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STUDIES ON THE *SARCOMENIA* GROUP OF THE RHODOPHYTA

By H. B. S. WOMERSLEY and E. ANN SHEPHERY

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Summary

A study of species placed in the genus *Sarcomenia*, and study of allied genera, shows that *Sarcomenia* includes only one species, *S. delesserioides* Sonder. Other species belong either to *Platysiphonia* Boergesen or to *Sarcotrichia* gen. nov. The Australian *Polysiphonia roeana* is shown to belong to the *Sarcomenia* group and is placed in a new genus, *Malaconema*. Other related genera which are discussed are *Cottoniella* Boergesen and *Taenioma* J. Agardh. *C. hawaiiensis* Doty & Wainwright is placed in a new genus, *Dotyella*.

These genera form a uniform group, distinguished largely on vegetative features since their reproductive structures are very similar. The *Sarcomenia* group forms an intermediate and linking group between the Delesseriaceae and Rhodomelaceae, but shows somewhat more features in common with the latter family and may have been derived from rhodomelaceous ancestors. The group is recognized as a subfamily, the Sarcomenioideae, of the Rhodomelaceae, and all other groups of the Rhodomelaceae are considered to form a second subfamily, the Rhodomeloideae. Phylogenetic relationships of the Sarcomenioideae are discussed.

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I. INTRODUCTION

The *Sarcomenia* group has been recognized as an entity since the tribe Sarcomeniaceae was first described by J. Agardh (1863), but its systematic position, and more recently the genera it includes, have been much debated. Agardh placed the *Sarcomenia* group in the Rhodomelaceae and included the following genera: *Sarcomenia*, *Taenioma*, *Vanvoorstia*, and *Claudea*. Although Agardh (1896, pp. 120-37; 1899, pp. 130-49) strongly maintained the rhodomelaceous affinities of the group, Schmitz (1889), Schmitz and Hauptfleisch (1897), and in particular Falkenberg (1901), were equally emphatic that the group belonged to the Delesseriaceae.

More recent authors have usually agreed with the delesseriaceous position of the *Sarcomenia* group, but Papenfuss (1937) split off *Claudea*, *Vanvoorstia*, and *Caloglossa* as the *Claudea* group of the Delesseriaceae. Kylin (1956) recognizes *Sarcomenia*, *Taenioma*, *Platysiphonia*, *Cottoniella*, and *Sonderella* as members of the *Sarcomenia* group.

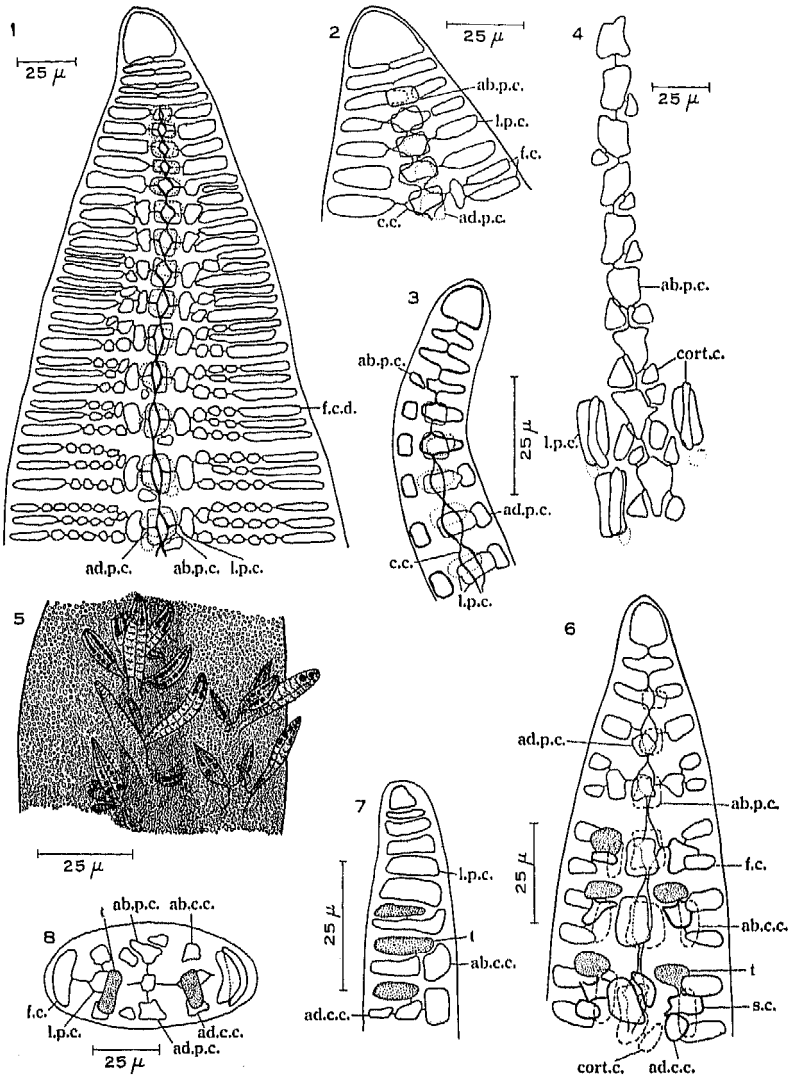
It is most noteworthy that only J. Agardh examined *Sarcomenia* in any detail. Falkenberg studied *Taenioma* as an example of the group, as also did Papenfuss (1944). Recent views on the position of the *Sarcomenia* group have thus not been based on the genus after which the group was named, and therefore are not well founded. This is in large measure due to the difficulty in studying dried material of *Sarcomenia* and allied genera, since they adhere closely to paper and largely disintegrate on being soaked off the paper. No species of *Sarcomenia* has been studied in full detail previously.

This study, based on adequate liquid-preserved material, was undertaken to clarify the position of the *Sarcomenia* group and its relationships to the Delesseriaceae and Rhodomelaceae. The genera investigated are those currently recognized by Papenfuss (1937) and Kylin (1956) after segregation of the *Claudea* group, with the exclusion of *Sonderella* Schmitz. This genus proves to be a member of the Rhodomelaceae allied to the *Amansia* group, and its structure and reproduction will be described in a separate paper.

II. MATERIAL AND METHODS

In most cases the material was preserved in 4 per cent. formalin-sea-water. No liquid-preserved material of certain species was available but the essential features were studied from herbarium specimens after brief soaking in detergent and careful removal from the paper. In general 1 per cent. aqueous aniline blue ($\frac{1}{2}$ min to a few minutes) fixed in dilute hydrochloric acid, was found to be an excellent stain. After washing, selected fragments were mounted directly in 50 per cent. Karo syrup, or, if more delicate, placed in 20 per cent. Karo syrup which was allowed to concentrate before mounting. Such mounts hardened considerably over a few weeks and proved much superior to glycerine mounts.

For studies of the segmentation of the lateral pericentral cells of the stichidia, to form the tetrasporangia and cover cells, the material was cleared in 5 per cent. potassium hydroxide and a whole branch mounted. Stichidia lying on edge could then be studied in optical longitudinal section, but in general the sequence of divisions



Figs. 1-8.—*Sarcomenia delesserioides*. Fig. 1.—Branch apex, showing formation of lateral chains of cells. Fig. 2.—Apex, showing segmentation. Fig. 3.—Side view of apex, showing formation of abaxial and adaxial pericentral cells. Fig. 4.—Development of cortication from the abaxial pericentral cells. Fig. 5.—Portion of thallus bearing stichidia. Fig. 6.—Upper part of a stichidium, showing formation of tetrasporangia and cover cells. Fig. 7.—Optical longitudinal view of a young stichidium, showing division of the lateral pericentral cells into a tetrasporangium and cover cells. Fig. 8.—Transverse view of a stichidium.

[For meaning of abbreviations see opposite page.]

could only be observed in very young stichidia. Older stichidia always showed formation of tetrasporangium and both cover cells between one segment and the next.

III. THE SPECIES PLACED UNDER SARCOMENIA SONDER

J. Agardh (1899, p. 148) recognized 13 species of *Sarcomenia*, 12 of which were Australian (including *S. miniata*). Of these 4 have proved to be synonymous with other species, leaving 7 species under *Sarcomenia*, plus *Platysiphonia miniata*. All these species are discussed below. *S. rhizocarpa* Harvey (1863, synop. No. 188) is probably a species of *Dasya*.

1. *Sarcomenia delesserioides* Sonder 1845: 56; 1846: 194. J. Agardh 1863: 1266; 1896: 137; 1899: 140. De Toni 1900: 742; 1924: 361. Harvey 1847: 21; 1854: 537; 1860: pl. 121. Kuetzing 1849: 880.

Figs. 1-19; Plate 1, Fig. 1

Type locality.—Western Australia (Preiss 2618).

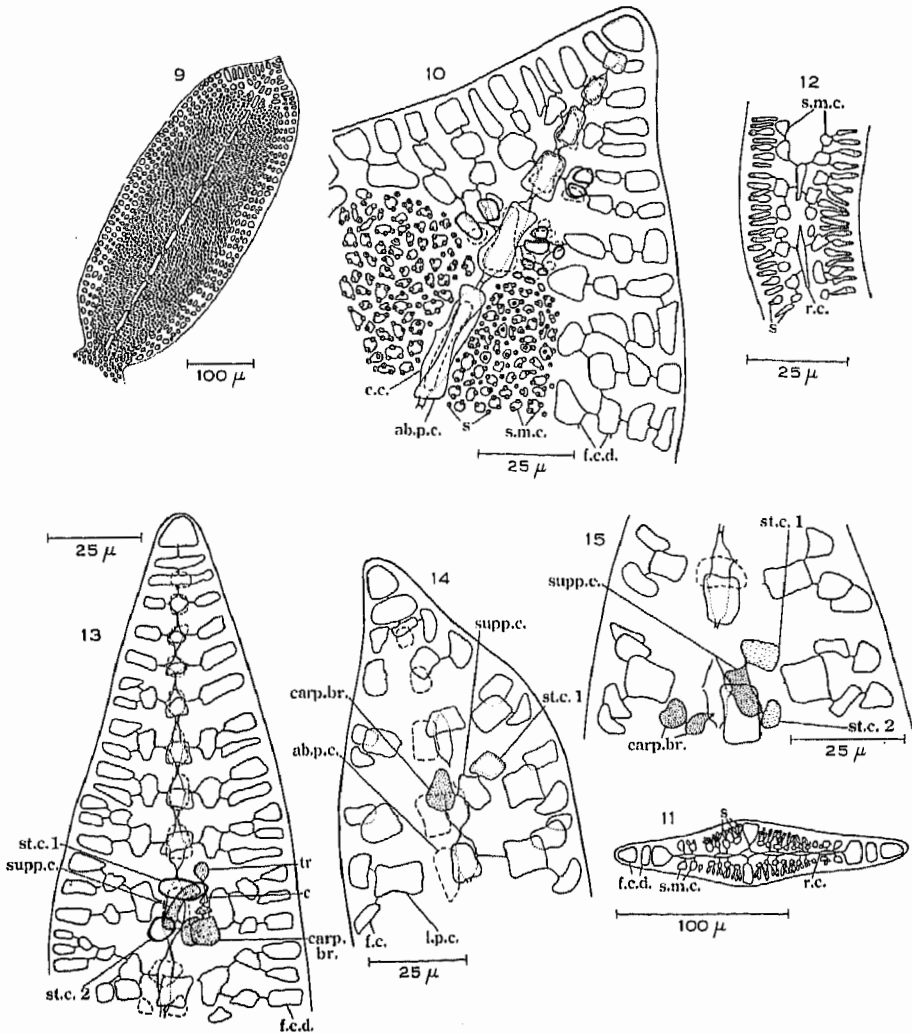
Type.—MEL (herbaria are abbreviated according to Lanjouw, J., and Stafleu, F. A. (1952).—"Regnum Vegetabile. Vol. 2. Index Herbariorum. Pt. I. The Herbaria of the World").

Distribution.—From Fremantle, W.A., to Western Port, Vic. Sublittoral on rough coasts.

Sarcomenia delesserioides, the type species of the genus, was described by Sonder in 1845 from material collected by Preiss on the south-west coast of Western Australia. The thallus is considerably larger than that of any other member of the group and is rather variable in width and degree of branching. It reaches 50 cm in height and may, in its older parts, attain a width of 2.5-3 cm. Most plants occurring around southern Australia are about 1 cm in width (Plate 1, Fig. 1). In some plants the branches terminate in curled tendrils. Intergrades between plants with broad and narrow thalli are common and it is difficult to delimit distinct forms as suggested by Harvey (1860, Plate 121). Lateral branches occur on both abaxial and adaxial surfaces (more commonly on the latter) at a position usually between midrib and margin. They arise endogenously from the central cells of the parent branch, but their point of origin from the thallus is displaced by later growth. Tetraspores, spermatia, and carpogonial branches occur on small blades (Figs. 5, 9) which develop similarly to lateral branches. The thallus, when fresh, has a greyish red iridescence, but on exposure to air or soon after collection changes to a bright rosy red colour and decomposes rapidly.

Abbreviations Applying to All Text Figures

ab.c.c., Abaxial cover cell; *ad.c.c.*, adaxial cover cell; *ab.p.c.*, abaxial pericentral cell; *ad.p.c.*, adaxial pericentral cell; *aux.c.*, auxiliary cell; *c.*, carpogonium; *carp.br.*, carpogonial branch; *c.c.*, central cell; *cort.c.*, corticating cell; *f.c.*, flanking cell; *f.c.d.*, flanking cell derivative; *fus.c.*, fusion cell; *gon.fil.*, gonimoblast filament; *gon.init.*, gonimoblast initial; *l.p.c.*, lateral pericentral cell; *r.c.*, residual cell; *s.*, spermatangium; *s.c.*, stalk cell; *s.m.c.*, spermatangium mother cell; *st.c. 1*, first sterile cell; *st.c. 2*, second sterile cell; *supp.c.*, supporting cell; *t.*, tetrasporangium; *tr.*, trichogyne.



Figs. 9-15.—*Sarcomenia delesserioides*. Fig. 9.—Mature spermatangial blade. Fig. 10.—Tip of spermatangial blade, showing development of spermatangial mother cells and spermatangia. Fig. 11.—Transverse section of spermatangial blade. Fig. 12.—Longitudinal section through lateral pericentral cell region of spermatangial blade. Fig. 13.—Young blade of a female plant, showing carpogonial branch and 2 sterile cells. Fig. 14.—Early development of a carpogonial branch, with the first sterile cell and carpogonial branch initial cut off from the supporting cell. Fig. 15.—A carpogonial branch at a 2-celled stage (slightly displaced), with 2 sterile cells.

Material on which these investigations have been carried out was collected, as drift, at Port McDonnell and Nora Creina Bay, S.A. (tetrasporic plants only) in August 1953 (AD: A19016); at Robe, S.A. (spermatangial and young cystocarpic plants) in March 1955 (AD: A19870); and at Nora Creina Bay, S.A. (mature cystocarpic plant) in November 1955 (AD: A21394).

Structure of thallus

Growth is initiated by a hemispherical apical cell, which cuts off cells posteriorly. In the third or fourth segment, a cell is cut off from the abaxial surface, forming the abaxial or dorsal transverse pericentral cell (Figs. 1-3). Two cells are next cut off laterally to form the lateral pericentral cells. No strict order for the formation of these 2 lateral cells has been observed. Shortly after the formation of the 2 lateral pericentral cells, a cell is cut off from the adaxial surface, thus forming the fourth pericentral cell (Figs. 2, 3). This order of pericentral cell development is that typical of the Rhodomelaceae and the abaxial pericentral cells are formed in a line. The lateral pericentral cells elongate and 2 cells (one anterior to the other) are cut off from each so as to leave a lateral pericentral cell of about the same size as the transverse pericentral cells (Figs. 1, 2). The upper of these 2 flanking cells again divides in the same way. Thus 3 elongate cells are produced from each lateral pericentral cell and further divisions occur at the inner edges of these, forming lateral chains of cells, always with an elongate cell at the edge of the blade. After the formation of the 4 pericentral cells as described above, a portion of the original saucer-shaped cell remains, forming the central cell (Figs. 1, 3). Central cells of successive segments are connected by large, distinct pit connections. Thin protoplasmic connections are visible between all other cells and their derivatives. In older parts of the thallus secondary pit connections develop, firstly between adjacent pericentral cells and later between the cells of the lateral chains.

Cortication of the thallus begins usually about 20 segments from the tip. The transverse pericentral cells cut off, by an oblique wall, a small cell at 1 posterior corner of the pericentral cell (Figs. 1, 4). Such cells are cut off at alternate posterior corners of successive pericentral cells. At a later stage a cell is cut off at the other posterior corner and later still, 2 cells are cut off at the anterior corners of these pericentral cells. At about the 25th segment cortication of the lateral pericentral cells commences, cells being cut off by periclinal divisions on both sides of the blade. Complete cortication occurs by similar periclinal divisions of all the lateral cell chains of the blade (Fig. 5).

Lateral branches arise endogenously from the central cells of a parent blade. The anterior end of a central cell cuts off a cell which acts as an apical initial, emerging to one side of the transverse pericentral cell and developing pericentral cells itself as described above.

Development of stichidia and tetrasporangia

Tetraspores are produced in small lateral blades or stichidia, which arise singly or in groups of up to 6. These groups are formed by younger stichidia developing at the base of an older one; often only the base of the older stichidium remains (Fig. 5). The tetrasporangia are formed in 2 regular, vertical rows in the stichidium and mature in acropetal succession (Figs. 5, 6). Stichidia are endogenous in origin, and cell development is similar to that of lateral branches.

However, the 2 derivatives (flanking cells) of each lateral pericentral cell do not divide to form chains of cells though each cuts off a small cell anteriorly. Thus there are 4 cells at the edge of the blade corresponding to each segment of the thallus.