Observations on reproductive morphology and new records of Rhodomelaceae (Rhodophyta) from the Canary Islands, including *Veleroa complanata* sp. nov.

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Polysiphonia funebris and *P. tenerrima* are examined mainly in relation to their vegetative and reproductive features. In *P. funebris* the procarps and cystocarps are described for the first time, and it is confirmed that the species exhibits all the vegetative and reproductive features presently used in the delineation of the genus *Polysiphonia*. The mainly Mediterranean *P. tenerrima* is reported for the first time in the Atlantic Ocean. This epi-endophyte on *Nemalion helminthoides* has ecorticate axes with four pericentral cells, abundant trichoblasts spirally arranged, rhizoids cut off from pericentral cells, tetrasporangia produced in spiral series and apparently three-celled carpogonial branches, all diagnostic characters of the genus *Neosiphonia*. Tetrasporangial plants in the western Atlantic species *Dipterosiphonia reversa* are described for the first time from a collection that represents the first record of this species in the eastern Atlantic Ocean. Tetrasporangia are produced (one per segment) in short linear series in pinnate laterals, with fertile segments consisting of five pericentral cells; the fertile pericentral cell cuts off two sporangial cover cells. *Veleroa complanata* Afonso-Carrillo & Rojas-González *sp. nov.*, known only from Tenerife in the Canary Islands, is unique among species of the genus *Veleroa* because of its progressively corticated polysiphonous axes and its two different types of spirally arranged, determinate, pigmented, persistent trichoblasts. These are unbranched in prostrate and fertile portions of erect axes, but branched, with up to eight alternate-distichous complanate laterals, in vegetative erect axes. A comparative table of the morphological attributes of the species currently accepted in *Veleroa* is given.

INTRODUCTION

Recent floristic studies have revealed that the morphologically diverse red algal family Rhodomelaceae is the largest in the Canary Islands (Afonso-Carrillo & Sansón 1999), although the taxonomy and morphology of its representatives are still only partially known in this region (Rojas-González & Afonso-Carrillo 2000). A continued study of rhodomelaceous collections made at several localities in the Canary Islands has allowed the study of species until now unreported in the Canary Islands, or in which significant aspects of the reproductive morphology were unknown or had been inadequately described previously. In this account, the procarps, mature cystocarps, tetrasporangia and spermatangial axes are examined in two species of *Polysiphonia* Greville. Three species are added to the seaweed flora of the Canary Islands, including *Veleroa complanata* Afonso-Carrillo & Rojas-González, *sp. nov.*, a taxon with persistent pigmented trichoblasts and belonging to a genus previously unreported in the Atlantic Ocean. The finding of this new species constitutes additional evidence of the richness and distinctiveness of the benthic marine flora of the Canary Islands, on which important advances have taken place in recent years (Afonso-Carrillo & Sansón 1999). The Canarian marine flora appears to be the result of a combination of the effects of its geographical position in the warm temperate eastern Atlantic, its prevailing

oceanographic conditions, and palaeoclimatic events (Prud'homme van Reine & Hoek 1990; Pakker & Breeman 1996; Pakker *et al.* 1996). Floristically, the algal flora can be characterized by the co-occurrence of elements from the Mediterranean Sea, the tropical western Atlantic Ocean, the warm temperate north Atlantic, and a small number of Canarian endemic species (Sansón *et al.* 2001). *Veleroa complanata* is added to other recently described endemic red algae belonging to the genera *Dudresnaya* P. Crouan & H. Crouan (Tabares *et al.* 1997; Afonso-Carrillo *et al.* 2002), *Ganonema* Fan & Wang (Afonso-Carrillo *et al.* 1998), *Helminthocladia* J. Agardh (O'Dwyer & Afonso-Carrillo 2001) and *Botryocladia* (J. Agardh) Kylin (Afonso-Carrillo & Sobrino 2003).

MATERIAL AND METHODS

Collections were made from 1984 to 2002 in the eulittoral and sublittoral zones at several localities in the Canary Islands. Material was studied while fresh, and was then preserved in 4% formalin in seawater. Permanent slides were prepared from liquid-preserved specimens. Selected fragments were stained in 1% aniline blue and mounted in 50% aqueous Karo syrup (Bestfoods, Englewood Cliffs, NJ, USA). Drawings were made using a camera lucida attached to a Zeiss Standard microscope (Carl Zeiss, Berlin, Germany). Micrographs were taken on a Zeiss photomicroscope. Herbarium abbreviations follow Holmgren *et al.* (1990).

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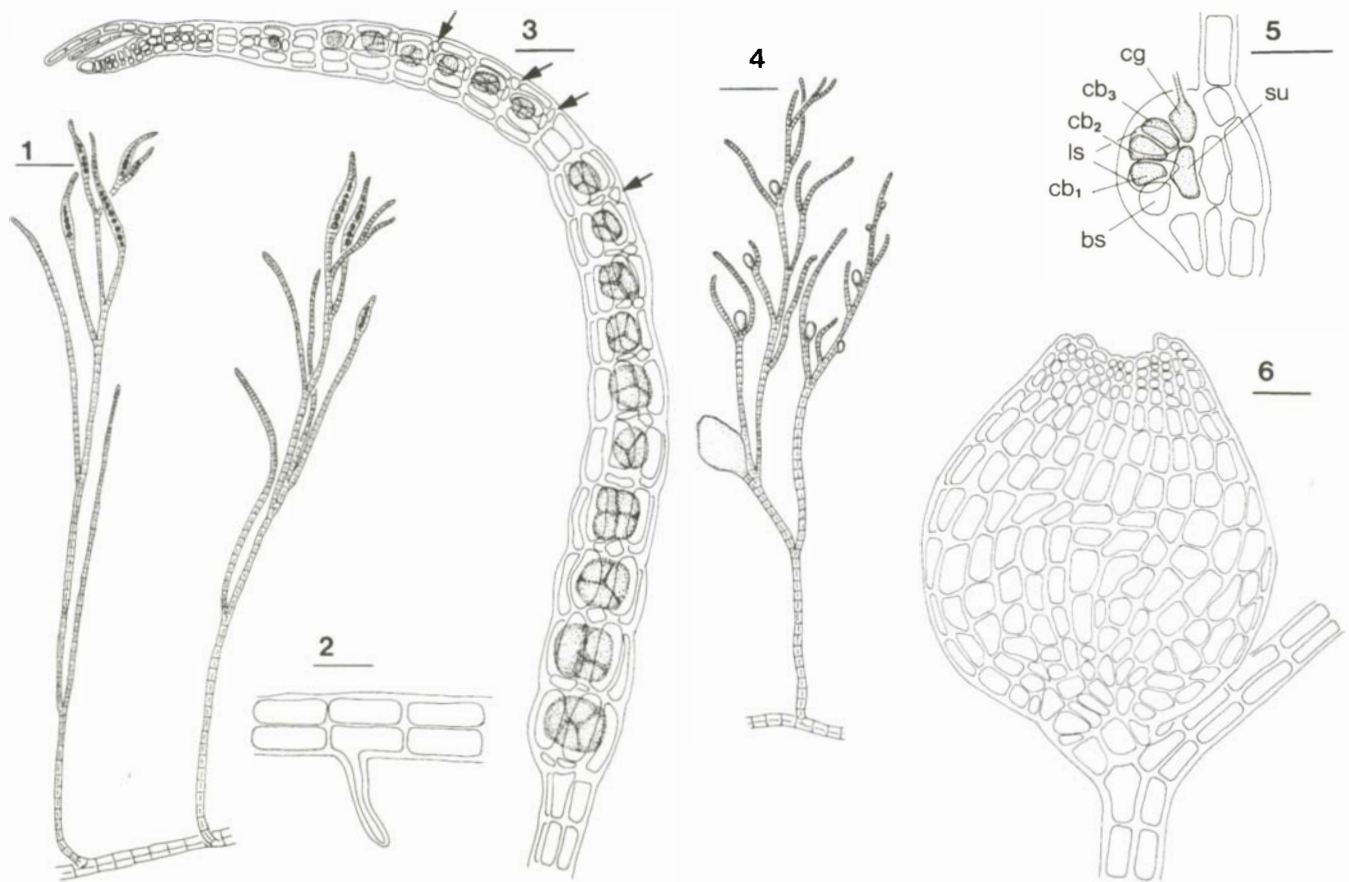
Figs 1–6. *Polysiphonia funebris* (TFC Phyc 9334).
  Fig. 1. Portion of the habit of a fertile tetrasporangial plant. Scale bar = 300 μm.
  Fig. 2. Prostrate axis with a nonseptate rhizoid. Scale bar = 50 μm.
  Fig. 3. Detail of fertile branch with tetrasporangia arranged in a straight row. Note postsporangial cover cells (arrows). Scale bar = 50 μm.
  Fig. 4. Portion of the habit of a fertile female plant. Scale bar = 300 μm.
  Fig. 5. Detail of the procarp (bs = basal sterile group; cb = carpogonial branch, with cell numbers; cg = carpogonium; ls = lateral sterile group; su = supporting cell). Scale bar = 20 μm.
  Fig. 6. Cystocarp showing outer pericarp polygonal cells. Scale bar = 50 μm.

OBSERVATIONS

Polysiphonia funebris J. Agardh (1863, p. 979)

Figs 1–6

TYPE LOCALITY: Genoa (Mediterranean Sea).

SELECTED COLLECTIONS: **Tenerife.** Las Teresitas (*B. Rojas-González & C. Ibeas,* 12 August 1992, TFC Phyc 9336; 28 July 1993, TFC Phyc 9335); Radazul (*B. Rojas-González & C. Ibeas,* 27 March 1993, TFC Phyc 9333); Puertito de Güímar (*B. Rojas-González & C. Ibeas,* 11 March 1993, TFC Phyc 9297). **La Palma.** Tazacorte (*B. Rojas-González & C. Ibeas,* 04 July 1993, TFC Phyc 9298, 9334).

The known distribution of this minute species is based on a limited number of reports and is restricted to several localities in the western Mediterranean Sea (see Gómez-Garreta *et al.* 2001), the nearby Atlantic coasts of Portugal (Ardré 1970), and the Canary Islands (Rojas-González *et al.* 1994). Until the finding of tetrasporic specimens by Pizzuto *et al.* (1996) at Lachea Island (western Mediterranean), the species was only characterized by its vegetative features. Canarian tetrasporic and cystocarpic specimens were collected in July, August and November, growing both in a higher-shore pool on the barnacle *Chthamalus stellatus* Poli and in the upper sublittoral zone on an anchor rope at 1–3 m depth. Plants consist of extensive prostrate axes that give rise to exogenously alternate-branched (in an alternate-subdistichous arrangement), erect axes that are up to 5 mm in height and 60–100 μm in diameter (Figs 1, 4). Axes are uncorticated, and have four pericentral cells, rhizoids in open connection with pericentral cells (Fig. 2), and very scarce trichoblasts (up to 210 μm long and arranged in a 1/4 short spiral series) that leave scar cells when they are shed. The tetrasporangia are borne in a straight series of 5–12 sporangia in the last two orders of branching; a single tetrasporangium occurs in each segment (Fig. 3). In sections of fertile branches, five pericentral cells are present, progressively expanded to one side as a result of the growth of the tetrasporangia. Mature tetrasporangia are irregularly spherical, 25–40 μm in diameter; they are tetrahedrally divided and covered by two enlarged presporangial cover cells and one small postsporangial cover cell (Fig. 3). The procarps arise on the second basal segment of a fertile trichoblast and consist of a four-celled carpogonial branch and two sterile-

cell groups (the lateral sterile group and the basal sterile group) borne on the supporting cell (Fig. 5). Mature cystocarps are ovoid, 375–425 μm long $\times$ 270–300 μm broad, and open by an ostiole 60–75 μm in diameter (Fig. 6). The outer pericarp cells are polygonal and arranged in irregular rows; they decrease in size towards the ostiole. The carposporangia are clavate, 47–75 μm long and 20–38 μm in diameter.

Although the plants examined are smaller and have less numerous trichoblasts than those from the Mediterranean, they exhibit the vegetative features used by Pizzuto *et al.* (1996) for the characterization of the Mediterranean plants. Nevertheless, the arrangement of tetrasporangia in the Canary Islands plants is in straight series, whereas Pizzuto *et al.* (1996) observed tetrasporangia in irregular right-handed spiral in the single previous report. This may not be a difference because the spiralling in the Mediterranean material may be secondary. Moreover, fertile segments of tetrasporangial plants contain five pericentral cells (instead of four in Mediterranean plants). Although Pizzuto *et al.* (1996) do not comment on this feature, five pericentral cells also occur in fertile segments of the type species of *Polysiphonia, P. stricta* (Dillwyn) Greville (Kim *et al.* 2000).

The plants examined exhibit an ensemble of attributes (four pericentral cells in vegetative axes, scarcity or absence of trichoblasts, nonseptate rhizoids, tetrasporangia in straight rows, and four-celled carpogonial branches) characteristic of the genus *Polysiphonia* Greville as recently delineated by Kim & Lee (1999) and Kim *et al.* (2000). This confirms that *P. funebris* is an unequivocal member of this genus. Among the species currently accepted in the redefined genus *Polysiphonia* (see Choi *et al.* 2001), *P. funebris* can be included in a small group of species [e.g. *P. namibiensis* Stegenga & Engledow (Stegenga *et al.* 1997) and *P. scopulorum* Harvey (Masuda *et al.* 2000)] that differ from the type species *P. urceolata* (Dillwyn) Greville [= *P. stricta* (Dillwyn) Greville] in having a small postsporangial cover cell that is lacking in the type species. According to Kim *et al.* (2000), the phylogenetic significance of this feature needs to be evaluated.

Polysiphonia tenerrima Kützing (1843, p. 417)

Figs 7–14

TYPE LOCALITY: Various syntype localities in Italy, western Mediterranean (Silva *et al.* 1996).

SELECTED COLLECTIONS: **Tenerife.** Punta Hidalgo (*J. Darias & R. González,* 26 February 1986, TFC Phyc 9360); Mesa del Mar (*B. Rojas-González & C. Ibeas,* 12 March 1993, TFC Phyc 9358); El Pris (*B. Rojas-González & C. Ibeas,* 7 April 1993, TFC Phyc 9359).

The Canarian collections represent the first report of this minute species in the Atlantic Ocean. This minute species, which grows as an epi-endophyte on *Nemalion helminthoides* (Velley) Batters, has previously been reported from the Mediterranean Sea (see Gómez-Garreta *et al.* 2001) and from Indonesia and the Seychelles in the Indian Ocean (Silva *et al.* 1996). Plants examined were up to 2 mm tall (Fig. 7) and in good agreement with previous descriptions (Kützing 1843, 1849, 1863; Agardh 1863; Falkenberg 1901; Athanasiadis 1987). Decumbent branches are attached by unicellular rhizoids up to 800 μm long, which cut off from the pericentral cells and penetrate deeply into the host tissue (Fig. 8). Erect branches are ecorticate with four pericentral cells. Segments

are 0.5–1 diameters long and up to 115 μm in diameter (Fig. 9). Trichoblasts are abundant and usually borne on every segment in 1/4 spiral divergence (Fig. 9), leaving conspicuous scar cells when shed. Lateral branches are formed at irregular intervals at the axils of trichoblasts. Plants are dioecious, and densely tufted spermatangial branches occur at the apices of young laterals. Spermatangial axes are formed at the first dichotomy of fertile trichoblasts, replacing one branch (Fig. 10). They are cylindrical, 110–135 μm long and 27–35 μm in diameter. Spermatangia are spherical to ovoid and about 3–4 μm in diameter. Procarps (although only one procarp was distinguished with certainty) have a three-celled carpogonial branch (Fig. 11); mature cystocarps are ovoid, 195–270 μm long and 165–225 μm broad, opening by an ostiole 35–50 μm in diameter (Fig. 12). The outer pericarp cells are polygonal and arranged in regular rows; they decrease in size towards the ostiole. Carposporangia are pyriform, 37–55 μm long and 12–23 μm in diameter (Fig. 13). In tetrasporangial plants, fertile segments have five pericentral cells; the second of these (placed next to the basal cell of the trichoblast) first cuts off two cover cells, and then divides into a lower stalk cell and an upper sporangium. Mature tetrahedrally divided tetrasporangia are arranged in a spiral series in upper branches and are 38–50 μm in diameter (Fig. 14).

Polysiphonia tenerrima was originally described by Kützing (1843) as an epiphyte on *Phlebothamnion grande* Kützing [= *Callithamnion granulatum*? (Ducluzeau) C. Agardh]. Hauck (1885) illustrated this plant under the name *Polysiphonia sertularioides* (Grateloup) J. Agardh β *tenerrima* Hauck and identified it as an epiphyte on *Nemalion lubricum* Duby (= *N. helminthoides*). Both Falkenberg (1901) and Athanasiadis (1987) recognized *P. tenerrima* as a separate species growing as an epi-endophyte on *Nemalion* Duby, although the latter author suggested that this taxon might represent a minute form of *P. sertularioides*. In the Canary Islands, *P. sertularioides* is common throughout the year on stones in tide pools and as an epiphyte on numerous seaweeds [*Padina pavonica* (Linnaeus) Thivy, *Colpomenia sinuosa* (Roth) Derbès & Solier, *Halimeda discoidea* Decaisne, and species of *Codium* Stackhouse]. These plants differ from those growing on *Nemalion* in several respects, for example: (1) they are longer (up to 30 mm long); (2) the segments in the lower portions are up to 3 diameters long and have spiralling pericentral cells; (3) the cystocarps are larger (up to 310 μm in diameter) and urceolate; and (4) the spermatangial axes are longer (up to 180 μm long). These differences support the retention of *P. tenerrima* as a separate species. However, the present concept of *P. tenerrima* could be wrong because the original diagnosis is not based on material growing in *Nemalion*. Although the name *P. tenerrima* has been widely used in the Mediterranean seaweed literature (see Gómez-Garreta *et al.* 2001), it is possible that the correct name for the plants growing in *Nemalion* should be *P. nemalionis* Zanardini (Zanardini 1843), a taxon included by Falkenberg (1901) among the synonyms of *P. tenerrima*. Comparison of the type material of both *P. tenerrima* and *P. nemalionis* is necessary to make a decision with confidence.

Plants of *P. tenerrima* seem to show the vegetative and reproductive characters used by Kim & Lee (1999) to define the genus *Neosiphonia* Kim & Lee: they have ecorticate axes with four pericentral cells, abundant spirally arranged tricho-
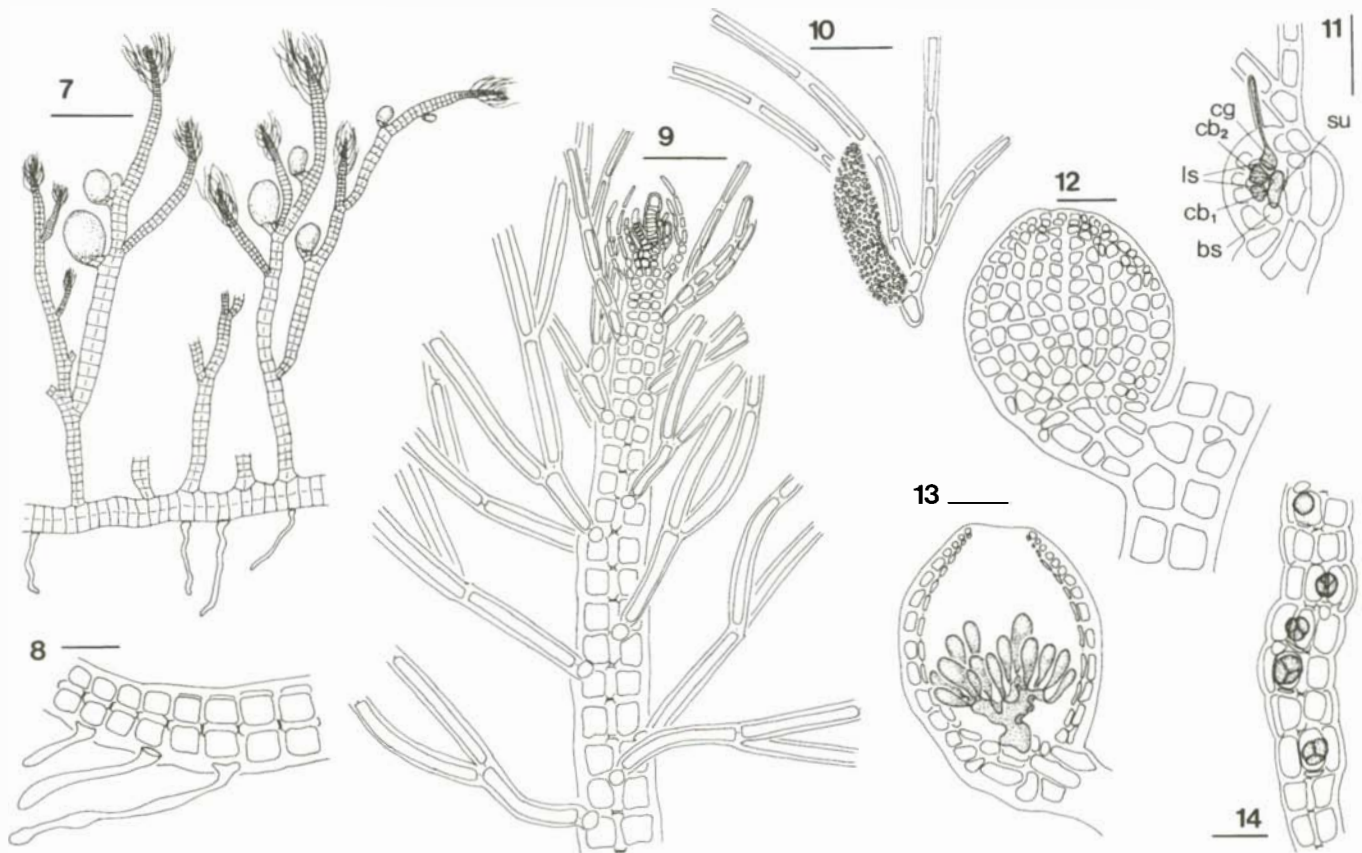
Figs 7–14. *Polysiphonia tenerrima* (TFC Phyc 9358).
Fig. 7. Portion of the habit of a fertile female plant. Scale bar = 300 μm.
Fig. 8. Prostrate axis with rhizoids cut off from pericentral cells. Scale bar = 50 μm.
Fig. 9. Apex of an erect axis showing abundant spiral arranged trichoblasts. Scale bar = 50 μm.
Fig. 10. Detail of fertile trichoblast with a spermatangial axis replacing a branch at the first dichotomy. Scale bar = 50 μm.
Fig. 11. Detail of the procarp (bs = basal sterile group; cb = carpogonial branch, with cell numbers; cg = carpogonium; ls = lateral sterile group; su = supporting cell). Scale bar = 20 μm.
Fig. 12. Cystocarp showing outer pericarp polygonal cells. Scale bar = 50 μm.
Fig. 13. Longitudinal section of a cystocarp showing the cellular fusion and carposporangia. Scale bar = 50 μm.
Fig. 14. Detail of fertile axis with spirally arranged tetrasporangia. Scale bar = 50 μm.

blasts, rhizoids that are cut off from pericentral cells, tetrasporangia that are produced in spiral series, and, apparently, procarps with a three-celled carpogonial branch. Nevertheless, at present, the circumscription of the genus *Neosiphonia* has not been clarified beyond excluding *Polysiphonia sensu stricto* (Kim *et al.* 2000) and some polysiphonous species (Choi *et al.* 2001). We prefer to retain the present status of *P. tenerrima* until these questions are clarified.

Dipterosiphonia reversa Schneider (1975, p. 392)
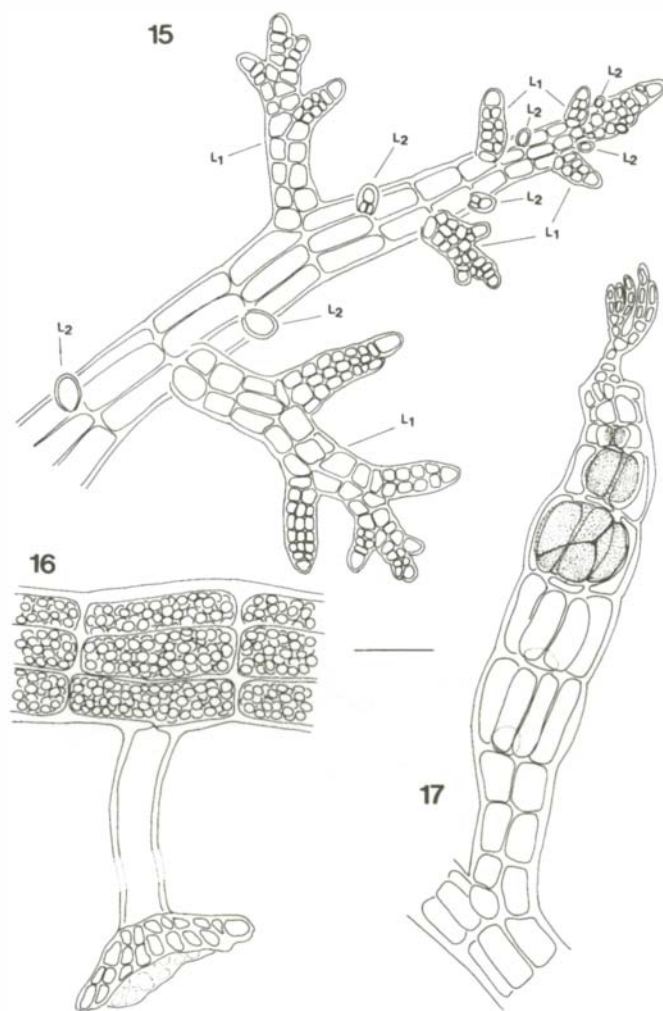
Figs 15–17

TYPE LOCALITY: North Carolina, western Atlantic.

SELECTED COLLECTIONS: **Tenerife.** Punta de Güímar (*G. Dionis,* 15 April 1984, TFC Phyc 10966).

Dipterosiphonia reversa was described by Schneider (1975) based on sterile off-shore specimens from North Carolina (western Atlantic), and was later reported from Georgia (Searles 1987). Up until now it has been considered to be a deep-water species endemic to the southeastern United States

(Schneider & Searles 1991). Only sterile plants of *D. reversa* were known until we found tetrasporangial plants in the Canary Islands.

The specimens of *D. reversa* were identified in a collection of maerl obtained by dredging at 50 m depth. They were abundant, growing among the protuberances of fruticose rhodoliths of *Lithothamnion corallioides* P. Crouan & H. Crouan. Plants examined matched previous descriptions of the species (Schneider 1975; Schneider & Searles 1991). Plants were largely sterile and only a few specimens had tetrasporangia. Plants are up to 15 mm in length, prostrate, polysiphonous, ecorticate (with five pericentral cells), dorsiventrally organized (Fig. 15), and attached by unicellular rhizoids that are cut off from the pericentral cells and end in a multicellular discoid holdfast (Fig. 16). Main indeterminate axes produce alternate pairs of lateral branches on opposite sides. The first-formed of each pair develops into a pinnate determinate or indeterminate branch, whereas the second-formed branch often does not develop or remains only a few cells in length (Fig. 15). According to Schneider (1975), *D. reversa* is unique among species of the genus *Dipterosiphonia* in having the

Figs 15–17. *Dipterosiphonia reversa* (TFC Phyc 10966). Scale bar = 50 μm.

Fig. 15. Detail of terminal portion of prostrate indeterminate axis showing alternate pairs of lateral branches. The first-formed of each pair (L_1) develops into a pinnate determinate branch and the second-formed branch (L_2) remains reduced to one or a few cells in length.

Fig. 16. Detail of a mature prostrate axis with a rhizoid cut off from a pericentral cell terminating in a multicellular discoid holdfast. Pericentral cells are filled with starch grains.

Fig. 17. Detail of a pinnate determinate branch showing tetrasporangia and a rudimentary trichoblast at the apex.

branched and unbranched members of alternate pairs in reverse sequence from all other taxa previously described. This branching sequence is evident at the apex of plants (Fig. 15), and it permits one to distinguish *D. reversa* easily from *D. dendritica* (C. Agardh) Schmitz and *D. rigens* (C. Agardh) Falkenberg, the other *Dipterosiphonia* species present in the Canary Islands (Afonso-Carrillo & Sansón 1999). Trichoblasts (up to 60 μm long and with two dichotomies) are developed singly at the apices of determinate laterals in fertile specimens (Fig. 17). One tetrasporangium is produced per segment in short linear series up to six segments long in the pinnate laterals (Fig. 17). Fertile segments also form five pericentral cells. The fertile pericentral cell initially cuts off two presporangial cover cells, and the pericentral cell next divides into a tetrasporangium and a stalk cell. A postsporangial cover

cell is not formed. Tetrasporangia segment by a single division, resulting in four tetrahedrally arranged spores. Mature tetrasporangia are spherical (up to 60 μm in diameter) and each segment swells (Fig. 17). The rare elaboration of specialized reproductive structures and the abundant accumulation of starch grains in the cells of the older portions of the plants (Fig. 16) suggest that vegetative spread occurs by extensive growth, followed by fragmentation of prostrate axes.

With the record of this taxon in the eastern Atlantic, *D. reversa* joins other amphi-Atlantic species with strictly warm temperate zone distributions, such as *Codium carolinianum* Searles, *Porphyra carolinensis* Coll & Cox, *Gloiocladia blomquistii* (Searles) R.E. Norris, *G. rubrispora* (Searles) R.E. Norris, and *Colaconema ophioglossum* (Schneider) Afonso-Carrillo, Sansón & Sangil (Schneider & Searles 1998; Sansón *et al.* 2002; Afonso-Carrillo *et al.* 2003). As with *D. reversa,* these species were initially thought to be endemic to the warm temperate northwest Atlantic Region (Hoek 1984; Schneider & Searles 1991) before their discovery in the Canary Islands (Chacana 1991; Reyes *et al.* 1993; Sansón *et al.* 2002; Afonso-Carrillo *et al.* 2003).

Veleroa complanata Afonso-Carrillo & Rojas-González, *sp. nov.*

Figs 18–33

Plantae saxicolae, repentes vel decumbentes, axibus polysiphoniis repentibus ad substratum per rhizoidea fasciculata affixis et axibus polysiphoniis erectis usque 30 mm altis, his persistentibus determinatis pigmentosis trichoblastis vestitis, dispositis spiraliter. Axes polysiphonii cylindrici, quattuor cellulis pericentralibus, progressive corticatis, usque 60–600 μm diametro. Trichoblasti exogeni, spiraliter dispositi, usque 20 cellulas longi et 400–600 μm longi, ferentes usque 6–8 ramos laterales alternidistiche complanate dispositos. Trichoblasti simplices (rare 1–4 subdichotome ramificati) in axibus decumbentibus et portionibus fertilibus axium erectorum restricti. Tetrasporangia, uno in quoque segmento, in portionibus terminalibus axium polysiphoniorum posita. Tetrasporangia spiraliter ordinata, subsphaerica, 40–70 μm diametro, divisa tetraedrice. Spermatangia et cystocarpia ignota.

Plants saxicolous, prostrate or decumbent, with creeping polysiphonous axes attached by clumped rhizoids and erect polysiphonous axes up to 30 mm in height, clothed with determinate pigmented persistent trichoblasts, spirally arranged. Polysiphonous axes terete, with four pericentral cells, progressively corticated, and 60–600 μm in diameter. Trichoblasts exogenous, spirally arranged, up to 20 cells long and 400–600 μm in length, with up to 6–8 laterals in an alternate-distichous complanate arrangement. Trichoblasts simple (rarely 1–4 times subdichotomously branched), restricted to prostrate axes and fertile portions of erect axes. Tetrasporangia one per segment in terminal portions of polysiphonous axes. Tetrasporangia formed in spirals, subspherical, 40–70 μm in diameter, and tetrahedrally divided. Spermatangia and cystocarps unknown.

HOLOTYPE: Canary Islands. Tenerife, Puerto de la Cruz, TFC Phyc 10971 (Fig. 18), tetrasporophyte, epilithic in a shaded crevice of lower-shore pool, 30 March 2002, leg. *J. Afonso-Carrillo.*

ETYMOLOGY: The specific epithet refers to the flattened ramification of the trichoblasts in erect axes.

REPRESENTATIVE SPECIMENS EXAMINED: **Canary Islands.** Tenerife, Puerto de la Cruz (*B. Rojas-González & C. Ibeas,* 1 February 1991, TFC Phyc 9214; 1 April 1991, TFC Phyc 9215; 22 January 1992, TFC Phyc 9216; 9 May 1992, TFC Phyc 9218; 29 July 1992, TFC Phyc 9219; 13 December 1992, TFC Phyc 9221; 12 February 1993, TFC Phyc 9222; 23 May 1993, TFC Phyc 9223; 25 July 1993, TFC Phyc 9224; *J. Afonso-Carrillo,* 9 March 1992, TFC Phyc 9217; 29 October 1992, TFC Phyc 9220; 14 September 2000, TFC Phyc

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Figs 18, 19. *Veleroa complanata.*
Fig. 18. Holotype specimen (TFC Phyc 10971). Scale bar = 5 mm.
Fig. 19. Young erect axes with branched trichoblasts formed from a prostrate axis. The prostrate axis is attached by vigorous rhizoids and exhibits unbranched trichoblasts. (TFC Phyc 9219). Scale bar = 300 μm.

10965; 28 April 2002, TFC Phyc 10972; 30 May 2002, TFC Phyc 10973; 29 June 2002, TFC Phyc 10974; 30 July 2002, TFC Phyc 10975; 29 August 2002, TFC Phyc 10976); Tenerife, San Marcos, Icod (*J. Reyes & E. Muñoz*, 25 May 1995, TFC Phyc 9682).

DISTRIBUTION: Tenerife, Canary Islands.

HABITAT AND SEASONALITY: An epilithic population of *V. complanata* growing on a vertical shaded surface in a small lower-shore pool in an area of high water movement has been periodically examined for the last twelve years. Prostrate axes are found throughout the year and are probably perennial, giving rise in November–March to erect axes that become fertile with tetrasporangia from January to May, and many persist as senescent until October–November. Other algae occurring in this habitat include *Gymnothamnion elegans* (C. Agardh) J. Agardh, *Microdictyon calodictyon* (Montagne) Kützing and *Rhodymenia pseudopalmata* (J.V.F. Lamouroux) Silva.

HABIT AND VEGETATIVE STRUCTURE: Plants are prostrate or decumbent, rose-red in colour, consisting of creeping branched polysiphonous axes attached by clumped rhizoids, and simple or little-branched erect polysiphonous axes up to 30 mm in height, clothed with spirally arranged, determinate, rhodoplastic, persistent trichoblasts (Fig. 18). Trichoblasts in infertile portions of erect axes are complanately branched and usually arranged in one plane in a falsely distichous pattern, giving the erect portions an oval–lineal outline (Fig. 19).

Prostrate axes are cylindrical and grow from dome-shaped apical cells that are 10–12 μm long and 8–10 μm in diameter (Fig. 20); four pericentral cells are formed in an alternating sequence. The polysiphonous segments are initially broader than long, but elongate subsequently to up to two diameters long (to 120 μm × 90 μm). The prostrate axes become extensively corticated, increasing in diameter (up to 600 μm) in older portions. Corticating initials are cut off from the posterior ends of pericentral cells at 15–20 segments from the apex (Figs 20, 21). These initials give rise to rhizoidal corticating filaments that grow only downwards, between the pericentral cells and over the surface of the axes. The compound rhizoids arise at irregular intervals from the proximal and adjacent distal ends of pericentral cells of successive polysiphonous segments (Figs 21–23), and all rhizoidal initials are pit-connected to a pericentral cell. The rhizoids reach up to 500 μm in length and end in a multicellular adhesive pad; their diameter increases up to 150 μm by cortical filaments (Fig. 23). Trichoblasts on prostrate axes arise exogenously from every segment in a 1/4 spiral divergence. They are up to 12-celled and 240 μm in length, pigmented, unbranched and slightly subulate (Fig. 20). The basal cell of each trichoblast is isodiametric (16–26 μm broad); the remaining cells are subcylindrical and progressively smaller (from 30 × 19 μm in proximal cells to 10 × 7 μm in distal cells), so the trichoblast ends in a pointed apical cell. Trichoblasts from prostrate axes are caducous, but the basal cells persist as scar cells.

The prostrate axes form erect axes and further prostrate axes at irregular intervals. Indeterminate erect axes arise exogenously in the position of a trichoblast, and show monopodial growth by means of a single, transversely dividing apical cell of the same size and shape as the apical cells of prostrate axes (Fig. 24). Pericentral cells are not cut off until the
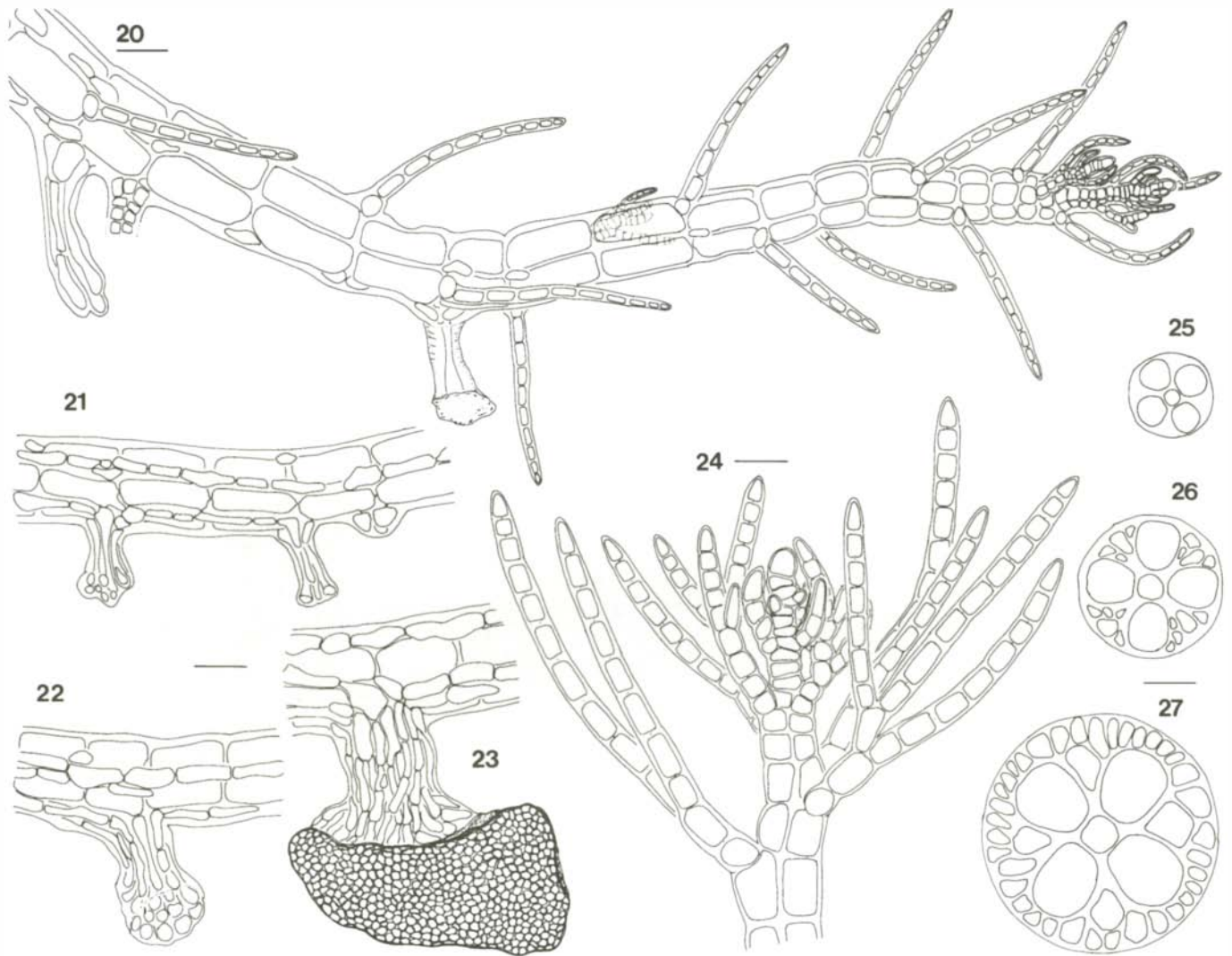
Figs 20–27. *Veleroa complanata.*
   Fig. 20. Apex of a prostrate axis with unbranched trichoblasts arranged in a spiral sequence. (TFC Phyc 9682). Scale bar = 50 μm.
   Figs 21–23. Successive developmental stages of compound rhizoids. (TFC Phyc 9214). Scale bar = 50 μm.
   **Fig. 24.** Apex of an erect axis showing production of trichoblasts from the third or fourth subapical segment cell in a ¼ clockwise descending spiral (TFC Phyc 9682). Scale bar = 20 μm.
   Figs 25–27. Transverse sections of polysiphonous axes showing the axial cell and the four pericentral cells progressively surrounded by cortical cells (TFC Phyc 9221). Scale bar = 50 μm.

6th to 12th segment from the apical cell. The sequence of initiation of pericentral cells appears to be invariable, and four pericentral cells are always formed per segment. The first pericentral cell is cut off directly below the basal cell of the trichoblast, the second next to the first on one side of the axial cell, the third next to the first on the other side, and the fourth between the third and the second pericentral cells. Pericentral cells are subcylindrical, reaching up to 100 μm in length and 50 μm in diameter; they delineate polysiphonous segments that are broader than long near the apices to nearly square (up to 100 μm long × 120 μm broad) before being obscured by cortication. Cortical cells are slowly produced as described for prostrate axes, increasing the diameter of proximal portions of mature erect axes to 600 μm (Figs 25–27).

A branched, pigmented, determinate, monosiphonous trichoblast is produced exogenously from every segment. Tri-choblasts are initiated from the third or fourth subapical segment cell and are cut off in a 1/4 clockwise descending spiral (Figs 24, 28, 29). Trichoblasts are up to 20 cells long, relatively stiff, and 400–600 μm in length. They develop monopodially and produce up to six to eight laterals on successive segments in an alternate-distichous arrangement, beginning from the suprabasal cell alternate (Figs 28, 29). The basal cell of trichoblasts is nearly isodiametric and up to 30 μm broad. The other cells of the trichoblasts are subcylindrical, 50 × 30 μm in proximal portions, becoming slightly shorter and thinner (30 × 18 μm) distally. The two or three subapical cells of each trichoblast are shorter, ending in a conical apical cell. Although trichoblasts arise radially, the erect axes frequently appear complanate because the branching of the trichoblasts occurs in the same plane as the polysiphonous axis. Proximal portions of senescent erect axes become partially denuded by
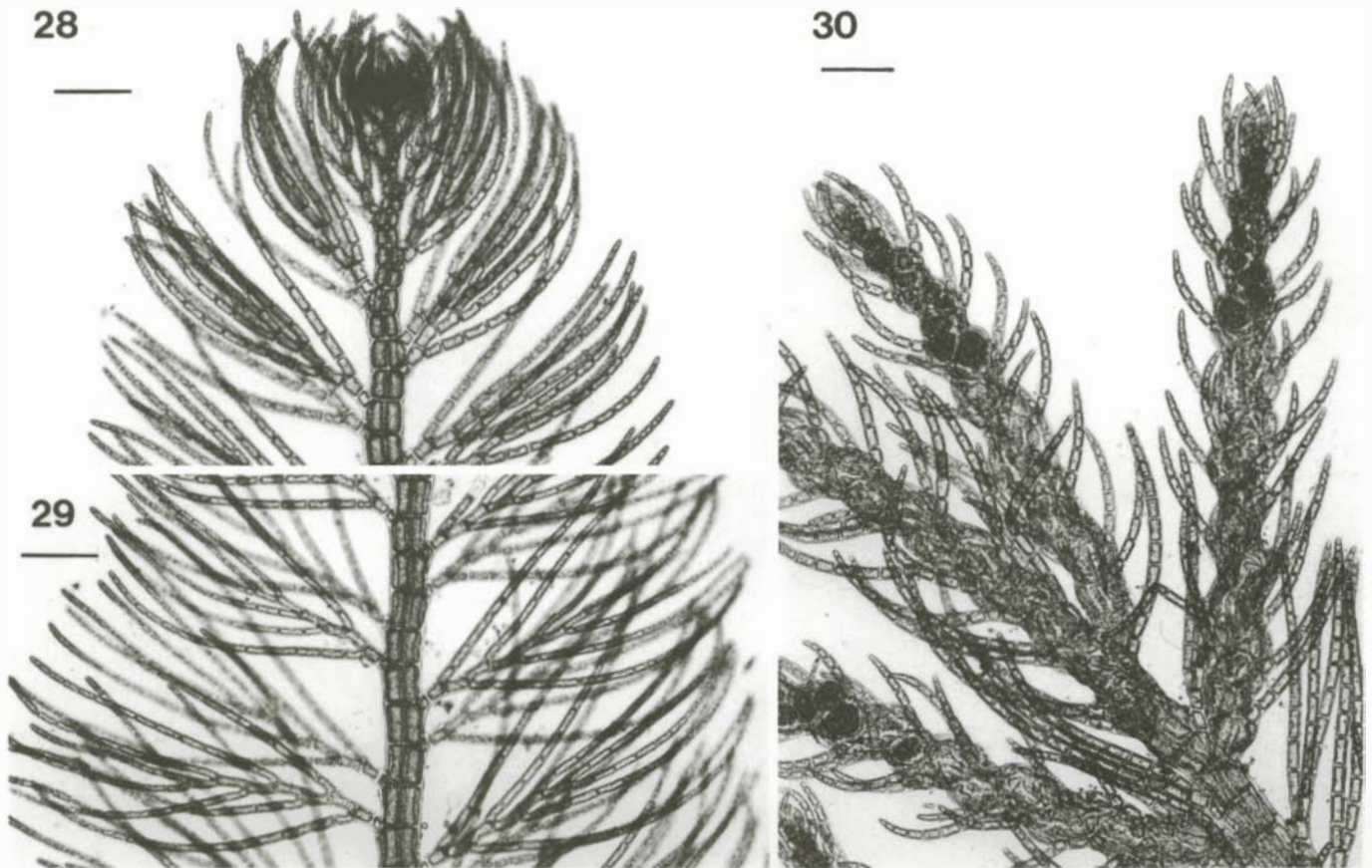
Figs 28–30. *Veleroa complanata* (TFC Phyc 9219).
Fig. 28. Apex of an erect axis. Scale bar = 100 μm.
**Fig. 29.** Detail of median portion of an erect axis. Scale bar = 100 μm.
Fig. 30. Fertile polysiphonous branches with tetrasporangia. Scale bar = 100 μm.

damage to the trichoblasts. Indeterminate polysiphonous lateral branches also arise exogenously, replacing a trichoblast at irregular intervals, and retaining the planar arrangement of the trichoblasts. These laterals are identical to the main indeterminate axis in their development and pattern of trichoblasts, but are thinner (60–80 μm in diameter) and generally much shorter.

REPRODUCTION: Tetrasporangia are produced singly per segment in indeterminate polysiphonous branches occurring in distal portions of erect axes (Figs 30, 31). Fertile branches are simple or branched proximally 1–4 times; they reach 2–5 mm in length and are clothed by unbranched (rarely 1–4 times subdichotomously branched), persistent, rhodoplastic, spirally arranged trichoblasts (Figs 30, 31). Unbranched trichoblasts from fertile branches resemble the trichoblasts on prostrate axes. They are 9–12 cells long, relatively stiff, slightly subulate, somewhat curved upward and up to 250 μm long. Tetrasporangia are formed in apical portions in an uninterrupted 1/4 spiral series of fertile segments (Fig. 31). They develop in a regular sequence in long indeterminate series; at least 10–20 tetrasporangia in different degrees of development occur simultaneously. In every segment, the fertile pericentral cell is the one next to the basal cell of the trichoblast. This cell cuts off three presporangial cover cells longitudinally and then

divides transversally to produce the sporangial initial and the stalk cell (Figs 32, 33). The mature tetrahedrally divided tetrasporangia are subspherical or slightly deformed by the pressure of tetrasporangia from neighbouring segments. Tetrasporangia enlarge to 40–70 μm in diameter and the cover cells stretch, producing a marked swelling on one side of the segment (Fig. 33). Successive swollen segments persist after tetrasporangia are discharged, delineating the stichidia-like appearance of the spiralled fertile branches. Spermatangia, procarps and cystocarps have not been observed.

REMARKS: Observations on *V. complanata* from the Canary Islands clearly show that this species is a member of the Rhodomelaceae. Despite the absence of information on the spermatangial branches and the procarps, a tribal and generic affiliation can be proposed with confidence because the new species exhibits at least two relevant features that are of limited distribution in the family. The elaboration of rhodoplastic persistent trichoblasts and the production of tetrasporangia within ordinary polysiphonous branches are attributes exclusive to the tribe Lophothalieae (Falkenberg 1901). Although Parsons (1975) proposed the subdivision of Lophothalieae into two tribes [Lophothalieae *sensu* Parsons (1975) and Brongniartelleae (Parsons 1975, 1980)], this proposal has recently been dropped (Womersley 2003). Parsons (1975) had based
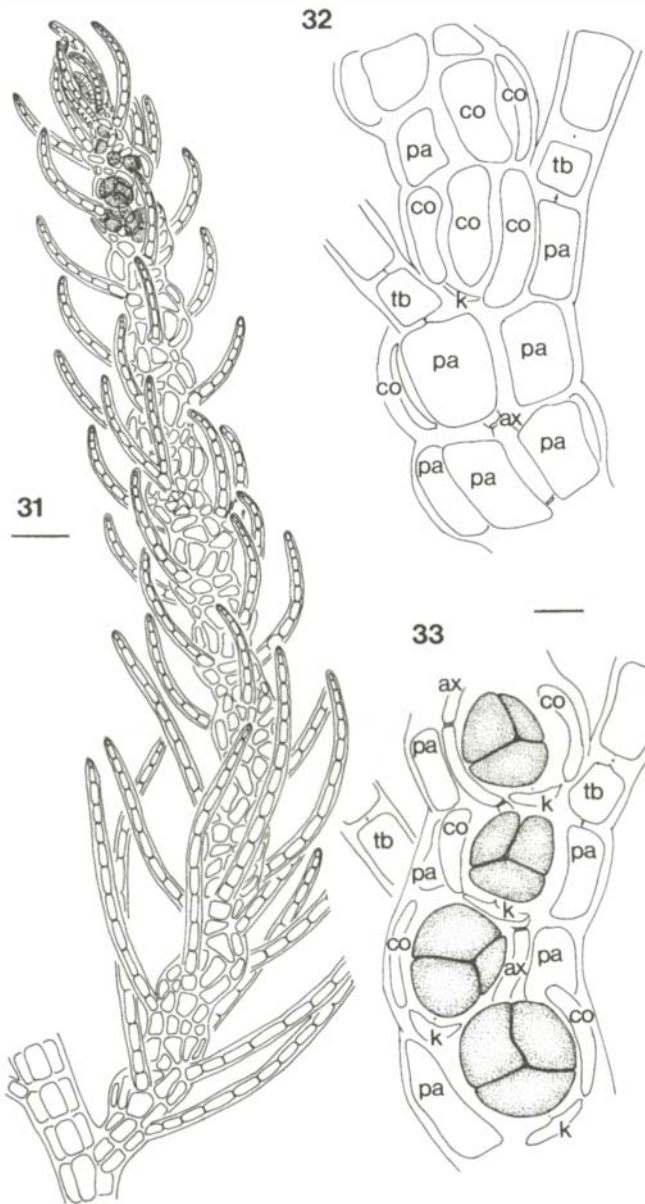
Figs 31–33. *Veleroa complanata*. (TFC Phyc 9214).
Fig. 31. Polysiphonous branch with tetrasporangia. Note spiral arrangement of exclusively simple trichoblasts. Scale bar = 100 μm.
Fig. 32. Details of four successive fertile segments with tetrasporangia in surface view. Scale bar = 20 μm.
Fig. 33. Optical axial section of the same axes in Fig. 32. Scale bar = 20 μm. (ax = axial cell; co = presporangial cover cell; k = stalk cell; pa = pericentral cell; tb = trichoblast). Scale bar = 20 μm.

his tribes on whether the procarp contained one (Lophothalieae) or two (Brongniartelleae) sterile cell groups, a feature that was scarcely confirmed in representatives of these tribes (Parsons 1975, 1980; Wynne & Norris 1982; Millar 2000a).

Within the tribe Lophothalieae *sensu lato,* an important defining feature is the number of pericentral cells per segment in polysiphonous axes (Falkenberg 1901; Kylin 1956; Millar 2000a, b). Comparisons between the 18 genera presently included in the tribe Lophothalieae reveal that only nine possess polysiphonous axes with four pericentral cells [*Doxodasya*

Falkenberg, *Endosiphonia* Zanardini, *Holotrichia* Schmitz, *Lophocladia* (J. Agardh) Schmitz, *Murrayella* Schmitz, *Murrayellopsis* Post, *Spyrocladia* Børgesen, *Veleroa* Dawson and *Wrightiella* Schmitz]. However, *Doxodasya, Endosiphonia, Holotrichia, Lophocladia, Spyrocladia* and *Wrightiella* have tetrasporangia formed in stichidia on modified trichoblasts (Kylin 1956) and thus cannot be allied to *V. complanata.* The remaining three genera (*Murrayella, Murrayellopsis* and *Veleroa*) all have tetrasporangia formed within normal polysiphonous indeterminate branches. But in *Murrayellopsis,* tetrasporangia are arranged in decussate pairs (Post 1962; Abbott & Hollenberg 1976), and in *Murrayella* in whorls of four (Børgesen 1920). The new species can only be accommodated in *Veleroa,* a genus characterized by its invariable number (four) of pericentral cells in the polysiphonous axes, radially developed axes, and production of a single tetrasporangium in each segment (Millar 2000b; Womersley 2003).

The genus *Veleroa* was established by Dawson (1944) and currently includes five species of minute polysiphonous plants that have been mainly defined by vegetative features such as the erect or decumbent nature of the habit, and the size, shape and branching of the trichoblasts (Saenger 1982; Millar 2000b; Womersley 2003). Species of *Veleroa* have been reported infrequently and appear to have very restricted distributions in the warm temperate to tropical Indo-Pacific. The type species *V. subulata* Dawson is known from the Gulf of California (the type locality), Santa Catalina Island in California and Hawaii (Abbott & Hollenberg 1976; Aguilar-Rosas *et al.* 2000; Millar 2000b). *Veleroa karuvalensis* (Varma) Krishnamurthy & Thomas (Krishnamurthy & Thomas 1971) is known from India (Varma 1960, as *Lynkiella karuvalensis* Varma) and Papua New Guinea (Coppejans & Millar 2000). *Veleroa elongata* Saenger (Saenger 1982) is known from Queensland (Australia), and *V. magneana* Millar (Millar 2000b) from the Coral Sea in the South Pacific. *Veleroa adunca* (J. Agardh) Womersley & Parsons in Womersley (2003) is known only from southern Australia and Tasmania [Falkenberg (1901), as *Brongniartella disticha* Falkenberg; Kylin (1956), as *Thaumatella disticha* (Falkenberg) Kylin]. Differences between species of *Veleroa* are presented in Table 1.

The new species is mainly distinguished by the branching pattern of the trichoblasts and the elaboration of the cortex in the polysiphonous axes. Trichoblasts in other members of the genus are reported to be simple or with up to three subdichotomous branches (Dawson 1963; Krishnamurthy & Thomas 1971; Saenger 1982; Millar 2000b) but never until now with up to eight laterals in an alternate-distichous arrangement (Table 1). The production of rhizoidal cortical cells around the polysiphonous axes has not been previously described in species of *Veleroa,* and consequently the genus has been characterized as ecorticate (Millar 2000b; Womersley 2003). Although both of these vegetative features demonstrate that *V. complanata* is different from the known species of *Veleroa* (Table 1), and the elaboration of cortication has been used as a diagnostic feature at genus level in Lophothalieae (Kylin 1956; Millar 2000b), they seem insufficient at the moment to justify the erection of a new genus. The radial arrangement of unbranched trichoblasts in the fertile tetrasporangial branches appears to justify the inclusion of *V. complanata* in *Veleroa* because this character is also shared by the type species *V. subulata* (Dawson 1944, 1963).

Table 1. Comparison of species of *Veleroa*.

Character	V. adunca[1]	V. complanata	V. elongata[2]	V. karuvalensis[3]	V. magneana[4]	V. subulata[5]
Distribution	Southern Australia, Tasmania	Canary Islands, Eastern Atlantic	Gladstone, Queensland, Australia	India and Papua New Guinea	Coral Sea, South Pacific	Pacific Mexico, California
Habit	decumbent	decumbent	erect	erect	decumbent	erect
Maximum height of erect axes (mm)	40	30	15	70	4	15
Maximum diameter of polysiphonous axes (μm)	170	600	320	210	64	70
Cortication	absent	present	absent	absent	absent	absent
Trichoblasts	branched with 1–3 subdichotomies	simple or branched with up to 8 alternate–distichous laterals	simple	simple	mostly simple, rarely up to 3 subdichotomies	mostly simple, rarely up to 3 subdichotomies
Maximum length of trichoblasts (μm)	1500	600	1500	1400	900	700
Number of cells in trichoblasts	no data	9–20	7–8	4–7	15–24	7–9
Shape of cells in trichoblasts	long and tapering gradually	short cylindrical, all similar in length	elongate cylindrical, much shorter in proximal and distal portions	elongate inflated, much shorter and thinner in proximal and distal portions	elongate cylindrical, all similar in length	short subulate, all similar in length
Maximum diameter of cells in trichoblasts (μm)	55	30	60	105	12	40
Number of fertile segments in tetrasporangial series	no data	indeterminate	6–15	no data	6–16	8–15
Spermatangial axes	ovoid	unknown	subcylindrical	spherical	subcylindrical	unknown
Cystocarps	ovoid with a pronounced neck	unknown	unknown	no data	unknown	unknown

[1] Data on *V. adunca* from Womersley (2003).
[2] Data on *V. elongata* from Saenger (1982).
[3] Data on *V. karuvalensis* from Krishnamurthy & Thomas (1971) and Varma (1960, as *Lynkiella karuvalensis* Varma).
[4] Data on *V. magneana* from Millar (2000b).
[5] Data on *V. subulata* from Dawson (1944, 1963).

Finally, one reproductive feature exhibited by the new species needs additional commentary. Before the formation of the sporangial initial, three presporangial cover cells are cut off longitudinally from the fertile pericentral cell in each segment of fertile axes. This unusual feature was previously observed also in *V. magneana* by Millar (2000b), whereas the Lophothalieae described in Parsons (1975) all have two presporangial and one postsporangial cover cells. The taxonomic significance of this important character is presently uncertain, due to the absence of appropriate observations on the reproductive morphology of many poorly known Rhodomelaceae. At the moment, *V. magneana* and *V. complanata* seem distinct on the basis of the cells covering the tetrasporangium. Even the potential usefulness of this feature as diagnostic of *Veleroa* needs confirmation for the remaining species of the genus, which were insufficiently described with respect to this characteristic.

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