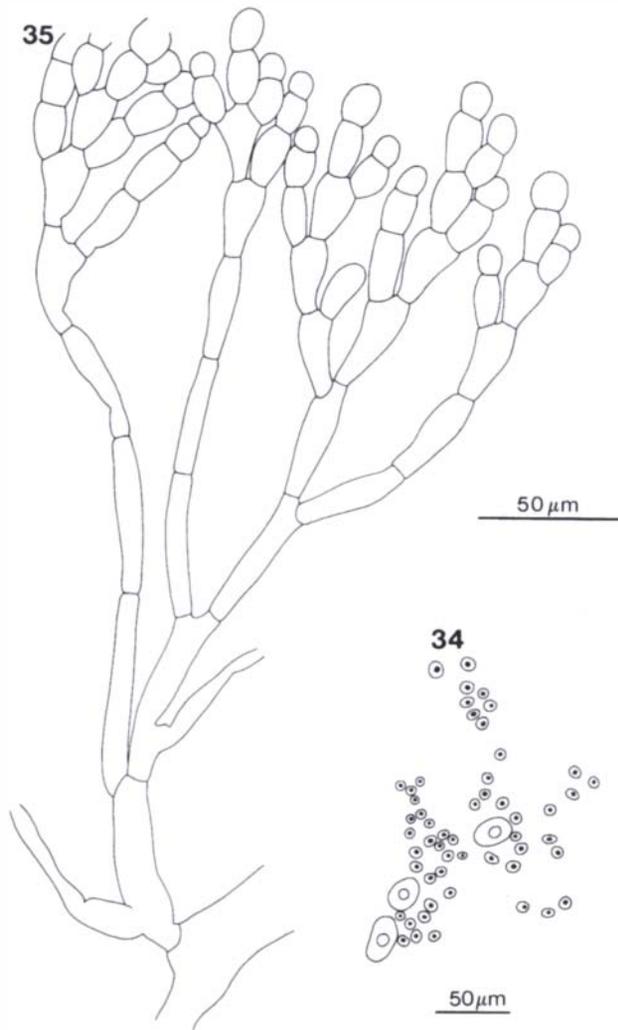
Fig. 24. Detail of assimilatory filament with curved 4-celled carpogonial branch (arrow), borne laterally on the middle of the supporting cell (TFC Phyc. 8491).

Fig. 25. Detail of assimilatory filament with carpogonial branch (arrowhead) and sterile filaments growing from adjacent cells (arrows) (TFC Phyc. 8491).

Figs 26–28. Successive stages in the growth of the gonimoblast (double arrow) with profuse formation of sterile filaments (arrows) (TFC Phyc. 8491).

Fig. 29. Mature carposporophyte showing gonimoblast filaments and carposporangia (C), surrounded by involucre filaments (arrows) (TFC Phyc. 8491).

Figs 30, 31. Portions of outer cortical filaments bearing spermatangia (arrows) (TFC Phyc. 8501).



Figs 34, 35. *Liagora canariensis* Børgesen.

Fig. 34. Detail of transverse section of medulla, showing thick medullary cells intermingled with thin rhizoidal cells (TFC Phyc. 8489).

Fig. 35. Assimilatory filament (TFC Phyc. 8507).

Mogán (*Kvaternik & Lanzadera*, 20.vi.1993; TFC Phyc. 8478). LANZAROTE: Laja del Cochino, P.N. Timanfaya (*Arráez*, 11.vii.1987; TFC Phyc. 5196. 12.viii.1987; TFC Phyc. 5226). Playa de La Madera, P.N. Timanfaya (*Arráez*, 14.vii.1987; TFC Phyc. 5227). P.N. Timanfaya (*Arráez*, 28.vii.1987; TFC Phyc. 5247). Playa del Paso, P.N. Timanfaya (*Arráez*, 13.vii.1987; TFC Phyc. 5225).

HABITAT: *Liagora canariensis* is always epilithic. It is usually found in areas of moderate to high water movement and has been collected from lower intertidal pools to 3 m depth.

HABIT AND VEGETATIVE STRUCTURE: Plants erect, densely tufted, dark rose, to 110 mm high; heavily calcified through, except at the tips, with common fractures along the thallus; axes terete, 1–1.5 mm wide, 3–12 times dichotomously branched in a fairly regular manner, 5–10 mm between dichotomies (Fig. 33); adventitious branches not observed. Medullary filaments 24–31 µm broad intermingled with rhizoidal filaments 4–8 µm broad (Fig. 34). Cortical assimilatory filaments 300–450 µm long, up to 7 times dichotomously

branched, with trichotomies common at the end of the filaments (Fig. 35); cells of the assimilatory filaments cylindrical, 7–15 × 55–85 µm at the base of the filaments, becoming progressively smaller and more rounded outwards, with oval apical cells, 7–12 × 14–20 µm (Fig. 35); rhizoidal filaments common, produced from the innermost cells of the assimilatory filaments (Fig. 35).

CARPOGONIAL BRANCH AND CARPOSPOROPHYTE: Plants dioecious. Carpogonial branches four- to five-celled, straight or slightly curved, 12–13 µm broad, borne on the mid-lateral face of the supporting cell, at the middle portion of the assimilatory filaments (Fig. 36). After presumed fertilization the cells above, below and adjacent to the supporting cell branch irregularly to form colourless involucre filaments, initially surrounding the carpogonial branch and becoming very profuse, directed almost exclusively outwards (Figs 37–39). Simultaneously, the carpogonium divides transversely (Fig. 37), then the upper cell divides longitudinally (Fig. 38) forming (Fig. 39), radiating, densely compact gonimoblast filaments that bear terminal carposporangia, 9–12 × 19–24 µm (Fig. 40). The mature compact carposporophyte and the well developed involucre measure 270–350 µm in diameter in surface view. Fusions between the cells of the carpogonial branch after fertilization were not observed.

SPERMATANGIA: Spermataegia spherical, 2–3 µm in diameter, occurring 1–3 on elongate spermataegial mother cells, 2–3 µm broad and 7–10 µm long, which are clustered and form dense heads (Figs 41, 42).

REMARKS: Both the type specimen (Fig. 32) and the recent collections of *Liagora canariensis* agree in all respects with the description given by Børgesen (1927). In habit, *L. canariensis* is close to *L. boergesenii* Yamada, *L. setchellii* Yamada and *L. valida* Harvey, but it is differentiated anatomically by the assimilatory filaments with relatively straight cell walls without constrictions, the mature carposporophyte surrounded by involucre filaments and the spermataegia forming dense heads. *L. canariensis* is a common species in the Canary Islands throughout the year, although in winter is less abundant.

Liagora tetrasporifera Børgesen 1927: 39, figs 21–24

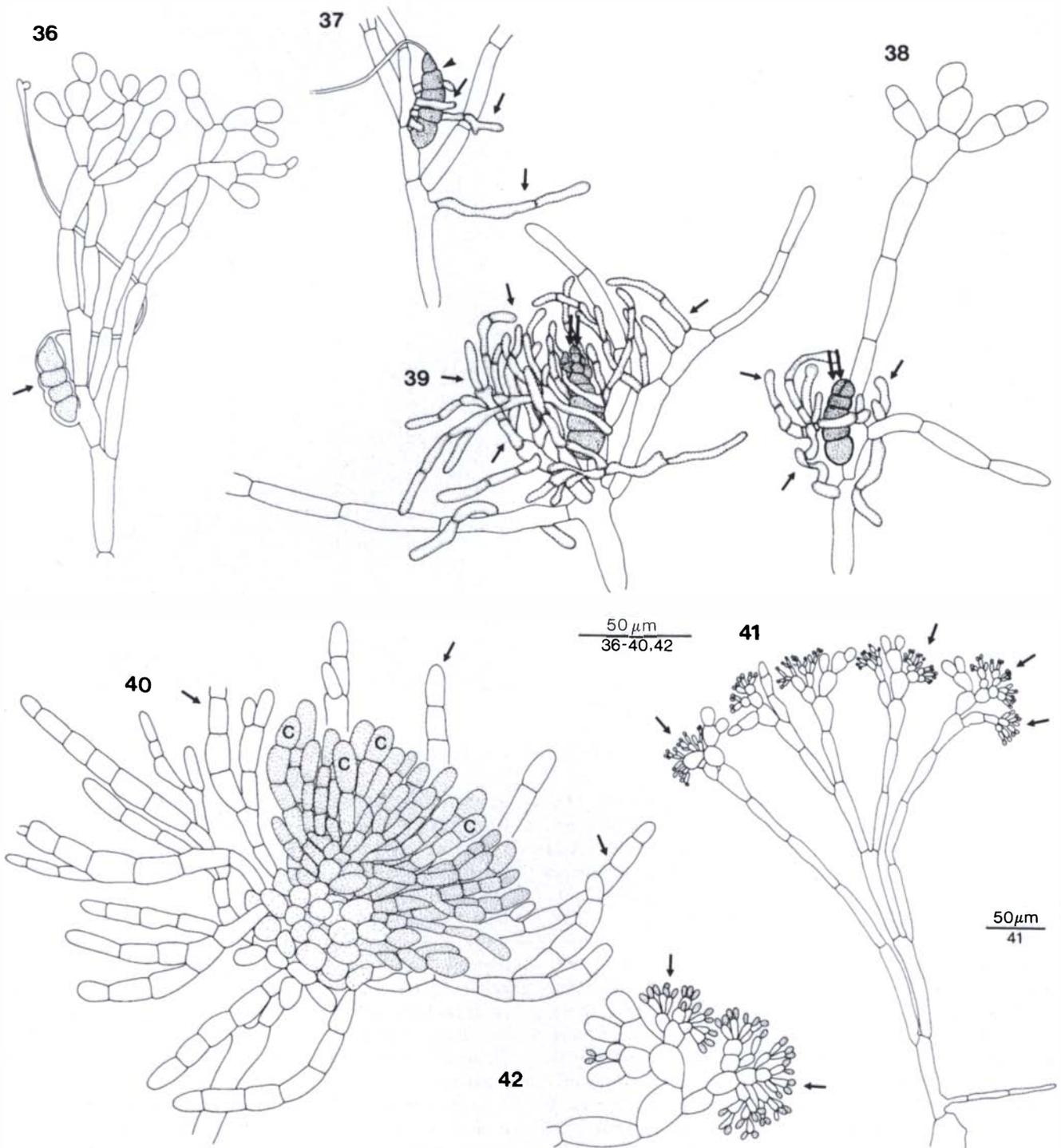
Kylin 1930: 8, fig. 3f; Couté 1976: pls 2,6,7.

HOLOTYPE: C Herb. Børgesen, *Algae marinae Canarienses*, No. 3538 (F. Børgesen, 1921; Fig. 43).

TYPE LOCALITY: Bahía del Confital, Gran Canaria, Canary Islands.

DISTRIBUTION: Warm temperate NE Atlantic: Western Mediterranean, Madeira, Salvage Islands and Canary Islands (El Hierro, Tenerife, Gran Canaria, Lanzarote and Fuerteventura).

REPRESENTATIVE SPECIMENS: EL HIERRO: Roque de Bonanza (*Rojas & Afonso-Carrillo*, 22.iv.1993; TFC Phyc. 8499). El Tocorón (*Rojas & Afonso-Carrillo*, 14.xi.1992; TFC Phyc. 8496). Arenas Blancas (*Rojas & Afonso-Carrillo*, 16.vi.1992; TFC Phyc. 8471). TENERIFE: Charco La Arena, Bajamar (*Gil-Rodríguez*, 30.v.1974; TFC Phyc. 320). Punta Hidalgo (*Acuña*, 1969; TFC Phyc. 78), (*Gil-Rodríguez*, ii.1971; TFC Phyc. 1211). Punta de Güimar (*Haroun*, 19.viii.1982; TFC Phyc. 4136). Porís de Abona (*Gil-Rodríguez*, v.1972; TFC Phyc. 1254), (*Haroun*, 28.vii.84; TFC Phyc. 4113). El Médano (*Gil-*



Figs 36–42. *Liagora canariensis* Børgesen.

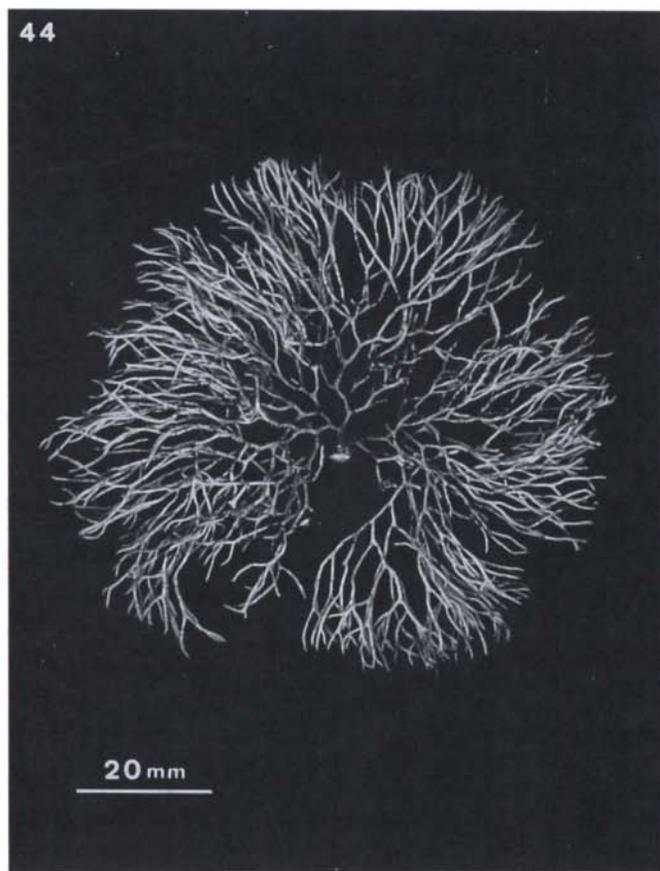
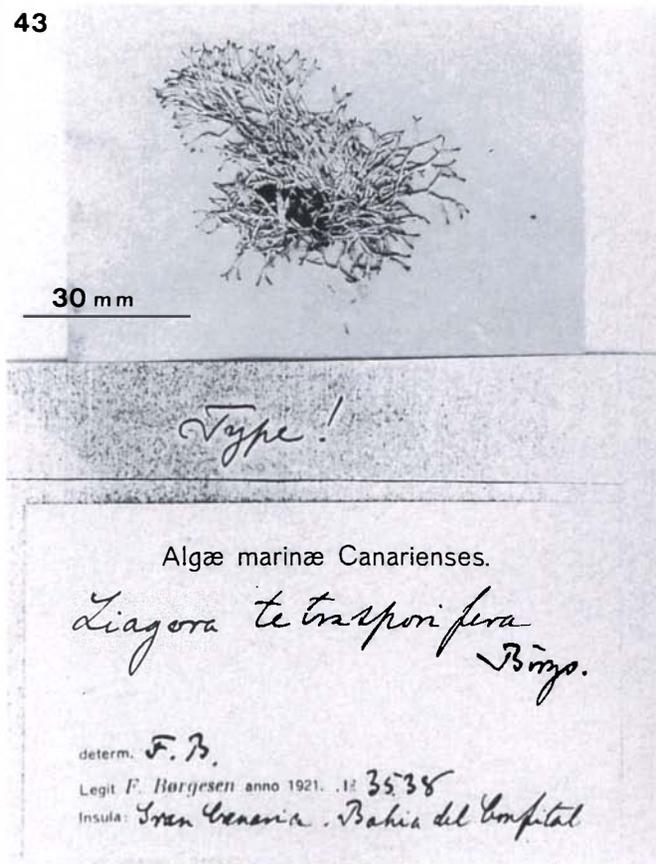
Fig. 36. Detail of assimilatory filament showing straight 4-celled carposporangial branch (arrow), borne laterally on the middle of the supporting cell (TFC Phyc. 8511).

Fig. 37. Carposporangial branch showing the first transverse division of the carposporangium (arrowhead) and sterile filaments growing from adjacent cells (arrows) (TFC Phyc. 8478).

Figs 38, 39. Early stages in the growth of the gonimoblast (double arrows) with profuse formation of sterile filaments (arrows) (TFC Phyc. 8511).

Fig. 40. Mature carposporophyte showing gonimoblast filaments and carposporangia (C), surrounded by involucre filaments (arrows) (TFC Phyc. 8478).

Figs 41, 42. Assimilatory filaments bearing spermatangia in terminal clusters (arrows) (TFC Phyc. 8509).



Figs 43, 44. *Liagora tetrasporifera* Børgesen.

Fig. 43. Holotype (C).

Fig. 44. Habit of a recently collected specimen in the Canary Islands (TFC Phyc. 8465).

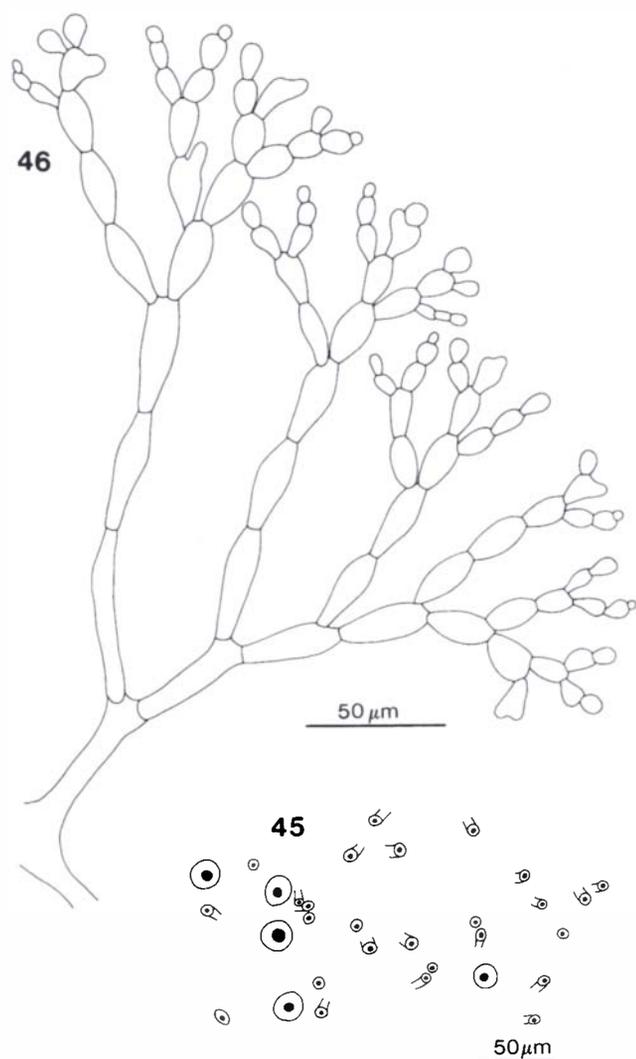
Rodríguez, xii.1976; TFC Phyc. 1296), (Reyes, 08.v.1992; TFC Phyc. 7825). Montaña Roja (Haroun, 27.xi.1982; TFC Phyc. 291). La Tejita (Gil-Rodríguez, iii.1974; TFC Phyc. 1210). Los Abrigos (Gil-Rodríguez, i.1974; TFC Phyc. 1242). Las Galletas (Cancap 3, 26.x.1978; TFC Phyc. 4301). GRAN CANARIA: BAÑA DEL CONFITAL (Børgesen, 1921; C. Herb. Børgesen No. 3538, holotype). Las Canteras (Cancap 3, 07.xi.1978; TFC Phyc. 4304), (Haroun, 22.xii.1978; TFC Phyc. 74; 10.iv.1979; TFC Phyc. 73), (Alumno, 26.xi.1979; TFC Phyc. 633), (González, 21.ii.1984; TFC Phyc. 5495; 03.vi.1985; TFC Phyc. 5471), (Kvaternik & Lanzadera, 01.iii.1993; TFC Phyc. 8469. 06.iv.1993; TFC Phyc. 8465). LANZAROTE: Arrecife (Gil-Rodríguez & Hernández, 26.x.1991; TFC Phyc. 8463), (Rojas & Ibeas, 07.v.1993; TFC Phyc. 8495). Orzola (Darias & González, 01.iii.1987; TFC Phyc. 5606). Caleta de Arriba, La Graciosa (Haroun & Viera, 16.iv.1984; TFC Phyc. 4968). FUERTEVENTURA: El Cotillo (Sansón & Reyes, 20.xi.1992; TFC Phyc. 8455. 21.xi.1992; TFC Phyc. 8454). Corralejo (Izquierdo, 14.ix.1982; TFC Phyc. 414). Sin localidad (Izquierdo, 14.ix.1982; TFC Phyc. 42).

HABITAT: *Liagora tetrasporifera* has been found growing epilithically and as an epiphyte on the rhizomes of the seagrass *Cymodocea nodosa* (Ucria) Ascherson. It has been collected from lower intertidal pools to 6 m depth, usually in areas of moderate water movement.

HABIT AND VEGETATIVE STRUCTURE: Plants tufted and entangled, whitish-rose, to 60 mm high heavily calcified except

at tips, with common fractures along the thallus, axes terete, 0.5–0.7(1) mm wide, 4–10 times sub- or dichotomously branched, 3–11 mm between dichotomies (Fig. 44); adventitious branches present on lower parts. Medullary filaments 16–22 μm broad, intermingled with rhizoidal filaments 5–7 μm broad (Fig. 45). Cortical assimilatory filaments 180–240 μm long, 4–8 times dichotomously branched in an irregular manner (Fig. 46); cells of the assimilatory filaments cylindrical, 7–12 \times 30–50 μm at the base of the filaments, becoming progressively smaller and more rounded outwards, with ovoid or spherical apical cells, 7–8 \times 9–12 μm (Fig. 46); rhizoidal filaments produced from the basal cells of the assimilatory filaments are rare.

CARPOGONIAL BRANCH AND CARPOSPOROPHYTE: Plants monoecious. Carpogonial branches three-celled, straight, 9–12 μm broad, borne on the distal portion of the supporting cell, about mid-level of the assimilatory filaments (Fig. 47). After presumed fertilization the cells above and adjacent to the supporting cell begin to develop the involucrel filaments (Figs 48–51). Simultaneously, the carpogonium divides transversely (Fig. 48) producing two cells, the upper one forms outwardly radiating lax filaments (Figs 49–51) that produce terminal quadripartite carposporangia, 9–12 \times 19–24 μm (Figs 52, 53). Cells of the carpogonial branch fuse together after fertilization (Fig. 49). Mature carposporophyte rather diffuse, 165–300 μm in diameter in surface view, with gonimoblast filaments and involucrel filaments intermingled.



Figs 45, 46. *Liagora tetrasporifera* Børgesen (TFC Phyc. 7825).
Fig. 45. Detail of transverse section of medulla, showing thick medullary cells intermingled with thin rhizoidal cells.
Fig. 46. Assimilatory filament.

SPERMATANGIA: Spermatangia spherical, *c.* 3 μm in diameter, 1–2 borne on spermatangial mother cells, 3 μm broad and 5 μm long, which arise on the terminal cells of the assimilatory filaments (Figs 54, 55).

REMARKS: Both the type specimen (Fig. 43) and the recent collections of *L. tetrasporifera* agree in all respects with the descriptions by Børgesen (1927). *L. tetrasporifera* is the only Atlantic species of the genus known to form multispored carposporangia. According to Guiry (1990) three other species form quadripartite carposporangia: *L. brachyclada* Decaisne from Juan Fernández Islands, *L. harveyana* Zeh from Australia and *L. papenfussii* Abbott from Hawaii and Japan. *L. papenfussii* has less developed involucre filaments and smaller carposporophytes than *L. tetrasporifera*. *L. brachyclada* and *L. harveyana* are closely related to *L. tetrasporifera* in habit and carposporophyte development but differ in carposporangial branch morphology. Both *L. brachyclada* and *L. harveyana* have curved four-celled carposporangial branches, whereas the type specimen and the recent collections examined

always showed, as described by Børgesen (1927), straight, three-celled carposporangial branches. Plants reported from the Mediterranean by Couté (1971, 1976) with curved four- or five-celled carposporangial branches should be reinvestigated. In culture studies of *L. tetrasporifera*, Couté (1971, 1976) found that spores from quadripartite carposporangia germinated to form erect fronds without developing a tetrasporophyte. Nevertheless, Guiry (1990) obtained tetrasporophytes from quadripartite carposporangia of *L. harveyana*, suggesting that the life history needs to be reinvestigated. *Liagora tetrasporifera* is a common species in the Canary Islands throughout the year, although in winter is less abundant.

***Liagora maderensis* Kützing 1858: 43, tab. 91, figs Ia–e**

LECTOTYPE: L, Herb. Kützing, ex Herb. Sonder (Fig. 56).

TYPE LOCALITY: Madeira.

DISTRIBUTION: Warm temperate NE Atlantic: Azores, Madeira and Canary Islands (El Hierro).

REPRESENTATIVE SPECIMENS: EL HIERRO: El Verodal (Rojas & Afonso-Carrillo, 16.vi.1992; TFC Phyc. 8472).

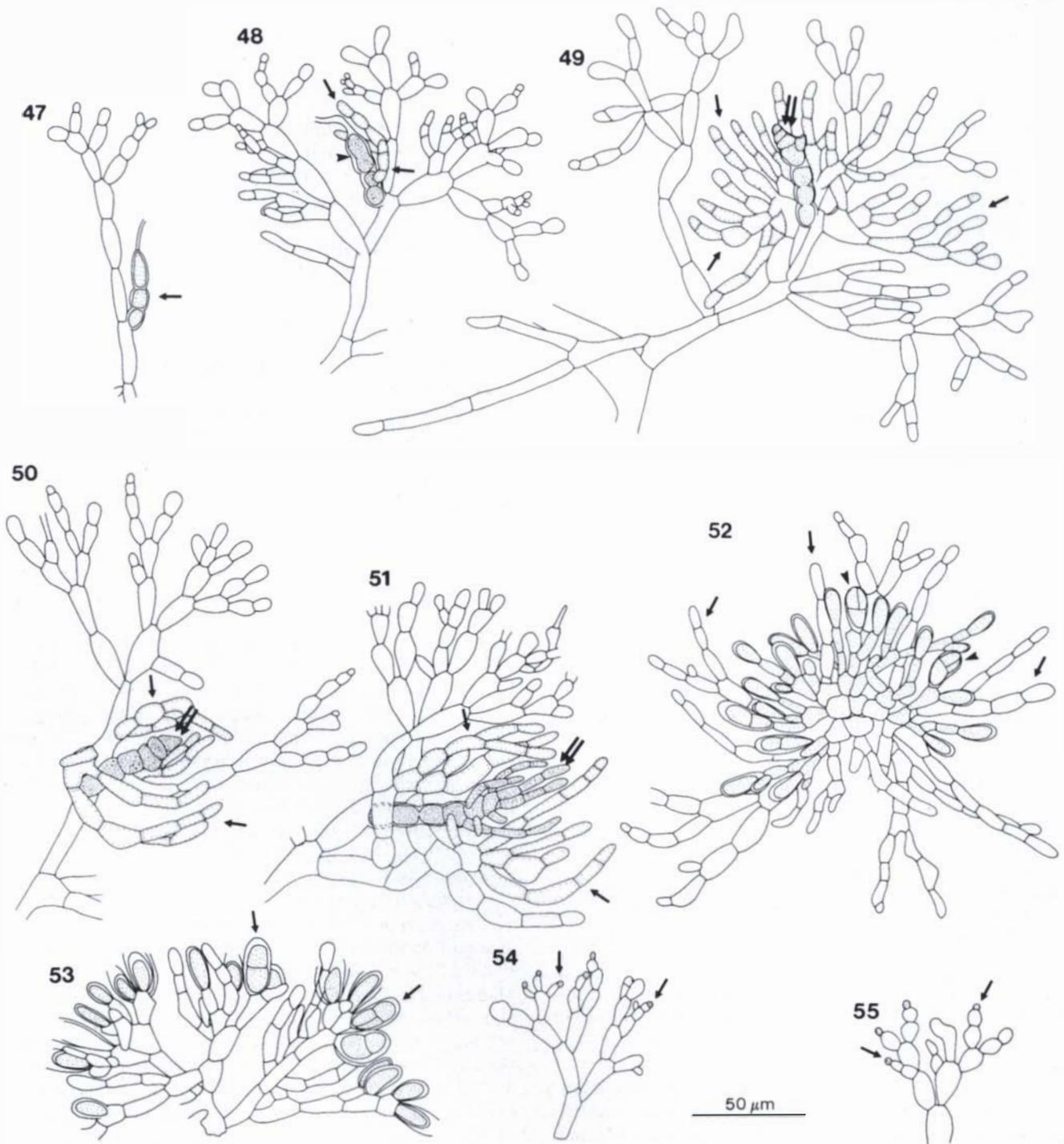
HABITAT: Specimens of *Liagora maderensis* examined were collected as drift together with plants of *L. canariensis*, *L. gymnarthron* and *L. valida*.

HABIT AND VEGETATIVE STRUCTURE: Plants erect, whitish to greenish, to 35 mm high, moderately calcified; axes terete, 0.7–1 mm wide, 3–8 times irregularly dichotomously branched, 2–7 mm between dichotomies, branching angles wide open (Fig. 57); dichotomously branched adventitious branches uncommon. Medullary filaments 36–84 μm broad, intermingled with rhizoidal filaments 6–12 μm broad (Fig. 58). Cortical assimilatory filaments 150–360 μm long, 5–7 times dichotomously branched, sometimes with apical trichotomies (Fig. 59); cells of the assimilatory filaments cylindrical, 9–22 × 24–55 μm at the base of the filaments, becoming shorter upwards, the uppermost ovoid or pyriform, 5–7 × 9–12 μm (Fig. 59); rhizoidal filaments produced from the basal cells of the assimilatory filaments are uncommon.

CARPOGONIAL BRANCH AND CARPOSPOROPHYTE: Plants monoecious. Carposporangial branches four-celled, strongly curved, arranged on the mid-line or slightly higher on the supporting cell, *c.* 12 μm broad, at the middle portion of the assimilatory filaments (Fig. 60). After presumed fertilization the cells above and below the supporting cell branch irregularly to form colourless involucre filaments (Figs 61–63). Simultaneously, the carposporangium divides transversely, the upper daughter cell divides again obliquely, producing two cells that continue dividing, forming a relatively compact gonimoblast (Figs 61–63) that produces terminal carposporangia, 7–10 × 14–22 μm (Fig. 64). The compact mature carposporophyte and the well developed involucre measure 250–300 μm in diameter in surface view. Fusions between the cells of the carposporangial branch after fertilization were not observed.

SPERMATANGIA: Spermatangia spherical, *c.* 2.5 μm in diameter, 1–2 borne on spermatangial mother cells arising on the terminal cells of the assimilatory filaments (Fig. 65).

REMARKS: *Liagora maderensis* was described by Kützing (1858) based on plants collected in Madeira and deposited in the Herbarium Sonder. It has not been reported since, and the name has often been cited as a synonym for *L. ceranoides* (Prud'homme van Reine *et al.* 1994). The lectotype collection



Figs 47–55. *Liagora tetrasporifera* Børgeesen.

Fig. 47. Detail of assimilatory filament with straight 3-celled carpopogonial branch (arrow), borne laterally on the distal portion of the supporting cell (TFC Phyc. 7825).

Fig. 48. Carpopogonial branch with the first transverse division of the carpopogonium (arrowhead) and sterile filaments growing from adjacent cells (arrows) (TFC Phyc. 7825).

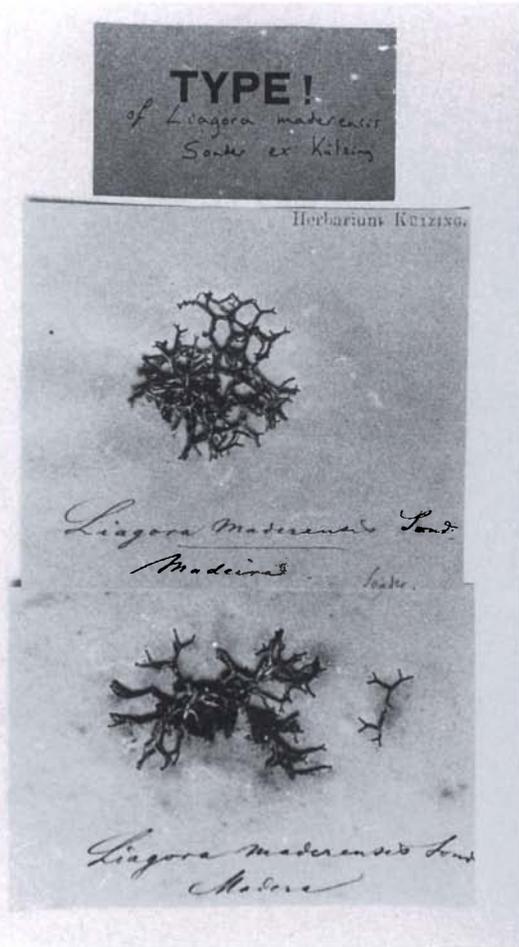
Figs 49–51. Early stages in the growth of the lax gonimoblast (double arrows) with profuse formation of sterile filaments (arrows) (TFC Phyc. 8471).

Fig. 52. Mature carposporophyte showing lax gonimoblast filaments intermingled with sterile filaments (arrows). Note quadripartite carposporangia (arrowheads) ending gonimoblast filaments (TFC Phyc. 7825).

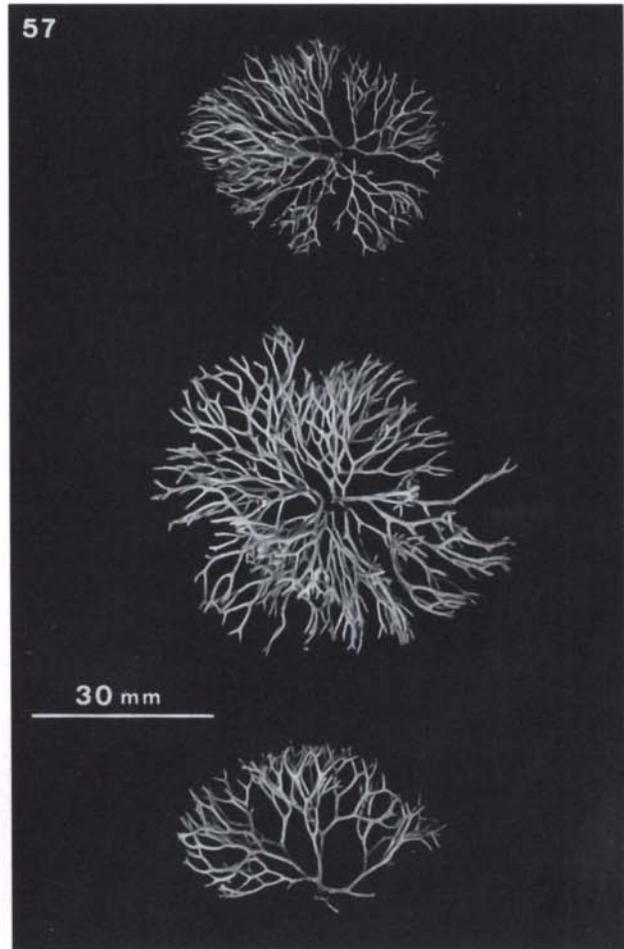
Fig. 53. Detail of gonimoblast filaments with immature and mature quadripartite carposporangia (arrows) (TFC Phyc. 8471).

Figs 54, 55. Portions of outer cortical filaments bearing spermatangia (arrows) (TFC Phyc. 8469).

56



57



Figs 56, 57. *Liagora maderensis* Kützing.

Fig. 56. Lectotype collection (L).

Fig. 57. Habit of recently collected specimens in the Canary Islands (TFC Phyc. 8472).

of *L. maderensis* is housed at L and consists of two small plants (to 32 mm long) (Fig. 56) that are dichotomously branched with wide angles. Anatomically, it presents medullary filaments 20–61 μm broad and rhizoidal filaments 6–12 μm broad; the cortical assimilatory filaments, 165–255 μm long and up to 7 times dichotomously branched, consist of cylindrical proximal cells 9–15 μm broad and 38–48 μm long, becoming shorter upwards and ending in ovoid cells, 5–7 μm broad and 10–12 μm long. Strongly curved four-celled carpogonial branches, c. 12 μm broad, arranged on the middle of the supporting cells, are evident in the type material. A compact mature carposporophyte examined is surrounded by a well developed involucre and measures c. 300 μm in diameter in surface view. Spermatangia were not observed. The Canarian collection is in close agreement with the type material.

Prud'homme van Reine *et al.* (1994) examined two isotype specimens housed at W and considered this taxon synonymous with *Liagora valida*. Nevertheless, the lectotype specimens differ remarkably from *L. valida* in having broader medullary filaments, a strongly curved carpogonial branch and a compact gonimoblast surrounded by a conspicuous involucre. In habit, *L. maderensis* is close to some small specimens of *L. viscida* but it is differentiated anatomically by the longer

assimilatory filaments, the strongly curved carpogonial branch and the compact carposporophyte. Recent collections from Azores housed at L and identified as *L. divaricata* Tseng are misidentifications of *L. maderensis* (Afonso-Carrillo, unpublished observations). The relationship between *L. divaricata* and *L. maderensis* needs to be investigated.

Liagora valida Harvey 1853: 38

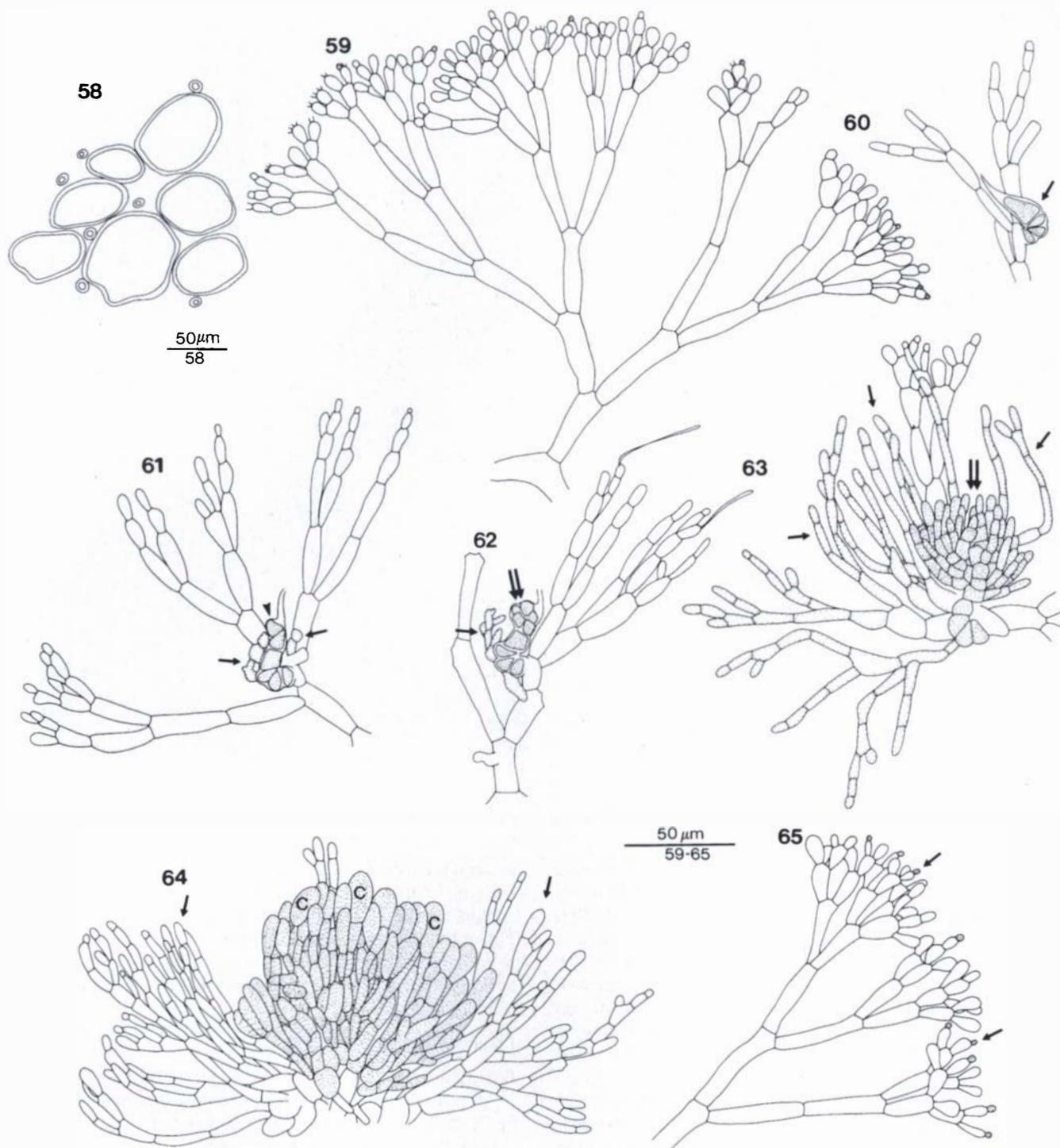
Børgesen 1915: 70, figs 71–75; Taylor 1928: 137; pl. 30, figs 7, 11; Abbott 1945: 160, figs 12–13; Taylor 1960: 327, pl. 43, fig. 2; Abbott & Yoshizaki 1982: 9, figs 1–16.

LECTOTYPE: TCD, leg. W. H. Harvey.

TYPE LOCALITY: Sand Key, Florida.

DISTRIBUTION: Widespread in warm temperate and tropical seas throughout the world. Eastern Atlantic: Morocco, Canary Islands (El Hierro, Tenerife, Gran Canaria and Fuerteventura) and Cape Verde Islands.

REPRESENTATIVE SPECIMENS: EL HIERRO: El Verodal (Rojas & Afonso-Carrillo, 16.vi.1992; TFC Phyc. 8477, 8497). TENERIFE: Bajamar (Kvaternik, 27.vi.1993; TFC Phyc. 8487). Igueste (Kvaternik, 27.vi.1993; TFC Phyc. 8487). Roque de Dentro, Anaga (Gil-Rodríguez *et al.*, 12.viii.1982; TFC Phyc. 690). El Médano (Reyes, 08.v.1992; TFC Phyc. 7373). GRAN CANARIA:



Figs 58–65. *Liagora maderensis* Kützing (TFC Phyc. 8472).

Fig. 58. Detail of transverse section of medulla, showing thick medullary cells intermingled with thin rhizoidal cells.

Fig. 59. Assimilatory filament.

Fig. 60. Detail of assimilatory filament with curved 4-celled carpoogonial branch (arrow), borne laterally on the middle of the supporting cell.

Fig. 61. Carpoogonial branch showing the first divisions of the carpoogonium (arrowhead) and sterile filaments growing from adjacent cells (arrows).

Figs 62, 63. Successive stages in the growth of the gonimoblast (double arrows) with profuse formation of sterile filaments (arrows).

Fig. 64. Mature carposporophyte showing gonimoblast filaments and carposporangia (C), surrounded by involucre filaments (arrows).

Fig. 65. Assimilatory filament bearing terminal spermatangia (arrows).

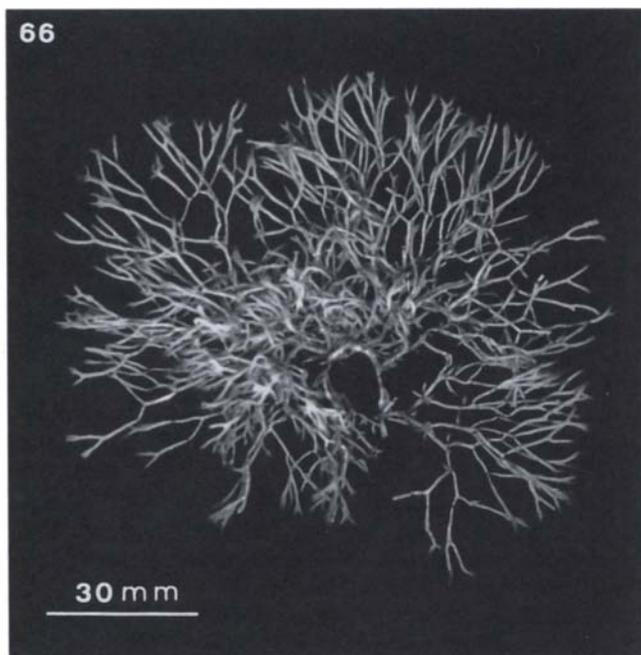


Fig. 66. *Liagora valida* Harvey. Habit of a recently collected specimen in the Canary Islands (TFC Phyc. 8497).

Las Canteras (González, 09.ii.1983; TFC Phyc. 5419). FUERTEVENTURA: Gran Tarajal (Gil-Rodríguez & Afonso-Carrillo, 02.v.1980; TFC Phyc. 2464).

HABITAT: *Liagora valida* has been found growing epolithically and also as an epiphyte on the rhizomes of the seagrass *Cymodocea nodosa*. It has been collected in the subtidal to 6 m depth, usually in areas of moderate water movement.

HABIT AND VEGETATIVE STRUCTURE: Plants erect, whitish, to 90 mm high, heavily calcified, sometimes cracked at dichotomies; axes terete, c. 1 mm wide, 5–10 times subdichotomously to dichotomously branched, 3–12 mm between dichotomies (Fig. 66); adventitious branches not observed. Medullary filaments 13–36 μm broad, intermingled with rhizoidal filaments 6–12 μm broad (Fig. 67). Cortical assimilatory filaments 240–410 μm long, 4–7 times dichotomously branched (Fig. 68), rarely with terminal clustered trichotomies at the ends of the filaments, cells of the assimilatory filaments, cylindrical, 7–12 \times 31–34 μm at the base of the filaments, becoming shorter and oval upwards, with oval or pyriform apical cells, 5–7 \times 9–12 μm (Fig. 68); rhizoidal filaments common, arising from the basal cells of the assimilatory filaments.

CARPOGONIAL BRANCH AND CARPOSPOROPHYTE: Plants monoecious. Carpogonial branches three- to four-celled, straight or slightly curved, c. 12 μm broad, arranged laterally on the distal portion of the supporting cell, at the middle portion of the assimilatory filaments (Fig. 69). After presumed fertilization involucre filaments arise from the cells adjacent, above and below the supporting cell (Figs 70–74). Simultaneously the carpogonium divides transversely (Fig. 70), the upper cell continues dividing obliquely (Figs 71–74), producing lax gonimoblast filaments morphologically similar to sterile filaments, eventually producing terminal carposporangia 5–8 \times 6–15 μm (Fig. 75). Mature carposporophytes measure

200–300 μm in diameter in surface view and show gonimoblast filaments intermingled with sterile filaments (Fig. 75). Fusions between the cells of the carpogonial branch after fertilization were not observed.

SPERMATANGIA: Spermatangia ovoid, 2–3 μm broad, 1–3 occurring on small spermatangial mother cells formed on terminal cells of the assimilatory filaments (Fig. 76).

REMARKS: *Liagora valida* seems to be a rare species in the Canary Islands, where has been observed from late winter to summer. In habit, it may be confused with *L. canariensis*, *L. tetrasporifera* or *L. maderensis*, but it is differentiated anatomically by the morphology of the assimilatory filaments and the characteristic carposporophyte with intermingled sterile involucre filaments and gonimoblast filaments.

Liagora ceranoides Lamouroux 1816: 239

Taylor 1928: 135, pl. 21, fig. 7, pl. 32, fig. 6, pl. 33, figs 4–5; Abbott 1945: 156, figs 8–9; Desikachary & Balakrishna 1957: 460, figs 15–27; Taylor 1960, 326, pl. 43, fig. 1, pl. 45, fig. 1.

HOLOTYPE: CN Herb. Lamouroux (Abbott 1990a: fig. 12).

TYPE LOCALITY: St Thomas; Virgin Islands, Western Atlantic.

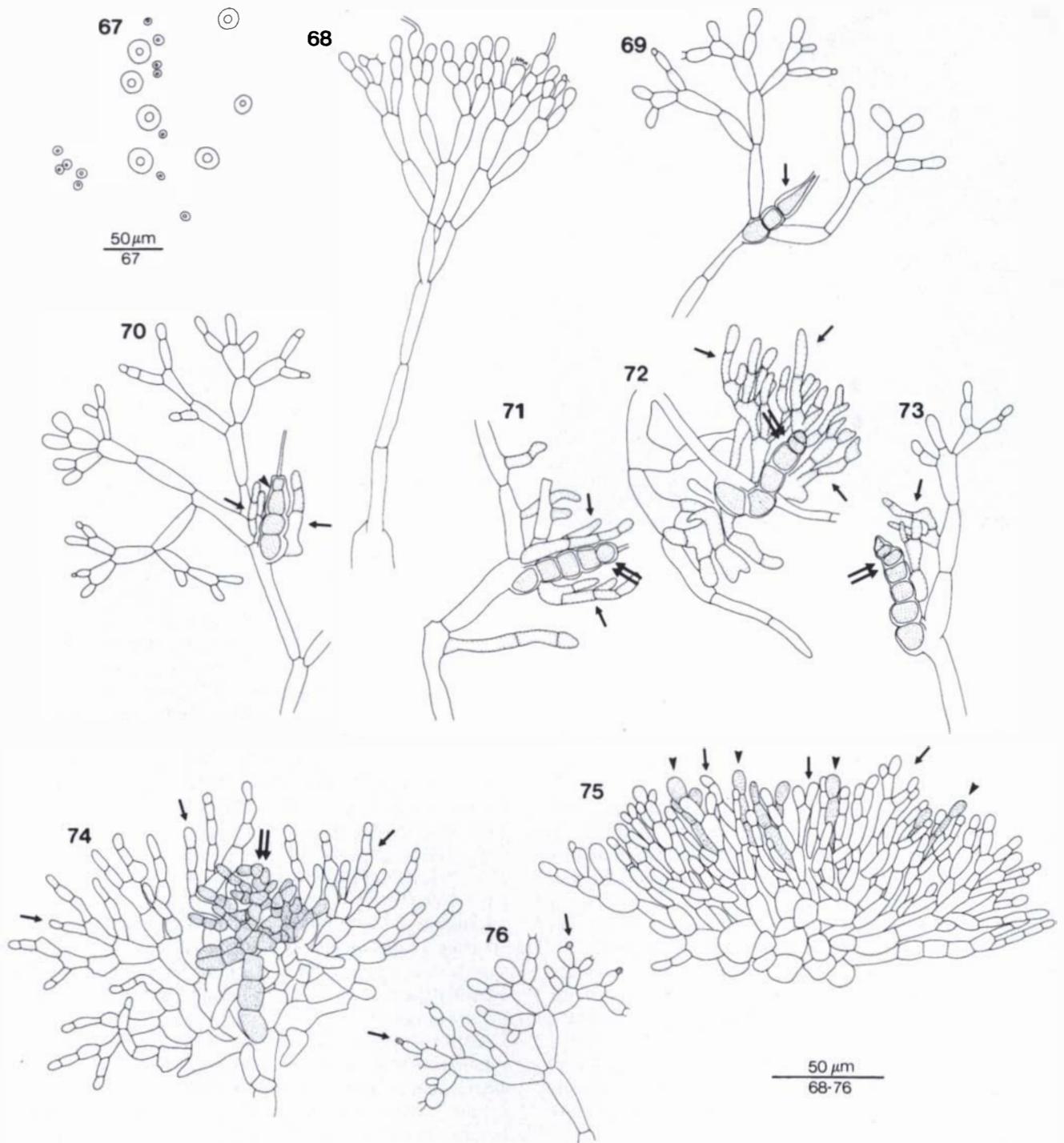
DISTRIBUTION: Widespread in warm temperate and tropical seas throughout the world. Eastern Atlantic: Western Mediterranean, Madeira, Salvage, Canaries (Tenerife, Gran Canaria and Lanzarote) and Cape Verde Islands.

REPRESENTATIVE SPECIMENS: TENERIFE: Bajamar (Kvaternik, 20.vi.1993; TFC Phyc. 8485, 12.vi.94; TFC Phyc. 8833). Punta Hidalgo (*Elejabeitia*, 02.vii.1991; TFC Phyc. 6839). Las Eras (*Guadalupe*, 26.vii.1993; TFC Phyc. 8486). El Médano (*Reyes & Afonso-Carrillo*, 08.v.1992; TFC Phyc. 7823, 8456), (*Sansón & Reyes*, 16.v.1992; TFC Phyc. 8466). Los Cristianos (*Gil-Rodríguez*, v.1972; TFC Phyc. 1347). GRAN CANARIA: Las Canteras (González, vii.1974; TFC Phyc. 1217, 05.vi.1985; TFC Phyc. 5470), (*Kvaternik & Lanzadera*, 06.iv.1993; TFC Phyc. 8481). LANZAROTE: Arrecife (*Gil-Rodríguez & Hernández*, 26.x.1991; TFC Phyc. 8464), (*Rojas & Ibeas*, 07.v.1993; TFC Phyc. 8506).

HABITAT: *Liagora ceranoides* has been found growing epolithically and as an epiphyte on the rhizomes of the seagrass *Cymodocea nodosa*. It has been collected from the lower intertidal pools to 5 m depth, usually in areas of moderate water movement.

HABIT AND VEGETATIVE STRUCTURE: Plants erect, rose-coloured with darker tips, to 80 mm high, moderately calcified, except at the tips, smooth and dusty surface; axes terete, c. 1 mm wide, dichotomously to fastigiately branched, up to 10 mm between dichotomies (Fig. 77); dichotomously branched adventitious branches relatively common. Medullary filaments 20–72 μm broad, intermingled with rhizoidal filaments 7–10 μm broad (Fig. 78). Cortical assimilatory filaments 156–216 μm long, 3–5 times irregularly dichotomously branched (Fig. 79); cells of the assimilatory filaments oval-elongate, 7–10 \times 28–36 μm , becoming gradually shorter, the uppermost nearly spherical, 4–10 μm broad, forming crowded terminal clusters (Fig. 79); elongate, branched rhizoidal filaments commonly produced from the basal cells of assimilatory filaments (Fig. 79).

CARPOGONIAL BRANCH AND CARPOSPOROPHYTE: Plants monoecious. Carpogonial branches three- to four-celled, slightly



Figs 67–76. *Liagora valida* Harvey (TFC Phyc. 8497).

Fig. 67. Detail of transverse section of medulla, showing thick medullary cells intermingled with thin rhizoidal cells.

Fig. 68. Assimilatory filament.

Fig. 69. Detail of assimilatory filament with straight 3-celled carpoogonial branch (arrow), borne laterally on the distal portion of the supporting cell.

Fig. 70. Carpoogonial branch showing the first transverse division of the carpoogonium (arrowhead) and sterile filaments growing from adjacent cells (arrows).

Figs 71–74. Successive stages in the growth of the gonimoblast (double arrows) with profuse formation of sterile filaments (arrows).

Fig. 75. Mature carposporophyte showing lax gonimoblast filaments intermingled with sterile filaments (arrows). Note terminal carposporangia (arrowheads).

Fig. 76. Portion of outer cortical filament bearing spermatangia (arrows).

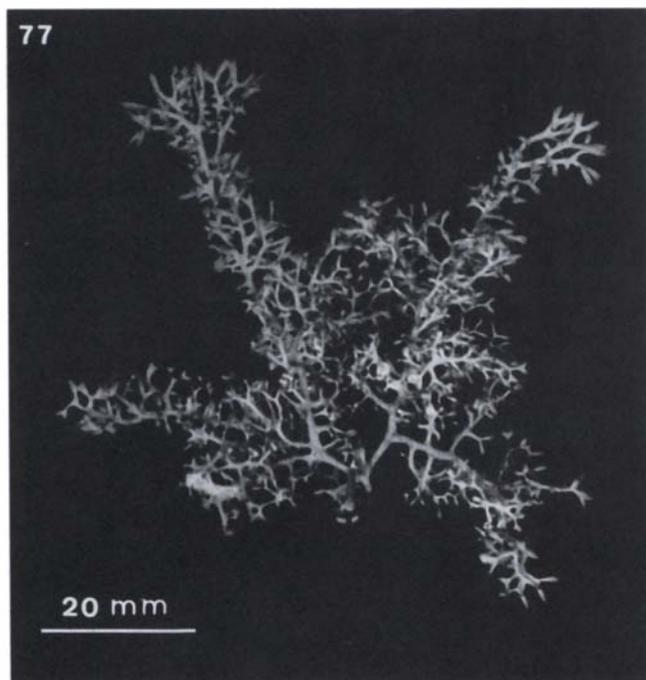


Fig. 77. *Liagora ceranoides* Lamouroux. Habit of a recently collected specimen in the Canary Islands (TFC Phyc. 8833).

curved, *c.* 10 μm broad, arranged laterally below the middle of the supporting cell, at the middle or lower portion of the assimilatory filaments (Fig. 80). After presumed fertilization the cells above, below and adjacent to the supporting cell form colourless involucre filaments (Figs 81, 82). Simultaneously, the gonimoblast initial divides, producing radiating, densely compact gonimoblast filaments (Figs 81–83) that produce terminal carposporangia, single or in short chains, 4–9 \times 7–17 μm (Figs 84, 85). The mature carposporophyte and the conspicuous involucre measure 240–300 μm in diameter in surface view. Cells of the carpogonial branch fuse after fertilization (Fig. 82).

SPERMATANGIA: Spermataegia spherical, *c.* 2.5 μm in diameter, 1–3 arranged on small spermataegial mother cells on the terminal cells of the assimilatory filaments (Fig. 86).

REMARKS: *Liagora ceranoides* seems to be a rare species in the Canary Islands, where it has been observed from late spring to summer. Plants examined were monoecious, although in the past *L. ceranoides* has always been described as dioecious. According to Abbott (1945, 1990a, b) some species of *Liagora* can be either monoecious or dioecious, and this variable character is not considered to be of diagnostic value. The species displays considerable variation in general habit, but it is consistent in anatomical and reproductive features. The abundant rhizoidal filaments produced from the basal cell of assimilatory filaments, the small gonimoblast and the relatively large diameter of the involucre, are useful features for species identification.

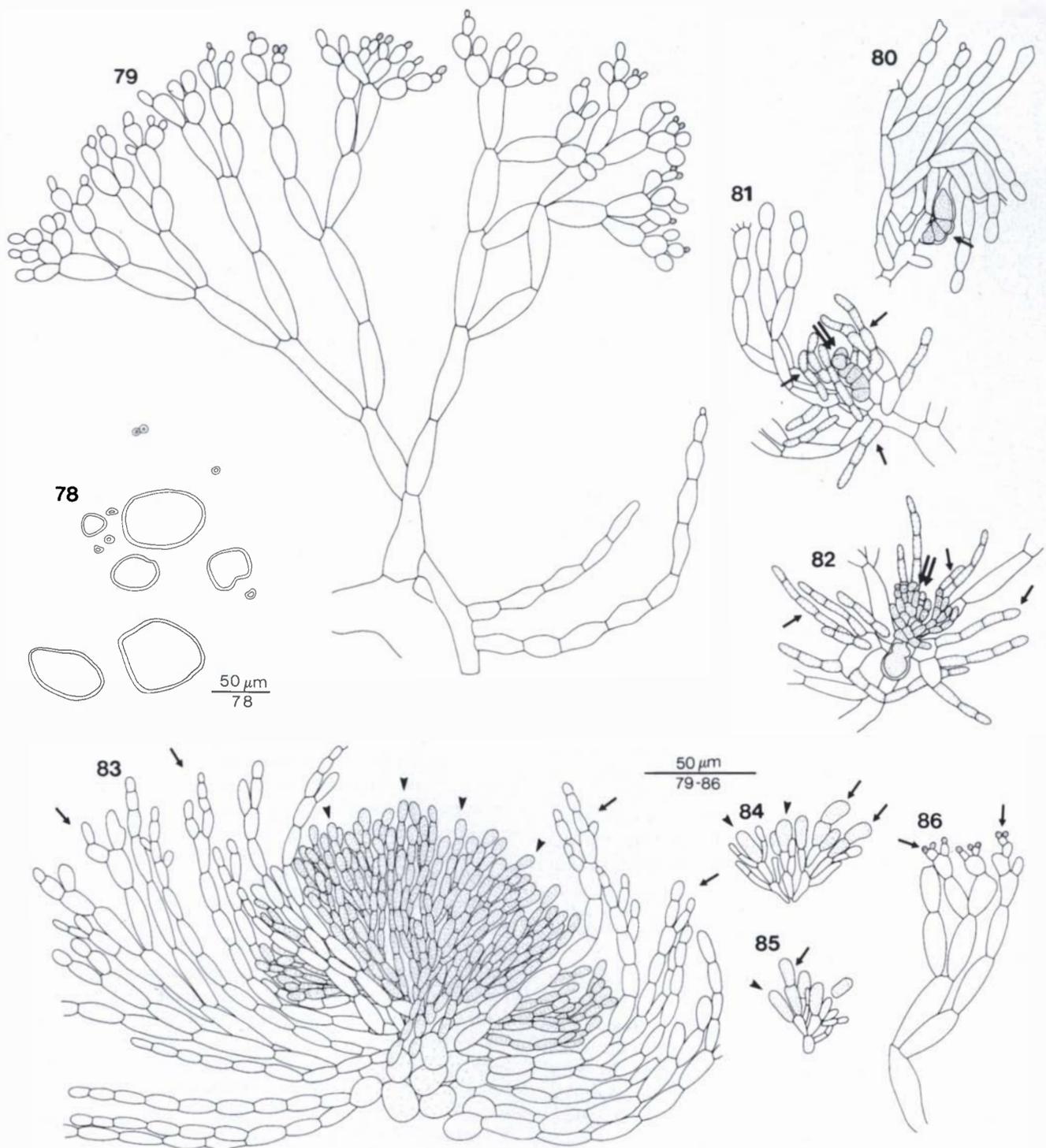
DISCUSSION

Species of *Liagora* are distributed in warm temperate and tropical waters in all oceans (Kraft 1989). Unfortunately, the

occurrence of many poorly known species prevents a general discussion about the distribution of the genus on a world scale. *Liagora* is represented in the Canary Islands by a large number of species with restricted distribution: *L. canariensis*, *L. distenta*, *L. gymnarthron*, *L. maderensis*, *L. tetrasporifera* and *L. viscida* are restricted to the Mediterranean Sea and nearby Atlantic coasts, and may be considered as endemics of the warm temperate NE Atlantic Region (Hoek 1984). The remaining species (*Liagora ceranoides* and *L. valida*) have a widespread world distribution (Abbott 1990a, b). Of the species previously reported from the Canary Islands, only *L. albicans* Lamouroux has not been confirmed in this study. The report of *L. albicans* (John *et al.* 1994) is based on old records of *L. decussata* Montague, considered by Abbott (1990a) as a later synonym of *L. albicans*. These records are doubtful because, according to Børgesen (1927: 53), the plants reported from Tenerife by Piccone (1884) as *L. decussata* are misidentifications of *L. canariensis*. A key to species of *Liagora* from the Canary Islands is presented in Appendix I.

Our observations have allowed the recognition of certain features considered sufficiently consistent to be of use in species delimitation. Morphology of cortical assimilatory filaments; shape, number of cells and relative position of the carpogonial branch on the supporting cell; and post-fertilization characters, together with the appearance of the mature carposporophyte are the most consistent features observed. The occurrence of a close correlation between morphology of assimilatory filaments and reproductive structures (carpogonial branches and carposporophytes) has a high practical value, and permits the identification of immature or male specimens in the dioecious species. Other vegetative features, such as habit or dimensions of medullary filaments, vary considerably and appear less useful for diagnostic purposes. Some Canarian species of *Liagora* present unique features useful as specific characters. *L. ceranoides* has long, branched rhizoidal filaments produced from the basal cell of assimilatory filaments, and *L. canariensis* presents spermataegia grouped in dense heads.

According to Kraft (1989), *Liagora* has generally been characterized by the following features: (1) carpogonial branch three to five-celled, curved, borne laterally on a mid-cortical supporting cell and after fertilization a fusion cell is formed by cells of the carpogonial branch; (2) gonimoblast compact, with densely aggregated, short-celled filaments; and (3) production of sterile subsidiary filaments ('involucre filaments') from several cells adjacent to the carpogonial branch. However, Kraft (1989), examining the criteria most widely used for generic characterization in the Liagoraceae, showed that the genus is particularly inconsistent with regard to its defining characters. Our observations on the species from the Canary Islands confirm the difficulties found by Kraft (1989). Curved carpogonial branches occur in most of the species examined including *L. viscida*, the lectotype species of the genus; however, *L. canariensis* and *L. valida* present straight or slightly curved carpogonial branches, and they are always straight in *L. tetrasporifera*. Fusion cells are formed in *L. viscida*, *L. tetrasporifera* and *L. ceranoides*, but in the rest of the species examined only slightly wide pit-connections were observed. The variability in the degree of curvature of the carpogonial branch and in the morphology of the fusion



Figs 78–86. *Liagora ceranoides* Lamouroux.

Fig. 78. Detail of transverse section of medulla, showing thick medullary cells intermingled with thin rhizoidal cells (TFC Phyc. 8506).

Fig. 79. Assimilatory filament (TFC Phyc. 8456).

Fig. 80. Detail of assimilatory filament with curved 4-celled carposporangial branch (arrow), borne laterally on the middle of the supporting cell (TFC Phyc. 8506).

Figs 81, 82. Successive stages in the growth of the gonimoblast (double arrows) with profuse formation of sterile filaments (arrows) (TFC Phyc. 8506).

Fig. 83. Mature carposporophyte showing gonimoblast filaments and carposporangia (arrowheads), surrounded by involucrel filaments (arrows) (TFC Phyc. 8456).

Figs 84, 85. Details of gonimoblast filaments showing terminal carposporangia, single (arrowheads) or in short rows (arrows) (TFC Phyc. 8464).

Fig. 86. Portion of outer cortical filament bearing spermatangia (arrows) (TFC Phyc. 8456).

cell supports Kraft's (1989) contention that these features alone may not be useful characters.

Liagora has generally been characterized as forming compact gonimoblasts, but rather diffuse carposporophytes were reported by Guiry (1990) in *L. harveyana* Zeh and in *L. viscida*, *L. tetrasporifera* and *L. valida* from the Canary Islands. Variation from somewhat loosely constructed carposporophytes to the more typical compact gonimoblasts was reported by Kraft (1989) as an obscure feature needing investigation.

Finally, all species examined showed sterile subsidiary filaments arising from cells adjacent to the carpogonial branch, although with different degrees of development. In *L. distenta* these filaments were only placed below the gonimoblast; in *L. canariensis*, *L. ceranoides*, *L. gymnarthron* and *L. maderensis* surrounding the gonimoblast, and in *L. viscida*, *L. tetrasporifera* and *L. valida* surrounding and intermingled with a lax gonimoblast.

At present, the features that characterize the genus *Liagora* are poorly defined, partly due to limited and contradictory information on the post-fertilization development of *Liagora viscida*, the lectotype species. Our observations on abundant fresh material collected in the Canary Islands have shown that the post-fertilization changes agree only in part with the descriptions by Kylin (1930) and Desikachary & Balakrishnan (1957). As seen in the present study, the carposporophyte of *L. viscida* has numerous and very well developed involucre filaments that surround and intermingle with a lax outwardly oriented filamentous gonimoblast. The vegetative cortical filaments described by Kylin (1930) as intermingling with the gonimoblast could be sterile involucre filaments.

The development in *Liagora viscida* of a lax gonimoblast, contrary to the compact gonimoblast used to characterize the genus *Liagora*, may have taxonomic implications. The degree of diffuseness in the carposporophyte has been used as an useful taxonomic feature at the generic level in the Liagoraceae. In *Cumagloia* Setchell et Gardner (Desikachary 1962), *Dermonema* Greville (Yoshizaki 1978), *Dotyophycus* Abbott (Abbott & Yoshizaki 1981), *Patenocarpus* Yoshizaki (Yoshizaki 1987) and *Yamadaella* Abbott (Abbott 1970), carposporophytes are very diffuse with gonimoblast filaments growing laterally and passing through surrounding cortical filaments. Less diffuse carposporophytes are present in *Cylindraxix* Kraft (Kraft 1989) and *Liagoropsis* Yamada (Doty & Abbott 1964) although in both genera gonimoblast filaments are outwardly oriented and lack sterile subsidiary filaments. *L. viscida* has a rather diffuse carposporophyte that allows the involucre filaments to intermingle with the outwardly oriented gonimoblast filaments.

It is likely that the species presently placed in *Liagora* could be segregated to different genera. Kraft (1989) remarked that the genus as presently delineated seems to be a continuum of morphology from somewhat loosely constructed carposporophytes to the more typically compact gonimoblasts. Our observations on post-fertilization development in species of *Liagora* from the Canary Islands permit differentiation of at least two distinct groups of species on the basis of the following carposporophyte morphologies: (1) carposporophyte lax, sterile subsidiary filaments, surrounding and intermingling with the gonimoblast filaments (*Liagora viscida*, *L. tetrasporifera* and *L. valida*); and (2) carposporophyte compact, sterile subsidiary filaments placed below the gonimo-

blast or forming a very conspicuous involucre (*Liagora canariensis*, *L. ceranoides*, *L. distenta*, *L. gymnarthron* and *L. maderensis*).

The taxonomic significance of these differences is difficult to assess at present, in the absence of carposporophyte information on numerous poorly known species now accepted as belonging to *Liagora*. It is possible that *Liagora* will have to be reserved for species with the features observed in *L. viscida*, and species with a compact gonimoblast will have to be segregated into a different genus. Further studies are needed before this matter can be firmly settled.

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REFERENCES

- ABBOTT I.A. 1945. The genus *Liagora* (Rhodophyceae) in Hawaii. *Occasional Papers of Bernice P. Bishop Museum* **18**: 145-169.
- ABBOTT I.A. 1970. *Yamadaella*, a new genus in the Nemaliales (Rhodophyta). *Phycologia* **9**: 115-123.
- ABBOTT I.A. 1990a. A taxonomic and nomenclatural assessment of the species of *Liagora* (Rhodophyta, Nemaliales) in the herbarium of Lamouroux. *Cryptogamie, Algologie* **11**: 111-136.
- ABBOTT I.A. 1990b. A taxonomic assessment of the species of *Liagora* (Nemaliales, Rhodophyta) recognized by J. Agardh, based upon studies of type specimens. *Cryptogamic Botany* **1**: 308-322.
- ABBOTT I.A. & YOSHIZAKI M. 1981. A second species of *Dotyophycus* (Nemaliales, Rhodophyta) that emphasizes the distinctness of a diffuse gonimoblast. *Phycologia* **20**: 222-227.
- ABBOTT I.A. & YOSHIZAKI M. 1982. *Liagora valida* Harvey (Rhodophyta) from Sand Key, Florida. *Japanese Journal of Phycology* **30**: 9-14.
- AFONSO-CARRILLO J. & SANSÓN M. 1989. *Clave ilustrada para la determinación de los macrófitos marinos de las Islas Canarias*. Departamento de Biología Vegetal La Laguna. 55 pp.
- AGARDH C.A. 1822. *Species Algarum I*. Stockholm. 396 pp.
- ATHANASIADIS A. 1987. *A Survey of the Seaweeds of the Aegean Sea with Taxonomic Studies on Species of the Tribe Antithamnieae (Rhodophyta)*. University of Gothenburg. Department of Marine Botany. 709 pp.
- BØRGENSEN F. 1915. The marine algae of the Danish West Indies, III. Rhodophyceae. *Dansk Botanisk Arkiv* **3**: 1-80.
- BØRGENSEN F. 1927. Marine algae from the Canary Islands, specially from Tenerife and Gran Canaria. III. Rhodophyceae. Pt. 1: Bangiales and Nemaliales. *Kongelige Danske Videnskabernes Selskab Biologiske Meddelelser* **6**(6): 1-97.
- BØRGENSEN F. 1932. A revision of Forsskål's algae mentioned in Flora Aegyptiaco-Arabica and found in his herbarium in the Botanical museum of the University of Copenhagen. *Dansk Botanisk Arkiv* **8**: 1-14.

- COPPEJANS E. 1983. *Iconographie d'algues Méditerranéennes*. Bibliotheca Phycologica 63. J. Cramer. 317 pp.
- COUTÉ A. 1971. Sur le cycle morphologique du *Liagora tetrasporifera* comparé à celui du *Liagora distenta* (Rhodophycées, Némaliales, Helminthocladiacées). *Compte Rendue Hebdomadaire, Séances de l'Académie des Sciences, Paris, Série D*, 273: 626–629.
- COUTÉ A. 1976. Etude comparative des cycles du *Liagora tetrasporifera* Borg. et du *Liagora distenta* (Mert.) C. Ag. en culture. *Revue Algologique* ns 11: 273–297.
- DESIKACHARY T.V. 1962. *Cumagloia* Setchell et Gardner and *Dermonema* (Grev.) Harv. *Journal of the Indian Botanical Society* 41: 132–147, pl. 7.
- DESIKACHARY T.V. & BALAKRISHNAN M.S. 1957. Post-fertilisation development in *Liagora*. *Journal of the Indian Botanical Society* 36: 457–471, pl. 17.
- DOTY M.S. & ABBOTT I.A. 1964. Studies in the Helminthocladiaceae, III. *Liagoropsis*. *Pacific Science* 18: 441–452.
- FAN K.C. & WANG Y.C. 1974. Studies on the marine algae of Hsisha Islands, China. I. *Ganonema* gen. nov. *Acta Phytotaxonomica Sinica* 12: 489–493.
- FORSSKÅL P. 1795. *Flora Aegyptiaco-Arabica*. Hauniae (Copenhagen). 219 pp.
- GALLARDO T., GOMEZ GARRETA A., RIBERA M.A., ALVAREZ M. & CONDE F. 1985. *A Preliminary Checklist of Iberian Benthic Marine Algae*. Real Jardín Botánico. Madrid. 83 pp.
- GIL-RODRÍGUEZ M.C. & AFONSO-CARRILLO J. 1980. *Catálogo de las algas marinas bentónicas (Cyanophyta, Chlorophyta, Phaeophyta y Rhodophyta) para el Archipiélago Canario*. Aula de Cultura de Tenerife. 47 pp.
- GUIRY M.D. 1990. The life history of *Liagora harveyana* (Nemaliales, Rhodophyta) from South-eastern Australia. *British Phycological Journal* 25: 353–362.
- HAMEL C. 1930. Floridées de France. VI. *Revue Algologique* 5: 61–109.
- HARVEY W.H. 1853. *Nereis Boreali-Americana*. II. *Smithsonian Contributions to Knowledge* 5(5): 1–138.
- HOLMGREN P.K., HOLMGREN N.H. & BARNETT L.C. 1990. *Index Herbariorum, Pt 1: The Herbaria of the World*. 8th edn. New York Botanical Garden, Bronx, New York. x+693 pp. [*Regnum Vegetabile*, vol. 120].
- HUISMAN J.M. & KRAFT G.T. 1994. Studies of the Liagoraceae (Rhodophyta) of Western Australia: *Glotrichus fractalis* gen. et sp. nov. and *Ganonema helminthaxis* sp. nov. *European Journal of Phycology* 29: 73–85.
- JOHN D.M., LAWSON G.W., PRICE J.H., PRUD'HOMME VAN REINE W.F. & WOELKERLING Wm J. 1994. Seaweeds of the western coast of tropical Africa and adjacent islands: a critical assessment. IV. Rhodophyta (Florideae) 4. Genera L–O. *Bulletin of the British Museum (Natural History), Botany Series* 24(1): 49–90.
- KRAFT G.T. 1989. *Cylindraxxis rotundatus* gen. et sp. nov. and its generic relationships within the Liagoraceae (Nemaliales, Rhodophyta.) *Phycologia* 28: 275–304.
- KÜTZING F.T. 1858. *Tabulae phycologicae oder Abbildungen der Tange* 8. Nordhausen. ii+48 pp+100 pl.
- KYLIN H. 1930. Über die Entwicklungsgeschichte der Florideen. *Lunds Universitets Årsskrift* 2, 26: 1–104.
- LAMOUREUX J.V.F. 1812. Extrait d'un mémoire sur la classification des Polypiers coralligènes non entièrement pierreux. *Nouveau Bulletin des Sciences, par la Société Philomatique de Paris* 3: 181–188.
- LAMOUREUX J.V.F. 1816. *Histoire des polypiers coralligènes flexibles, vulgairement nommées zoophytes*. Poisson, Caen. lxxxiv+560 pp., 19 pls.
- MIRANDA F. 1931. Sobre las algas y cianofíceas del Cantábrico, especialmente de Gijón. *Trabajos del Museo Nacional de Ciencias Naturales, Serie Botánica* 25: 1–106.
- PICCONE A. 1884. *Crociera del Corsaro alle Isole Madera e Canarie del capitano Enrico d'Albertis. Alghe*. Genova. 60 pp.
- PRUD'HOMME VAN REINE W.F., HAROUN R.J. & AUDIFFRED P.A.J. 1994. A reinvestigation of Macaronesian seaweeds as studied by A. Piccone with remarks on those studied by A. Grunow. *Nova Hedwigia* 58: 67–121.
- ROTH A.G. 1806. *Catalecta botanica* 3. Lipsiae (Leipzig). vii+350 pp+12 pl.
- SOUTH G.R. & TITTLER I. 1986. *A Checklist and Distributional Index of the Benthic Marine Algae of the North Atlantic Ocean*. Huntsman Marine Laboratory and British Museum (Natural History), St Andrews and London. 76 pp.
- TAYLOR W.R. 1928. The marine algae of Florida, with special reference to the Dry Tortugas. *Bibliotheca Phycologica* 2: 1–219. Reprint 1967.
- TAYLOR W.R. 1960. *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas*. University of Michigan Press, Ann Arbor. ix+(iii)+870 pp.
- VAN DEN HOEK C. 1984. World-wide latitudinal and longitudinal seaweed distribution patterns and their possible causes, as illustrated by the distribution of Rhodophytan genera. *Helgoländer Meeresuntersuchungen* 38: 227–257.
- YOSHIZAKI M. 1978. Morphology and taxonomy of the Japanese representatives of the Nemaliales. 2. Thallus structure and reproductive organs of *Dermonema dichotomum* and *D. pulvinatum*. *Journal of Japanese Botany* 53: 17–25.
- YOSHIZAKI M. 1987. The structure and reproduction of *Patencarpus paraphysiferus* gen. et sp. nov. (Dermonemataceae, Nemaliales, Rhodophyta). *Phycologia* 26: 47–52.

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APPENDIX I

Key to the species of *Liagora* from the Canary Islands

- (1) Carposporophyte rather diffuse, sterile subsidiary filaments surrounding and intermingling with the gonimoblast filaments 2
- (1) Carposporophyte compact, sterile subsidiary filaments placed below or forming a very conspicuous involucre 4
- (2) Cortical assimilatory filaments short, less than 150 μm long *L. viscida*
- (2) Cortical assimilatory filaments longer, more than 150 μm long 3
- (3) Cortical assimilatory filaments 180–240 μm long; carpogonial branch 3-celled, straight, borne on the distal portion of the supporting cell; quadripartite carposporangia present *L. tetrasporifera*
- (3) Cortical assimilatory filaments 240–410 μm long; carpogonial branch 3 or 4-celled, slightly curved, borne below the middle of the supporting cell; quadripartite carposporangia absent *L. valida*
- (4) Cortical assimilatory filaments short, less than 120 μm long; sterile filaments persist under the gonimoblast and do not surround the mature carposporophyte *L. distenta*
- (4) Cortical assimilatory filaments longer, more than 120 μm long; mature carposporophyte surrounded by a well developed involucre 5
- (5) Cortical assimilatory filaments 300–450 μm long; spermatangia forming quite dense heads *L. canariensis*

- (5) Cortical assimilatory filaments shorter; spermatangia in digitate clusters 6
 - (6) Long and branched rhizoidal filaments produced from the basal cell of assimilatory filaments very common; carpogonial branch slightly curved; carposporangia single or in short chains *L. ceranoides*
 - (6) Long and branched rhizoidal filaments absent; carpogonial branch strongly curved; carposporangia single 7
- (7) Cortical assimilatory filaments short, 132–192 μm long; carposporangia 10–12 μm broad and 21–30 μm long; mature carposporophyte and involucre less than 250 μm in diameter in surface view *L. gymnarthron*
- (7) Cortical assimilatory filaments longer, 150–360 μm long; carposporangia smaller, 7–10 μm broad and 14–22 μm long; mature carposporophyte and involucre more than 250 μm in diameter in surface view *L. maderensis*