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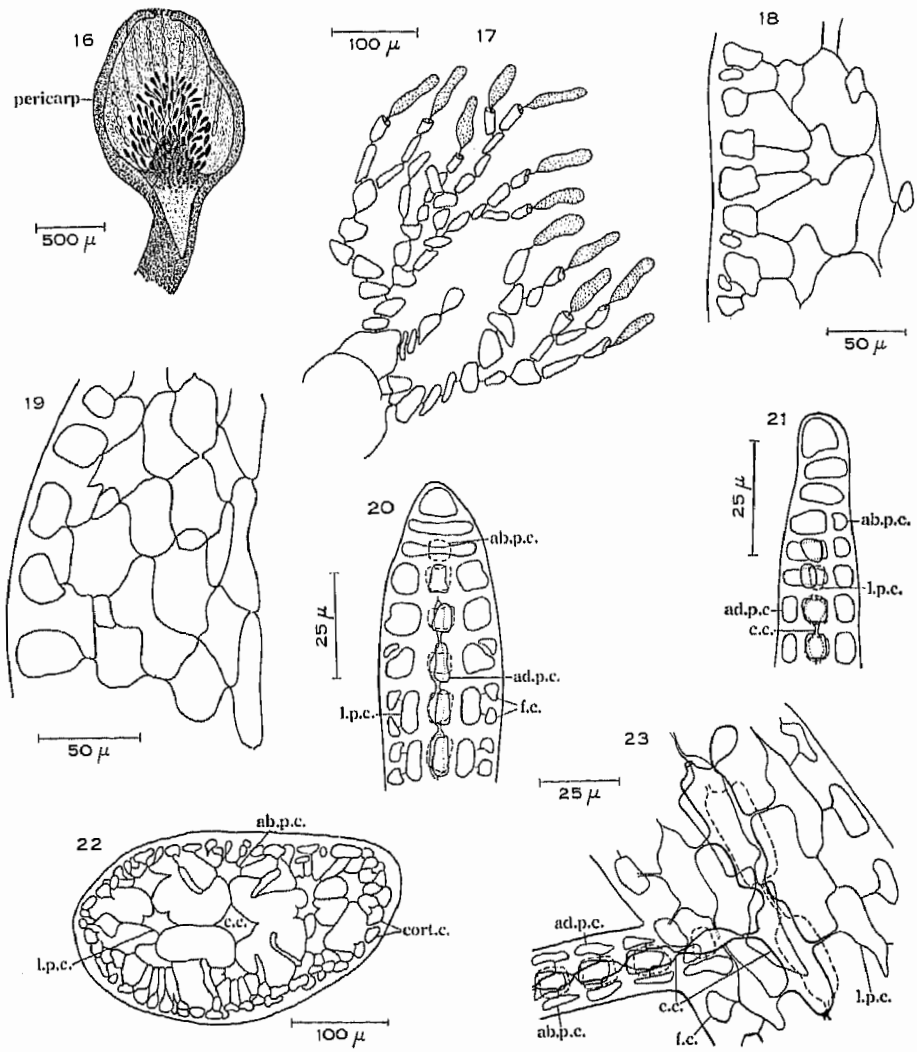


Figs. 16–19.—*Sarcomenia delesserioides*. Fig. 16.—Sectional view of a mature cystocarp. Fig. 17.—Upper part of the carposporophyte with terminal carposporangia. Fig. 18.—Transverse section of pericarp. Fig. 19.—Longitudinal section of pericarp. Figs. 20–23.—*Sarcomenia victoriae*. Fig. 20.—Tip of branch, showing cell segmentation. Fig. 21.—Side view of branch apex, showing development of transverse pericentral cells. Fig. 22.—Transverse section of a mature branch. Fig. 23.—Formation of a lateral endogenous branch.

These outer cells become curved and elongate horizontally, thus forming a protective covering around the developing tetrasporangium (Fig. 8).

The lateral pericentral cell cuts off the sporangium and 2 cover cells in very rapid succession. In all but the youngest stichidia they are all formed in passing from one segment to the next. Several very young stichidia were observed, however,

in which the sporangium was first cut off by a curved wall (Fig. 7) in such a way that it was exposed on the adaxial side of the stichidium but protected on the abaxial side by an extension of the old pericentral cell. The abaxial (dorsal) cover cell is next cut off, and still protects the sporangium on that side. The abaxial (ventral) cover cell is cut off last and remains small so that the sporangia are more or less exposed on that side of the stichidium (Figs. 6, 7).

As the tetrasporangium develops, the cover cells and flanking cells enlarge but the stalk cell becomes considerably stretched laterally, forming a very thin yet conspicuous cell in the stichidium. The tetraspores, which are tetrahedrally arranged, are liberated from the adaxial surface of the blade and after their liberation the cover cells undergo division to form small groups of cells which later merge with the general cortication of the old stichidium. Owing to the acropetal formation of the tetrasporangia, in one stichidium there are usually immature and mature tetrasporangia as well as the corticated basal region from which the tetraspores have been shed.

Development of spermatangial blades

Spermatangial blades develop endogenously from the central cells. Although these blades often appear to arise from the lateral wing of the branch, their central cell row can always be traced back, within the thallus, to the central cell row of the parent branch. As in normal branch development 3 marginal cell initials are formed at each edge of a segment, and in the spermatangial branches these undergo limited division, forming short lateral chains of cells. Thus a narrow winged blade is produced (Figs. 9, 10). The lateral pericentral cells cut off by obliquely periclinal walls 2–4 cortical cells (on each surface), each of which divides by anticlinal walls into 4 or more cells. The number of divisions in each of these series is variable, but ultimately a block of about 16 cells lying in the surface plane is formed. These are the spermatangial mother cells, each of which cuts off 2–4 elongate spermatangia (Figs. 10–12). The distal ends of these cells are densely protoplasmic and become rounded and budded off as spermatia (Fig. 12).

Although spermatangia production commences from the lateral pericentral cells, it gradually spreads outwards to involve the inner cells of the lateral wing of the spermatangial blade. However, a sterile margin of 3–4 undivided cells is maintained surrounding the spermatangial cells (Figs. 9, 10). The transverse pericentral cells take no part in spermatia production, but remain as a sterile "midrib" of cells in each spermatangial blade (Fig. 9). A small amount of cortication develops at the base of the spermatangial blade where it unites with the parent branch.

Development of procarp

Carpogonial branches form in small fertile blades which are similar to a lateral branch but show only limited division of the 3 lateral initials in each segment. The carpogonial branches develop only from the adaxial transverse pericentral cell. In a fertile segment, the adaxial pericentral cell first cuts off a cell towards its anterior end (Fig. 14). This is the first "sterile cell", and comes to lie horizontally across the anterior end of the central cell (Fig. 13). Following this, another cell is cut off laterally from the adaxial pericentral cell, this being the carpogonial branch

initial (Fig. 14). Thus the adaxial pericentral cell itself functions as the supporting cell of the carpogonial branch. By the time the carpogonial branch has become 2-celled, a second sterile cell is cut off laterally, on the opposite side of the supporting cell to the carpogonial branch (Fig. 15). The mature carpogonial branch is 4-celled, the second cell being the largest, and the small carpogonium bears a very short trichogyne, terminating in a large globular head (Fig. 13).

Development of cystocarp

Changes taking place immediately following fertilization have not been studied, as only fully mature cystocarps have been observed. These are produced adaxially from small branchlets formed on both surfaces of the blade. Since the procarps develop near the apex of the fertile branchlets, the cystocarps appear pedicellate. The cystocarp wall is considerably corticated except for the cells around the ostiole. The inner layer of the pericarp is composed of vertical chains of cells, from each of which usually 2 cells are produced externally. Each of these outer cells cuts off several smaller cortical cells and these produce another layer of small cells which form the outer layer of the pericarp. Thus the pericarp wall is composed of 4 layers of cells (Figs. 16, 18, 19)—the inner vertical rows of cells, developing from the pericarp initials, and 3 layers of cortical cells. The cystocarp in this species is far more densely corticate than in any other species of the group.

The carposporophyte shows a thick erect central axis from which the gonimoblast filaments arise sympodially, developing from near the base as well as from the upper part (Figs. 16, 17).

Old cystocarps often break off, leaving the basal part of their pedicel projecting from the blade. Several young procarp-forming branchlets may develop from each of these broken pedicels.

2. **Sarcomenia victoriae** Harvey ex J. Agardh 1863: 1262; 1896: 135; 1899: 145. De Toni 1900: 739; 1924: 359.

Figs. 20–42; Plate 1, Fig. 2; Plate 2, Fig. 1

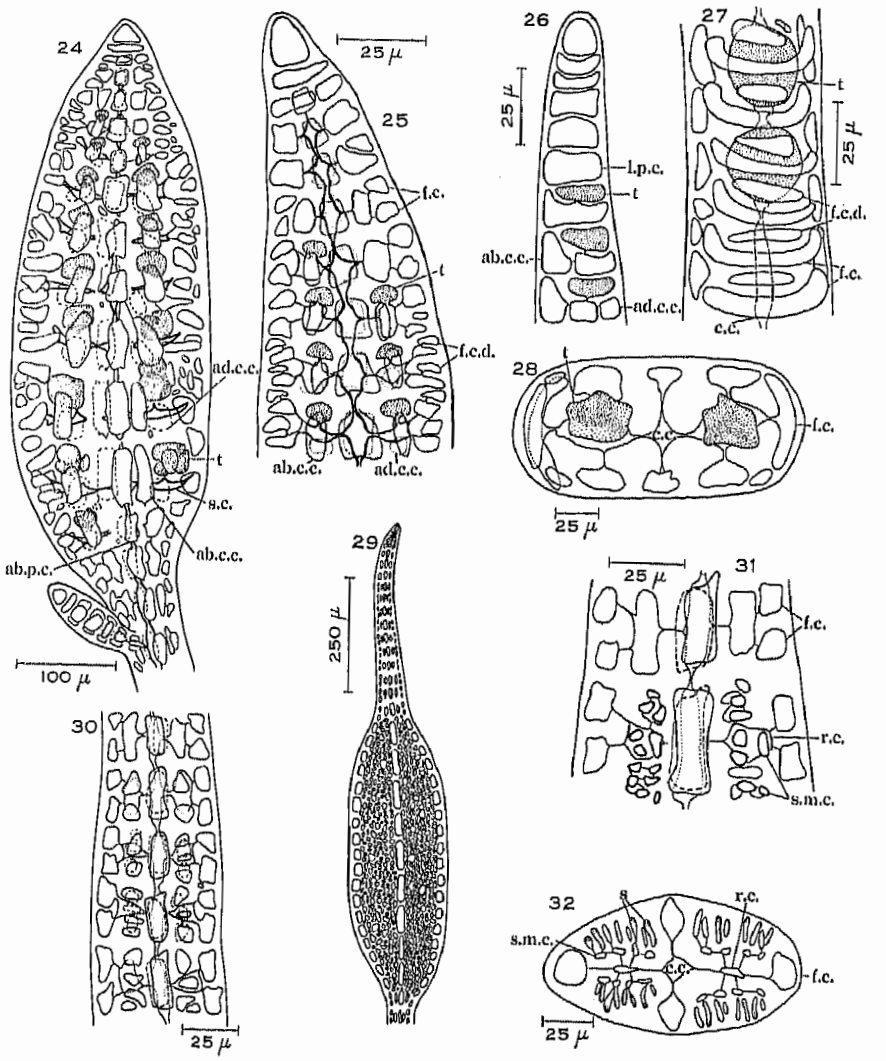
Polysiphonia victoriae Kuetzing 1864: 20, t. 56.
Sarcomenia dasyoides J. Agardh 1863: 1263; 1896: 134; 1899: 141. De Toni 1900: 738; 1924: 359.
Sarcomenia opposita J. Agardh 1899: 142, 146. De Toni 1924: 359.
Sarcomenia wilsonis J. Agardh 1899: 142. De Toni 1924: 360.

Type locality.—Port Phillip, Vic. (*Harvey* 188).

Type.—In Herb. Agardh, Lund (No. 43373).

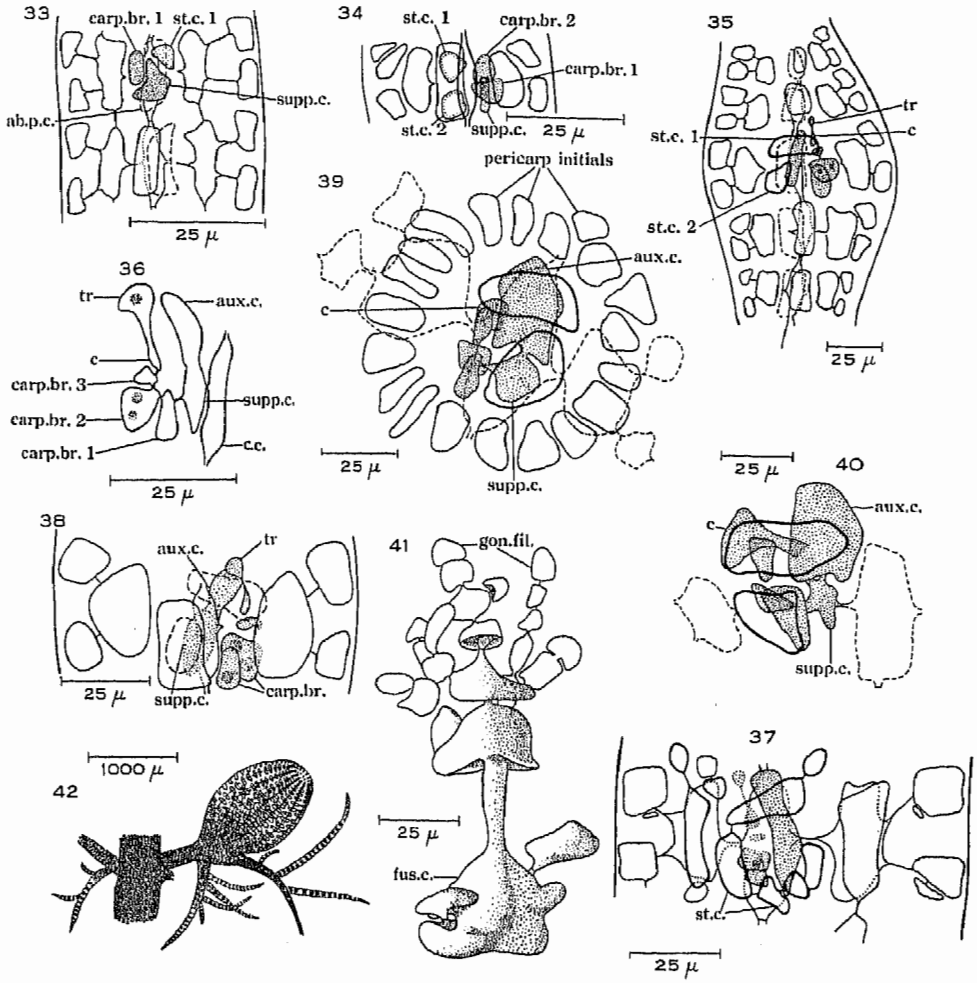
Distribution.—From Elliston, S.A., to Western Port, Vic. Sublittoral or in deeper rock platform pools on rough coasts.

Sarcomenia victoriae was first described by J. Agardh from material collected by Harvey at Port Phillip, Vic. The thallus reaches 30–35 cm in height, becoming terete in the lower regions owing to extensive cortication, while the younger branches are flattened. Branching occurs largely from the adaxial surface of the blades and is rather irregular (Plate 1, Fig. 2). The tetraspores and spermatia both develop



Figs. 24–32.—*Sarcomenia victoriae*. Fig. 24.—Mature stichidium from the abaxial side. Fig. 25.—Tip of a stichidium, showing formation of tetrasporangia and cover cells. Fig. 26.—Longitudinal optical view of a young stichidium, mostly through the lateral pericentral cells, showing the development of the tetrasporangium and cover cells. Fig. 27.—Edge view of a stichidium, showing the curved flanking cells and their derivatives. Fig. 28.—Transverse section of a stichidium. Fig. 29.—A mature spermatangial blade. Figs. 30, 31.—Stages in the development of spermatangial mother cells. Fig. 32.—Transverse section of a spermatangial blade.

on small lateral blades which are of determinate growth. Procarps develop near the base of young lateral branchlets, and fertilization of the carpogonium and the ensuing development of the cystocarp appear to inhibit further growth of the branch, so that the cystocarp is usually seen with a short spur at the base formed by the



Figs. 33–42.—*Sarcomenia victoriae*. Fig. 33.—Part of thallus, showing the first sterile cell, carpogonial branch initial, and supporting cell. Fig. 34.—The same, with 2 sterile cells and 2-celled carpogonial branch. Fig. 35.—Thallus with mature carpogonial branch and sterile cells. Fig. 36.—Side view of carpogonial branch, immediately after fertilization, with the supporting cell cutting off the auxiliary cell. Fig. 37.—Division of sterile cells and degeneration of unfertilized carpogonium. Fig. 38.—Formation of auxiliary cell from supporting cell. Fig. 39.—Fusion of carpogonium and auxiliary cell, surrounded by a ring of pericarp initials. Fig. 40.—Fusion of carpogonium and auxiliary cell by a tubular connection. Fig. 41.—A young carposporophyte, showing production of gonimoblast filaments from the erect fusion cell. Fig. 42.—Mature cystocarp.

branch from which it originally arose. At times short lateral branches occur on this spur (Fig. 42).

The thallus when fresh has a greyish iridescence. On exposure or drying it turns a rosy red and disintegrates very rapidly.

It has been impossible to find any real distinction between *S. victoriae* (Plate 1, Fig. 2) and *S. dasyoides* J. Agardh (Plate 2, Fig. 1) apart from rather more regular branching in the former and a more luxurious development of these branches. These differences seem readily accounted for as of environmental nature, where the more sparse, stunted *S. dasyoides* form comes from reef growth in rougher water and the *S. victoriae* form from more sheltered growth in bays or deeper and calmer water. This is supported by the localities from which the specimens seen have been recorded.

The type specimen of *S. opposita* J. Agardh (LD: No. 43381) is a reef form showing slightly more prominent opposite branching than usual, and *S. wilsonis* J. Agardh (LD: No. 43406) also appears to be only a form of *S. victoriae*.

Harvey distributed *S. dasyoides* and also *S. corymbosa* J. Agardh under the former name. The type of *S. dasyoides* (a Harvey specimen) is in Herb. Agardh (LD: No. 43398), but Harvey's 143E in MEL is *S. corymbosa*. J. Agardh (1863, p. 1264) also remarks on this confusion among the specimens of *S. dasyoides* distributed by Harvey. *S. victoriae* and *S. dasyoides* were both first described by J. Agardh (1863) in the same publication. As there is this confusion in Harvey's specimens of *S. dasyoides*, it is proposed to retain the name *S. victoriae*, relegating *S. dasyoides* to synonomy.

This investigation is based largely on material collected at Elliston on the west coast of Eyre Peninsula, S.A. These plants were growing under rough conditions in upper sublittoral reef pools and are of the more sparsely branched reef form of this species (= *S. dasyoides*). Cystocarpic, spermatangial, and tetrasporangial plants were all collected at the same time, in February 1954 (AD: A13518).

Structure of thallus

Growth is initiated by a single apical cell, which divides by transverse walls concave to the apex to form saucer-shaped cells (Fig. 20). The number of such cells present depends on the rate of growth at any one time. The abaxial pericentral cell is first formed, then the 2 lateral pericentral cells, and finally the adaxial pericentral cell, leaving the central cell (Figs. 20, 21). Each of the lateral pericentral cells cuts off a small cell at its anterior outer edge and later a similar cell is cut off posteriorly. These flanking cells elongate until each is about half as long as the lateral pericentral cell from which it was derived (Fig. 20). Further changes are produced only by the enlargement of the existing cells and by their cortication. Secondary pit connections develop between adjacent pericentral cells (Fig. 23) and these connections are later found more generally throughout the older blade. Lateral branches develop endogenously (Fig. 23). A single cell is cut off from the anterior end of a central cell and this acts as an apical initial, emerging anteriorly to the transverse pericentral cell and developing to form a lateral branch as described above. These lateral initials form only from the anterior end of any central cell.

Cortication of the thallus does not occur until several lateral branches have been initiated, but then follows rapidly and does not appear to follow a very definite pattern—being brought about by numerous periclinal divisions of all pericentral cells and the flanking cells (Fig. 22). The first divisions always occur in the transverse

pericentral cells, usually in the vicinity of a lateral branch, and owing to more intense cortication about the transverse pericentral cells the branch becomes almost terete. Both primary and corticated branches show strong regeneration after damage or breaking.

Development of stichidia and tetrasporangia

The stichidia are formed in dense masses in the position of lateral branches. Development of stichidia follows the same pattern as that of lateral branches. Tetrasporangia develop in each stichidium in 2 regular longitudinal rows. The tetrasporangium and 2 cover cells are cut off from the lateral pericentral cells in rapid succession (Figs. 24, 25), so that the order of their formation can only be seen in young actively growing stichidia. At about the sixth or seventh segment from the tip, the tetrasporangium is cut off by an oblique wall, leaving an upturned tip to the remaining cell (Fig. 26). The abaxial cover cell, which includes this upturned tip, is next cut off, thus protecting the sporangium on the dorsal side of the stichidium. The adaxial cover cell is last formed (Fig. 26). In most cases the adaxial cover cell is only about half the length of the abaxial cover cell and situated posteriorly to the young sporangium, thus leaving the tetrasporangium at least partially exposed. The remaining part of the lateral pericentral cell, now the stalk cell, remains very thin but is nevertheless conspicuous in the stichidium (Fig. 24). Tetrasporangia develop in acropetal succession. While tetrasporangia are still being formed at the tip of the stichidium, gaps occur near the base, from which mature tetraspores have been liberated. After the liberation of the tetrahedrally arranged tetraspores, the cover cells undergo division to form groups of about 6–7 small cells to fill the gap left by the tetraspores. During the development of the tetrasporangia the flanking cells divide further, each cutting off a small cell at its anterior edge (Fig. 25). The original flanking cells, although narrow, are very extended horizontally and curved (Figs. 27, 28), thus forming a protective framework round the edges of the stichidium, while the flanking cell derivatives are far less extended and lie centrally with regard to the flanking cells, i.e. actually at the edge of the stichidium (Fig. 27).

Development of spermatangial blades

Spermatangia develop in small lateral branches similar in size to the stichidia (Fig. 29). The spermatangial blades have a distinctive appearance since only the lateral pericentral cells are fertile. Thus each spermatangial blade in surface view shows a distinct "midrib" (the transverse pericentral cells) and margin (the flanking cells) of undivided cells. The production of spermatangial mother cells from the lateral pericentral cells does not occur until about the 16th–18th segment from the apex of the blade, leaving a sterile awn at the end of each spermatangial blade. This gives quite a distinctive appearance and appears to be typical of the species (Fig. 29).

Each lateral pericentral cell first cuts off by obliquely periclinal walls 2–4 cortical cells on each side of the blade (Figs. 30, 31). These then divide anticlinally to form ultimately a group of about 16 cells—the spermatangial mother cells—lying in the surface plane. When only 2 cortical cells are formed from 1 pericentral cell, these first divide to form a row of 4, then each of these forms a row of 4 cells

all lying in the same plane. If more than 2 cortical cells are formed, the development of the group of spermatangial mother cells is more irregular. The much attenuated remains of the lateral pericentral cell is visible in the median plane of spermatangial branches. Each of the spermatangial mother cells cuts off 3–4 elongate spermatangia with dense protoplasmic contents from which rounded spermatia are budded off (Fig. 32).

Development of procarp

Carpogonial branches develop only from the adaxial pericentral cells, near the base of young blades. Only 1 cystocarp develops in each branch, although occasionally 2 or even 3 young carpogonial branches may be seen in 1 blade. A cell is cut off the anterior end of the fertile adaxial pericentral cell by an oblique wall. This is the first sterile cell (Fig. 33), which comes to lie horizontally across the anterior part of the pericentral cell (Fig. 35). Next the ventral pericentral cell cuts off, laterally, the carpogonial branch initial (Fig. 33). By the time 2 cells of the carpogonial branch have been formed, the second sterile cell has been cut off from the adaxial pericentral cell and lies laterally to this on the opposite side to the carpogonial branch (Fig. 34). Thus the remainder of the adaxial pericentral cell functions as the supporting cell of the carpogonial branch.

A mature carpogonial branch is 4-celled, with the carpogonium surmounted by a short trichogyne with a broad, expanded tip (Figs. 35, 36). Of this 4-celled carpogonial branch the second cell is the largest and is frequently seen to be binucleate (Fig. 36). The larger second cell also lies nearer the adaxial surface of the blade than the other cells of the carpogonial branch, which all lie in the same plane. The large second cell of the carpogonial branch thus occupies the space between the 2 sterile cells on the ventral surface of the blade. The third cell of the carpogonial branch is the smallest. The carpogonium and trichogyne in all cases point towards the tip of the branch.

If fertilization fails to take place the 2 sterile cells divide further and the carpogonial branch disintegrates (Fig. 37). These sterile cell derivatives are the start of cortication of the branch.

Development of cystocarp

Following fertilization of the carpogonium, the anterior end of the supporting cell enlarges and is cut off to form the auxiliary cell (Figs. 38, 39), with which the enlarging carpogonium comes to lie in close proximity. A short tube forms between the carpogonium and this auxiliary cell (Figs. 39, 40) and the carpogonial branch soon begins to disintegrate. Fusions occur between the supporting cell, auxiliary cell, and central cell to form a large, irregular fusion cell, from which an erect prolongation develops (Fig. 41). From this arise numerous much-branched gonimoblast filaments which ultimately develop terminal oval carposporangia which are 80–100 μ in length and densely cytoplasmic. The cytoplasmic connections between the fusion cell and the lower cells of the carposporophyte become very much enlarged and a massive column is formed from which the gonimoblast filaments arise (Fig. 41). The upper cells of this column are characteristically umbrella-shaped. The 2 sterile

cells undergo no further development, and following fertilization they appear to disintegrate.

Following fertilization of the carpogonium and formation of the auxiliary cell, the development of the protective pericarp is initiated by the lateral pericentral cells and flanking cells of the fertile segment and the adaxial pericentral cells of the segments anterior and posterior to the fertile one (Fig. 39). From these cells are formed a ring of vertical chains of cells, which surround the developing carposporophyte. Each of the cells of these vertical chains cuts off, one above the other, 2 laterally elongate cells on the outside, so that the cystocarp has a double wall of cells. Cells of the adjacent outer rows usually alternate. Secondary pit connections develop between the horizontal outer cells but not between the vertical rows of cells. The globose pericarp opens at the apex by a small circular ostiole, through which the mature carpospores are liberated (Fig. 42). The cystocarp increases greatly in size, reaching 800–1000 μ in width and 900–1400 μ in length, by enlargement of the cells and their separation during growth. As the cystocarp matures, cortication of the basal portion occurs along with cortication of the parent branch.

3. **Sarcomenia corymbosa** J. Agardh 1896: 134. De Toni 1900: 737; 1924: 359.

Figs. 43–50; Plate 2, Fig. 2

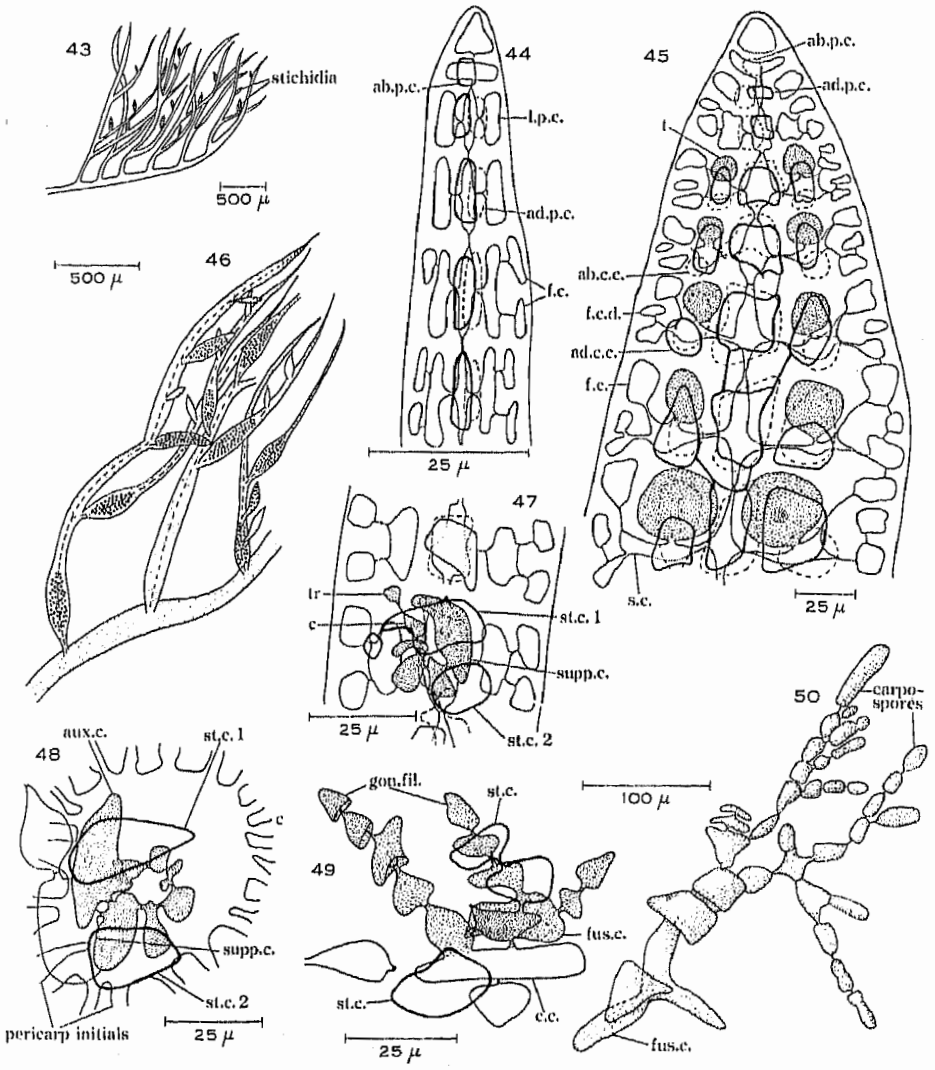
Type locality.—Western Port, Vic. (*J. B. Wilson* No. 41).

Type.—Herb. Agardh, Lund (No. 43355).

Distribution.—From Sturt Bay, S.A., to Phillip I., Vic., and the north coast of Tasmania. Sublittoral on rough coasts.

The thallus of this species reaches a height of about 30 cm. The main branches are generally alternate, while the tips of the branches show very distinct unilateral branching (Plate 2, Fig. 2). Branching is largely from the adaxial surface of the parent branch. Owing to this and to the density of branching in the younger parts of the thallus, the top of the plant tends to be flat or corymbose in form. When the plant is undergoing rapid vegetative growth all of these upper unilateral branches are uncorticate. Fertile specimens show a greater degree of cortication in these upper branches, although even then the younger branches are not corticate. There has been some confusion between *S. victoriae* and *S. corymbosa*, but study of the types of both species and a range of specimens shows the following distinctions.

S. victoriae has basically opposite branching, often with long lateral branches from near the base of the plant. Lesser branches are pinnately arranged and the plant is densely corticate except for the ultimate branches. *S. corymbosa* has alternate branching in the older parts and the ultimate branches are distinctly unilateral, arising adaxially. Thus the upper parts of *S. corymbosa* are dense and corymbose. Branches formed near the base of the plant are often lost relatively early. In rapidly growing plants the upper branches up to the fourth and sometimes higher orders are uncorticate. The spermatangial branches of *S. victoriae* and *S. corymbosa* are also distinct, those of the former being simple and determinate while in the latter they are often branched and relatively indeterminate.



Figs. 43–50.—*Sarcomenia corymbosa*. Fig. 43.—Upper part of thallus with stichidia and showing unilateral branching. Fig. 44.—Branch apex, showing segmentation. Fig. 45.—Upper part of a stichidium. Fig. 46.—Branches of a male plant bearing spermatangial sori. Fig. 47.—Mature carpogonial branch and sterile cells (one of which has divided). Fig. 48.—Fusion between auxiliary cell and carpogonium, and initiation of pericarp. Fig. 49.—Fusion between auxiliary cell and central cell, and early formation of gonimoblast filaments. Fig. 50.—Upper part of a gonimoblast filament with young terminal carposporangia.

As *S. corymbosa* is very similar to *S. victoriae* in many details of its structure and development, the main features only are described. The material available permitted a detailed study of all phases of the species.

Material of *S. corymbosa* was collected at Vivonne Bay, Kangaroo I., S.A., Jan. 1946 (AD: A2855), at Port McDonnell, S.A., Aug. 1953 (AD: A18991), and Robe, S.A., Dec. 1953 (AD: A19937).

Structure of thallus

Segmentation of the apical cell, the order of development of pericentral cells and flanking cells (Fig. 44), and the development of endogenous lateral branches are the same as described for *S. victoriae*.

The basal portions of plants of *S. corymbosa* are densely corticate and become terete. Depending on the stage of growth, the upper parts of the thallus are more or less densely corticate. The corticating cells in this species tend to be rather elongate and occur in longitudinal rows, in contrast to *S. victoriae*, *S. mutabilis*, and *S. hypneoides*, where the corticating cells are rhomboidal in form.

Development of stichidia and tetrasporangia

The stichidia are always produced adaxially on the parent branches (Fig. 43) and are essentially similar in form to those already discussed in *S. victoriae*. The tetrasporangia and 2 cover cells are cut off in rapid sequence from the lateral pericentral cells, the abaxial cover cell usually being the larger, though occasionally the abaxial and adaxial cover cells alternate in size in successive segments (Fig. 45). Secondary pit connections may occur between the cover cells and transverse pericentral cells (Fig. 45). In the stichidium the posterior of the 2 flanking cells in each segment divides horizontally before the anterior one, but eventually 4 cells are formed (Fig. 45). These cells, especially the original flanking cells, elongate horizontally and form a curved protective edge around the stichidium. After the tetraspores are liberated, cell divisions occur in and around the small ventral cover cell (occasionally also around the dorsal cover cell), and the ends of the curved flanking cells may also be cut off.

Development of spermatangial blades

The spermatangial blades of *S. corymbosa* differ from those of all other species investigated. They are lateral branches of unlimited growth and the patches of spermatia occur near their base (Fig. 46). These branches continue to grow in length and also themselves produce branches which may bear spermatia. The spermatangia are formed from the 2 lateral pericentral cells. In a few cases transverse pericentral cells were seen to divide to form spermatangia, but this was exceptional. Each lateral pericentral cell cuts off a group of spermatangial mother cells on both surfaces of the blade. From each of these spermatangial mother cells 2 or 3 elongate spermatangia are formed by anticlinal divisions and spermatia are budded off from their tips.

Development of procarp

Procarps develop from the adaxial pericentral cells in lateral branches. The first sterile cell is cut off from the anterior end of the pericentral cell, followed by the carpogonial branch initial. By the time the carpogonial branch is 2-celled, a second sterile cell has been cut off from the adaxial pericentral cell, lying lateral to the pericentral cell and opposite the young carpogonial branch.

The mature carpogonial branch is 4-celled, the second cell being the largest and often showing 2 nuclei (Fig. 47). The carpogonium is surmounted by a short trichogyne with a globular tip.

Development of cystocarp

After fertilization of the carpogonium the anterior part of the supporting cell is cut off to form the auxiliary cell. The carpogonium enlarges and lies in close proximity to this cell and fusion occurs between the fertilized carpogonium and the auxiliary cell (Fig. 48). Subsequently fusions also occur between the auxiliary cell, central cell, and supporting cell (Fig. 49), forming the large basal fusion cell, from which the erect carposporophyte structure develops in an irregularly sympodial manner, producing gonimoblast filaments with terminal, ellipsoidal carposporangia (Fig. 50).

Following fertilization of the carpogonium, the pericarp is initiated and a ring of cells develops round the procarp. These cells divide to form upright chains of cells and each cuts off externally 2 more or less isodiametric cells lying horizontally. The wall of the mature, urceolate cystocarp thus consists of 2 distinct cell layers. Corticating cells develop in the basal part of the cystocarp when cortication of the supporting branch occurs.

4. **Sarcomenia hypneoides** Harvey 1854: 537; 1858: pl. 12. J. Agardh 1863: 1266; 1896: 137; 1899: 143. De Toni 1900: 741; 1924: 360.

Figs. 51–54; Plate 3, Fig. 1

Type locality.—"Fremantle and Garden Island", W.A. (*Harvey* 142)

Type.—In Herb. Harvey (TCD) No. 142A.

Distribution.—Only known from Fremantle and Garden I., W.A. Apparently rare.

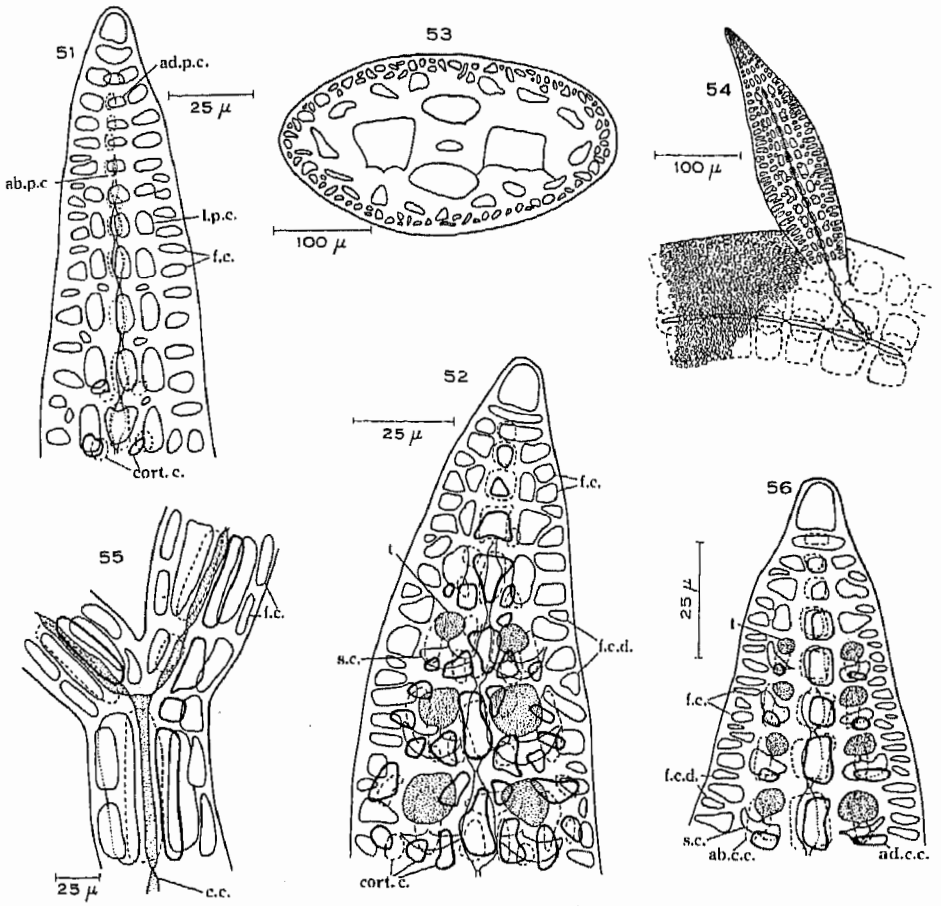
This species has been studied from dried herbarium specimens only (AD: A18446, A18301) collected near Fremantle by Harvey and G. Clifton. The thallus, which reaches a height of about 20 cm, shows opposite branching in most parts. In one specimen (Plate 3, Fig. 1) the ends of several branches had become curled in a tendril-like manner—similar to those found in some specimens of *S. delesserioides*. The thallus is basically like *S. victoriae* in structure, differing principally in the greater degree of cortication, which produces a coarser plant.

Structure of thallus

Growth is initiated by a hemispherical apical cell, which cuts off segments by transverse walls (Fig. 51). Each of these subapical cells very soon develops 4 pericentral cells, the abaxial pericentral cell being formed first. This is followed by the 2 lateral pericentral cells and lastly by the adaxial pericentral cell. Each of the lateral pericentral cells cuts off 2 flanking cells towards the edge of the blade (Fig. 51).

Lateral branches arise endogenously from the anterior end of a central cell. The lower segments of lateral branches are immersed in the thick thallus and the

basal 6 segments or so do not develop pericentral cells or flanking cells. A chain of central cells may be seen between the lateral branch and the central cell of the parent branch (Fig. 54). Cortication occurs very rapidly following branch initiation, leaving only the growing tips ecorticate (Fig. 51). Cortical cells are cut off first by the abaxial pericentral cells and this is followed by divisions of the adaxial pericentral



Figs. 51–54.—*Sarcomenia hypneoides*. Fig. 51.—Apex of branch, showing segmentation and early cortication. Fig. 52.—Apex of a stichidium, showing early cortication. Fig. 53.—Transverse section of a branch. Fig. 54.—Young lateral branch. Figs. 55, 56.—*Sarcomenia mutabilis*. Fig. 55.—Departure of a lateral branch. Fig. 56.—Apex of a stichidium.

cells and later the lateral pericentral cells and flanking cells. All the branches become covered by several layers of small corticating cells (Figs. 53, 54), which are rhomboidal in shape, similar to those of *S. victoriae*. The branches remain slightly flattened even when fully corticate. Prominent secondary pit connections are visible between the pericentral and flanking cells. Secondary connections are also visible between the corticating cells.

Development of stichidia and tetrasporangia

The stichidia (Fig. 52) are similar in form to those of *S. victoriae*. The tetrasporangia are produced from the lateral pericentral cells and 2 cover cells are cut off almost simultaneously. The cover cell formed on the adaxial surface of the blade is generally only half the length of the abaxial cover cell, which is equal to the transverse pericentral cell in length. Each flanking cell in the stichidium divides horizontally into two. Cortication of the stichidium commences even before the formation of the tetrasporangia and cover cells (Fig. 52), cells being cut off from both transverse pericentral cells. After the tetraspores have been liberated, the adaxial cover cell divides further, merging with the general cortication. As in the vegetative thallus, the stichidium of *S. hypneoides* is more heavily corticated than in other species.

5. **Sarcomenia mutabilis** (Harvey) J. Agardh 1863: 1261; 1896: 134. De Toni 1900: 736; 1924: 359.

Figs. 55, 56; Plate 3, Fig. 2

Polysiphonia mutabilis Harvey 1854: 540. Kuetzing 1864: 20, t. 55*d–g*.

Type locality.—Fremantle, W.A. (on *Zostera*).

Type.—In Herb. Harvey (TCD) No. 116A. *Isotype.*—AD: A18300.

Distribution.—From Fremantle, W.A., to Port Stephens, N.S.W., and Low Head, Tas. Sublittoral, not common.

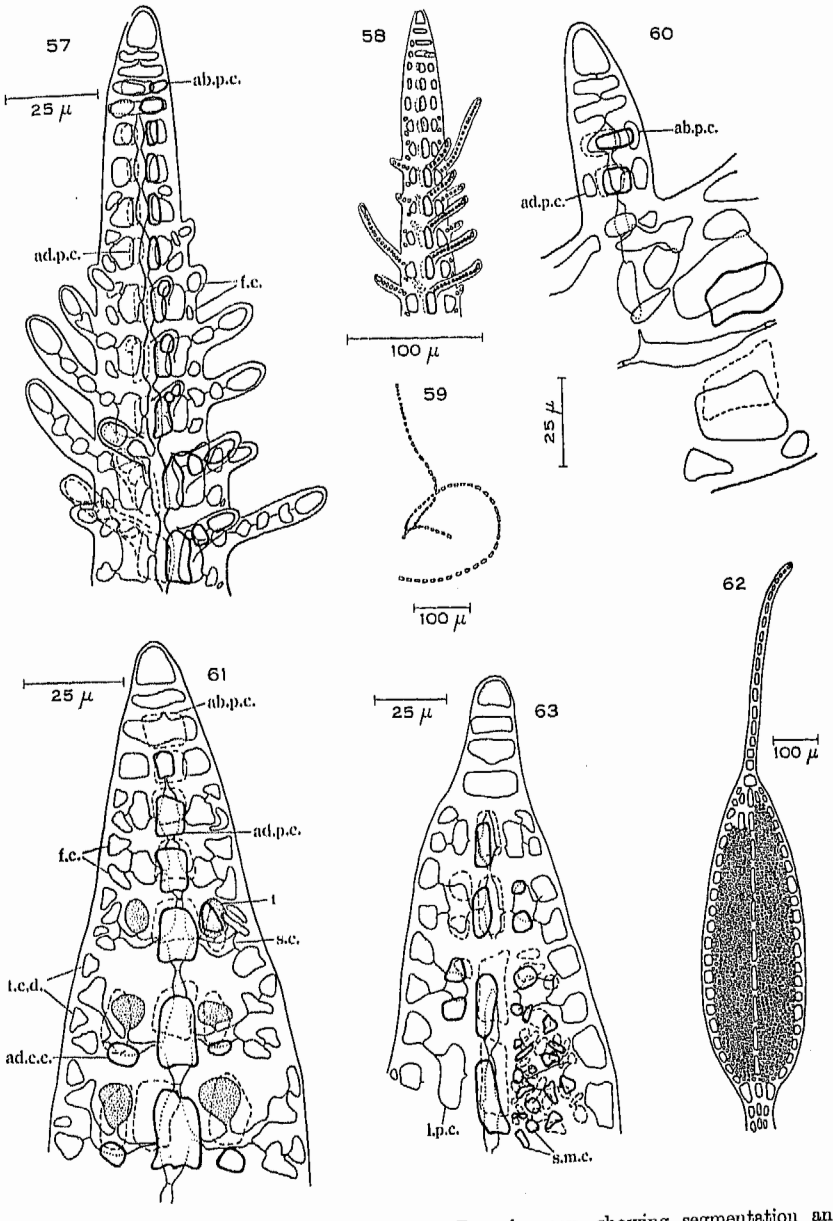
Sarcomenia mutabilis was available for study only from dried herbarium specimens. Isotype material (AD: A18300) was used for the most part, but other specimens were also studied. Stichidia were present on the isotype material. The thallus is of delicate form and usually 4–10 cm in height (Plate 3, Fig. 2). The size, form, and slight degree of cortication satisfactorily separate *S. mutabilis* from all other species of the group.

Structure of the thallus

As in the other species of the *Sarcomenia* group already discussed, growth is initiated by a hemispherical apical cell (Fig. 56). The cells cut off by horizontal divisions each produce 4 pericentral cells. The abaxial pericentral cell is formed first, followed by the lateral pericentral cells and finally the adaxial pericentral cell. Each lateral pericentral then cuts off 2 flanking cells, giving a flattened branch 5 cells wide and 3 cells thick in the centre. The statement of Silva and Cleary (1954, p. 259) that flanking cells are lacking in *S. mutabilis* is based on a misidentification of *Polysiphonia roeana* (see below).

Branching is endogenous (Fig. 55), originating from the anterior end of a central cell. The basal segment of a lateral branch often lacks flanking cells.

Cortication is slight and only becomes complete in the lower branches of the thallus. The corticating cells are small and generally rhomboidal in outline, similar to those formed in *S. victoriae*.



Figs. 57–63.—*Sarcomenia tenera*. Fig. 57.—Branch apex, showing segmentation and development of monosiphonous filaments. Fig. 58.—Branch apex, further developed than in Fig. 57. Fig. 59.—A branched monosiphonous filament. Fig. 60.—Origin of a lateral branch. Fig. 61.—Apex of a stichidium, adaxial view. Fig. 62.—A mature spermatangial blade. Fig. 63.—Apex of a young spermatangial blade, showing development of spermatangial mother cells.

branches, become more scattered away from the tip, and are usually entirely absent from older branches.

Lateral branches develop endogenously from the anterior end of a central cell (Fig. 60), similarly to previously described species. Cortication commences relatively early in *S. tenera* (usually at about the 15th–18th segment) and only the young growing tips are uncorticate. Corticating cells are first cut off from the transverse pericentral cells, then from the lateral pericentral cells and flanking cells, until the branch becomes completely corticate and terete. A greater degree of cortication occurs in this species than in *S. victoriae*.

Development of stichidia and tetrasporangia

Solitary stichidia are produced laterally from mature corticated branches, mainly from the adaxial surface. The stichidia develop similarly to lateral branches (Fig. 61). Each of the flanking cells cuts off a small cell anteriorly and these flanking cells become horizontally elongate and curved, forming a protective edge to the stichidium. The lateral pericentral cells of the stichidium cut off the tetrasporangium, abaxial cover cell, and adaxial cover cell in rapid succession as in other species of the *Sarcomenia* group and the sporangium is partly exposed on the adaxial side of the stichidium. Following the liberation of the tetrahedrally arranged tetraspores, the cover cells undergo further division and the stichidium becomes progressively corticate from the base.

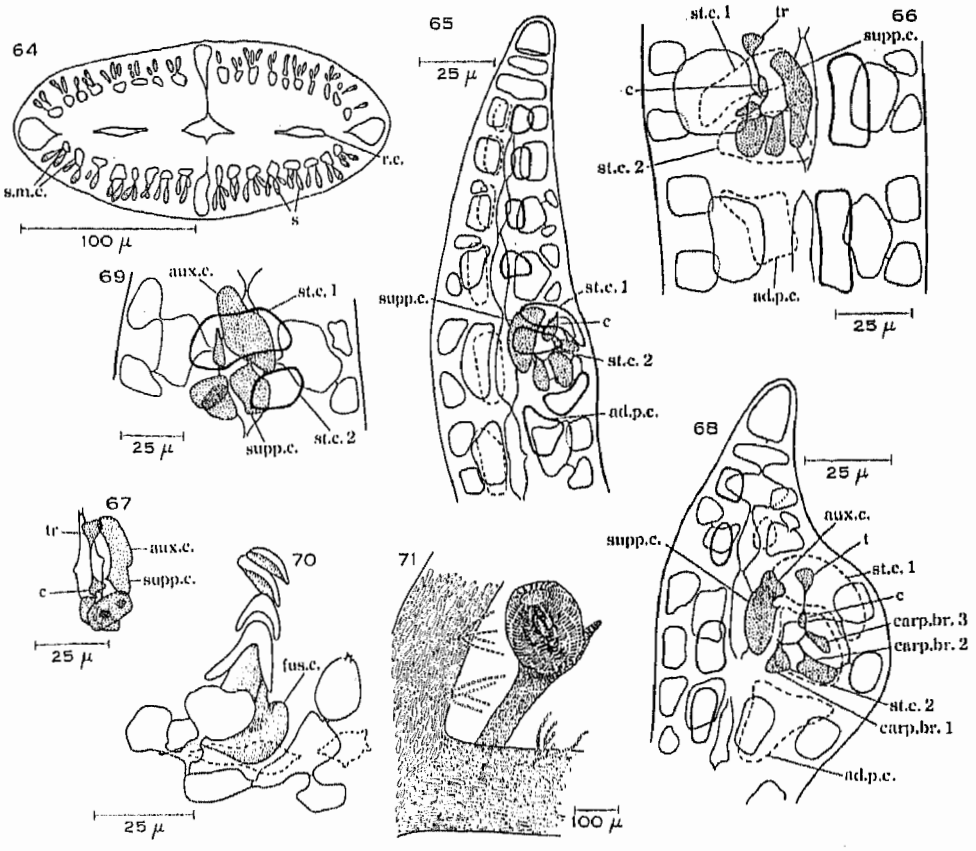
Development of spermatangial blades

Small spermatangial blades are formed in groups on the main branches. They develop as normal lateral branches, and spermatangial mother cells are formed by anticlinal division of cortical cells cut off from the lateral pericentral cells (Figs. 62, 63). More spermatangial mother cells (16–32) are produced from each lateral pericentral cell in this species than in other species of the group. In a transverse section of the spermatia-producing blade (Fig. 64) about 8 spermatangial mother cells correspond to each lateral pericentral cell, compared to about 4 in the previously discussed species of *Sarcomenia*. Initiation of divisions producing spermatangial mother cells appears to depress formation of pericentral cells and flanking cells, so that each spermatia-producing blade is surmounted by a long monosiphonous awn (Fig. 62).

Development of procarp

Initiation of the procarp occurs near the tip, usually in about the fifth to eighth segment, of a lateral branch (Fig. 65). Owing to this position of procarp initiation the mature cystocarp is borne on a longer "stalk" than in some other species (e.g. *S. victoriae*), where procarp initiation occurs nearer the base of the fertile lateral branch. In each fertile lateral branch usually only one procarp is initiated. The first sterile cell is cut off at the anterior end of the fertile adaxial pericentral cell. A cell is then cut off laterally by the pericentral cell and this acts as initial for the 4-celled carpogonial branch. A second sterile cell is next cut off and lies over the carpogonial branch. The remainder of the adaxial pericentral cell acts as the supporting cell of the carpogonial branch (Figs. 65, 66). The 4-celled

carpogonial branch is surmounted by a short trichogyne with a very prominent tip (Fig. 66) and the second cell of the carpogonial branch is the largest and frequently binucleate. In *S. tenera* additional protection is given to the developing procarp by the adaxial pericentral cell of the next posterior segment, which acts as an extra



Figs. 64–71.—*Sarcomenia tenera*. Fig. 64.—Transverse section of a spermatangial blade. Figs. 65, 66.—Mature carpogonial branches, with 2 sterile cells and protection also from a derivative of the adaxial pericentral cell of the posterior segment. Figs. 67, 68.—Division of the supporting cell to cut off the auxiliary cell after fertilization. Fig. 69.—Auxiliary cell with old carpogonial branch. Fig. 70.—Formation of "capping cells" from the erect fusion cell. Fig. 71.—A mature cystocarp.

"cover cell". This pericentral cell may itself extend toward the procarp (Figs. 66, 68) or it may cut off an additional cell which performs this protective function (Fig. 65). If fertilization fails to occur, the sterile cells divide and initiate cortication in the region of the procarp.

Development of cystocarp

After fertilization the auxiliary cell is cut off from the anterior portion of the supporting cell (Figs. 67, 69). The fertilized carpogonium increases in size and comes to lie nearer the enlarging auxiliary cell. Fusion occurs between these 2 cells by

means of a short fusion tube and a binucleate cell is formed. This cell enlarges considerably and produces large "capping cells" connected by wide pit connections (Fig. 70). Fusions occur between auxiliary cell, supporting cell, and central cell to form the large fusion cell from which the vertical structure of capping cells arises. Repeated sympodial branching of this structure produces numerous gonimoblast filaments, each of which terminates in a large ellipsoidal carposporangium.

The developing carposporophyte is surrounded by a protective pericarp which is initiated only after fertilization of the carpogonium has occurred. The adaxial pericentral cells anterior and posterior to the fertile segment, the lateral pericentral cells, and the flanking cells all take part in the production of the pericarp. A complete ring of cells is formed which grows up around the developing carposporophyte. Each cell of the ring produces a vertical chain of cells, from each of which, except the apical cell, 2 cells are cut off externally, one above the other, lying horizontally across the inner row of cells. Thus the protective pericarp is made up of 2 layers of cells (Fig. 71).

7. **Sarcomenia dolichocystidea** J. Agardh 1896: 135; 1899: 145. De Toni 1900: 740; 1924: 361.

Figs. 72–82; Plate 4, Fig. 2

Type locality.—Brighton Beach, Port Phillip, Vic. (*Harvey* 209F).

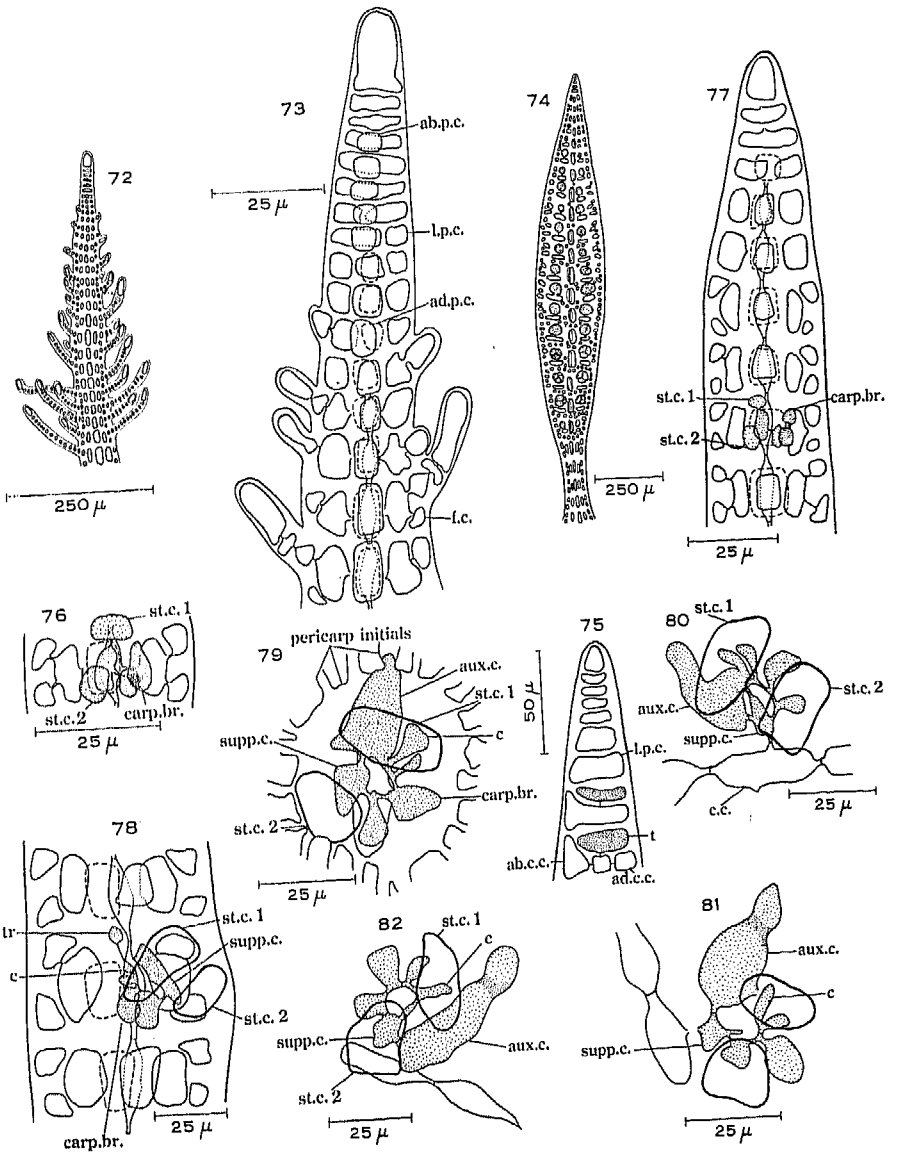
Type.—In Herb. Agardh, Lund (No. 43444).

Distribution.—From King George's Sound, W.A., to Port Phillip, Vic., and at Gordon, Tas. Usually found in relatively sheltered places, sublittoral.

This species is similar to *S. tenera* but is of more slender form and in general smaller at maturity (Plate 4, Fig. 2). Cortication is dense and only the young growing tips are uncorticate. The older parts of the thallus are terete. The apices of the branches are densely clothed with monosiphonous filaments which give a distinctive appearance to the species (Fig. 72). These monosiphonous filaments contain numerous chromatophores and may branch on older parts of the thallus, frequently each filament having 3 branches. The filaments are sparse away from the actual growing tip and finally in older parts of the thallus they are lost altogether. As with other species of the *Sarcomenia* group, *S. dolichocystidea* on exposure or when confined in a small amount of water becomes a bright rosy red and rapidly disintegrates. The material used in this investigation was collected in August 1954 at American River Inlet, Kangaroo I., S.A. (AD: A19788).

Structure of the thallus

In cell structure and cell formation *S. dolichocystidea* differs from *S. tenera* only in the position of the monosiphonous filaments. Only the upper of each pair of flanking cells produces filaments, i.e. the filaments are formed only laterally (Figs. 72, 73). At first the filaments tend to be formed on alternate sides in successive segments, but later they form on both sides of the same segment. The filaments themselves are rather coarser than those of *S. tenera*, this being especially evident in the terminal cell of the filament, which is here much longer and somewhat broader,



Figs. 72–82.—*Sarcomenia dolichocystidea*. Fig. 72.—Apex of a branch, with monosiphonous filaments from the flanking cells only. Fig. 73.—Branch apex, showing segmentation and formation of monosiphonous filaments. Fig. 74.—A stichidium. Fig. 75.—Optical longitudinal view (through the lateral pericentral cells) of the apex of a stichidium, showing formation of the tetrasporangium and cover cells. Fig. 76.—A 2-celled carpogonial branch. Fig. 77.—Branch apex with a 3-celled carpogonial branch. Fig. 78.—A mature carpogonial branch. Fig. 79.—Fusion between carpogonium and auxiliary cell and initiation of pericarp. Figs. 80, 81.—Development of fusion cell. Fig. 82.—Further development of fusion cell, and a connection between carpogonium and supporting cell.

measuring on an average 20 by 8·5 μ (Fig. 72). Lateral branches are formed endogenously, as in *S. tenera* and the other species discussed previously.

Corticating cells are formed, as in *S. tenera*, on the branches quite near the growing point and although the young branches are flat the rest of the thallus is terete in form.

Development of stichidia and tetrasporangia

The stichidia in this species are rather longer than those of *S. tenera* (Fig. 74) and tend to become considerably corticated. However, the formation and development of tetraspores occur in the same manner as described for *S. tenera*, with the tetrasporangium being cut off before the cover cells (Fig. 75).

Development of spermatangial blades

Blades producing spermatia are exactly like those of *S. tenera* in structure and formation of spermatia-bearing cells. These blades have the same sterile monosiphonous awn at the tip of the spermatia-bearing tissue as in *S. tenera*.

Development of procarp and cystocarp

Formation and development of procarps follow the normal pattern previously described for other species. The fertile adaxial pericentral cell cuts off the carpogonial branch initial and 2 sterile cells, itself remaining as the supporting cell (Figs. 76, 77). The mature carpogonial branch is 4-celled and the trichogyne has a very pronounced globular tip at the end of a short, slender stalk (Fig. 78). After fertilization the supporting cell cuts off the auxiliary cell towards the tip of the branch, and the carpogonium and auxiliary cell fuse (Figs. 79–81). Also, in this species, connection has been seen between the carpogonium and the supporting cell (Fig. 82). Gonimoblast filaments develop as described previously and carposporangia are produced terminally. The structure of the pericarp is the same as in *S. tenera*, the wall of the cystocarp being composed of 2 layers of cells. The lower part of the urceolate cystocarp becomes corticated and this cortication merges with that of the branch bearing the cystocarp.

IV. Other Taxa Allied to Sarcomenia

1. **Platysiphonia miniata** (C. Agardh) Boergesen 1931: 1–9. Silva and Cleary 1954: 251. Cribb 1956: 187.

Figs. 83–99

Hutchinsia miniata C. Agardh 1828: 94.
Polysiphonia miniata (C. Agardh) Kuetzing 1849: 820.
Sarcomenia miniata (C. Agardh) J. Agardh 1863: 1260; 1896: 133. Weber van Bosse 1896: 281–5, t. 359. De Toni 1900: 735; 1924: 359.

Type locality.—Cadiz, Spain (*Cabrera*).

Type.—In Herb. Agardh, Lund (No. 43346).

Distribution.—From Kangaroo I., S.A., around the south-east coast of Australia to the Burnet River, Qld. Mostly sublittoral, extending into lower littoral at least on Kangaroo I. Cribb (1956: 187) has recorded *P. miniata* from Devonport, Tas. Also known from Spain, South Africa, and India.

Study of *P. miniata* was made on preserved material collected from rock platform pools at Vivonne Bay, Kangaroo I., Jan. 1950 (AD: A12914). This material has been compared with the type and agrees with it well. Individual plants are only $\frac{1}{2}$–$1\frac{1}{2}$ cm high, and together form a turf-like mat with small coralline algae. Tetrasporic plants were abundant, spermatangial plants rare, and a very few female plants were found.

The Vivonne Bay material is dioecious, as was that studied by Boergesen (1931) from India, and Silva and Cleary (1954) from South Africa. Weber van Bosse (1896) stated that her only sexual plant was monoecious.

The genus *Platysiphonia*, based on *Sarcomenia miniata* (C. Agardh) J. Agardh, was described by Boergesen in 1931. He also suggested that *S. intermedia* and *S. mutabilis* should be placed in *Platysiphonia*. Boergesen based his new genus primarily on the great difference in size between *P. miniata* and the type species of *Sarcomenia* (*S. delesserioides*), and on the difference in thallus construction between them. The fact that a basal prostrate system is developed in *S. miniata* was also taken into consideration. At present the genus *Platysiphonia* includes *P. miniata* (C. Agardh) Boergesen, *P. mutabilis* (J. Agardh) Boergesen, *P. clevelandii* (Farlow) Papenfuss, *P. intermedia* (Grunow) Boergesen, and *P. parva* Silva & Cleary. *P. mutabilis* is described above as *Sarcomenia mutabilis*, though as shown later it is a species of *Platysiphonia*. *P. miniata* has been studied by Weber van Bosse (1896), Boergesen (1931), and Silva and Cleary (1954). A brief account only, based on the Vivonne Bay material, is given here.

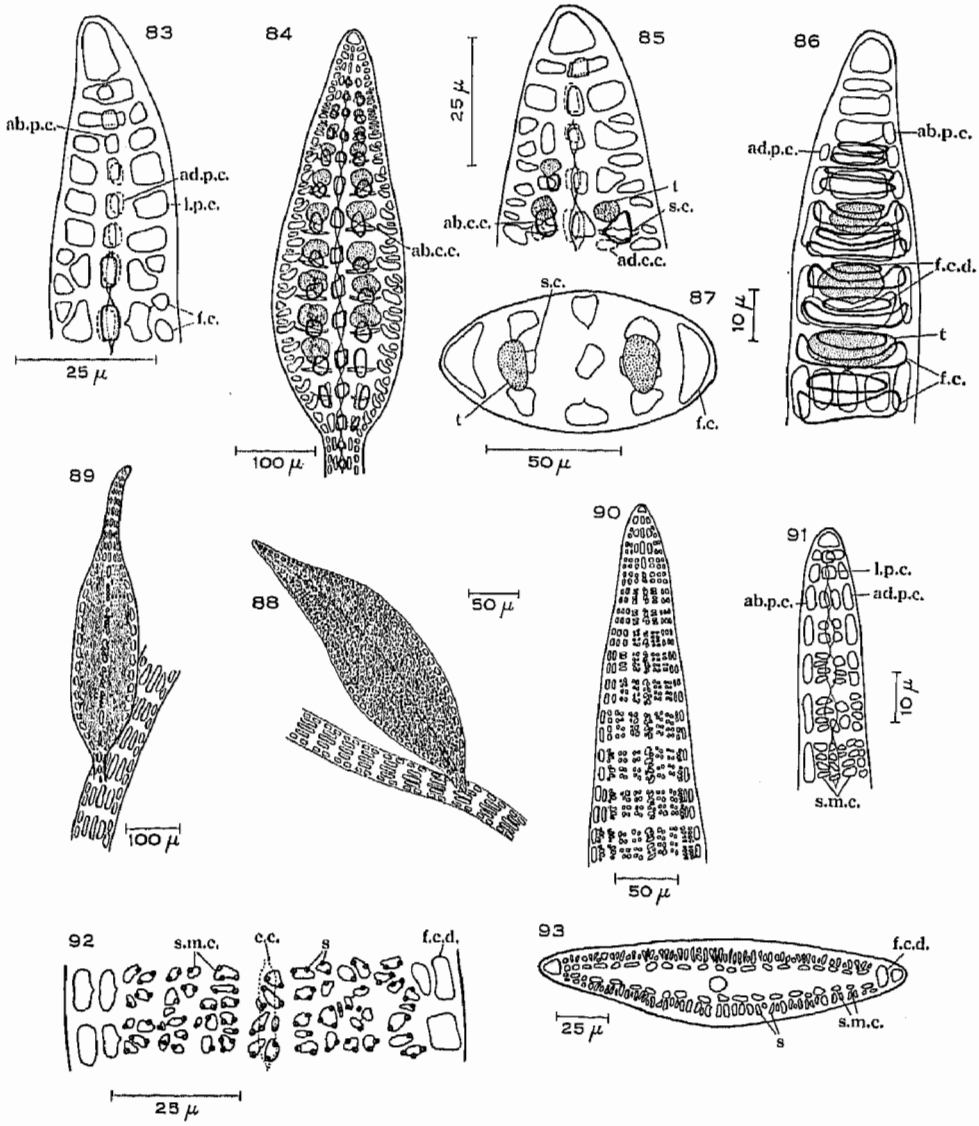
Structure of the thallus

In general structure and arrangement of cells *P. miniata* is essentially similar to *Sarcomenia victoriae* and *S. corymbosa*.

Growth is initiated by a hemispherical apical cell (Fig. 83). The abaxial pericentral cell is formed first, followed by the 2 lateral pericentral cells, and the adaxial pericentral cell is produced last. Weber van Bosse (1896) considered that the 2 lateral pericentral cells are formed first. Silva and Cleary (1954), however, found that the abaxial pericentral cell is formed first in South African material of *P. miniata*, and this is certainly so in the Vivonne Bay specimens. Two flanking cells are cut off by each lateral pericentral cell, and each elongates to half the length of the lateral pericentral cell. Lateral branches arise endogenously from the central cells, and pericentral cell formation follows as in the parent branch. The erect branches in *P. miniata* arise from prostrate basal branches which are attached to the substratum by unicellular rhizoids developed from the anterior flanking cells, usually on one side only. The thallus is ecorticate.

Development of stichidia and tetrasporangia

Stichidia develop as small lateral branches as in previously described species of the group, but very little if any cortication occurs even after the tetraspores are shed (Fig. 84). Each lateral pericentral cuts off first the tetrasporangium, followed by the abaxial cover cell, and last the adaxial cover cell (Figs. 85–87). The latter is about half the length of the transverse pericentral cells, and as the tetrasporangia



Figs. 83-93.—*Platysiphonia miniata*. Fig. 83.—Branch apex, showing segmentation. Fig. 84.—A stichidium. Fig. 85.—Apex of a stichidium, showing formation of tetrasporangia and cover cells. Fig. 86.—The same, side view. Fig. 87.—Transverse section of a stichidium. Fig. 88.—Mature spermatangial blade in which the transverse pericentral cells have formed spermatangia. Fig. 89.—Spermatangial blade, showing partial division of transverse pericentral cells. Fig. 90.—Apex of a spermatangial blade, showing segmentation. Fig. 91.—Optical longitudinal view of apex of a young spermatangial blade, showing the transverse pericentrals (outer rows) and direct division of the lateral pericentral to form spermatangial mother cells without a residual cell. Fig. 92.—Surface detail of a spermatangial blade. Fig. 93.—Transverse section of a mature spermatangial blade.

mature all the cells of the stichidium separate further, so that at maturity the tetrasporangia receive little protection from either of the cover cells.

Weber van Bosse (1896) refers only to a dorsal (abaxial) cover cell formed before the tetrasporangium, but Silva and Cleary (1954) have also found that this was not so in South African material. Each flanking cell divides horizontally soon after its formation, cutting off a derivative anteriorly. These marginal cells elongate considerably and become strongly curved, especially the posterior one of each pair (Figs. 84, 86). In mature segments the marginal cells give as much, if not more, protection to the tetrasporangia as do the cover cells. No stichidia were seen with the posterior of each pair of marginal cells divided vertically as stated by Weber van Bosse (1896). Silva and Cleary (1954) found that the posterior cell usually remains undivided in South African material.

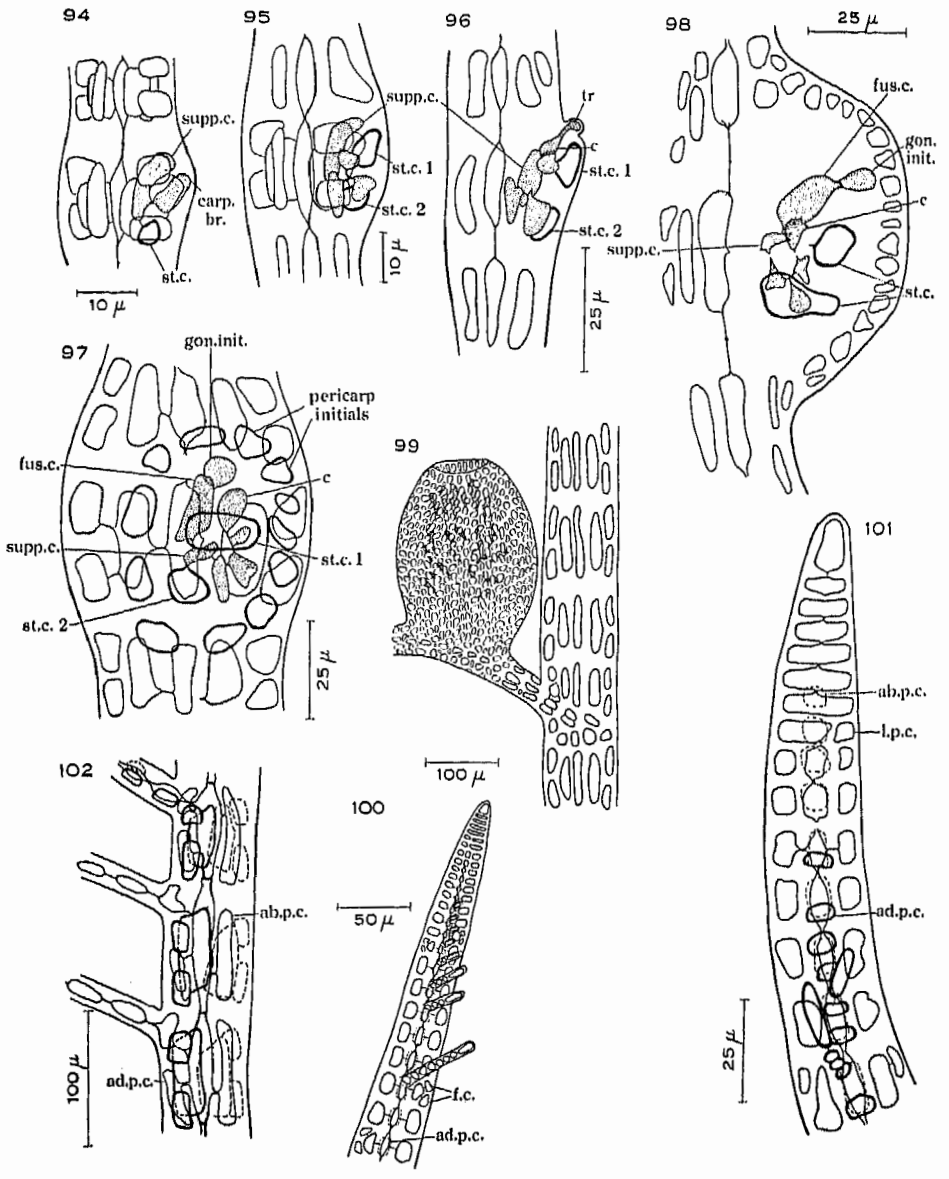
Development of spermatangial blades

The spermatia are formed on small lateral branches, similar to but more delicate than those previously described (Figs. 88, 89). They differ, however, in that the transverse pericentral cells are usually involved in spermatia production, and thus the branch lacks the distinct "midrib" of undivided pericentral cells (Fig. 88).

Boergesen (1931) also noted the activity of the transverse pericentral cells in spermatia production, but Weber van Bosse (1896) and Silva and Cleary (1954) found spermatia produced only from the lateral pericentral cells in South African material. Whether or not the transverse pericentral cells divide to form spermatia is apparently variable, since various stages showing partial involvement of the cells, or in some cases no divisions, were observed in the Vivonne Bay material. Figure 89 illustrates a spermatangial branch showing various degrees of division of the transverse pericentral cells. The flanking cells of the spermatangial branch of *P. miniata* divide longitudinally up to 3 times, and the first- and often the second-formed derivatives contribute to spermatia formation. On the margin of the blade a rather irregular line of undivided flanking cell derivatives remains, sometimes 1 and sometimes 2 cells wide (Fig. 90).

The lateral pericentral cells divide by a longitudinal periclinal wall into two, each of which divides anticlinally to give a row of 4 cells on each surface (Figs. 90, 91). Further anticlinal divisions may take place, giving on each surface 2 rows of up to 8 cells each from each lateral pericentral cell. These are the spermatangial mother cells. The derivatives of the flanking cells divide similarly but usually give a single row of 4 spermatangial mother cells. The transverse pericentral cells divide directly into a row of 4 spermatangial mother cells (Figs. 90, 91). Each spermatangial mother cell cuts off by oblique anticlinal walls 2–4 spermatangia (Figs. 92, 93).

Thus, in our spermatangial material of *P. miniata* there is no residual cell resulting from the first division of the lateral pericentral cells (Figs. 91, 93), in contrast to all other species of the *Sarcomenia* group. Boergesen (1931) found no residual cells in Indian material of *P. miniata*, but Silva and Cleary (1954) believed



Figs. 94–99.—*Platysiphonia miniata*. Fig. 94.—A young procarp, with 1 sterile cell and the carpogonial branch initial. Fig. 95.—A young procarp, with a 3-celled carpogonial branch and 2 sterile cells. Fig. 96.—A mature carpogonial branch. Fig. 97.—Post-fertilization development of the fusion cell and initiation of the pericarp. Fig. 98.—Sectional view of a young cystocarp, showing development of the fusion cell. Fig. 99.—A mature cystocarp. Fig. 100.—*Cottoniella arcuata*. Branch apex, showing occasional formation of flanking cells and formation of endogenous monosiphonous filaments anterior to the adaxial pericentral cell (the latter shown by a broken line). Figs. 101, 102.—*Cottoniella filamentosa*. Fig. 101.—Branch apex, showing segmentation and formation of monosiphonous filaments anterior to the small adaxial pericentral cell. Fig. 102.—Side view of older part of a branch, showing origin of monosiphonous filaments.

him to be mistaken on the grounds that "in all Delesseriaceae the spermatangium mother cells represent cortical cells, at least in part".

Development of procarp

Both Weber van Bosse (1896) and Boergesen (1931) had only very limited female material of *P. miniata*, and only a very few of the Vivonne Bay plants were female. Weber van Bosse and Boergesen both described and figured the mature cystocarp, and Boergesen also described what he thought were stages in procarp development. He shows, however, a well-developed pericarp in his figures, and it seems likely, as Silva and Cleary (1954) have stated, that Boergesen was dealing with post-fertilization stages. In the Vivonne Bay material the pericarp is not initiated until after fertilization, as in all other species of the *Sarcomenia* group.

Procarps arise on the adaxial surface of young lateral branches which develop rapidly, so that the procarp and later the mature cystocarp occur near the base of a long branch. The adaxial pericentral cell cuts off 2 sterile cells and the initial cell of the carpogonial branch (Figs. 94, 95), the latter being formed before the second sterile cell. The carpogonial branch is 4-celled, the first cell becoming elongate and only lightly staining; the second cell is the largest (Fig. 96). The carpogonium bears a short trichogyne with a bulbous end, as in other members of the *Sarcomenia* group.

Development of cystocarp

Adequate material was not available to follow the post-fertilization development, but initial development of the fusion cell resembles that in previously described species (Figs. 97, 98). The pericarp is initiated after fertilization (Fig. 97). The mature cystocarp is relatively small (about 200 μ across), globose, and sessile on a short lateral branch (Fig. 99). The carposporophyte bears terminal carpospores but does not show the massive, erect basal part found in the species of *Sarcomenia* described above.

The pericarp is 2 cells thick. The inner erect filaments of cells each cut off 2 cells (sometimes 3 near the base) externally, but these cells remain more or less isodiametric in surface view and do not elongate horizontally. The very few cystocarps in the Vivonne Bay material agree with Boergesen's figure (1931, Fig. 5) but not with that of Weber van Bosse (1896, Fig. 9), who shows horizontally elongate cells.

2. Cottoniella Boergesen

Cottoniella was established by Boergesen (1919, p. 333) for an alga, from St. Thomas in the West Indies, which he named *C. arcuata*. A second species was added to the genus in 1920 when Boergesen transferred *Sarcomenia filamentosa* Howe (1905) which was based on a specimen from Cape Florida. *C. sanguinea* was described by Howe (1928) from Brazil and *C. fusiformis* by Boergesen (1930, p. 144) from the Canary Is. Schotter (1951), however, regarded *C. arcuata*, *C. filamentosa*, and *C. fusiformis* as forms of one species, in which he described a new variety *algeriensis* from Algeria.

A comparison of the published figures of *C. arcuata*, *C. fusiformis*, and Schotter's var. *algeriensis* shows certain marked differences. Boergesen's (1919, pp. 336, 337) figures of *C. arcuata* in general do not show flanking cells, yet when describing *C. fusiformis* Boergesen (1930) compares it with *C. arcuata* and *C. filamentosa* and states that all three species are closely related and almost identical in cell development. Flanking cells are formed regularly by each segment of *C. fusiformis* and *C. filamentosa*. *C. arcuata* var. *algeriensis* appears to be identical with *C. filamentosa*. The latter is discussed below on the basis of material from Florida. *C. fusiformis* is distinguished from the other taxa of *Cottoniella* by the formation of monosiphonous filaments, usually in pairs anterior to the adaxial pericentral cells. Boergesen states that this is not always so, but on present knowledge this appears to be an adequate character on which to separate *C. fusiformis* from the other species of *Cottoniella*.

In view of the discrepancy between Boergesen's original figures of *C. arcuata* (without flanking cells) and his later inferences of close resemblance between this species and others, type material from St. Thomas of *C. arcuata* has been examined. This material, kindly made available by Dr. Tyge Christenson, had been preserved in liquid in the Botanical Museum in Copenhagen, but had dried up. A small fragment was found amongst other algal material, as recorded by Boergesen. This material shows that Boergesen's figures are essentially accurate, but what he referred to as corticating cells (Boergesen 1919, Fig. 336*c* and probably 335*g*) are actually flanking cells which are formed only spasmodically along the branches. This is shown in our Figure 100. This appears to give a clear-cut distinction between *C. arcuata* and *C. filamentosa*, which otherwise are very similar.

On present knowledge it appears that *C. arcuata* Boergesen, *C. filamentosa* (Howe) Boergesen, and probably *C. fusiformis* Boergesen should be recognized as distinct species. Schotter's Algerian variety should be known as *C. filamentosa* var. *algeriensis* (Schotter) comb. nov. *C. sanguinea* Howe is discussed below.

Although *C. arcuata* only forms flanking cells occasionally, and the other species do so in each segment, the characteristic endogenous monosiphonous filaments formed anterior to the adaxial pericentral cells, and the characteristic habit of the species, indicate that they should be classed in one genus.

Reproductive organs are completely unknown in *Cottoniella*, but thallus structure allies it with other genera of the *Sarcomenia* group.

Cottoniella filamentosa (Howe) Boergesen 1920: 477.

Sarcomenia filamentosa Howe 1905: 571, pl. 29, fig. 6. De Toni 1924: 362. Schotter 1951: 279.

Type locality.—Florida (*Howe*).

Type.—In Herb. New York Botanical Garden (No. 2844).

The basic structure of *C. filamentosa* as given by Howe (1905), Boergesen (1919), and Schotter (1951), and as observed in material of *C. filamentosa* from Bald Point, Florida (coll. *H. J. Humm*), is summarized below.

Structure of thallus

The hemispherical apical initial cuts off segments which divide to form 4 pericentral cells. The abaxial pericentral cell is first formed, followed by the 2 lateral pericentral cells, and finally the adaxial pericentral cell (Fig. 101). Schotter (1951) states that the lateral pericentral cells are formed first in his Algerian material but Silva and Cleary (1954) found the abaxial pericentral to be formed first in *C. arcuata* from Bermuda. This is also true in the type material of *C. arcuata* Boergesen. The lateral pericentral cells each form 2 flanking cells each about half as long as the pericentral cell. This basic structure is typically that of the *Sarcomenia* group.

The distinctive feature of *Cottoniella* is the formation of monosiphonous filaments from the adaxial face of the branches. Cells of the filaments contain chromatophores. The filaments are conspicuous near the branch apices but fall off away from the tip. They develop endogenously from the central cell, at the anterior end of the adaxial pericentral cell, which is shorter in length than the other pericentral cells (Figs. 101, 102). They arise very shortly after the adaxial pericentral cell is formed. These filaments tend to emerge from the branch in 2 rows, alternately to either side. When the filaments are shed the basal cell only is retained. Monosiphonous filaments are not formed near the base of lateral branches; here the adaxial pericentral cell is about as long as the other pericentral cells.

The endogenous origin, anterior to the adaxial pericentral cell, of the monosiphonous filaments distinguishes *Cottoniella* from *Sarcomenia tenera* and *S. dolichocystidea*, where the filaments arise exogenously from the flanking cells or from the transverse pericentral cells. *Cottoniella hawaiiensis* Doty & Wainwright from the Hawaiian Is. lacks flanking cells except in the stichidia, and the monosiphonous filaments, superficially like those in *C. filamentosa*, arise exogenously from a lateral pericentral cell. These features separate *C. hawaiiensis* generically from *C. filamentosa* (see below).

Lateral branches arise endogenously from the central cells in *C. filamentosa* and cortication commences some distance from the apex and develops extensively, at least in some varieties. The thallus is attached by means of several-celled rhizoids from prostrate branches.

Cottoniella sanguinea Howe 1928

Cottoniella sanguinea Howe from Brazil is apparently known only from the type material. It is described as differing in the presence of 5 pericentral cells instead of 4.

The type material (NYBG, fragment in AD) is strongly adherent to the mounting paper and difficult to examine. Near the tip there appear to be only 4 pericentral cells, but 5 in older parts. In a few cases it appeared that the fifth cell might be cut off from one of the first 4 pericentrals but lie in the same circle of pericentral cells. The monosiphonous filaments were short and rather unlike those of *C. filamentosa*; their origin could not be determined. Flanking cells are not present.

C. sanguinea is probably not a species of *Cottoniella* though it may well belong to the *Sarcomenia* group, but its affinities cannot be established without better material.

3. **Cottoniella hawaiiensis** Doty & Wainwright 1958

Figs. 103–105

Doty and Wainwright (1958) have recently described a new species of *Cottoniella* from Hawaii. Their account, and an examination of type material kindly made available by Dr. M. S. Doty, shows, however, that this species cannot be placed in *Cottoniella*. A brief description and reasons for placing this alga in a new genus are given below.

The thallus consists of prostrate filaments attached to other algae by rhizoids and bearing lax unilateral branch systems up to 2 cm tall. The thallus is ecorticate, with 4 pericentral cells but no flanking cells in the vegetative parts (Fig. 103). The pericentral cells are formed in typical Rhodomelaceae fashion—abaxial, lateral, and adaxial in that order. Lateral branches arise endogenously from the adaxial surface of the thallus.

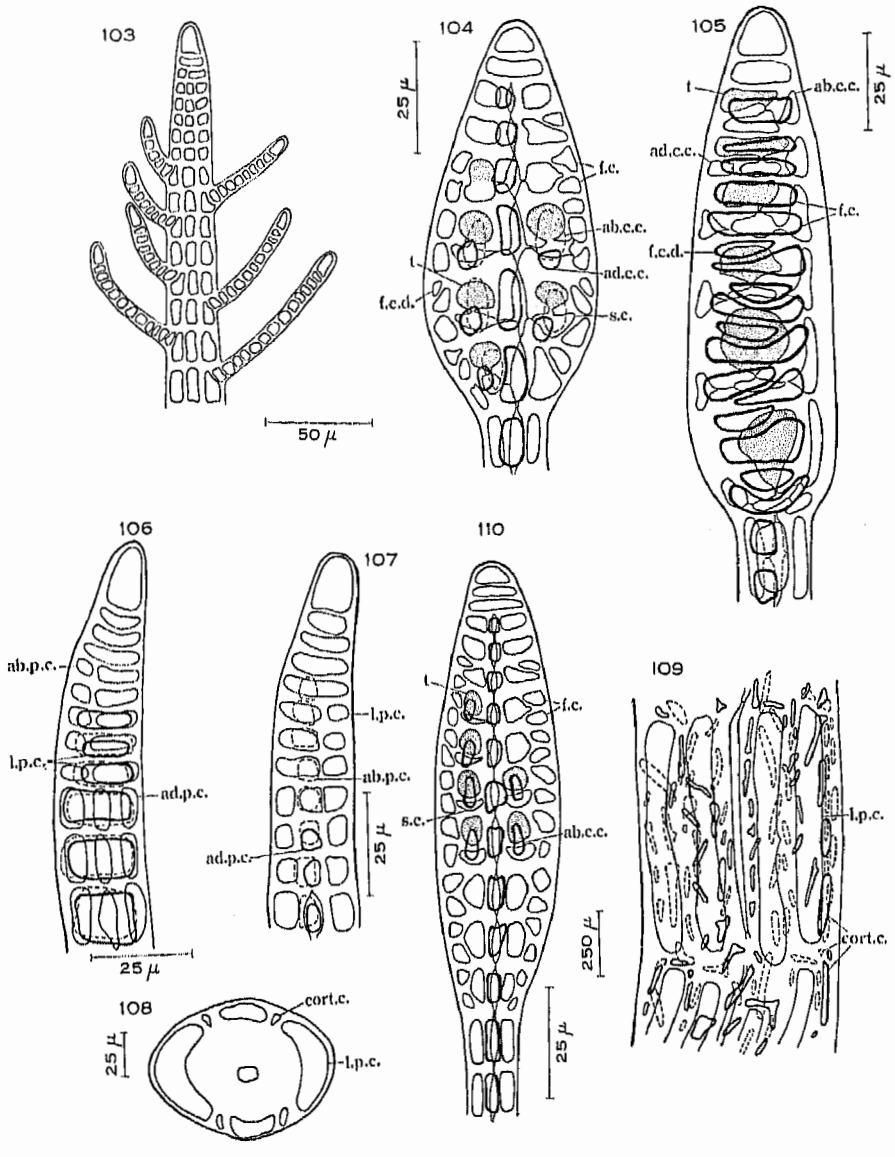
Monosiphonous filaments, containing chromatophores, are formed in characteristic manner from the lateral pericentral cells and are thus exogenous in origin. They occur alternately on the right and left pericentral cells of successive segments (Fig. 103), but are lost from older parts of the thallus. Branches tend to be concave towards the parent axis, and both rows of monosiphonous filaments are turned towards the concave side, i.e. adaxially.

The only reproductive organs known are stichidia. These are typical of the *Sarcomenia* group. The lateral pericentral cells each cut off 2 flanking cells (referred to by Doty and Wainwright as "cover" cells) which may each cut off a smaller cell (Figs. 104, 105). The tetrasporangium is cut off before the 2 cover cells on the abaxial and adaxial surfaces, of which the first-formed cover cell is extended anteriorly to partly protect the tetrasporangium while the last-formed cover cell is small and leaves the tetrasporangium exposed on that surface of the stichidium (Fig. 105). The flanking cells become curved and greatly extended horizontally, often with enlarged ends which give some protection to the tetrasporangia (Fig. 105). The flanking cell derivatives elongate but not to the same extent. Doty and Wainwright state that only an adaxial cover cell is formed, but both abaxial and adaxial cover cells are clearly present in our material. Doty and Wainwright also do not mention division of the flanking cells.

The stichidium, development and number of pericentral cells, and endogenous lateral branching clearly ally this plant with the *Sarcomenia* group. It differs from *Cottoniella*, however, in two important points:

(1) Flanking cells are completely lacking from the vegetative thallus.

(2) The monosiphonous filaments, superficially somewhat like those of *Cottoniella*, are exogenous in origin, from the lateral pericentral cells, whereas in *Cottoniella* they are endogenous, from the central cells.



Figs. 103–105.—*Cottoniella hawaiiensis*. Fig. 103.—Branch apex, showing formation of exogenous monosiphonous filaments from the lateral pericentral cells. Fig. 104.—A young stichidium. Fig. 105.—Side view of a young stichidium, showing cover cells and flanking cells. Figs. 106–110.—*Polysiphonia rocana*. Fig. 106.—Side view of a slightly flattened branch apex, showing cell segmentation. Fig. 107.—Face view of a branch apex. Fig. 108.—Transverse section of a branch, with slight cortication. Fig. 109.—An older branch, showing cortication. Fig. 110.—A stichidium, showing tetrasporangia, cover cells, and flanking cells.

On these grounds *C. hawaiiensis* is considered generically distinct from *Cottoniella* and is renamed *Dotyella* in honour of Dr. Maxwell S. Doty (see below).

4. **Polysiphonia roeana** Harvey 1854: 540; 1858: pl. 35. J. Agardh 1863: 967; Kuetzing 1864: 20, t. 55*a–c*. De Toni 1903: 877.

Figs. 106–110; Plate 5, Fig. 1

Type locality.—Fremantle, W.A. (*Harvey*).

Type.—In Herb. Harvey (TCD), No. 169A.

Distribution.—Fremantle, W.A., Torrens Strait and American River Inlet on Kangaroo I., S.A. Sublittoral under calm conditions.

The thallus is composed of fine, much-branched filaments reaching a height of 20 cm (Plate 5, Fig. 1). The branches of the thallus frequently show a distinct, though slight, lateral flattening (Fig. 108). The thallus has a greyish iridescence when fresh which very quickly changes to rosy red on exposure or on confinement in a limited volume of water. Degeneration and decomposition of the thallus occur rapidly. The material studied was collected as drift at American River Inlet, Kangaroo I., in July 1947 (AD: A5784), August 1954 (AD: A19787), and May 1955 (AD: A21393). No fertile material was included in these collections, although some hundreds of plants of the August 1954 collection were examined. The material from Fremantle, originally described and figured by Harvey, was not fertile, and no reproductive organs have ever been described. However, a specimen in Adelaide University Herbarium (AD: A1459) from "Torrens Strait" (probably Torrens I. near Outer Harbour, S.A.) proved to be tetrasporic.

Structure of thallus

Growth is initiated by a large hemispherical apical cell, which cuts off disc-shaped segments posteriorly. These segments each form 4 pericentral cells around the central cell. The abaxial pericentral cell is the first formed (Figs. 106, 107), followed by the 2 lateral pericentral cells, and finally by the adaxial pericentral cell. In the vegetative parts no lateral flanking cells are produced after the formation of the 4 pericentral cells. The cells of each segment elongate considerably, until in the older corticated branches each segment measures up to 1 mm in length. Small, elongate corticating cells are formed in fairly regular longitudinal rows from the external surfaces of each pericentral cell (Fig. 109). Lateral branches are endogenous in origin, developing from the anterior end of the central cell of the parent branch. Branching is largely from the adaxial face of the parent branch. The branches show a definite, although slight, lateral flattening, due to the larger diameter of the lateral pericentral cells (Fig. 108). The typical trichoblasts of *Polysiphonia* are completely absent.

Development of stichidia and tetrasporangia

The single dried tetrasporic specimen of *P. roeana* available did not prove suitable for a detailed study of stichidial development, but the broad features can be given with some assurance.

Tetrasporangia form near the ends of lateral branches and the stichidia are less well defined than in other species of the *Sarcomenia* group. Small lateral branches may be largely fertile, but more usually only the end 10 or more segments of a long