

Lomentaria benahoarensis (Lomentariaceae, Rhodophyta), a diminutive epiphytic new species from La Palma, Canary Islands (eastern Atlantic Ocean)

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Abstract

The marine red alga *Lomentaria benahoarensis* sp. nov. from the Canary Islands is described. Plants grow epiphytically on *Corallina elongata* forming turfs of creeping axes attached by lateral discoid holdfasts and erect axes up to 12 mm high. Erect axes are terete to slightly compressed, 200–300(–1000) µm broad, radially branched up to three orders, with laterals progressively thinner, constricted only at the bases of terminal axes. The cortex is three-layered with the outermost cortical cells arranged in a near-continuous surface layer. Medullary filaments form a loose network of narrow elongate cells, which bear secretory cells. Gametophytes are dioecious with spermatangia formed in continuous spermatangial sori; cystocarps are urceolate and ostiolate. Tetrasporangia are subspherical and formed in depressed rounded sori in slightly swollen regions in the middle of fertile terminal axes. The new species has no single unique feature, but differs from the other *Lomentaria* species by a distinctive combination of attributes. Closest related species to *Lomentaria benahoarensis* appear to be *L. corallicola*, *L. gracillima*, *L. monochlamydea*, *L. orcadensis*, *L. rawitscheri*, and *L. tenerrima*. Although all these species have a diminutive, decumbent habit and lack regular constrictions in axes, the number of cortical cell layers and the arrangement of outer cortical cells distinguish them.

Keywords: Canary Islands; *Lomentaria benahoarensis*; Lomentariaceae; Rhodophyta; Rhodymeniales.

Introduction

Although the marine algal flora of the Canary Islands is considered to be well-documented (Afonso-Carrillo and Sansón 1999, Haroun et al. 2002), recent studies have concluded that present knowledge is still incomplete, because the finding of new records and undescribed

species are relatively frequent (Afonso-Carrillo et al. 2006a,b, 2007, Sansón et al. 2006, Cassano et al. 2008, García-Jimenez et al. 2008, Gil-Rodríguez et al. 2009). The present account includes the description of a diminutive epiphytic new species of *Lomentaria*, collected from lower eulittoral habitats of La Palma, the Canary Islands.

Among the Lomentariaceae (Schneider and Wynne 2007), the genus *Lomentaria* Lyngbye (1819) currently includes erect or prostrate species with hollow mucilage-filled terete or compressed axes. The structure is multiaxial and the axis walls consist of 2–6 cortical cell layers lined inside with medullary filaments bearing inwardly directed secretory cells. Monostromatic septa are absent, but medullary filaments compact into a plug at constrictions and/or branch bases. The carpogonial branches are three-celled, most of the gonimoblast develops into carposporangia and the cystocarp protrudes outwards; the spermatangia are cut off from initials on cortical cells, and the tetrahedrally divided tetrasporangia, which originate terminally from cortical cells, are arranged in depressed sori (Kylin 1931, Lee 1978, Womersley 1996).

Species of *Lomentaria* have been defined by a combination of features: (1) external features, such as habit (erect from a single small holdfast, caespitose with prostrate and erect axes, or completely prostrate), shape of axes, occurrence of constrictions in axes, and branching pattern; (2) anatomical vegetative features, such as number of cell layers in the cortex and the arrangement of the outer cortical cells; and (3) reproductive features, such as morphology of the cystocarp and position and shape of tetrasporangial sori (Ercegovic 1956, Womersley 1996, Wynne 1998). Approximately 40 species are currently assigned to *Lomentaria* (Womersley 1996, Guiry and Guiry 2009), most of them from temperate to tropical seas in both hemispheres, where they grow epilithically or epiphytically from the lower eulittoral down to the deep sublittoral. Womersley (1996), Stegenga et al. (1997), Wynne (1998), and Kawaguchi et al. (2002) added new species recently. Among the 19 species known from the Atlantic Ocean and the Mediterranean Sea (Table 1), 11 were described from material collected in the Adriatic Sea or the Mediterranean Sea. In the Mediterranean basin, the genus *Lomentaria* is highly diversified, and only a few of these species also occur in the eastern Atlantic (Table 1). Three among the remaining species are based on materials from European localities, two from American localities, and one from South Africa. Finally, two species were originally described from localities in the Indian and Pacific Oceans (Table 1). From the Canary Islands, five species have been reported: *L. articulata* (Hudson) Lyngbye, *L. baileyana* (Harvey) Farlow, *L. chy-*

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Table 1 Distribution of Atlantic and Mediterranean species of *Lomentaria*.

| | Type locality | Distribution | References |
|---|--|--|--|
| <i>Lomentaria articulata</i> (Hudson) Lyngbye | Cornwall, England | NE Atlantic Ocean (from Scandinavia to Cameroon, Azores, Madeira, Salvage and Canaries), Mediterranean Sea | Newton (1931), Irvine and Guiry (1983) |
| <i>Lomentaria baileyana</i> (Harvey) Farlow | Peconic Bay, Long Island, New York, USA | NW Atlantic Ocean (from Maritimes to Brazil), NE Atlantic Ocean (Azores, Canaries, Mauritania) | Taylor (1957, 1960), Schneider and Searles (1991), Litter and Litter (2000) |
| <i>Lomentaria chlyocladie/ella</i> Funk | Gulf of Naples, Italy | NE Atlantic Ocean (Canary Islands), Mediterranean Sea | Funk (1955), Boudouresque (1974), Afonso-Carrillo et al. (2007) |
| <i>Lomentaria clavaeformis</i> Ercegovic | Jakuba Island, Croatia, Adriatic Sea | Mediterranean Sea | Ercegovic (1956), Furnari and Scammacca (1971), De Masi and Gargiulo (1981) |
| <i>Lomentaria clavellosa</i> (Turner) Gallon | Norfolk, England | NE Atlantic Ocean (from Scandinavia to Portugal), Mediterranean Sea | Irvine and Guiry (1983) |
| <i>Lomentaria clavellosa</i> var. <i>conferta</i> (Meneghini) J. Feldmann | Italy | NE Atlantic Ocean (Spain and Portugal), W Mediterranean Sea | Kützing (1865, as <i>Chondrothamnion confertum</i> Meneghini), Feldmann (1942), Ercegovic (1956), Boudouresque et al. (1977) |
| <i>Lomentaria compressa</i> (Kützing) Kyllin | Gulf of Naples, Italy | Mediterranean Sea | Kyllin (1931), Kützing (1843, 1849, 1865, as <i>Chondrosiphon compressus</i> Kützing), Funk (1927), Ercegovic (1956) |
| <i>Lomentaria corallicola</i> Børgesen | Kharg Island, Iran | NW Atlantic Ocean (Colombia and Brazil), Indian and Pacific Oceans | Børgesen (1939), Cribb (1983), Norris (1987) |
| <i>Lomentaria diffusa</i> Stegenga, Bolton et Anderson | Kraalbaai, Langebaan Lagoon, Cape Province, South Africa | SE Atlantic Ocean (South Africa) | Stegenga et al. (1997) |
| <i>Lomentaria ercegovicii</i> Verlaque, Boudouresque, Meinesz, Giraud et Marcot-Coqueugniot | Jabuka Island, Croatia, Adriatic Sea | Mediterranean Sea | Verlaque et al. (1977), Ercegovic (1956, as <i>Lomentaria tenera</i> Ercegovic) |
| <i>Lomentaria hakodatensis</i> Yendo | Hakodate, Hokkaido, Japan | NE Atlantic Ocean (France and Spain), W Mediterranean Sea, Pacific Ocean (N America, Asia and Pacific islands) | Lee (1978), Lee and West (1980), Cabioc'h and Magne (1987), Curriel et al. (2006) |
| <i>Lomentaria jabukae</i> Ercegovic | Jabuka Island, Croatia, Adriatic Sea | Adriatic Sea, W Mediterranean Sea | Ercegovic (1956) |
| <i>Lomentaria linearis</i> (Zanardini) Zanardini ex Kützing | Adriatic Sea | NE Atlantic Ocean (Canary Islands), Mediterranean Sea | Funk (1955), Ercegovic (1956) |

(Table 1 continued)

| | Type locality | Distribution | References |
|---|--------------------------------------|--|--|
| <i>Lomentaria orcadensis</i> (Harvey) F.S. Collins | Orkney, Scotland | NE Atlantic Ocean (from Scandinavia to Portugal), NW Atlantic Ocean (from Nova Scotia to North Carolina) | Taylor (1957), Irvine and Guiry (1983), Bárbara et al. (1996) |
| <i>Lomentaria rawitscheri</i> A.B. Joly | Itapeva, São Paulo State, Brazil | NW Atlantic Ocean (Cuba, Puerto Rico, Colombia and Brazil) | Joly (1957), Sazima (1979), Ballantine et al. (2002) |
| <i>Lomentaria subdichotoma</i> Ercegovic | Bisevo Island, Croatia, Adriatic Sea | NE Atlantic Ocean (Canary Islands), Adriatic Sea, W Mediterranean Sea | Ercegovic (1956), Ballesteros (1992), Ballesteros et al. (1992) |
| <i>Lomentaria tenerrima</i> (Esper) P.C. Silva | Trieste, Adriatic Sea | NE Atlantic Ocean (Senegal), Adriatic Sea, W Mediterranean Sea | Kylin (1931), Ercegovic (1956) as <i>Lomentaria firma</i> (J. Agardh) Kylin |
| <i>Lomentaria uncinata</i> Meneghini ex Zanardini | Venice, Adriatic Sea | Adriatic Sea, W Mediterranean Sea | Zanardini (1840), Kützing (1849, 1865, as <i>Chondrosiphon uncinatus</i> Kützing and <i>Chondrosiphon meneghinianus</i> Kützing) |
| <i>Lomentaria verticillata</i> Funk | Gulf of Naples, Italy | Adriatic Sea, W Mediterranean Sea | Funk (1955), Boudouresque (1974) |

locladiella Funk, *L. linearis* (Zanardini) Zanardini ex Kützing, and *L. subdichotoma* Ercegovic (Ballesteros et al. 1992, Afonso-Carrillo and Sansón 1999, Afonso-Carrillo et al. 2007). *Lomentaria benahoarensis* sp. nov. is now added as the first endemic species of the genus in the Canary Islands.

Materials and methods

Plants were collected at La Salemera, southeast of La Palma, Canary Islands (Figure 1). Liquid-preserved specimens were fixed in 4% formalin in seawater. Permanent slides were prepared from selected fragments stained in 1% aniline blue in distilled water, and mounted in a 50% Karo® corn syrup solution (Bestfoods, Englewood Cliffs, NJ, USA). Sections were made by hand with a razor blade. Camera lucida drawings were made with the aid of a Zeiss standard microscope (Zeiss, Berlin, Germany). Micrographs were taken using a Nikon Coolpix 4600 digital camera (Nikon, Tokyo, Japan) attached to a Zeiss compound microscope. Voucher herbarium specimens and slides have been lodged at TFC (Departamento de Biología Vegetal, Universidad de La Laguna, Canary Islands).

Results

Lomentaria benahoarensis sp. nov. (Figures 2–23)

Diagnosis *Plantae epiphyticae super Corallina elongata, caespitosae, praebentes axes prostratos multis lateralibus hapteronis discoidis adhaerentes et axes erecti usque 12 mm alti. Axes principales cylindrici ad parce compressos, usque 1000 µm crassi, sparsim et radiatim ramificati usque ordines 3, cum ramis lateralibus cylindricis et gradatim decrecentibus sine regularibus constrictionibus etsi cum basi constricta. Cortex tubularis cum tribus stratis cellularum, interius cellulis hyalinis, magnis, elongatis, ovalibus-oblongis (20–50 µm latis et 40–80 µm longis), stratum medium cellulis brevioribus (6–11 µm diametro), et exterius quasi continuum cellulis corticalibus ovodeis (3–5 µm diametro). Medulla filamentosa reticulatim et laxa cum cellulis tenuibus, elongatis, subcylindricis (3–7 µm diametro et 50–110 µm longis). Cellulae secretoriae e subsphaericis ad ovoideas-pyriformes usque 7–10 µm latae et 10–20 µm longae. Gametophyta dioica. Spermatangia super cellulas matrixales, spermatangiales elongatas in cortice exterius soris spermatangialibus continuis. Cystocarpia prominentia conspicue, urceolata (300–500 µm diametro et 350–600 µm longa) cum ostiolo visibili et carposporangia ovoidea (14–19 µm lata et 19–26 µm longa) Tetrasporangia subsphaeirica (40–60 µm diametro) tetraedrice divisa, soris orbicularibus depressis (120–180 µm diametro) in regionibus tenuiter tumidis in medio axium fertilium terminalium.*

Plants epiphytic on *Corallina elongata* Ellis et Solander forming turfs of creeping axes attached by many lateral discoid holdfasts and erect axes up to 12 mm long. Main erect axes terete to slightly compressed, up to 1000 µm

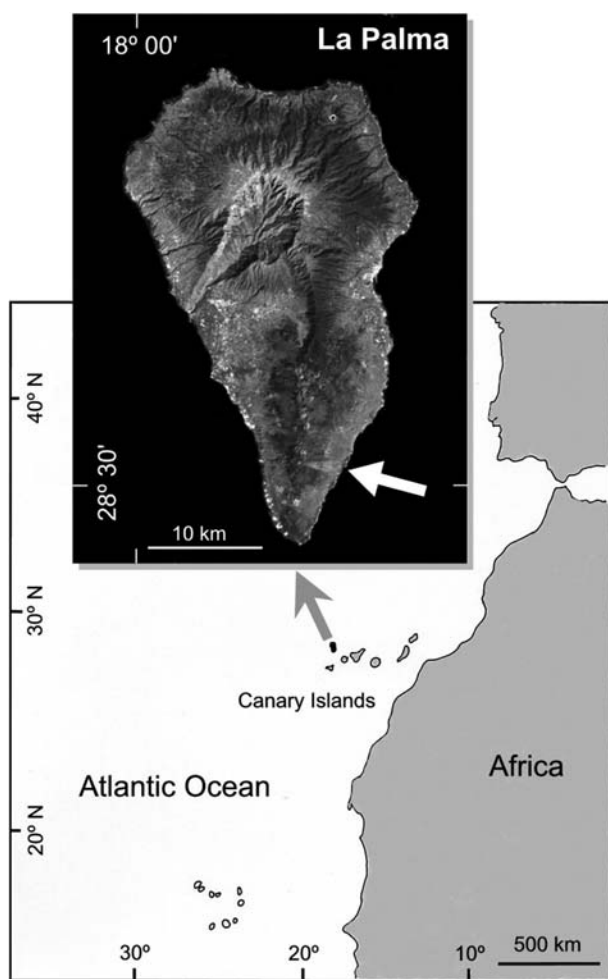


Figure 1 *Lomentaria benahoarensis*: location of the type locality La Salemera (white arrow), La Palma, the Canary Islands.

broad, sparsely radially branched up to three orders, with laterals terete and progressively thinner, lacking regular constrictions but constricted at the base. Cortex tubular with three cell layers comprising the innermost layer made up of non-pigmented, large, elongate, oval-oblong cells (20–50 μm broad and 40–80 μm long), the intermediate layer of smaller cells (6–11 μm in diameter), and the near-continuous surface layer of ovoid cells (3–5 μm in diameter). Medullary filaments forming a loose network of narrow, elongate, subcylindrical cells (3–7 μm in diameter and 50–110 μm long). Secretory cells subspherical to ovoid-pyriform up to 7–10 μm broad and 10–20 μm long. Gametophytes dioecious. Spermatangia borne on elongate spermatangial mother cells in outer cortex in continuous spermatangial sori. Cystocarps strongly prominent, urceolate (300–500 μm in diameter and 350–600 μm long), with a distinctive ostiole and ovoid carposporangia (14–19 μm wide and 19–26 μm long). Tetrasporangia subspherical (40–60 μm in diameter), tetrahedrally divided, in depressed rounded sori (120–180 μm in diameter) located in slightly swollen regions in the mid-portion of fertile terminal axes.

Holotype TFC Phyc 13340 (Figure 4). Female gametophyte. Lower eulittoral, La Salemera, La Palma, Canary Islands, 3 April 2004; leg. C. Sangil.

Etymology The specific epithet refers to the native name (Benahoare) of the type locality La Palma.

Isotypes TFC Phyc 13099, sterile, male and female gametophytes; TFC Phyc 14338, sterile; TFC Phyc 14339 and 14341, female gametophytes; TFC Phyc 14342, male gametophyte; TFC Phyc 14343, tetrasporophyte. Lower eulittoral, La Salemera, La Palma, Canary Islands, 3 April 2004; leg. C. Sangil.

Other specimens examined TFC Phyc 13100, male, female, and sporangial plants. Lower eulittoral, La Salemera, La Palma, Canary Islands, 20 May 2004; leg. C. Sangil.

Distribution Known only from the type locality.

Habitat *Lomentaria benahoarensis* grows as an epiphyte on dense turfs dominated by *Corallina elongata* (geniculate, Corallinaceae) in the lower eulittoral at moderately exposed sites. *Lomentaria* forms small dispersed groups of plants through the turf, where the prostrate axes grow among the branches of *Corallina*, resulting in attachment by means of adherent lateral discs; only the erect axes are slightly exposed outwards. Male, female, and sporangial plants occur simultaneously in spring and are probably annual.

Habit and vegetative structures Plants are red-yellow to pinkish, forming relatively stiff turfs composed of entangled creeping axes bearing erect axes up to 12 mm long (Figures 2–7). Prostrate axes are terete, 200–300 μm in diameter, lacking constrictions, irregularly branched and attached by many lateral discoid holdfasts up to 350 μm in diameter (Figures 7 and 12). Main erect axes are terete or slightly compressed, up to 1000 μm broad, sparsely radially branched up to three orders, with laterals terete and progressively thinner, the highest order nearly 200–300 μm in diameter. Axes lack regular constrictions, but terminal branches are constricted at the bases (Figure 8). Anastomoses and adherent secondary discs occur between axes of the same individual (Figure 13). Fertile plants are more densely branched, with branches nearly verticillate in female gametophytes (Figure 5), radially to subverticillate in male gametophytes (Figure 6) and nearly opposite and distichous in tetrasporophytes (Figure 7).

Axes are hollow and filled with watery mucilage (Figure 10), except for branch bases in which the hollow interior of younger axes is separated by a plug of medullary cells. The cortex is tubular and relatively leathery, ranging from 40 to 60 μm in thickness, and consisting of three cell layers (Figures 10 and 14). The innermost is composed of non-pigmented, large, elongate, oval-oblong cells, 20–50 μm broad and 40–80 μm long in surface view (Figure 15), and surmounted by two layers of progressively smaller pigmented cells (Figure 14). Rounded cells, 6–11 μm in diameter, form a discontinuous subsurface layer. On the outside are ovoid, loosely arranged cortical cells, 3–5 μm in diameter, which form a near-continuous surface layer (Figure 9). The cortex is lined inside with medullary filaments composed of narrow, elongate, sub-



Figures 2–7 *Lomentaria benahoarensis* sp. nov.: liquid preserved specimens.

(2) Detail of the habit of a sterile specimen showing decumbent axes attached by several points to branches of *Corallina elongata*. Note the sparse and radial branching (TFC Phyc 14338). (3) Female specimen with erect axes bearing a cystocarp (arrow) (TFC Phyc 14339). (4) Detail of a female specimen showing cystocarps (arrows) on an erect, densely ramified branch (TFC Phyc 14340). (5) Detail of erect branches of a female specimen showing a dense, nearly verticillate branching (TFC Phyc 14341). (6) Detail of erect branches of a male specimen (TFC Phyc 14342). (7) Sporangial specimen showing swollen fertile regions at the middle portion of terminal axes (arrows). Note the attachment to *C. elongata* by prostrate axes and the nearly distichous arrangement of laterals in erect axes (TFC Phyc 14343). Specimen in Figure 4 is the holotype, the remainder are isotypes. Scale bars=1 mm.

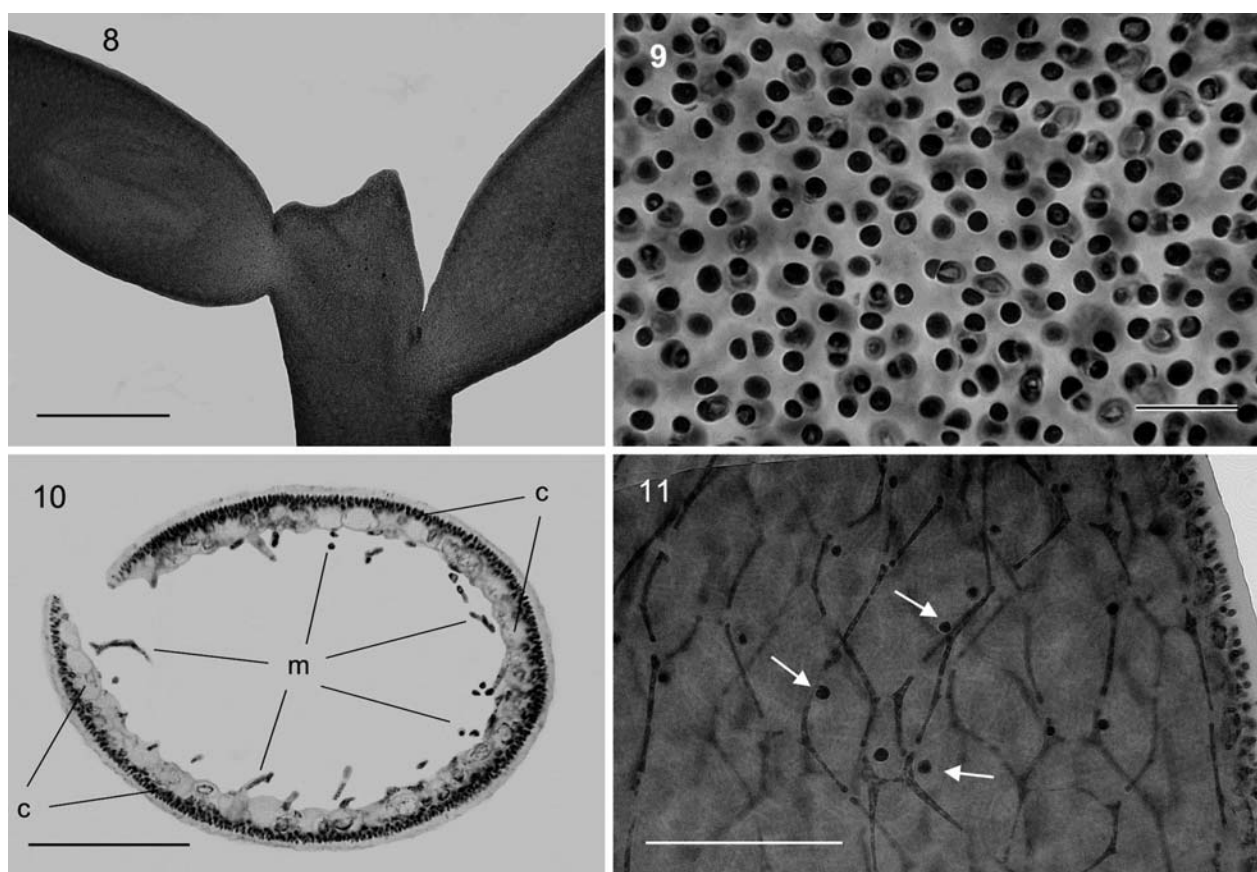
cylindrical cells, 3–7 μm in diameter and 50–110 μm long, which are laterally connected by pit-connections forming a loose network (Figure 11). Medullary cells bear irregularly scattered secretory cells that project into the cavity. They are subspherical when young, 5–10 μm in diameter, and elongate progressively to ovoid-pyriform, 7–10 μm broad and 10–20 μm long (Figures 11, 14, and 15).

Reproductive structures The gametophytes are dioecious. Male plants form continuous patches of spermatangial sori in the distal portions of axes. All outermost cortical cells form elongate spermatangial mother cells (2–3 μm in diameter and up to 8 μm long), which cut off ovoid spermatangia outwards (2–3 μm in diameter and 3–5 μm long) (Figure 16). Early stages of carpogonial branch formation and stages of cystocarp development were not examined in female plants (Figures 17–19). Cystocarps are scattered in the distal portions of the axes and frequently arise on the axil of a short lateral branch. Mature cystocarps are strongly prominent, urceolate, 300–500 μm in diameter and 350–600 μm long, with the ostiole up to 300 μm wide (Figures 17–19). The gonimoblast is subglobose to subconical, 115–250 μm in diameter and 150–350 μm long; it is composed entirely of ovoid carposporangia, which are 14–19 μm wide and 19–26 μm long, each supported by a basal columnar fusion cell (Figure 20). No tela arach-

noidea was observed in the cavity of the cystocarp. The pericarp, 20–30 μm thick, consists of three cell layers that are arranged as in the vegetative axes (Figure 20). Tetrasporangia are formed in depressed sori located in slightly swollen regions in the mid-portion of fertile terminal axes of tetrasporophytes (Figures 7, 21, and 22). Tetrasporangial sori are rounded, 120–180 μm in diameter; they result from invaginations of the cortex, and occur at a frequency of 2–5 per branch (Figures 21 and 22). Tetrasporangia are terminally formed outwards from small cells of a network of cortical filaments that cover the depression (Figure 23). A single sorus contains 8–15 subspherical tetrasporangia, each 40–60 μm in diameter, with tetrahedrally arranged spores (Figures 22 and 23).

Discussion

Lomentaria benahoarensis is one of a group of diminutive species that have been overlooked in regions with well-known floras (Alongi et al. 2008). The new species has no unique features, but differs from other species of the genus by a distinctive combination of characters. The other species of *Lomentaria* reported from the Canary Islands (*L. articulata*, *L. baileyana*, *L. chylocladiella*, *L. linearis*, and *L. subdichotoma*) are easily distinguished in external appearance. *L. articulata*, *L. linearis*, and *L. subdichotoma* have regularly constricted axes (Ercegovic



Figures 8–11 *Lomentaria benahoarensis* sp. nov.

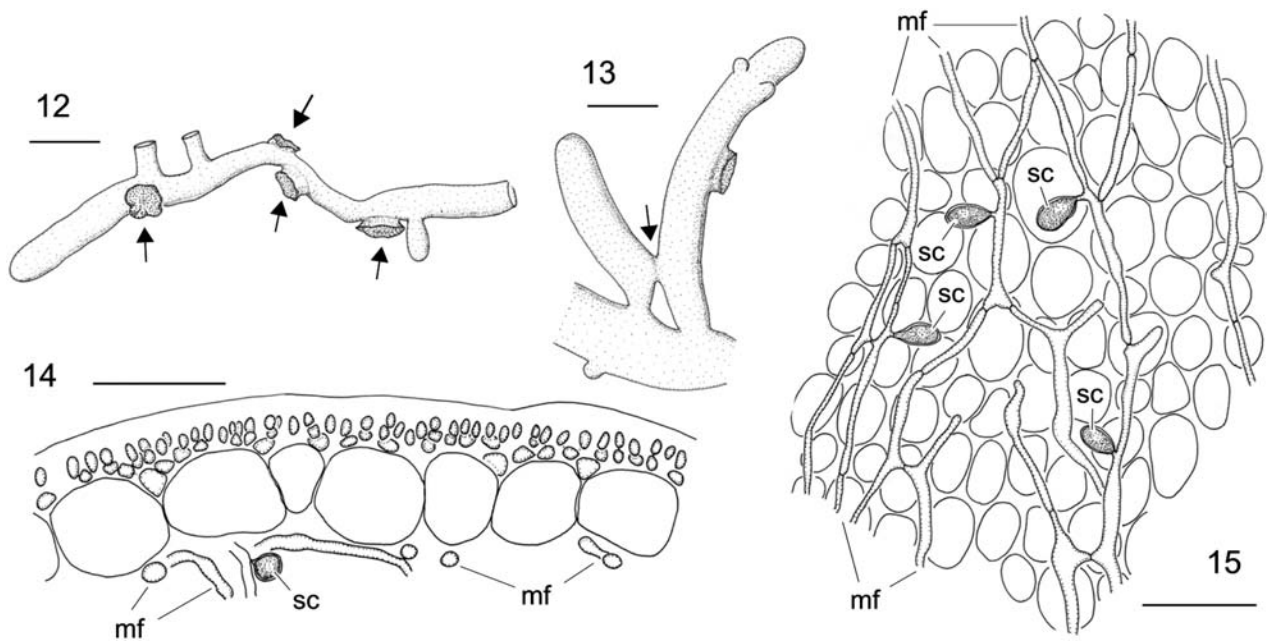
(8) Detail of the basal constriction in two successive laterals (TFC Phyc 13099). (9) Surface view of cortex with outer cortical cells forming a nearly continuous layer (TFC Phyc 14340). (10) Transverse section of an axis showing cortical cells (c) and medullary cells (m) (TFC Phyc 14340). (11) Longitudinal section of an axis showing the peripheral network of medullary filaments, with some projecting secretory cells (arrows) (TFC Phyc 14340). Scale bars: Figure 8=500 μm , Figure 9=20 μm , Figure 10=200 μm , Figure 11=100 μm .

1956, Irvine and Guiry 1983, Ballesteros et al. 1992), whereas in *L. benahoarensis*, the axes are regularly cylindrical and only terminal branches are constricted at the bases. *L. chylocladiella* forms indefinite entangled masses of filiform axes that are completely unconstricted (Boudouresque 1974, Afonso-Carrillo et al. 2007); *L. baileyana* is a larger species that habitually reaches up to 70 mm long, and, although it has terminal branches constricted at the base, it differs in its outer cortex of few scattered cells sometimes arranged in rosettes (Taylor 1957, 1960, Schneider and Searles 1991, Littler and Littler 2000), whereas in *L. benahoarensis*, outer cortical cells form a near-continuous surface layer.

Lomentaria benahoarensis differs from the remaining Atlantic or Mediterranean species compiled in Table 1. *L. clavellosa*, *L. compressa*, *L. hakodatensis*, and *L. uncinata* are larger species that are also easily distinguished in external appearance. The habit in *L. clavellosa* is completely erect from a small holdfast; it is pyramidal in outline and up to 400 mm long, has broader axes, and the outer cortical cells are arranged in a continuous surface layer (Irvine and Guiry 1983). *L. compressa* also has a completely erect habit forming pyramidal to subfastigiate tufts up to 70 mm long arising from a small holdfast, broader axes, and a continuous layer of outer cortical cells (Funk 1927, Ercegovic 1956). *L. hakodatensis* forms dense tufts of prostrate axes, which give rise to erect

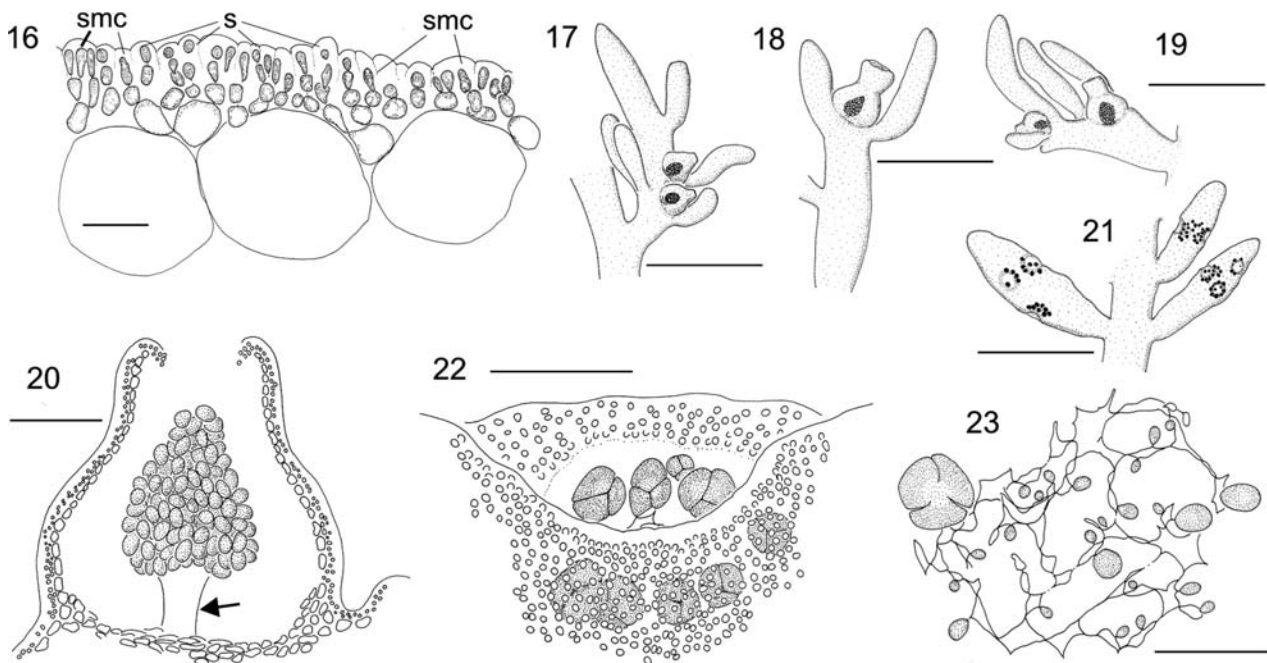
axes up to 100 mm long, with broader axes and a continuous outer cortical layer (Lee and West 1980, Cabioc'h and Magne 1987, Curiel et al. 2006). Finally, *L. uncinata* is characterized by its erect entangled axes, 20–60 mm long, arising from a small discoid holdfast; axes frequently end in hamate tips, and the arrangement of outer cortical cells is in a continuous layer (Zanardini 1840).

The other *Lomentaria* species previously reported from the Atlantic or the Mediterranean basin (Table 1) are diminutive species lacking regular constrictions in axes; they seem to be more closely related to *L. benahoarensis*. A detailed comparison of their attributes is compiled in Table 2. Among them, *L. clavaeformis*, *L. clavellosa* var. *conferta*, *L. ercegovicii*, and *L. verticillata* differ by possessing habits that are completely erect and arise from small discoid holdfasts lacking creeping axes. In addition, *L. clavaeformis*, *L. ercegovicii*, and *L. verticillata* differ clearly in cortex structure, which is thinner and comprises only two cell layers, viz., the inner layer of large hyaline cells forming a continuous layer, and the outer of small pigmented cells arranged in rosettes (Funk 1955, Ercegovic 1956, Boudouresque 1974, Verlaque et al. 1977). All three species form a closely related assemblage that may constitute a single taxonomic entity (Wynne 1998). *L. clavellosa* var. *conferta* differs by possessing branches that are mainly opposite and



Figures 12–15 *Lomentaria benahoarensis* sp. nov.

(12) Detail of a prostrate axis showing many lateral discoid holdfasts (arrows) (TFC Phyc 13099). (13) An anastomosis by an adherent disc between two contiguous branches (arrow) (TFC Phyc 13099). (14) Detail of a transverse section of an axis showing medullary filaments (mf) bearing a secretory cell (sc), which are surrounded by a three-layered cortex consisting of an inner layer of large cells surmounted by two layers of progressively smaller cells (TFC Phyc 14340). (15) Detail of longitudinal section of an axis showing the network of narrow medullary filaments (mf), with some projecting ovoid-pyriform secretory cells (sc) (TFC Phyc 14340). Scale bars: Figures 12, 13=500 μm , Figures 14, 15=50 μm .



Figures 16–23 *Lomentaria benahoarensis* sp. nov.

(16) Transverse section of an axis through a spermatangial sorus showing elongate spermatangial mother cells (smc) cutting off spermatangia (s) on the outer side (TFC Phyc 14342). (17–19) Details of branches showing the disposition of cystocarps (TFC Phyc 14340). (20) Longitudinal section of a cystocarp with the basal columnar fusion cell (arrow) giving rise to a conical mass of carposporangia (TFC Phyc 14340). (21) Detail of terminal branches showing tetrasporangial sori in swollen portions of the axes (TFC Phyc 13099). (22) Surface view of a depressed rounded tetrasporangial sorus with mature tetrasporangia (TFC Phyc 13099). (23) Detail of the network of cortical filaments that cover the depression of a tetrasporangial sorus showing terminally formed sporangia in different development stages (TFC Phyc 13099). Scale bars: Figure 16=20 μm , Figures 17–19, 21=1 mm, Figures 20, 22=100 μm , Figure 23=50 μm .

Table 2 *Lomentaria benahoarensis* sp. nov.: comparison with other diminutive congeners lacking regular constrictions in axes.

| Habitat | Habit | Constriction at the bases of terminal axes | Shape and thickness of axes (μm) | Branching of erect axes | Cell layers in cortex | Outer cortex and outer cortical cell size (μm) | Position, shape and size of cystocarps (μm) | Spermatangial sori | Location of tetrasporangia | Position and size of tetrasporangia (μm) | References |
|---|--|--|---|--|-----------------------|---|--|-----------------------|---|---|--|
| <i>Lomentaria benahoarensis</i> sp. nov. Epiphytic on <i>Corallina elongata</i> in lower eulittoral | Caespitose, forming tufts of creeping axes that produce erect axes up to 12 mm long | Present | Cylindrical to slightly compressed, 200–300 (–1000) | Irregularly alternate and radial; opposite to distichous in sporangial axes; radial to whorled in cystocarpic axes | 3 | Near continuous, 3–8 | Strongly protuberant, urceolate, 300–500×350–600 | In continuous patches | Swollen portions of terminal branches | Rounded sori in small depressions, 40–60 | This paper |
| <i>Lomentaria clavaeformis</i> Ercegovic Epiphytic on algae from eulittoral to 20 m depths | Erect as a single unbranched, club-shaped axis, 2–4 mm long | Absent | Clavate, 150–500 | Absent | 2 | Arranged in rosettes, 5–9 | Partially immersed, globose to urceolate, 220–250 | n.d. | Near the apex of club-shaped axes | Rounded sori in small depressions, 45–50 | Ercegovic (1956), Furnari and Scammacca (1971), De Masi and Gargiulo (1981) |
| <i>Lomentaria clavellosa</i> var. <i>conferta</i> (Meneghini) J. Feldmann Epilithic or epiphytic from lower eulittoral to upper sublittoral, both at sheltered and exposed areas | Erect with branched axes, usually flattened in outline, up to 10 mm long, arising from a small holdfast | Present | Cylindrical, rarely compressed, 100–300 | Opposite and distichous, rarely alternate | 2 | Near continuous, 6–8 | Strongly protuberant, conical, 200–350 | n.d. | Slightly swollen portions of terminal branches | Rounded sori in small depressions, 40–50 | Kützing (1865, as <i>Chondrothamnion confertum</i> Meneghini), Feldmann (1942), Ercegovic (1956), Boudouresque et al. (1977) |
| <i>Lomentaria corallicola</i> Bergesen On corals or epiphytic in algal turfs from eulittoral to 20 m depths | Caespitose, forming dense tufts of decumbent axes that coalesce by rhizoids, giving rise to erect axes 2–8 mm long | Present | Cylindrical, 300–500 | Absent or sparsely and irregular | 2 | Few scattered cells to arranged in rosettes, 5×8 | Strongly protuberant, urceolate, ca. 600×770 | n.d. | Near the apex in broad, obovate-ellipsoidal terminal axes | Rounded sori in small depressions, 40–50 | Bergesen (1939), Cribb (1983), Norris (1987) |
| <i>Lomentaria diffusa</i> Stegenga, Bolton et Anderson Epiphytic or epilithic in the upper sublittoral | Caespitose, forming dense clumps of interwoven and anastomosing prostrate and erect axes 20–30 mm long | Present | Subcylindrical, up to 1500 | Irregular, or lateral in a double row on the outside of the slightly curved axes | ca. 5 | Continuous, 5–16 | Strongly protuberant, ovate to urceolate, 500×500–700 | n.d. | In broad, obovate-ellipsoidal terminal axes | Rounded sori in deep depressions, up to 70 | Stegenga et al. (1997) |

(Table 2 continued)

| | Habitat | Habit | Constriction at the bases of terminal axes | Shape and thickness of axes (μm) | Branching of erect axes | Cell layers in cortex | Outer cortex and outer cortical cell size (μm) | Position, shape and size of cystocarps (μm) | Spermatangial sori | Location of tetrasporangia | Position and size of tetrasporangia (μm) | References |
|--|--|---|--|---|--|-----------------------|---|--|--------------------|--------------------------------------|---|---|
| <i>Lomentaria ercegovicii</i> Verlaque, Boudouresque, Meinesz, Giraud et Marcot-Coqueugniot | Epiphytic on algae in the sublittoral (50–80 m) | Erect, forming pyramidal to subfastigiate tufts 15–20 mm long, arising from a small holdfast | Absent | Cylindrical or compressed, 300–600 | Opposite and distichous | 2 | Arranged in rosettes, 6–10 | Partially immersed, subglobose-conical, ca. 400 | n.d. | Terminal filiform axes | Scattered or in small groups, 50–60 | Verlaque et al. (1977), Ercegovic (1956, as <i>Lomentaria tenera</i> Ercegovic) |
| <i>Lomentaria gracillima</i> Masuda et Kogame in Kawaguchi et al. | Epiphytic on brown algae in the upper sublittoral | Caespitose, with fleshy arcuate axes up to 8 mm long arising from a discoid holdfast and secondarily attached by additional holdfasts | Present | Cylindrical or compressed, 100–250 | Secund | 2–4 | Continuous, 5–12 | Strongly protuberant, ovoid, 400–450 \times 420–480 | n.d. | Compressed portions of erect axes | Rounded sori in small depressions, 60–70 | Kawaguchi et al. (2002) |
| <i>Lomentaria jabukae</i> Ercegovic | Epiphytic on eulittoral algae | Prostrate, forming compact and adherent pulvinate clumps of 1–3 mm in thickness, constituted by entangled creeping axes | Absent | Cylindrical (150–200) to compressed (400–700) | Irregular, opposite, unilateral or alternate | 3 | Nearly continuous, 6–8 | n.d. | n.d. | n.d. | n.d. | Ercegovic (1956) |
| <i>Lomentaria monochlamydea</i> (J. Agardh) Kylin | Epilithic in the upper sublittoral | Caespitose, with prostrate cylindrical axes producing compressed erect axes 5–20 mm long | Present | Cylindrical or compressed 500–2000 | Alternate or secund | 3–4 | Few, scarcely forming rosettes, 10–22 | n.d. | n.d. | Erect unmodified axes | Irregularly elongate depressed sori, 30–50 | Millar (1990), Womersley (1996) |
| <i>Lomentaria orcadensis</i> (Harvey) F.S. Collins in Taylor | Epilithic or epiphytic in the sublittoral down to 20 m | Caespitose, with erect compressed axes up to 30 mm long arising from prostrate axes | Present | Compressed, 1300–3000 | Opposite, 1–2 times pinnate | 2 | Arranged in rosettes, 4–8 | Strongly protuberant, hemispherical to conical, 400–600 | n.d. | Middle portions of terminal segments | Rounded sori in small depressions, 33–55 | Taylor (1957), Irvine and Guiry (1983), Bárbara et al. (1996) |

(Table 2 continued)

| Habitat | Habit | Constriction at the bases of terminal axes | Shape and thickness of axes (μm) | Branching of erect axes | Cell layers in cortex | Outer cortex and outer cortical cell size (μm) | Position, shape and size of cystocarps (μm) | Spermatangial sori | Location of tetrasporangia | Position and size of tetrasporangia (μm) | References |
|---|--|--|---|---|-----------------------|---|--|-----------------------|---------------------------------------|---|--|
| <i>Lomentaria rawitscheri</i> A.B. Joly | Epiphytic on geniculate coralline algae | Absent | Cylindrical, 300–1000 | Irregularly alternate | 2–3 | From few scattered cells to arranged in rosettes, ca. 5 | Strongly protuberant, spherical, 680–740 | In continuous patches | Terminal inflated axes | Rounded sori in small depressions, 29–74 | Joly (1957), Sazima (1979), Ballantine et al. (2002) |
| <i>Lomentaria tenerima</i> (Esper) P.C. Silva in Silva et al. | Epilithic, mainly in upper sublittoral next to harbors | Absent | Cylindrical to compressed, 200–1000 | Irregularly alternate, opposite or unilateral | 4–5 | Continuous, 12–20 | Strongly protuberant, hemispherical, 300–600 (–850) | n.d. | Swollen portions of terminal branches | Rounded sori in small depressions, n.d. | Kylin (1931), Ercegovic [1956 as <i>Lomentaria firma</i> (J. Agardh) Kylin], Silva et al. (1996) |
| <i>Lomentaria verticillata</i> Funk | Epiphytic on algae from eulittoral to 30 m depths | Absent | Cylindrical, up to 350 | Irregularly alternate, whorled or absent | 2 | Arranged in rosettes, 5–12 | Partially immersed, ovoid-conical, ca. 300 | n.d. | Near the apex in terminal axes | Scattered under the cortical layer, up to 80 | Funk (1955), Boudouresque (1974) |

n.d.=no data.

distichous, the cortex is two-layered and the cystocarps are conical and smaller (Feldmann 1942, Ercegovic 1956, Boudouresque et al. 1977). In contrast, *L. jabukae* is very different in possessing a completely prostrate habit. This species forms entangled prostrate axes in compact and adherent pulvinate clumps, and the terminal axes are not constricted at the bases (Ercegovic 1956).

Lomentaria corallicola, *L. diffusa*, *L. orcadensis*, *L. rawitscheri*, and *L. tenerrima* have decumbent habits comprising erect axes arising from prostrate axes. In addition, *L. orcadensis* differs in possessing erect axes compressed and pinnately branched, the cortex is two-layered, and the outermost cortical cells are arranged in rosettes (Irvine and Guiry 1983, Bárbara et al. 1996). *L. tenerrima* forms fastigate tufts with terminal branches unconstricted at the bases, the cortex has four or five cell layers, and the outermost cortical cells are large and arranged in a continuous surface layer (Ercegovic 1956, as *L. firma*). In *L. diffusa*, the plants reach up to 30 mm long, the cortex is broader with five cell layers, and the outermost cells form a continuous layer (Stegenga et al. 1997). In *L. corallicola*, erect axes are shorter, simple, or sparsely and irregularly branched, the cortex is two-layered with an incomplete outer cortical layer of few scattered cells sometimes arranged in rosettes (Børgesen 1939, Cribb 1983, Norris 1987). Finally, *L. rawitscheri* differs in possessing axes irregularly alternately branched, terminal branches not constricted at the bases, cortex comprising 2–3 cell layers, and an outer layer consisting of few to several discontinuous cortical cells arranged in rosettes, greater spherical cystocarps, and tetrasporangia formed in terminal inflated axes (Joly 1957, Sazima 1979, Ballantine et al. 2002). Although Bula-Meyer and Norris (2001) considered *L. rawitscheri* to be conspecific with *L. corallicola*, Ballantine et al. (2002) showed that *L. rawitscheri* has a distinctive feature in its spherical non-ostiolate cystocarp.

Among the non-Atlantic/Mediterranean species, *Lomentaria benahoarensis* seems most closely related to *L. gracillima* Masuda et Kogame from Pulau Sipadan, Malaysia (Kawaguchi et al. 2002) and *L. monochlamydea* (J. Agardh) Kylin from Australia (Millar 1990, Womersley 1996). Both species are diminutive; they are compared in Table 2. *L. gracillima* differs from *L. benahoarensis* by possessing fleshy arcuate axes, thinner axes with secondarily arranged branches, a continuous outer cortex, ovoid cystocarps and tetrasporangia in compressed portions of erect axes (Kawaguchi et al. 2002). *L. monochlamydea* has broader flattened axes alternately or secondarily branched, the cortex consisting of 3–4 cell layers, large outer cortical cells forming a very discontinuous surface layer and tetrasporangia in non-swollen portions of erect axes (Millar 1990, Womersley 1996).

The type species *Lomentaria articulata* has multilayered plugs constricting the medullary cavity at regular intervals, a feature absent in *L. benahoarensis* and the remainder of the species included in Table 2. Guiry (cited in Irvine and Guiry 1983) suggested that species lacking regular constrictions or with them occurring only at the bases of the branches could be removed to a separate genus, *Chondrothamnion* Kützinger (1843: 438), based on *Fucus clavellus* Turner. Nevertheless, a boundary between these genera is difficult to establish. *Lomentaria*

species are mainly separated by different combinations of morphological features; most do not have a unique diagnostic character, and recent molecular results strongly support an alliance between *L. articulata* and *L. orcadensis*, in contrast to Guiry's proposal (Le Gall et al. 2008). Further vegetative and reproductive information is needed in many poorly known *Lomentaria* species, and molecular studies are necessary to reach a satisfactory knowledge of the genus.

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