

First report of *Reticulocaulis mucosissimus* (Naccariaceae, Rhodophyta) for the Atlantic Ocean

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Abstract – The finding of *Reticulocaulis mucosissimus* in the Canary Islands represents the first record in the Atlantic Ocean of *Reticulocaulis*, a marine red algal genus very rarely reported and previously known only from the central Pacific (Hawaii) and the northwestern Indian Ocean (Oman and Yemen). The vegetative and reproductive morphology of a female gametophyte from La Palma (Canary Islands) is described in detail. The Canarian plant exhibits the distinctive characters of *R. mucosissimus*, although the range of morphological variation is extended for certain features like the occurrence of sinusoidal apices, the early appearance of both periaxial cells, and the slightly longer carpogonial branches. The infrequent sublittoral occurrence of ephemeral gametophytes and undersampling of subtidal habitats can explain the disjunct distribution presently exhibited by *R. mucosissimus*.

Canary Islands / marine algae / morphology / Naccariaceae / *Reticulocaulis mucosissimus* / Rhodophyta

Résumé – Première récolte de *Reticulocaulis mucosissimus* (Naccariaceae, Rhodophyta) dans l'Océan Atlantique. Le signalement du *Reticulocaulis mucosissimus* dans les îles Canaries représente le premier report pour l'Océan Atlantique du *Reticulocaulis*, un genre d'algues rouge marine très rarement observé et seulement connu de l'Océan Pacifique central (Hawaï) et au nord-ouest de l'Océan Indien (l'Oman et le Yémen). La morphologie végétative et reproductrice d'un gamétophyte femelle trouvé à La Palma (îles Canaries) est décrite en détail. La plante des Canaries présente les caractères distinctifs du *R. mucosissimus*, bien que la variation morphologique soit très large pour quelques caractères comme la présence des apex sinusoïdaux, l'apparition précoce des deux cellules périaxiales, et les rameaux carpogoniaux légèrement plus longs. La présence peu fréquente et éphémère des gamétophytes dans le sublittoral et le peu d'échantillonnage des habitats sublittoraux peuvent expliquer l'actuelle distribution disjointe du *R. mucosissimus*.

Algues marines / Iles Canaries / morphologie / Naccariaceae / *Reticulocaulis mucosissimus* / Rhodophyta

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INTRODUCTION

Recent studies of the distribution of benthic assemblages along the littoral of La Palma, eastern Atlantic, revealed new species records for the Canary Islands (Sangil *et al.*, 2003, 2004a, 2004b). In the present account, we document the first record of *Reticulocaulis mucosissimus* Abbott for the Atlantic Ocean.

The red algal genus *Reticulocaulis* was established by Abbott (1985) for the single species *R. mucosissimus*, a rare gelatinous spring alga of the Hawaiian marine flora. Initially it was considered as a Hawaiian endemic monotypic genus (Abbott, 1999), but recently the genus has been reported for the Arabian Sea: *R. mucosissimus* was recorded for Masirah Island (Oman) and a second species, *R. obpyriformis* Schils was described from Socotra Island (Yemen) (Schils *et al.*, 2003). Representatives of the Naccariaceae (species of *Naccaria* Endlicher, *Atractophora* P.L. et H.M. Crouan and *Reticulocaulis*) show ephemeral seasonal gametophytes with an infrequent occurrence (Millar, 1990; Womersley, 1996). The range of morphological variation within species is only partially known, as the number of available specimens limits morphological studies. The finding of *R. mucosissimus* in the Canary Islands provided an opportunity to examine the morphology in detail and to elaborate its description for this new distribution area.

MATERIALS AND METHODS

A single specimen of *Reticulocaulis mucosissimus* (TFC Phyc 13058, 25 April 2003, leg. C. Sangil) was collected in Profs de Tegalate (La Palma, Canary Islands). Sampling efforts at this site during the spring and the summer of 2004 and 2005 did not reveal another finding of the species. Extra-Canarian material of *Reticulocaulis* was examined for comparative purposes: *R. mucosissimus* from the Hawaiian Islands, Mahukona, Hawaii Island (GENT slides IA23471, 26 May 1998, K.J. McDermid, female gametophyte); Kawaihoa, Oahu Island (GENT slides IA17225, 10 May 1985, W.H. Magruder & S. Carper, female gametophyte); Hanalei Bay, Kauai Island (Abbott collection, slides IA21966, 2 June 1993, K.J. McDermid, female gametophyte); *R. mucosissimus* from Oman, Masirah Island (GENT slides MAS138, 9 November 1999, T. Schils, female and male gametophytes); *R. obpyriformis* from Yemen, Socotra Island (GENT slides SMM446, 30 April 2000, T. Schils, monoecious gametophyte).

The liquid-preserved specimen was fixed in a 4% formalin-seawater solution. Selected fragments were stained in 1% aniline blue in distilled water, mounted in a 50% Karo[®] corn syrup solution, and slightly squashed to separate the filaments. Drawings were made using a camera lucida attached to a Zeiss Standard microscope. Micrographs were taken on a Zeiss photomicroscope. Herbarium abbreviations follow Holmgren *et al.* (1990).

OBSERVATIONS

The specimen of *Reticulocaulis mucosissimus* grew epilithically on a cobble in a sand flat at 10 m depth, together with other ephemeral red algae such as *Acrosymphyton purpuriferum* (J. Agardh) Sjöstedt, *Ganonema lubricum*

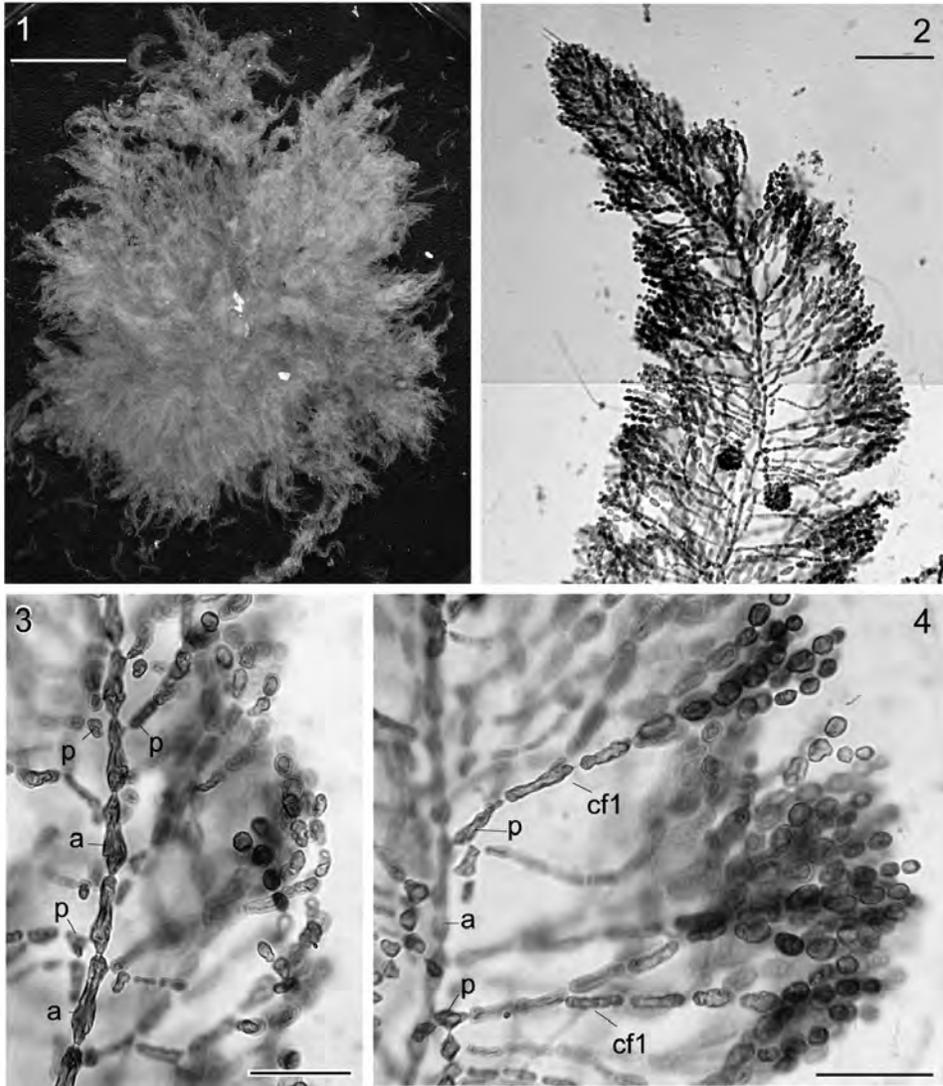
Afonso-Carrillo, Sansón *et* Reyes, *Helminthocladia reyesii* O'Dwyer *et* Afonso-Carrillo and *Scinaia complanata* (Collins) Cotton.

The plant is erect, arising from a single small discoid holdfast, up to 5 cm in height, slightly pink in colour, delicate, smooth, gelatinous and slippery (Fig. 1). Six main axes, each terete and up to 3 mm in diameter, arise from the holdfast. Three of the main axes are quickly truncate, and the remaining axes are densely irregularly radially branched for up to five orders. Laterals arise perpendicularly, but curve upwards while growing, hereby forming acute axils. Laterals are terete and gradually decrease in diameter, with younger branches 100-200 μ m in diameter, tapering progressively to relatively acute apices (Fig. 2).

Growth of indeterminate axes is by means of a single, dome-shaped apical cell, about 8 μ m in diameter (Fig. 5), that divides obliquely to form an initially sinusoidal axial filament. Young axial cells are subspherical (6-8 μ m in diameter) and gradually elongate, becoming slender and cylindrical, reaching more than 300 μ m in length in old portions. Differing in the timing of their initiation, two initials of determinate cortical fascicles ('periaxial cells') are produced at opposite ends in an irregular 1/4 spiral from each axial cell (Figs 3, 4, 5). The first periaxial cell (the 'distal' periaxial cell) is cut off from the subapical cell (Fig. 5), and the second periaxial cell (the 'proximal' periaxial cell) is formed from cells 12-14 below the apex and in 1/4 spiral divergence to the first periaxial cell (Fig. 5). The distal periaxial cell becomes elongated and subcylindrical, and will be retained in its subterminal position; whereas the proximal periaxial cell remains approximately isodiametric, and will be displaced to a middle position, as a consequence of the elongation of the axial cells (Figs 6, 7). The periaxial cells quickly branch to form primary cortical fascicles. Cortical fascicles are 10- to 12-celled, up to 400 μ m in length, and are six to eight times pseudodichotomously branched (Figs 4, 9). The five to six proximal cells of cortical fascicles are colourless and subcylindrical, 12-23 μ m in diameter and 70-95 μ m long, becoming pigmented upwards, shorter and ovoid to subspherical, 20-30 μ m in diameter (Figs 4, 9). The rhodoplasts are discoid, 2-4 μ m in diameter. Indeterminate lateral branches arise at irregular intervals, replacing a proximal cortical fascicle and developing new axes (Fig. 9).

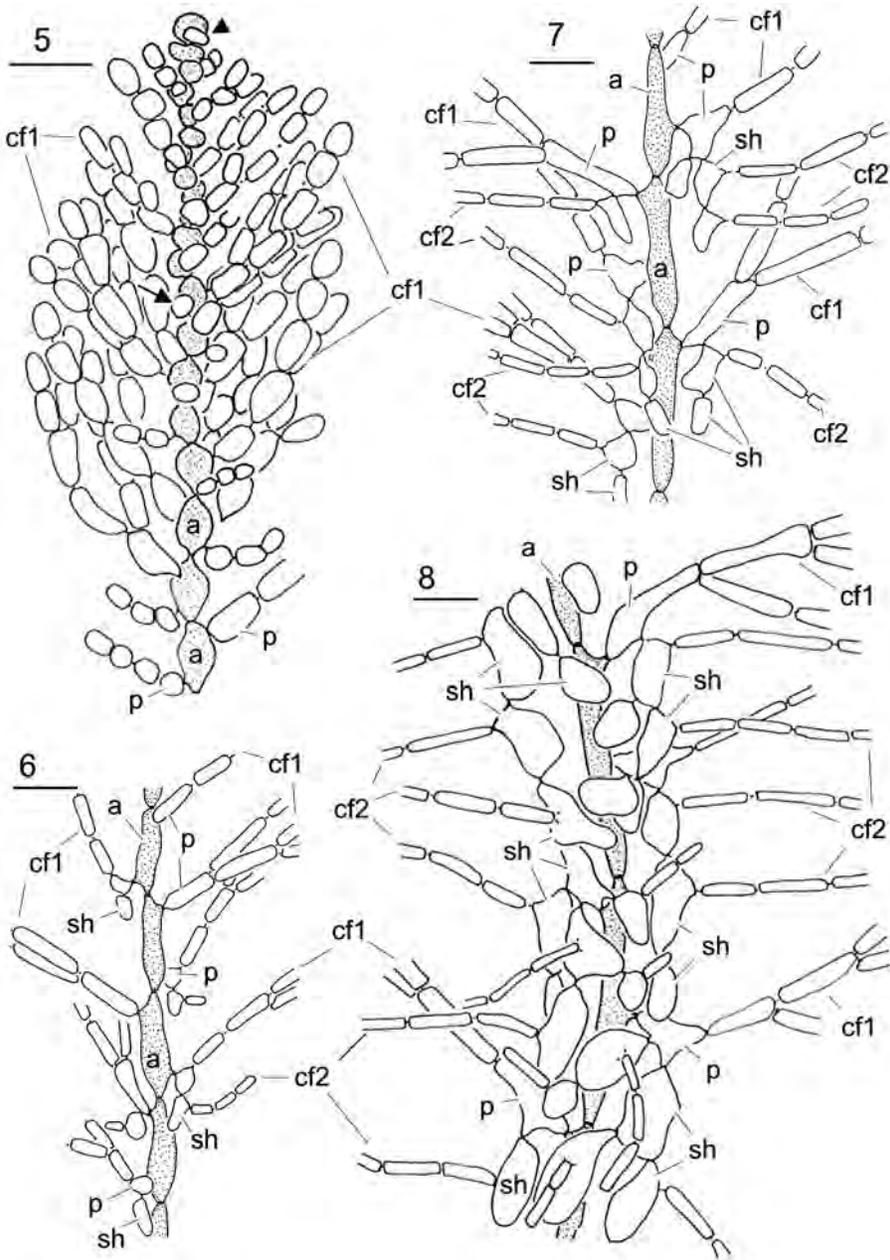
Twenty to thirty cells from the apex, downwardly growing rhizoidal filaments arise from both periaxial cells (Figs 3, 4, 6, 7). The periaxial cells and rhizoidal cells inflate progressively, forming a pseudoparenchymatous, colourless, net-like sheath around the axial strand, in which the neighbouring cells are connected by secondary pit connections (Figs 8-10). Twenty millimetres from the apex, inflated cells reach up to 100 μ m wide and 150 μ m long, and the axial sheath has increased up to 300 μ m in thickness (Fig. 11). In addition to the cellular elongation, new growth downwards increases the thickness of the sheath: addition of new inflated cells surrounding the initial sheath, and elaboration of unbranched rhizoidal filaments consisting of slender subcylindrical cells. In older parts of the plant, rhizoidal filaments densely cover the inflated cells. Upon sheath initiation, each sheath cell produces a perpendicular subsidiary (secondary) cortical filament (Figs 8, 10), which divides until reaching the length of the cortical fascicles. Most of the secondary cortical filaments only branch in the distal parts, thus differing from the primary cortical fascicles. However, some secondary filaments remain unbranched, and its terminal cells are subcylindrical in shape.

The solitary collected specimen is a female gametophyte. Carpogonial branches are formed abundantly in young portions of branches as downwardly growing filaments adjacent to the axial sheath (Figs 12-18). They arise singly from the periaxial cell or the second cell (rarely from the third cell) of the proximal

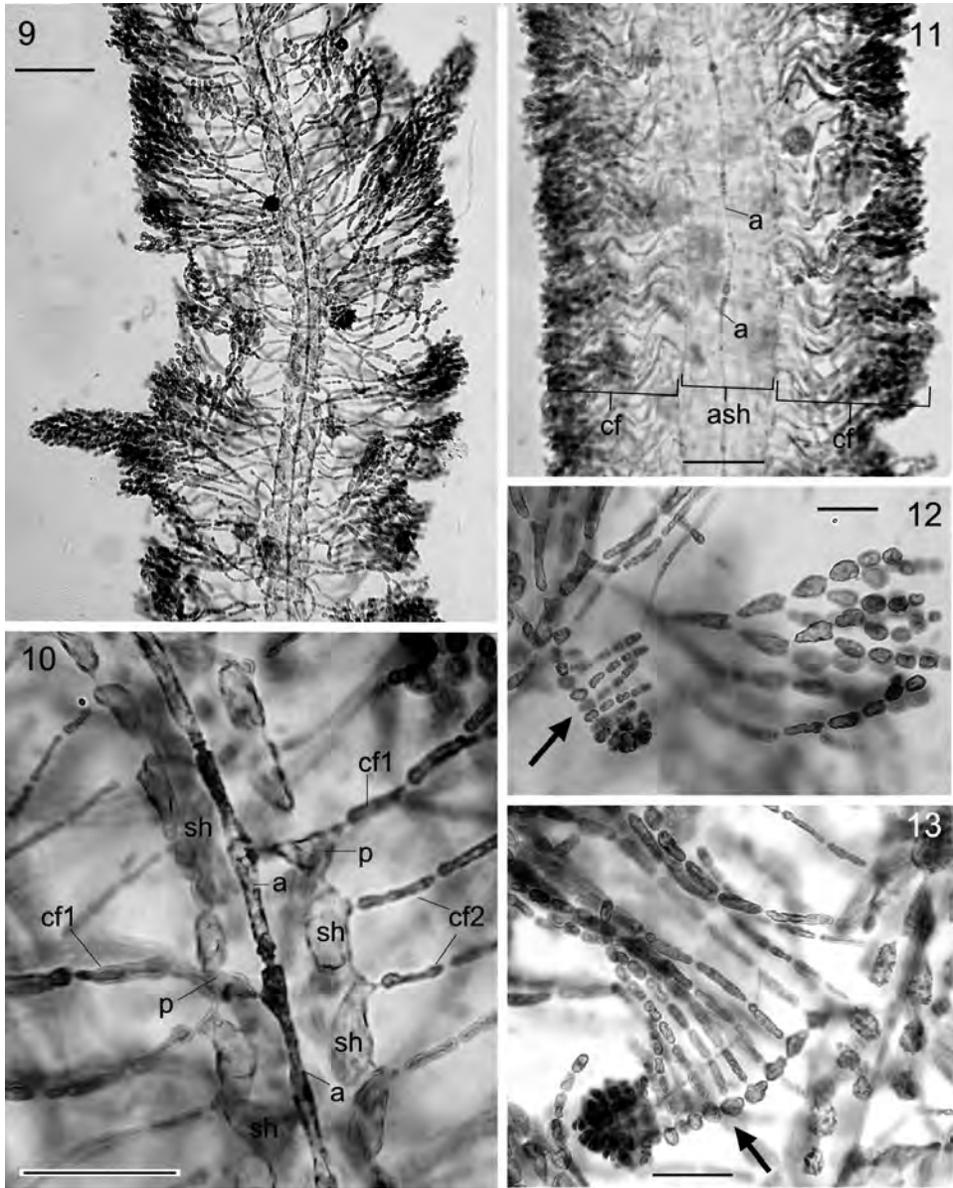


Figs 1-4. *Reticulocaulis mucosissimus* Abbott (TFC Phyc 13058). **1.** Habit of the liquid preserved specimen. Scale bar = 20 mm. **2.** Young branch showing a relatively acute apex and cortical fascicles. Scale bar = 100 μ m. **3, 4.** Detail of young branches showing axial cells and primary cortical fascicles. Scale bars = 50 μ m. (a, axial cell; cf1, primary cortical fascicle; p, periaxial cell).

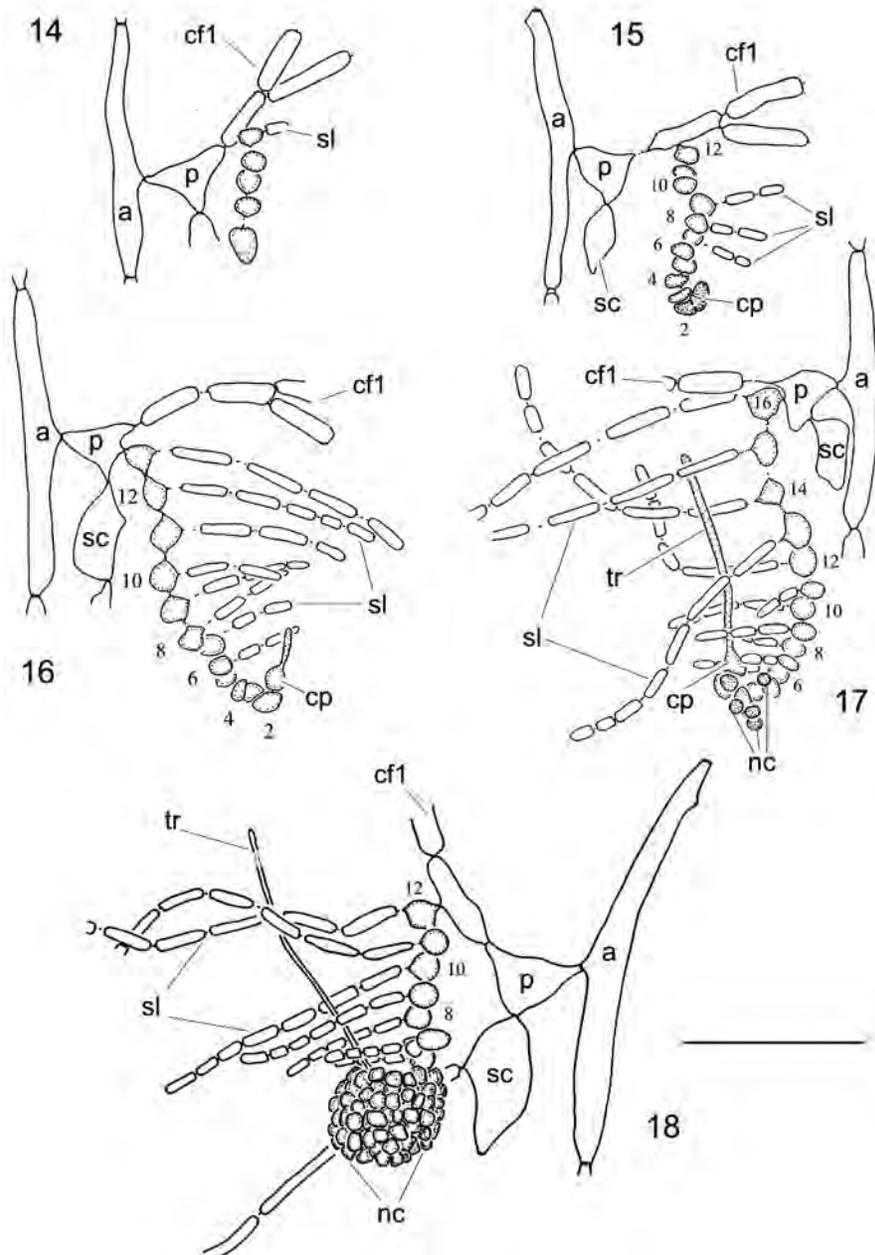
cortical fascicle. Carpogonial branches arising on cells of the distal cortical fascicles, the secondary cortical fascicles or the axial sheath, or occurring in pairs on a single supporting cell were not observed. Carpogonial branches are composed of 11-13 (-16) cells (designated by numbers in Figs 16-18, starting with the terminal carpogonium: #1) in an evident zigzag arrangement, a consequence of the eccentric position of its primary pit connections. The carpogonium results from a transverse division and the apex of the carpogonial branch becomes



Figs 5-8. *Reticulocaulis mucosissimus* Abbott (TFC Phyc 13058). **5.** The first periaxial cell (arrowhead) is cut off from the subterminal cell, and the second periaxial cell (arrow) is cut off in cell positioned 13 below the apex. Note an sinusoidal arrangement in first axial cells. **6-7.** Initiation of rhizoidal down-growths from periaxial cells of primary cortical fascicles in young branches. **8.** Cells from rhizoidal down-growths inflate to form the axial sheath. A secondary cortical filament arises from each sheath cell. Scale bars = 20 μ m. (a, axial cell; cf1, primary cortical fascicle; cf2, secondary cortical fascicle; p: periaxial cell; sh: sheath cell).



Figs 9-13. *Reticulocaulis mucosissimus* Abbott (TFC Phyc 13058). **9.** Portion of a young branch showing the axial sheath, cortical fascicles and indeterminate branches. Scale bar = 100 μm. **10.** Detail of the axial sheath surrounding the axial strand. Scale bar = 50 μm. **11.** Portion of a mature branch with a wide axial sheath and outer cortex. Scale bar = 100 μm. **12.** Immature carpoogonial branch (arrow) in the inner cortex. Scale bar = 50 μm. **13.** Mature carpoogonial branch (arrow). Scale bar = 50 μm. (a, axial cell; ash: axial sheath; cf: cortical fascicles; cf1, primary cortical fascicle; cf2, secondary cortical fascicle; p: periaxial cell; sh: sheath cell).



Figs 14-18. *Reticulocaulis mucosissimus* Abbott (TFC Phyc 13058). Carpogonial branch morphology. **14.** First stages of the development of a carpogonial branch. **15, 16.** Young carpogonial branches with terminal immature carpogonium and sterile laterals growing from the lower cells. **17.** Mature sixteen-celled carpogonial branch bearing nutritive-cells on the hypogynous cell and on cell #3 and cell #4, and sterile laterals on more proximal cells. **18.** An apparently unfertilised carpogonium is surrounded by a mass of nutritive cells in a mature carpogonial branch. Scale bar = 50 μ m. (a, axial cell; cf1, primary cortical fascicle; cp: carpogonium; nc: nutritive cells; p, periaxial cell; sh: sheath cell; sl: sterile lateral; tr: trichogyne).

reflexed outwards (Figs 15, 16). The carpogonium is extended by a relatively straight trichogyne up to 500 μm in length, which grew between the cortical fascicles towards the surface of the branches (Figs 17, 18). Simple sterile laterals up to 12 cylindrical cells in length, rarely distally branched, arise perpendicularly and adaxially from proximal cells of the carpogonial branches (Figs 16-18). On the four terminal cells these sterile laterals are replaced by clusters of nutritive cells formed on cells #2, #3, and #4 (Fig. 17). These clusters divide and branch to form a distally and abaxially arranged compact mass of globose to angular nutritive cells, 5-8 μm in diameter (Fig. 18). No fertilizations were observed for the numerous mature carpogonial branches that were examined. The largest cluster of nutritive cells measured 50 μm in diameter (Fig. 18). Spermatangia were not observed.

DISCUSSION

Representatives of the Naccariaceae generally grow amidst sublittoral gelatinous red algae communities and the occurrence of gametophytes is described as seasonal, infrequent and ephemeral (Abbott, 1985; Millar, 1990; Womersley, 1996). This ensemble of characteristics with respect to habitat and seasonality also holds for *Reticulocaulis mucosissimus* from the Canary Islands. Recent studies carried out on shallow sublittoral cobble and bare-rock substrata at the Canary Islands have allowed the recognition of a rich flora composed of ephemeral spring-annual species, including new and previously unrecorded species (Afonso-Carrillo & Tabares, 2004). Most of these gelatinous red algae exhibit simple vegetative morphologies and relatively primitive modes of sexual reproduction, e.g. genera as *Ganonema* Fan et Wang and *Helminthocladia* J. Agardh (Liagoraceae), *Acrosymphyton* Sjöstedt (Acrosymphytaceae), *Dudresnaya* P.L. et H.M. Crouan (Dumontiaceae), *Schimmelmanna* Kützing and *Thuretella* Schmitz (Gloiosiphoniaceae), *Predaea* De Toni (Nemastomataceae), and *Naccaria* (Naccariaceae) (Afonso-Carrillo & Tabares, 2004). *Reticulocaulis* complements this set of genera.

Until now, only one specimen has been documented for the Canary Islands and intensive surveys afterwards did not yield new sightings. At present *Reticulocaulis mucosissimus* has been only reported from six collections from Hawaii (Abbott, 1999) and one from Oman (Schils *et al.*, 2003). Although the life history has not been completely established for *Reticulocaulis*, the genus apparently exhibits a heteromorphic life history observed in other Naccariaceae (Chemin, 1927; Boillot & L'Hardy-Halos, 1975). Abbott (1999) reported that, under culture conditions, a filamentous phase was obtained from carpospores, but it did not reach maturity. Unpredictable occurrence of seasonal gametophytes might result from the growth regulation by critical values for one or several seasonal environmental factors (i.e., daylength, temperature, nutrients, sand movement) which do not concur yearly (Dring, 1984; Kain & Norton, 1990).

The present disjunct geographical distribution exhibited by *Reticulocaulis mucosissimus* (Hawaii in the central Pacific, Oman in the northwestern Indian Ocean, and the Canary Islands in the eastern Atlantic) can be explained by the infrequent ephemeral sublittoral occurrence of gametophytes and undersampling of sublittoral habitats. On a world-wide scale, the distribution of the above listed

gelatinous red algae is restricted to the tropical regions or regions that border the original Tethyan Ocean (Hommersand, 1986). *Reticulocaulis mucosissimus* grows in these regions and the eastern Atlantic record might represent a relict distribution instead of a recent introduction.

Abbott (1985) distinguished *Reticulocaulis* from the closely related genus *Naccaria* by (1) the different pattern in which the inflated cells of the sheath surround the axial strand, (2) the more elaborate carpogonial branches (longer, more branched, and with small clusters of nutritive cells on the hypogynous and adjacent carpogonial branch cells), and (3) the compact carposporophyte occurring in the mid to outer cortex. Although the Canarian specimen lacks carposporophytes, the morphological features that distinguish *R. mucosissimus* from *R. obpyriformis* are evident (*i.e.* axial cells slender instead of broadly inflated; gradual transition of cortical cells from cylindrical to spherical instead of abrupt transition from cylindrical-obpyriform to spherical-ovoid; and dioecious instead of monoecious) (Schils *et al.*, 2003). Comparative observations with specimens from Hawaii and Oman have allowed identification with confidence. However, the alga from the Canary Islands exhibits a few minor differences in vegetative and reproductive morphology. The apical axial cells show a sinusoidal arrangement before the axial cells become aligned, lacking the nearly straight arrangement observed by Schils *et al.* (2003). Both periaxial cells appear earlier than previously reported (Schils *et al.*, 2003). The first periaxial cell is cut off from the subterminal cell (instead of three axial cells from the apex), and the second periaxial cell is cut off from axial cells positioned 12-14 (instead 15-20) from the apex. Finally, carpogonial branches are slightly longer with more carpogonial branch cells than those previously reported. Most of the abundant carpogonial branches present in the Canarian material were 11-13 celled, reaching occasionally up to 16 cells, and differing in this way from the 6-11 celled branches observed by Abbott (1985) and the 7-13 celled described by Schils *et al.* (2003). The limited number of examined specimens prevents a taxonomic evaluation of these morphological differences, although it raises the point that our current knowledge of morphological variation within the species is rather incomplete.

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