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lateral branch bear tetraspores. The order of cell formation in the stichidium could not be followed, but it is clear (Fig. 110) that:

(1) Typical flanking cells are produced by all fertile segments of the flattened stichidium, but they appear to remain undivided.
(2) Tetrasporangia are produced in 2 longitudinal rows from the lateral pericentral cells.
(3) Adaxial and abaxial cover cells appear to be formed.
(4) The tetrasporangia are only partly protected by the cover cells and the flanking cells. The latter become elongate and curved, but not to the same extent as in previously discussed species of the *Sarcomenia* group.
(5) The tetraspores are tetrahedrally divided.

*The affinity of* Polysiphonia roeana

The order of pericentral cell formation, absence of trichoblasts, tendency to slight flattening of the thallus, rapid disintegration of the thallus under drying or crowding after collection, and the typical *Sarcomenia*-type stichidia all point to *P. roeana* being a member of the *Sarcomenia* group. The absence of flanking cells in the vegetative thallus separate it from all other genera of the group except *Dotyella hawaiiensis*. The relationships of *P. roeana* are further discussed below.

5. **Taenioma** J. Agardh

*Taenioma* is usually referred to the *Sarcomenia* group. It has been investigated in detail by Papenfuss (1944) and Tseng (1944), who had only tetrasporic material. The only record, with brief descriptions, of cystocarpic and spermatangial material is that of Thompson (1910), on *T. perpusillum*, though Dickinson and Foote (1950) reported female material from the Gold Coast. Desikachary and Balakrishnan (1957) described vegetative and tetrasporic *T. perpusillum* and vegetative *T. nanum* from India. Tetrasporic *T. perpusillum* is known from South Australia (Scott's Bay on Eyre Peninsula, and Second Valley, both specimens in AD), and agrees well with the descriptions of Papenfuss and Tseng. *T. perpusillum* has been recorded from Queensland by Cribb (1954, p. 26).

*Taenioma* is a most distinctive genus, particularly in the presence of indeterminate and determinate branches, the latter surmounted by 2 or 3 long hairs. Flanking cells occur only on the determinate branches.

*Taenioma* differs from other genera of the *Sarcomenia* group in that the order of pericentral cell formation is typically delesseriaceous, i.e. the 2 lateral pericentrals are formed first. The apical hairs, which may be interpreted as monosiphonous filaments formed only on the distal 2 or 3 segments, complicate the position, however, and perhaps undue weight should not be placed on this difference in pericentral cell formation. Although the hairs appear to be meristematic near their bases, Papenfuss has shown this to be due to more rapid elongation of the upper cells after cell division of the terminal cell ceases. The upper parts at least of the hairs are also colourless, in contrast to the assimilatory nature and longer-retained apical meristem of the monosiphonous filaments of *Cottoniella*, *Sarcotrichia*, and *Dotyella*.

Lateral branches in *Taenioma* arise exogenously, in contrast to other genera of the *Sarcomenia* group.

The formation of flanking cells, tetrasporangia, and cover cells is similar to that in other members of the *Sarcomenia* group. The flanking cells, however, do not divide and do not elongate horizontally and curve so as to partially protect the tetrasporangia as in other species. The tetrasporangia in *Taenioma* are virtually unprotected on either face of the stichidium.

Thompson (1910) describes spermatangial branches and also the mature cystocarp of *T. perpusillum*. Spermatangia are formed on the determinate branches, ultimately covering the whole surface. The flanking cells first divide, and the inner derivatives as well as the lateral pericentral cells are involved in spermatia formation. The transverse pericentrals and outer flanking or marginal cells remain as distinct lines of larger undivided cells. Thompson does not mention residual cells from the first divisions of the lateral pericentral cells, and this point is doubted by Papenfuss (1944, p. 203) since residual cells are normally present in Delesseriaceae. Papenfuss (personal communication) has since examined cystocarpic and spermatangial material of *T. perpusillum* from the Gold Coast and states that residual cells are present in the spermatangial blades.

Thompson (1910) also describes the structure of mature cystocarps. These are borne on terete branches and are urceolate in shape with a prominent neck and osteole. The wall consists of an outer layer of angular cells with inner filaments of cells running from the base to the osteole. The gonimoblast shows a large, erect, basal cell from which branched filaments of cells arise with terminal carpospores. This cystocarp appears to be very similar in structure to that of *Platysiphonia miniata* and others of the *Sarcomenia* group.

## V. The Distinctive Features of the Sarcomenia Group

The genera and species which have been described above are usually classed together as the *Sarcomenia* group and placed in the Delesseriaceae. They have the following features in common.

(1) Thallus with 4 pericentral cells, the 2 lateral pericentral cells larger than the transverse ones, and each producing (at least in the stichidia) 2 flanking cells each about half the length of the pericentral cells.

(2) The abaxial pericentral cell is first formed, followed by the 2 lateral pericentral cells, and finally the adaxial pericentral cell. (Exception: *Taenioma*.)

(3) Each cell contains numerous ovoid to elongate chromatophores.

(4) The complete absence of typical rhodomelaceous trichoblasts, but the presence in certain genera (*Sarcotrichia*, *Cottoniella*, *Dotyella*, and *Taenioma*) of monosiphonous chromatophore containing filaments which arise exogenously (Exception: *Cottoniella*.) from the pericentral cells.

(5) Lateral branches develop endogenously. (Exception: *Taenioma*.)

(6) Stichidia with 2 longitudinal rows of tetrahedrally divided sporangia formed from the lateral pericentral cells prior to the formation of both adaxial and abaxial cover cells. The abaxial cover cell is usually larger than the adaxial and gives

some protection to the tetrasporangium, whereas the latter is largely exposed on the adaxial side. The flanking cells extend horizontally, frequently curve, and give some protection to the tetrasporangium. Division of each flanking cell horizontally into two occurs in most species.

(7) Spermatangial blades show division of the lateral pericentrals into cortical cells on each surface, leaving a central residual cell. (Exceptions: *Platysiphonia miniata*, *Taenioma perpusillum*?)

The cortical cells divide anticlinally to form spermatangial mother cells, each of which forms 2–4 spermatangia. Derivatives of the flanking cells may also form spermatangia, with (e.g. *S. delesserioides*) or without (*P. miniata*, *P. parva*) the formation of residual cells.

The spermatangial blade usually shows a margin of one or more rows of undivided cells (flanking cells or their derivatives) and a central row of undivided transverse pericentral cells. (Partial exception: *P. miniata*.)

(8) Procarps arise on the adaxial side only of young branches, from the adaxial pericentral cell which acts as the supporting cell. A first sterile cell, the carpogonial branch initial, a second sterile cell, and then the other 3 cells of the carpogonial branch develop in that order. The second cell of the carpogonial branch is usually the largest and is often binucleate. The carpogonium bears a short trichogyne with a bulbous end. Normally only 1 procarp per branch develops.

Following fertilization, the anterior end of the supporting cell is cut off as the auxiliary cell, and fusion occurs between this and the carpogonium by means of a short tube. Other cells may or may not fuse, and the fusion cell becomes more or less erect and often elongate, developing gonimoblast filaments sympodially with terminal carposporangia.

The 2 sterile cells eventually disintegrate as the gonimoblast develops. If fertilization does not occur they may, in some species, divide further and contribute to cortication of the blade. The pericarp is initiated from the pericentral and flanking cells after fertilization, and develops an urceolate shape with a terminal osteole. The wall consists of inner erect filaments not connected laterally, which cut off externally 2 (rarely 3) cells each. These outer cells may be arranged horizontally or vertically; if the latter they usually elongate horizontally and separate considerably in the mature cystocarp.

(9) The thallus when living is usually an iridescent greyish red, but on exposure to air or crowding after collection rapidly turns rosy red and disintegrates. (*Dotyella* and *Taenioma* are unknown in this respect.)

## VI. The Genera and Species of the Sarcomenia Group

Various authors, including Grunow (1870), J. Agardh (1899), Howe (1905), and Boergesen (1920) have realized that *Sarcomenia* was not a natural genus, but owing to the difficulties of studying dried material little could be done to clarify the group. Boergesen (1919) described *Cottoniella* and later (1931) segregated *Platysiphonia*.

The most important changes now made are the inclusion of several other species in *Platysiphonia*, and the two species with monosiphonous filaments (*S. tenera*, *S. dolichocystidea*) in a new genus, *Sarcotrichia*. *Platysiphonia* now includes eight species which differ most conspicuously in size and degree of cortication but are similar in fundamental structure. Only one species, *S. delesserioides* Sonder, is now left in *Sarcomenia*. *Polysiphonia roeana* Harvey has been shown above to be almost certainly a member of this group, and is here placed in a new genus, *Malaconema*.

Generic differences within the group are based largely on vegetative structure since reproductive organs, where known, are very similar. A key to the genera is given below, followed by brief taxonomic diagnoses.

KEY TO GENERA OF THE SARCOMENIA GROUP

1. Thallus without flanking cells from the lateral pericentral cells of vegetative (indeterminate) branches ..... 2
1. Thallus with flanking cells from the lateral pericentral cells ..... 4
2. Thallus without monosiphonous filaments ..... *Malaconema*
2. Thallus with monosiphonous filaments ..... 3
3. Monosiphonous filaments from the lateral pericentral cells, turned to the adaxial side ..... *Dotyella*
3. Monosiphonous filaments in 2's or 3's surmounting determinate branches ..... *Taenioma*
4. Free monosiphonous filaments present ..... 5
4. Free monosiphonous filaments not formed ..... 6
5. Monosiphonous filaments formed endogenously from the central cells anterior to the adaxial transverse pericentral cell ..... *Cottoniella*
5. Monosiphonous filaments formed exogenously from the anterior flanking cells of each segment and in *S. tenera* from the transverse pericentrals ..... *Sarcotrichia*
6. Flanking cells not dividing further in the vegetative thallus ..... *Platysiphonia*
6. Flanking cells dividing further, the anterior one producing 2 chains of cells, the posterior one a single chain of cells, which remain laterally adherent giving a strongly compressed thallus ..... *Sarcomenia*

**Sarcomenia** Sonder 1845. Type and only species: *S. delesserioides* Sonder 1845.

Thallus arising from a branched holdfast, erect, to 50 cm high; branches strongly flattened, up to 2 cm broad. Branching endogenous from the central cells, issuing usually to the side of the midrib. Pericentral cells 4; lateral pericentral cells each forming 2 flanking cells, the upper of which forms 2 chains of cells, the lower 1 chain of cells, all lying in the one plane and laterally adherent to form the broad, flat branches; cell divisions restricted to the marginal end cells of the chains. Thallus heavily corticated to near the apices.

Cystocarps and stichidia corticated. Spermatangia formed from lateral pericentral cells and several series of flanking cell derivatives. Otherwise reproductive organs as in the *Sarcomenia* group.

**Platysiphonia** Boergesen 1931. Type species: *P. miniata* (C. Agardh) Boergesen.

Thallus arising from a prostrate basal part attached by rhizoids or from a branched holdfast, variable in size. Branches compressed when young, becoming more or less terete when corticated. Lateral branches endogenous from the central

cells, issuing above or laterally to the central cells. Pericentral cells 4; lateral pericentral cells each forming 2 flanking cells which do not divide further (except in the spermatangial branches of certain species). Thallus varying from ecorticate in some species to heavily corticate in others. Cystocarps and stichidia not or only slightly corticated near the base. Reproductive organs as in the *Sarcomenia* group.

*Platysiphonia* includes the following species as well as the type:

*P. intermedia* (Grunow) Boergesen 1931.
*P. mutabilis* (Harvey) Boergesen 1931.
*P. clevelandii* (Farlow) Papenfuss 1944.
*P. parva* Silva & Cleary 1954.
*P. victoriae* (Harvey ex J. Agardh) comb. nov. (*Sarcomenia victoriae* Harvey ex J. Agardh 1863: 1262.)
*P. corymbosa* (J. Agardh) comb. nov. (*Sarcomenia corymbosa* J. Agardh 1896: 134.)
*P. hypneoides* (Harvey) comb. nov. (*Sarcomenia hypneoides* Harvey 1854: 537.)

KEY TO THE SPECIES OF PLATYSIPHONIA

1. Thallus to a few centimetres high, not or only very slightly corticate ..... 2
1. Thallus 6–40 cm high, heavily corticate below ..... 5
2. Flanking cells of stichidium undivided ..... 3
2. Flanking cells of stichidium divided into two ..... 4
3. Thallus to 1 cm high, epiphytic on *Codium* (Guadalupe Is.) ..... *P. parva* Silva & Cleary
3. Thallus not epiphytic on *Codium*, to 8 cm high (South Africa, St. Paul) ..... *P. intermedia* (Grunow) Boergesen
4. Flanking cells in stichidium divided horizontally into two. Lateral branches emerging in line with the longitudinal axis of the parent branch ..... *P. miniata* (C. Agardh) Boergesen
4. Flanking cells in stichidium divided vertically giving an outer marginal row of cells. Lateral branches emerging obliquely laterally from the longitudinal axis of the parent branch ..... *P. clevelandii* (Farlow) Papenfuss
5. Branching mostly unilateral from the adaxial surface of parent branches ..... *P. corymbosa* (J. Agardh) comb. nov.
5. Branching more irregular ..... 6
6. Branches corticate only near their bases, plant relatively slender ..... *P. mutabilis* (Harvey) Boergesen
6. Branches corticate nearer their apices, plant robust, stem to 2 mm thick below ..... 7
7. Branches corticate almost to the apices, branch ends curled, stichidia corticate ..... *P. hypneoides* (Harvey) comb. nov.
7. Younger branches and stichidia ecorticate ..... *P. victoriae* (Harvey ex J. Agardh) comb. nov.

**Sarcotrichia** gen. nov. Type species: *S. tenera* (Harvey) comb. nov. (*Dasya tenera* Harvey 1854: 543.)

Thallus arising from a branched holdfast, to 30 cm high. Branches compressed above, more or less terete and heavily corticate below. Lateral branches endogenous from the central cells. Pericentral cells 4; lateral pericentral cells each forming 2 flanking cells. Anterior flanking cells (and in *S. tenera* the transverse pericentral cells also) forming slender, monosiphonous filaments from their anterior ends;

filaments completely free, deciduous on older branches. Cystocarps and stichidia not corticated. Spermatangia on small lateral blades.

Thallus oriens ex haptero ramoso, ad 30 cm altus. Superni rami compressi, inferne rami teretiores et corticatissimi. Laterales rami endogeni e cellulis centralibus. 4 cellulae pericentrales; quaque cellula latero-pericentralis producens 2 marginales cellulas. Cellulae marginales anteriores (et in *S. tenera* etiam cellulae pericentrales transversae) producentes tenuia, monosiphona filamenta ex anterioribus extremis; filamenta toto separata, cadentia in ramis maturis. Cystocarpia et stichidia non corticata. Spermatangia in ramulis lateralibus.

*Sarcotrichia* also includes *S. dolichocystidea* (J. Agardh) comb. nov. (*Sarcomenia dolichocystidea* J. Agardh 1896: 135.)

KEY TO THE SPECIES OF SARCOTRICHIA

1. Monosiphonous filaments produced from the anterior flanking cells and the transverse pericentral cells ..... *S. tenera* (Harvey) comb. nov.
1. Monosiphonous filaments produced from the anterior flanking cells only ..... *S. dolichocystidea* (J. Agardh) comb. nov.

**Cottoniella** Boergesen 1919. Type species: *C. arcuata* Boergesen 1919.

Thallus slender, arising from prostrate parts attached by rhizoids, up to 12 cm high, corticate below. Lateral branches endogenous, above more or less arcuate. Pericentral cells 4; lateral pericentral cells each forming 2 flanking cells (only occasional in *C. arcuata*) which do not divide further. Monosiphonous filaments formed endogenously from the central cells, anterior to the adaxial pericentral cell, in 1 or 2 rows. Reproductive organs unknown.

**Dotyella** gen. nov. Type species: *D. hawaiiensis* (Doty & Wainwright) comb. nov. (*Cottoniella hawaiiensis* Doty & Wainwright 1958: 229.)

Thallus slender, to 2 cm high, with erect branches arising from prostrate parts attached by rhizoids; ecorticate. Lateral branches endogenous from the central cells. Pericentral cells 4. No flanking cells formed in vegetative parts. Monosiphonous filaments arising from the lateral pericentral cells, alternately on opposite sides, turned towards the adaxial side of the branch. Stichidia with flanking cells, developing as in the *Sarcomenia* group. Cystocarps and spermatia unknown.

Thallus tenuis, ad 2 cm altus, cum ramis erectis orientibus e partibus prostratis adfixis a rhizoidibus; ecorticatus. Laterales rami endogeni e cellulis centralibus. 4 cellulae pericentrales. Marginales cellulae deficientes in partibus sterilibus. Filamenta monosiphona orientia e cellulis latero-pericentralibus et alternato in lateribus oppositis, versa ad adaxiale latus rami. Stichidia marginalibus cellulis sicut in Sarcomenioideis. Cystocarpia et spermatia incognita.

**Malaconema** gen. nov. Type species: *M. roeana* (Harvey) comb. nov. (*Polysiphonia roeana* Harvey 1854: 540.)

Thallus very slender, to 20 cm high, terete or slightly flattened. Lateral branches irregular, endogenous from the central cells. Thallus lightly corticate

below. Pericentral cells 4, the 2 lateral ones largest. No flanking cells formed in vegetative parts. No monosiphonous filaments formed. Ends of tetrasporangial branches broader, similar to stichidia of the *Sarcomenia* group. Stichidia with 2 flanking cells formed from each lateral pericentral cell. Cystocarps and spermatangial branches unknown.

Thallus tenuissimus, ad 20 cm altus, teres aut compressior. Rami laterales irregulares, endogeni e centralibus cellulis. Thallus paulum corticatus inferne. 4 cellulae pericentrales, quarum 2 laterales cellulae maximae. Marginales cellulae deficientes in partibus sterilibus. Filamenta monosiphona deficientia. Fines tetrasporangialium ramorum latiores sicut stichidia Sarcomenoidearum. Stichidia cum 2 marginalibus cellulis formatis ex quaque cellula latero-pericentrali. Cystocarpia et spermatia incognita.

**Taenioma** J. Agardh. Type species: *T. perpusillum* (J. Agardh) J. Agardh. (*Polysiphonia perpusilla* J. Agardh.)

Thallus minute, with prostrate, terete, indeterminate branches attached by rhizoids and with 4 pericentral cells only, and erect, flattened, determinate branches arising from the indeterminate branches. Determinate branches with 2 flanking cells from each lateral pericentral, the whole branch surmounted by 2 or 3 long monosiphonous filaments. Tetrasporangia and spermatangia formed in determinate branches, cystocarps on terete branches.

## VII. Taxonomic Relationships of the Sarcomenia Group

*Sarcomenia*, when originally described by Sonder (1845, p. 56; 1846, p. 194) was placed in the Delesserieae, and this was followed by Kuetzing (1849). At this time *S. delesserioides* Sonder was the only known species of the genus. Harvey (1847, 1854, 1860), however, suggested that it belonged to the Rhodomeleae, and this was supported by J. Agardh (1863) when he described several other species of *Sarcomenia*, based largely on Harvey's collections. J. Agardh described the tribe Sarcomenieae of the order Rhodomeleae, including in it *Taenioma*, *Vanvoorstia*, and *Claudea* as well as *Sarcomenia*. The distinctive feature of this tribe was the presence of half-length marginal cells outside the lateral pericentral cells. Later J. Agardh (1896, 1899) discussed the species of *Sarcomenia* remarkably thoroughly considering that he had only dried material, and he considered that the group definitely belonged to the Rhodomeleae. Schmitz (1889) and Schmitz and Hauptfleisch (1897), however, placed the Sarcomenieae as a subfamily of the Delesseriaceae, distinguished from the rest of the Delesseriaceae by the tetrasporangia being formed in a single layer only and by the prominent globose cystocarps. They included in the Sarcomenieae the following genera: *Caloglossa*, *Taenioma*, *Sarcomenia*, *Sonderella*, *Claudea*, *Vanvoorstia*, and *Zellera*.

Falkenberg (1901) strongly supported the affinities of the *Sarcomenia* group with the Delesseriaceae, and strongly criticized J. Agardh's placing of it as a tribe of the Rhodomelaceae. Falkenberg used two features in particular in placing the Sarcomenieae in the Delesseriaceae, viz. the method of division of the apical cell

to form pericentral cells, and the cutting off by the lateral pericentral cells of two marginal or flanking cells each half the length of the pericentral cells. The order of pericentral cell formation, first elucidated by Naegeli (1847), is probably still the best character on which to separate the Rhodomelaceae and Delesseriaceae, but Falkenberg apparently based his concepts of the *Sarcomenia* group on *Taenioma*, whereas J. Agardh had studied in considerable detail the species of *Sarcomenia* itself. As is shown in the present study, all the species then placed in *Sarcomenia* show the rhodomelaceous order of pericentral cell formation, whereas *Taenioma* is exceptional (for the *Sarcomenia* group) in showing the delessereaceous order of pericentral cell formation.

More recent authors who have studied members of the *Sarcomenia* group have not had adequate material on which to form opinions on the position of the group. Papenfuss (1944) and Tseng (1944) both studied *Taenioma perpusillum*, and support Falkenberg's findings.

From the Sarcomenieae as recognized by Schmitz and Hauptfleisch, *Caloglossa*, *Claudea*, and *Vanvoorstia* have been separated by Papenfuss (1937) as the *Claudea* group; *Caloglossa*, however, was later removed from this group by Papenfuss (1944) because of its exogenous branching and is placed by Kylin (1956) in a group of its own. *Zellera* is little known but probably belongs also to the *Claudea* group. *Sonderella* is not a member of the group but belongs to the Rhodomelaceae, possibly near the *Amansia* group; this will be discussed in a separate account.

The *Sarcomenia* group thus contains *Sarcomenia*, *Platysiphonia*, *Cottoniella*, and *Taenioma*, and the three genera described in this account: *Sarcotrichia*, *Malaconema*, and *Dotyella*. The distinctive features of these genera have been outlined above, and can now be discussed further in relation to the taxonomic position of the *Sarcomenia* group.

Recent discussion of the *Sarcomenia* group has centred mainly on whether it should be recognized as an independent subfamily of the Delesseriaceae or merged with the Delesserieae. Kylin (1923, 1928) first advocated the latter course, on the grounds that the procarps were formed on the midrib of the blade, in contrast to the Nitophylleae, where they occur scattered over the surface. Kylin (1924 and previously), however, while studying in detail many Delesserieae and Nitophylleae, did not study any members of the Sarcomenieae. Kylin was supported by Papenfuss (1937) on the basis of a study of *Claudea* and *Vanvoorstia* and by Papenfuss (1944) on *Taenioma*, but the first two genera are not members of the *Sarcomenia* group and *Taenioma* is certainly not a typical representative. Fritsch (1945, p. 746), however, retains the Sarcomenieae as a distinct subfamily of the Delesseriaceae. The present study shows that there are other features more significant than the procarp position which separate the *Sarcomenia* group from the Delesseriaceae.

### (*a*) *Vegetative Features*

The order of pericentral cell formation in all genera of the *Sarcomenia* group except *Taenioma* is the abaxial pericentral cell first, followed by the 2 lateral pericentral cells, and finally by the adaxial pericentral cell. This order is typical of the Rhodomelaceae, in contrast to the Delesseriaceae, where the lateral pericentral

cells are first formed; and since being elucidated by Naegeli (1847) this has proven one of the most satisfactory distinctions between the two families. Papenfuss (1944, p. 200) states that not a single exception to this separation of the two families has been found. This, however, was before the *Sarcomenia* group had been adequately investigated and, as stated before, the example of this group (*Taenioma*) studied by Falkenberg, Papenfuss, and others is exceptional in its pericentral cell formation. The situation in *Taenioma* is not easy to evaluate owing to the restriction of monosiphonous filaments to the apex of the branches and the very rapid formation of determinate and indeterminate apices at the branch ends.

If the distinction on pericentral cell formation is regarded as of primary importance, then the *Sarcomenia* group must be classed under the Rhodomelaceae, and *Taenioma* must be regarded as doubtfully a member of the group.

A more important exception to the above separation of the families Delesseriaceae and Rhodomelaceae occurs in the *Claudea* group of the former, where *Claudea* shows the delesseriaceous plan but *Vanvoorstia* the rhodomelaceous plan of pericentral cell formation (see Section IX).

Other vegetative features of the *Sarcomenia* group indicate that its affinities are with the Delesseriaceae rather than the Rhodomelaceae, but exceptions are known in each case.

All Delesseriaceae possess 4 pericentral cells, whereas the basic number (at least in fertile parts) in the Rhodomelaceae is 5. In this respect the *Sarcomenia* group is similar to the Delesseriaceae.

In the Delesseriaceae the first-formed pericentral cells lie in a row, whereas in many Rhodomelaceae but not all they are spirally arranged. In the *Sarcomenia* group the first-formed pericentral cells lie in a linear row.

The Delesseriaceae without exception lack typical trichoblasts, which are a feature of most but not all of the Rhodomelaceae. Typical trichoblasts are strictly exogenous (Scagel 1953, p. 9) and arise very close to the apical cell before the ring of pericentral cells is fully developed. They are usually colourless, lacking chromatophores (exception: Lophothalieae), and almost always bear the sex organs. Trichoblasts are not known in *Bostrychia* or in the vegetative state of *Polyzonia* (Scagel 1953, p. 8). The monosiphonous filaments of certain genera of the *Sarcomenia* group (*Sarcotrichia*, *Dotyella*), are exogenous but do not arise till after pericentral cell formation, while those of *Cottoniella* are endogenous from the central cells. In these genera of the *Sarcomenia* group the cells of the monosiphonous filaments contain abundant chromatophores. They appear therefore to be distinct in both origin and structure from typical trichoblasts.

The presence of flanking cells, produced in pairs from the lateral pericentral cells, has been regarded as a distinctive character of the Delesserieae. This was one of the main reasons why Falkenberg (1901) and others referred the *Sarcomenia* group to the Delesseriaceae. In most Delesserieae the flanking cells give rise to initials which produce rows of cells. In a few genera of Rhodomelaceae where flanking cells are formed, only one is cut off by each pericentral cell and this later divides lengthwise into two (Papenfuss 1944, p. 201). The *Sarcomenia* group

resembles the Delesserieae in that both flanking cells originate directly from the lateral pericentral cells. In certain genera, however, flanking cells are formed only in the stichidia.

Branching in the Rhodomelaceae is basically exogenous, originating close to the apical cell, but endogenous branches occur in *Metamorphe*, the Amansieae, and the Lophosiphonieae (Scagel 1953, p. 9; Kylin 1956). The Delesserieae show endogenous branching exclusively except for *Caloglossa* (and *Taenioma*) (Papenfuss 1944, p. 207). Branching in the *Sarcomenia* group is endogenous except for the monosiphonous filaments in *Sarcotrichia* and *Dotyella*.

While the form and habit of *Sarcomenia delesserioides* is delesseriaceous, that of other species of the *Sarcomenia* group is distinctly rhodomelaceous or dasyaceous, as the thalli in general are more or less terete and much branched.

Thus while the most important vegetative distinction between the Delesseriaceae and Rhodomelaceae, the order of pericentral cell formation, places the *Sarcomenia* group in the Rhodomelaceae (which it also resembles in general appearance), other vegetative features show similarity with the Delesseriaceae.

### (*b*) *The Procarp and Cystocarp*

Papenfuss (1944, p. 203), following similar expressions by earlier authors, states that there are "no sharply defined and constant differences between the Rhodomelaceae and Delesseriaceae with respect to the development and structure of the cystocarp". Kylin (1956), however, separates these two families primarily on the method of branching of the gonimoblast filaments. This is monopodial in the Delesseriaceae and sympodial in the Rhodomelaceae. This distinction was first recognized by Falkenberg (1901) but has not been emphasized by other authors except Kylin. The use of this feature warrants further careful investigation, and some doubt may be felt as to its significance from figures given by Kylin (1956) of gonimoblasts in various Delesseriaceae and Rhodomelaceae.

The gonimoblast development in the *Sarcomenia* group is sympodial, if somewhat irregular, and Kylin would doubtless have placed it in the Rhodomelaceae had he known this.

The position of the procarp provides a good distinction between the Delesseriaceae and Rhodomelaceae, with a few exceptions in the latter family. In the Delesseriaceae the procarp is always borne directly on the blades, but in the Rhodomelaceae it occurs on trichoblasts with few exceptions (*Rhodomela*, *Bostrychia*). In this respect the *Sarcomenia* group agrees with the Delesseriaceae.

Procarps in the Delesserieae (excluding the *Claudea* group) are formed on both surfaces of the blade, but in the *Sarcomenia* group they occur on only one series (adaxial) of transverse pericentral cells. The 2 sterile cells of the procarp of the *Sarcomenia* group ultimately disintegrate unless fertilization does not occur, when they may divide in some species and contribute to cortication of the blade. In this respect they are similar to the sterile cells in the Delesserieae (Kylin 1923, p. 102; 1937, p. 286; Papenfuss 1944, p. 210).

Carpospores in the *Sarcomenia* group are produced singly and terminally, as they are also in the *Claudea* group. In other groups of the Delesseriae carpospores are produced in rows (Kylin 1956, p. 417). In the Nitophylleae and Rhodomelaceae carpospores are also formed terminally and singly.

The mature cystocarp of the *Sarcomenia* group is an external, urceolate structure similar to that in most Rhodomelaceae. The cystocarp of the Delesseriaceae in contrast is partly or largely immersed in the thallus. The pericarp is initiated after fertilization in most Delesseriaceae, whereas in most Rhodomelaceae (one exception is *Bostrychia* (Fritsch 1945, p. 707)) it is initiated before fertilization. In the *Sarcomenia* group the pericarp is not initiated until after fertilization.

The pericarp wall of the Delesseriaceae cystocarp usually consists of several layers of cells of similar size, arranged in vertical rows and originating from the cortical cells which surround the procarp (Kylin 1956, p. 415) or sometimes from the pericentral cells. In the Rhodomelaceae the pericarp is normally 2 cells thick, formed of an inner layer of erect filaments, the cells of which each cut off 2 or 3 outer cells (which may be interpreted as pericentral cells). Further cortication occurs in some species. The pericarp of the *Sarcomenia* group cystocarp is of the latter type, and the 2 (or 3) outer cells, cut off from each vertical filament cell, may lie horizontally or one above the other. In the latter case they become considerably elongate horizontally. The mature pericarp cells separate considerably from each other.

Thus while differences in procarp and cystocarp structure between the Delesseriaceae and Rhodomelaceae are mostly relatively minor, the position of the procarp of the *Sarcomenia* group is more typically delesseriaceous, but Kylin's distinction of the families on the method of gonimoblast branching would definitely place the *Sarcomenia* group in the Rhodomelaceae. In other respects, in the restriction of procarps to one series of transverse pericentral cells, the general form of the cystocarp and the structure of the pericarp (but not its post-fertilization origin) the *Sarcomenia* group is also rhodomelaceous.

### (c) *Spermatangial Blades*

Spermatangia in the Delesseriaceae are produced on small lateral blades and arise from spermatangial mother cells formed by subdivision of cortical cells. In the Rhodomelaceae the spermatangia are usually formed on the trichoblasts, except in *Euzoniella*, *Bostrychia*, *Lophothalia*, and *Rhodomela*, where they are produced from the pericentral cells of polysiphonous branches (Scagel 1953, p. 11). Otherwise there appear to be no constant differences between the two families in spermatangial development. The *Sarcomenia* group, in species in which spermatangia are known, forms spermatangia on small lateral blades, in general from spermatangial mother cells. These are derived from cortical cells cut off from the lateral pericentral cells or derivatives of the flanking cells. While in most species a residual cell remains after division of the lateral pericentral cells to form cortical cells, in *Platysiphonia miniata* the pericentral cells divide directly into two, each of which divides to form spermatangial mother cells.

Spermatangial blades in the *Sarcomenia* group are distinctive in that the marginal cells (flanking cells or their derivatives) and the transverse pericentral cells remain undivided and play no part in spermatangium formation. The blades thus show a central "midrib" and a margin of undivided cells. In most Rhodomelaceae all pericentral cells take part in spermatangium formation, leaving no sterile cells on the surface, but in *Euzoniella* (Scagel 1953, p. 86, Fig. 17) a situation superficially resembling that in the *Sarcomenia* group is found. Here the spermatangial blade is triradiate, with undivided marginal cells in each of the 3 flanges, which are derived from the 3 pericentral cells of vegetative blades.

The distinctive spermatangial blades of the *Sarcomenia* group are not seen in the Delesseriaceae in general, but the situation and origin of the spermatangia are similar. Spermatangial blades of the Delesseriaceae show more irregular fertile areas, without the distinctive lines of sterile transverse pericentral and marginal cells.

Thus the spermatangial blades help little in showing the affinities of the *Sarcomenia* group, but are uniform and distinctive within the group.

### (*d*) *Stichidia and Tetrasporangia*

One of the best distinctions that has been recognized between the Delesseriaceae and the Rhodomelaceae lies in the order of sporangium and cover cell development in the stichidium (Papenfuss 1944). In the Delesseriaceae the tetrasporangium is initiated first from the pericentral (or some other) cell, followed by the 2 cover cells, which only partly protect the sporangium. In the Rhodomelaceae the cover cells are formed first and completely protect the sporangium. The *Sarcomenia* group in this respect conforms with the Delesseriaceae and not the Rhodomelaceae.

In the Rhodomelaceae the sporangia are formed from pericentral cells only, except in the Laurencieae and Chondrieae (Scagel 1953, p. 12). In the Delesseriaceae the sporangia in general arise from cortical cells and not pericentral cells, except in *Claudea*, where both types of cells are involved, and *Vanvoorstia*, where pericentral cells only are concerned (Papenfuss 1937). In *Caloglossa* also the sporangia are cut off in a single layer from the lateral pericentral cells and from successive cells of the cell rows of the second order. The *Sarcomenia* group shows more similarity to the Rhodomelaceae on the origin of the sporangia.

The *Sarcomenia* group was originally separated from the Delesserieae as the tetrasporangia occur in a single layer, whereas they occur in two layers in the latter. With the separation of *Claudea* and *Vanvoorstia* from the *Sarcomenia* group by Papenfuss (1937) this distinction now applies with the exception of *Caloglossa*.

While the distinction of the Delesseriaceae and Rhodomelaceae on the order of sporangium and cover cell development appears generally satisfactory, the relationship of the flanking cells and abaxial and adaxial cover cells may be considered with regard to the possible origin of the *Sarcomenia* type of stichidium.

In the Rhodomelaceae the stichidia nearly always possess 5 pericentral cells, whatever the number of vegetative pericentrals. In most genera only 1 pericentral cell per segment is fertile and these are spirally arranged, but in some (Amansieae,

*Rhodomela*, *Odonthalia*) the sporangia occur in 2 longitudinal rows in a flattened stichidium, while in others (*Bostrychia*, *Pleurostichidium*) every pericentral cell of a segment is fertile. The fertile pericentral cell cuts off first 2 or 3 cover cells (which may divide further) and these form a continuous cover protecting the tetrasporangium, which is cut off subsequently from the pericentral cell. In sectional longitudinal view the stichidium commonly shows the fertile pericentral cell with the sporangium anteriorly and the 2 or 3 cover cells laterally (e.g. Fritsch 1945, Fig. 291*G*, *I*; Scagel 1953, Figs. 7*c*, 12*f*).

Such longitudinal views of stichidia with 2 rows of sporangia are strikingly similar to the *Sarcomenia*-type stichidia, the only difference lying in the cells on the abaxial and adaxial surfaces of the stichidium. Whereas in the Rhodomelaceae such stichidia have 2 pericentral cells on one surface and 1 on the other, there is a single abaxial and single adaxial pericentral cell in the *Sarcomenia* type. Further, the fertile pericentral cells of the Rhodomelaceae do not cut off cells on the abaxial and adaxial surfaces comparable to the cover cells of the *Sarcomenia* group.

The usual interpretation of the first-formed derivatives of the lateral pericentral cells of the *Sarcomenia* group as "flanking cells" and the post-sporangial derivatives as "cover cells" derives largely from the presence of similar flanking cells in the vegetative thallus and also in the Delesseriae generally.

It is possible, however, that the flanking cells of the *Sarcomenia* group stichidium should be interpreted as cover cells comparable to those of the Rhodomelaceae, and the abaxial and adaxial "cover cells" as extra cells developed in the *Sarcomenia*-type stichidium to give some protection to the tetrasporangia, which otherwise lie completely exposed owing to the flattening of the stichidium and the presence of only 4 pericentral cells. This is supported by the fact that both the cover cells of the Rhodomelaceae and flanking cells are formed radially to the stichidium axis, whereas the *Sarcomenia* group cover cells are formed by the lateral pericentral cells at right angles to the plane of the stichidium. It is noteworthy also that in *Vanvoorstia coccinea* the "flanking cells" of the stichidium do not form a wing to the stichidium, but act as "cortical cells" (Papenfuss 1937, p. 58) or cover cells similar to those cut off by the 2 abaxial and 1 adaxial pericentral cell, a terete stichidium resulting.

On the basis of this interpretation (the cover or flanking cells being formed before the sporangium), the *Sarcomenia* group stichidium can be interpreted as having been derived from the rhodomelaceous type. Other features of the stichidium, while not conclusive, also resemble the Rhodomelaceae rather than the Delesseriaceae.

The lack of flanking cells in vegetative parts of *Malaconema* and *Dotyella* and their partial occurrence in *Cottoniella arcuata* may also indicate the derivation of the *Sarcomenia* group from rhodomelaceous ancestors.

### (*e*) *Conclusions as to the Position of the* Sarcomenia *Group*

The above discussion shows that of the three distinguishing features between the Delesseriaceae and Rhodomelaceae which have been considered most important, two (the order of pericentral cell development and the branching of the gonimoblast) place the *Sarcomenia* group in the Rhodomelaceae and one (the order of sporangium

and cover cell development) is apparently similar to the Delesseriaceae but may be derived from the Rhodomelaceae.

Other vegetative features (position of the procarps, presence of flanking cells, lack of trichoblasts, endogenous branching) are more typical of the Delesseriaceae. The wall structure and general morphology of the cystocarp are rhodomelaceous, but the post-fertilization origin of the pericarp is in general delesseriaceous. The spermatangial blades are distinctive for the *Sarcomenia* group but help little in relationships. Other features of the stichidia are rhodomelaceous rather than delesseriaceous.

The *Sarcomenia* group shows so many features which are characteristic of either the Delesseriaceae or the Rhodomelaceae that it must be recognized as forming an intermediate or linking group between the two families. It could be placed as a subfamily, the Sarcomenioideae, of either family or even recognized as an independent family. The majority of features, however, point to its relationships to the Rhodomelaceae, from which it could have been derived, and it seems best to place the Sarcomenioideae as a subfamily of the Rhodomelaceae. All other groups currently placed in the Rhodomelaceae (Scagel 1953, p. 13) comprise a second subfamily, the Rhodomeloideae, within which these groups are probably best ranked as tribes.

The Sarcomenioideae differ from the Rhodomeloideae in the following respects:

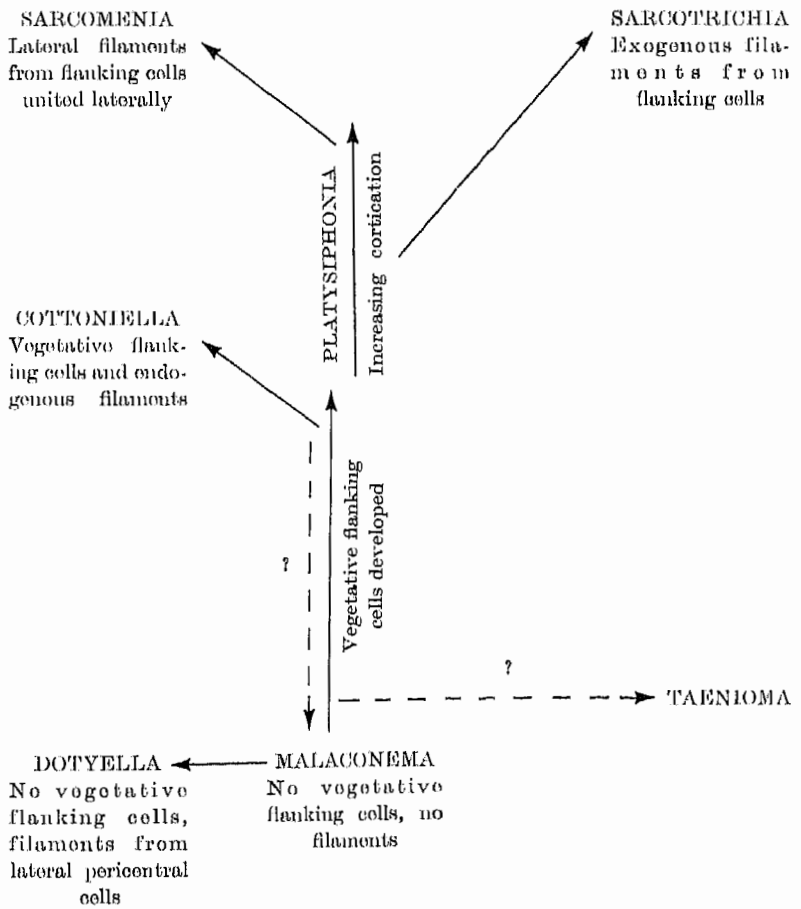
(1) Complete lack of typical trichoblasts (also in *Bostrychia* and a very few other species of Rhodomeloideae).
(2) Endogenous branching (also in Amansieae and Lophosiphonieae).
(3) Reproductive organs borne on small thallus branches, not on trichoblasts.
(4) Spermatangial blades flattened, with sterile transverse pericentral cells and flanking cells (or their derivatives).
(5) Stichidia with 2 longitudinal rows of sporangia; sporangia formed after the "flanking cells" but before the "cover cells".

## VIII. Phylogenetic Relationships of the Sarcomenioideae

The genera of the Sarcomenioideae may be related to each other as expressed in the diagram opposite.

On the basis that the simplest type of structure found in a group usually (but not always) indicates its possible origin, the genus *Malaconema* is of significance. This genus is unfortunately still incompletely known, no female or male plants having been found. Previously it was placed under *Polysiphonia*, as *P. roeana* Harvey. A form such as this could have evolved from a rhodomelaceous alga with 4 pericentral cells by restriction of sporangial production to opposite pericentral cells of a stichidium which had 4 pericentral cells, and by the production of extra cover cells from the stalk cell after sporangium formation. The first-formed rhodomelaceous cover cells would then constitute the flanking cells without significant modification. Associated changes would involve loss of trichoblasts and development of endogenous branching; both these changes occur in some Rhodomelaceae.

It is noteworthy that in most genera of the Sarcomenioideae the cover cells give little protection to the sporangium, especially on the adaxial side. In *Taenioma* neither cover cell protects the sporangium (Papenfuss 1944, p. 207). In the Delesserieae the cover cells are better developed and do protect the sporangium. Actually the curved flanking cells of some members of the Sarcomenioideae give more protection to the sporangia than do the cover cells.




Further developments within the Sarcomenioideae involve:

(1) Spreading of flanking cell development to the vegetative thallus (shown in all genera except *Malaconema* and *Dotyella*, and only partly in *Cottoniella arcuata*).

(2) Further development from the flanking cells or pericentral cells of filaments, usually free (*Sarcotrichia*) but laterally united in *Sarcomenia*.

(3) Increased cortication, especially within the genus *Platysiphonia*.

The possibility that *Malaconema* is a reduced form from a type such as *Platysiphonia*, with loss of vegetative flanking cell development, cannot be excluded.

The position of *Taenioma* is uncertain. This genus differs from other members of the Sarcomenioideae in the apparently delesseriaceous type of pericentral cell formation, in the exogenous branches, and in the restriction of monosiphonous filaments to the apex of determinate branches. Yet the tetrasporangial blades seem to ally *Taenioma* sufficiently with the rest of the Sarcomenioideae to place it in this group. Papenfuss (1944, p. 207), however, considered *Taenioma* to be the simplest of known Delesseriaceae, and further investigations may prove that it is not a member of the Sarcomenioideae.

Papenfuss (1944, p. 210, 211) considers that both the Delesseriaceae and Rhodomelaceae may have evolved from ancestors of the present-day Dasyaceae, and he also agrees with the views of Kylin (1956 and previously) that they represent two parallel lines of evolution, with the Rhodomelaceae somewhat higher than the Delesseriaceae.

The *Sarcomenia*-type stichidium could equally well have evolved from that of the Dasyaceae (which bears several sporangia in each segment, with 2 cover cells cut off after the sporangium) as from the rhodomelaceous stichidium. However, the order of pericentral cell formation sets the Dasyaceae apart from the Rhodomelaceae, and in other features the Sarcomenioideae have more in common with the latter than the former family.

Thus while discussion of the phylogeny of the families of the Ceramiales is very largely speculative, it seems clear that the Sarcomenioideae, while best placed as a distinctive subfamily of the Rhodomelaceae, represents a link between this family and the Delesseriaceae. Further, the stichidium of the Sarcomenioideae could possibly have evolved by reduction of the rhodomelaceous stichidium (with sporangia only from the lateral pericentral cells) and development of extra "cover cells" transversely from the lateral pericentral cells after sporangium formation. The flanking cells would then correspond to the Rhodomelaceae cover cells. Associated changes from the Rhodomelaceae are loss of trichoblasts and restriction to endogenous branching.

In turn the Delesserieae could have evolved from primitive types of the Sarcomenioideae by a change in the plan of pericentral cell formation, to monopodial development of the gonimoblast, and in other less important characters.

## IX. Other Genera Possibly Related to the Sarcomenioideae

Other genera that have previously been placed in the *Sarcomenia* group are *Caloglossa*, *Claudea*, *Vanvoorstia*, *Sonderia*, and *Sonderella*. *Caloglossa* is now placed in a group of its own (Papenfuss 1944; Kylin 1956) and *Claudea*, *Vanvoorstia*, and also *Zellera* are placed in the *Claudea* group (Papenfuss 1937; Kylin 1956) of the Delesseriaceae. Papenfuss (Sept. 1956) and Kylin (Oct. 1956) both refer *Sonderia bennettiana* (Harvey) F. Muell. to *Vanvoorstia* as *V. bennettiana*, and *Implicaria reticulata* which Kylin places in the *Claudea* group, has been shown by Segawa (1941, p. 270) to be identical with *Vanvoorstia coccinea*. *Sonderella* is not a member of the Sarcomenioideae and will be discussed elsewhere.

*Claudea* and *Vanvoorstia* resemble the Sarcomenioideae and differ from other Delesseriaceae in that procarps are formed from only 1 series of transverse pericentral

cells (but abaxial in *Claudea* and *Vanvoorstia* while adaxial in the Sarcomenioideae), the cystocarp is urceolate, and the tetrasporangia are formed entirely (*Vanvoorstia*) or mostly (*Claudea*) from pericentral cells. They differ from the Sarcomenioideae in the net formation of the thallus, in the plan of pericentral cell formation in *Claudea* (but not in *Vanvoorstia*), in the formation of sporangia from more than the 2 lateral pericentral cells, and in the pericarp structure, which appears to be more delesseriaceous. The method of branching of the gonimoblast has not been established, though the figures of Papenfuss (1937) indicate that *Claudea* and *Vanvoorstia* may differ in this respect.

Papenfuss (1937) found that the order of pericentral cell formation in *Claudea multifida* is typically delesseriaceous, and he appears to consider the same true of *Vanvoorstia spectabilis* and *V. coccinea*. However, Silva and Cleary (1954, p. 259) state that *Vanvoorstia* follows the rhodomelaceous plan of pericentral cell formation, and this is certainly true of material of *V. spectabilis* from Ceylon that we have examined. However, the adaxial pericentral cell appears to be formed first, in contrast to the abaxial pericentral cell in the Sarcomenioideae. *Claudea elegans* agrees with *C. multifida* in showing the delesseriaceous plan. This appears to be a unique case of two apparently very closely related genera differing in a feature which has been recognized as the best distinction between the families Delesseriaceae and Rhodomelaceae.

Little is known of *Zellera*, but a herbarium specimen of *Z. tawalliana*, from the Malay Archipelago, which we have examined shows formation of the 2 lateral pericentral cells first, while the cell lineages of the blade are similar to those of *Caloglossa* or the *Hypoglossum* group of the Delesseriaceae, i.e. each cell of the chain derived from the anterior flanking cell produces a chain of cells posteriorly, with all tertiary apical cells reaching the thallus edge. The position of *Zellera* is dependent on examination of fertile material, but the net formation derived from anastomosing of 4 orders of blades, and endogenous branching from the central cells, show close affinity with the *Claudea* group.

The *Claudea* group appears to differ significantly from the Sarcomenioideae, though showing some features in common, and is probably correctly placed as a group of the Delesseriaceae.

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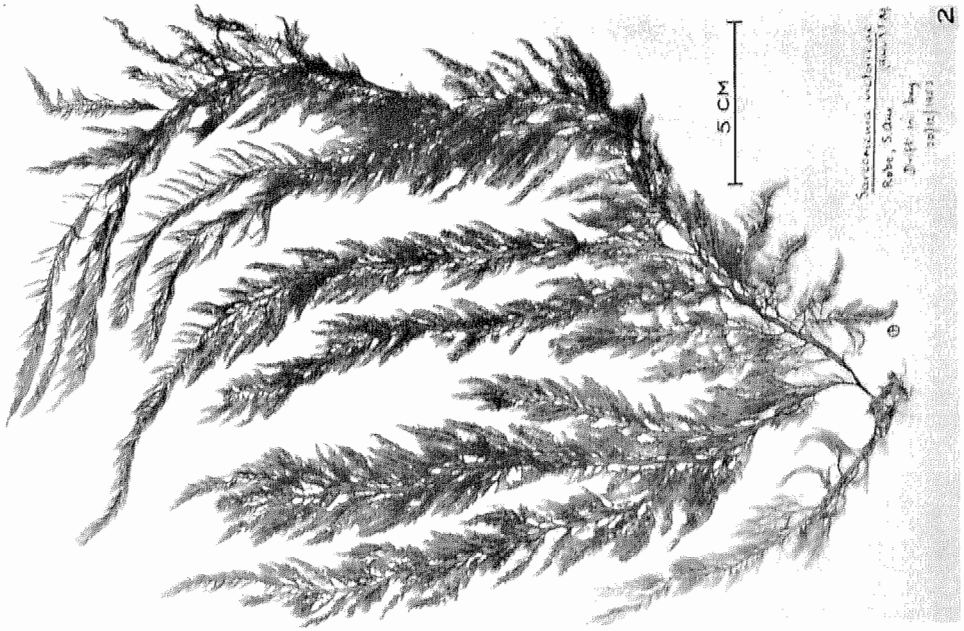


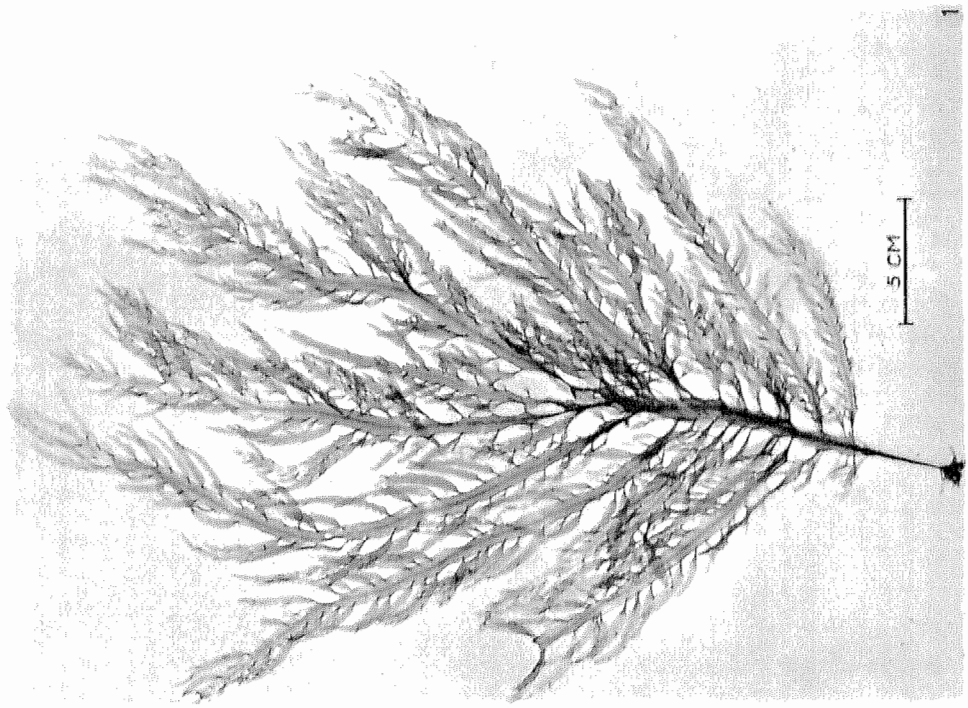

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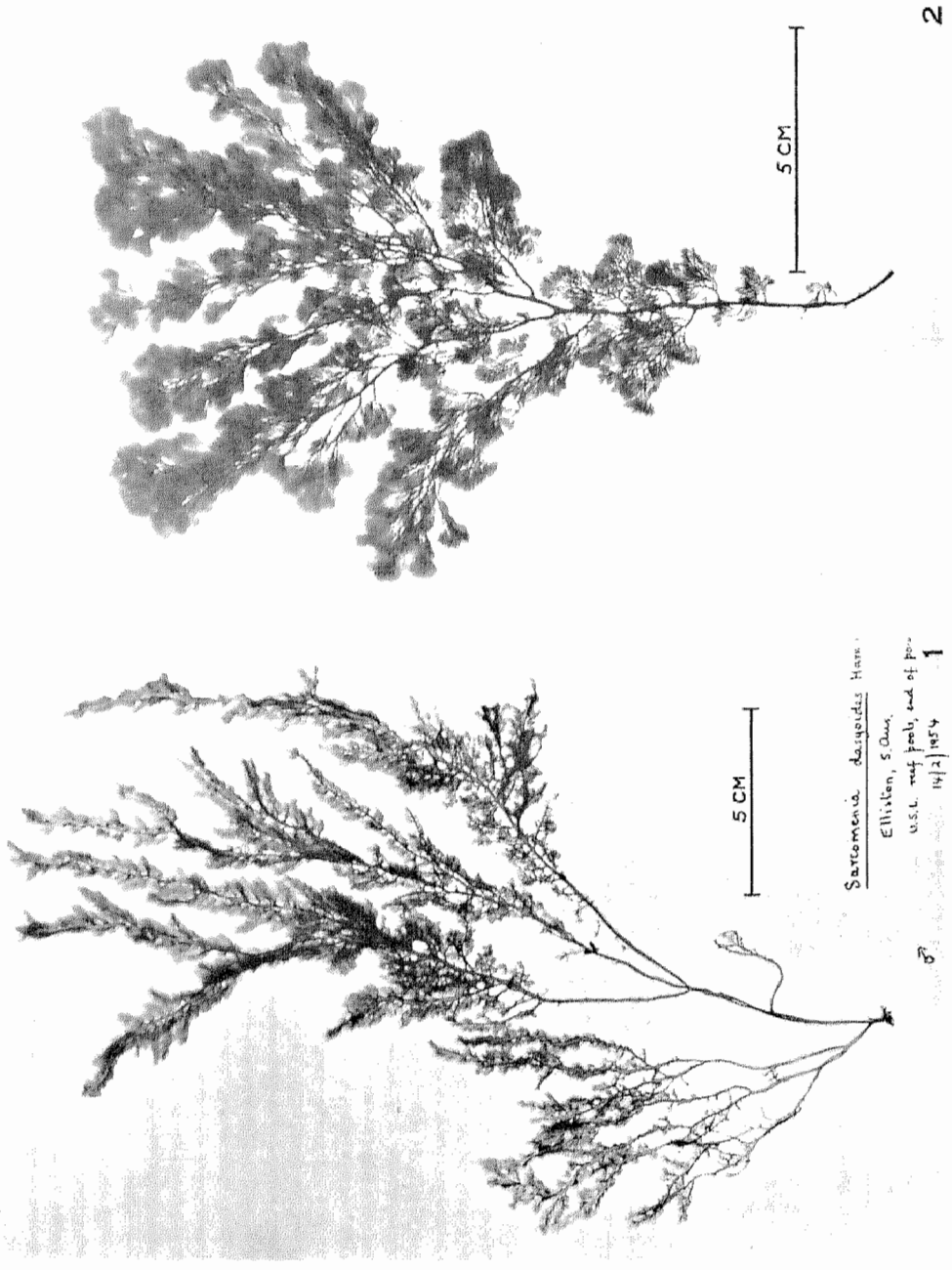

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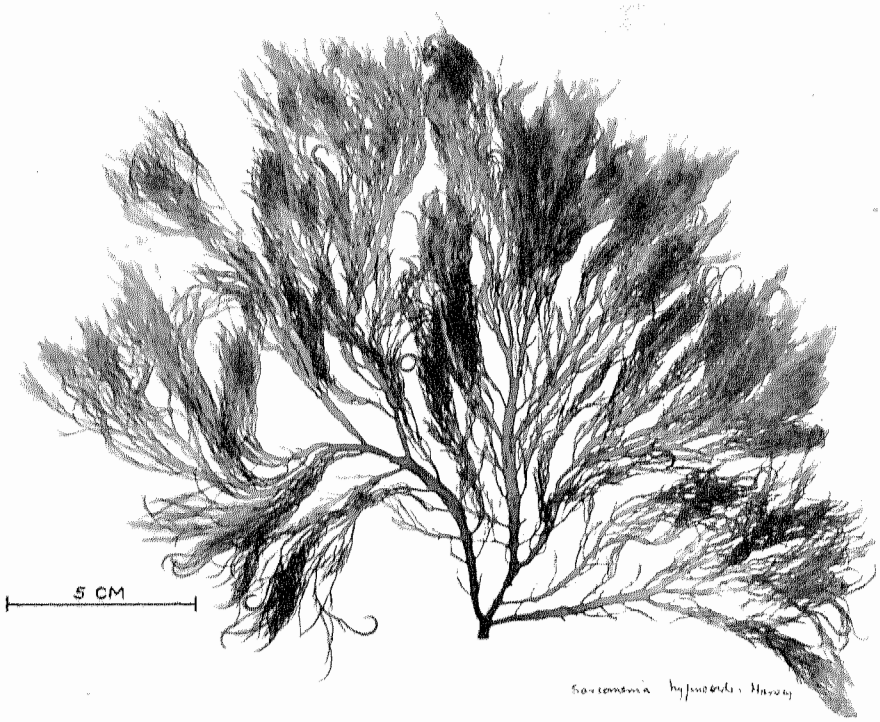


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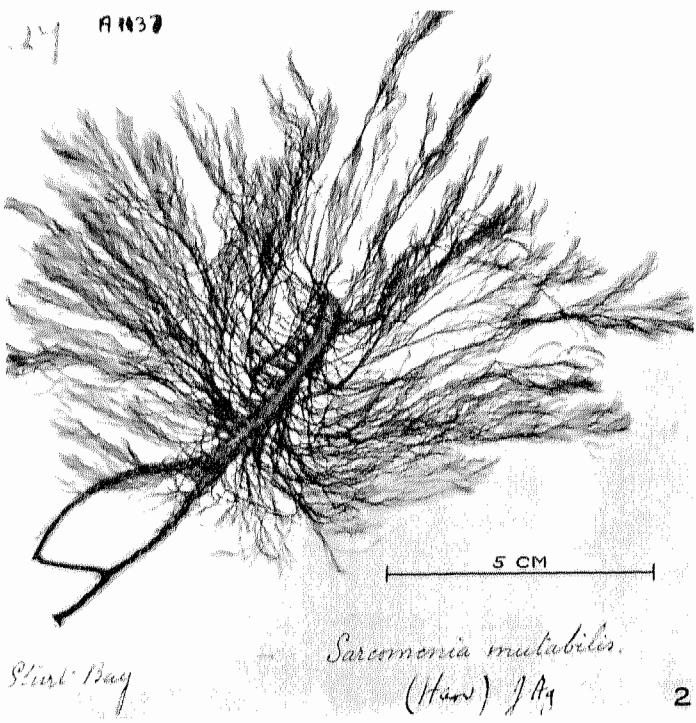

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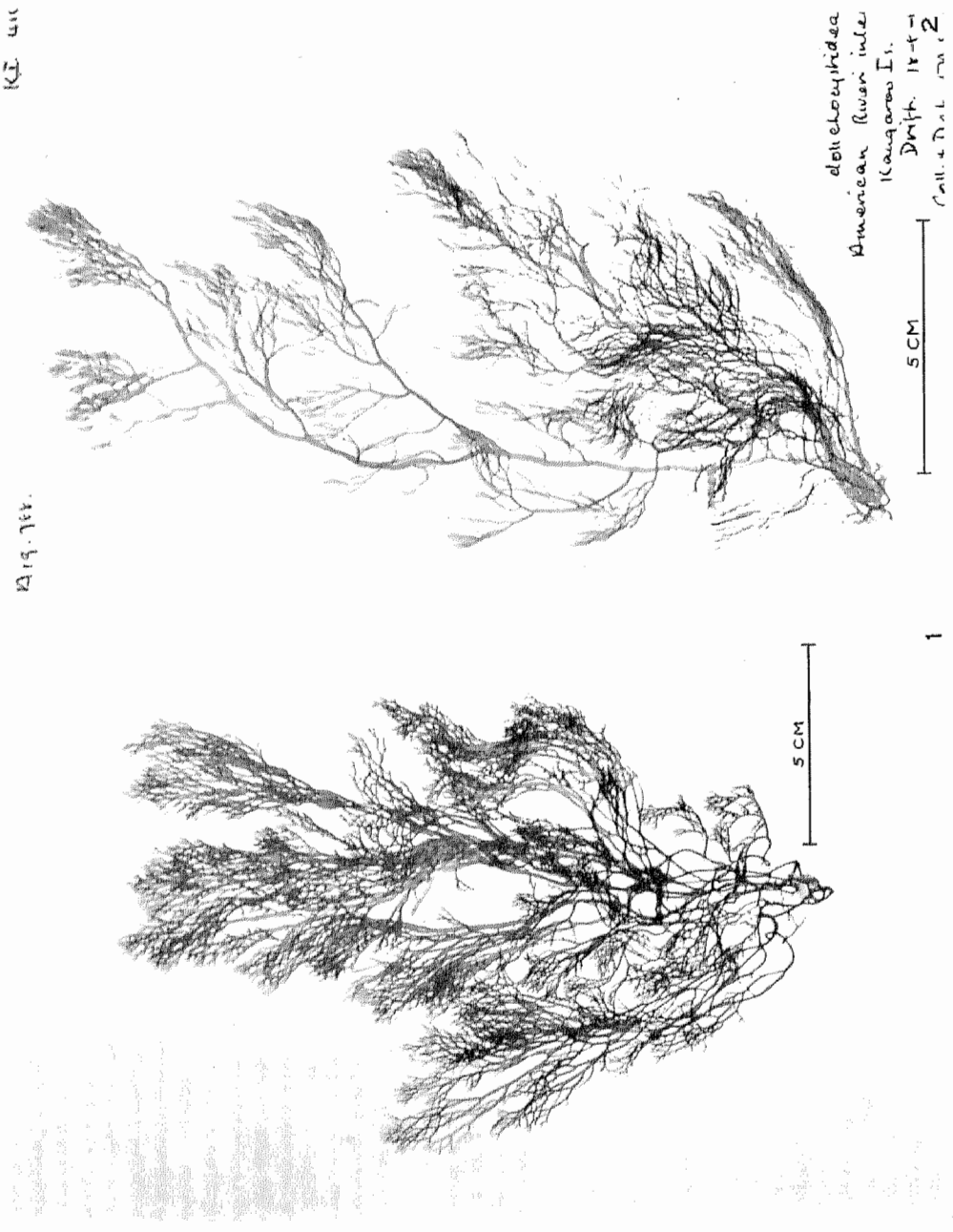
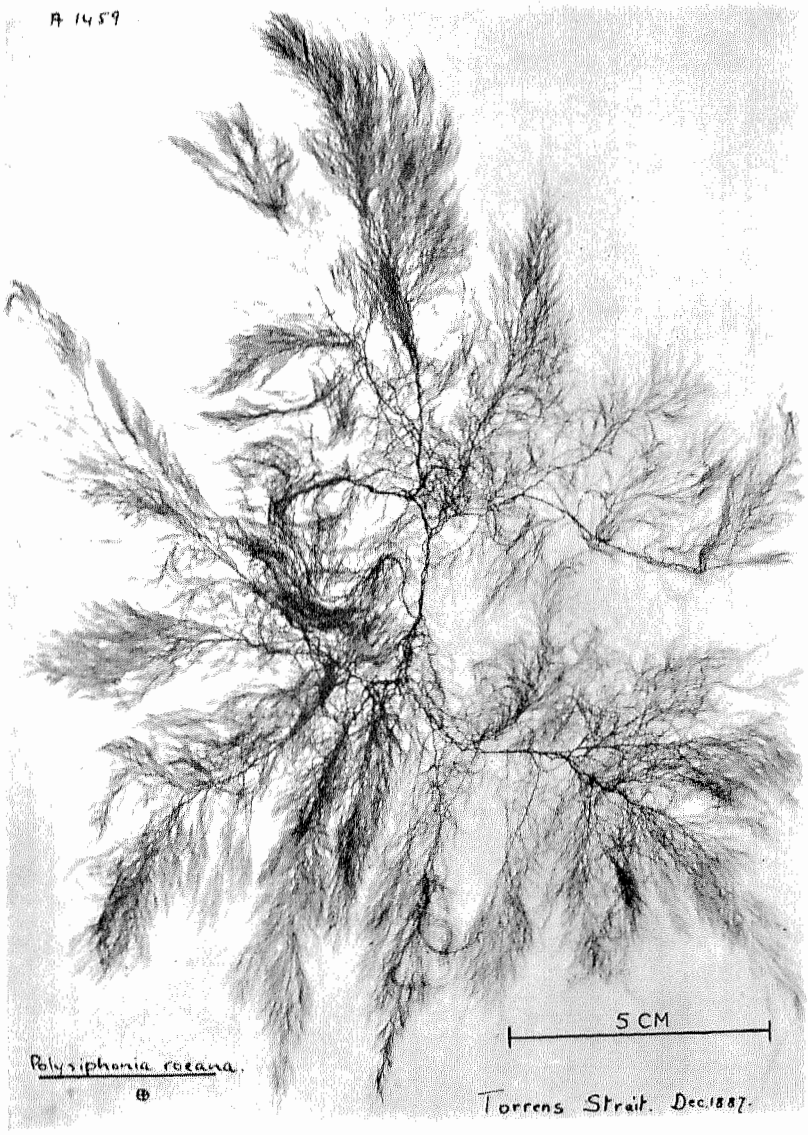


STUDIES ON SARCOMENIA GROUP



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## EXPLANATION OF PLATES 1–5

### PLATE 1

Fig. 1.—*Sarcomenia delesserioides* Sonder. Robe, S.A. (AD: A19872).

Fig. 2.—*Sarcomenia victoriae* Harvey ex J. Agardh. Robe, S.A. (AD: A19124).

### PLATE 2

Fig. 1.—*Sarcomenia victoriae* Harvey ex J. Agardh. Reef form (= *S. dasyoides* J. Agardh). Elliston, S.A. (AD: A19423).

Fig. 2.—*Sarcomenia corymbosa* J. Agardh. Port McDonnell, S.A. (AD: A18991).

### PLATE 3

Fig. 1.—*Sarcomenia hypneoides* Harvey. Western Australia (AD: A18301).

Fig. 2.—*Sarcomenia mutabilis* (Harvey) J. Agardh. Marion Bay, S.A. (AD: A1137).

### PLATE 4

Fig. 1.—*Sarcomenia tenera* (Harvey) J. Agardh. Marion Bay, S.A. (AD: A16097).

Fig. 2.—*Sarcomenia dolichocystidea* J. Agardh. American River Inlet, Kangaroo I., S.A. (AD: A19788).

### PLATE 5

*Polysiphonia rocana* Harvey. Torres Strait, S.A. (AD: A1459).