MORPHOLOGY AND TAXONOMY OF SOUTHERN AUSTRALIAN GENERA OF CROUANIEAE SCHMITZ (CERAMIACEAE, RHODOPHYTA).

by

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This is to certify that material contained in this thesis is the work of the author except where otherwise acknowledged.

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I. SUMMARY

The southern Australian species of the tribe Crouanieae Schmitz (Ceramiaceae, Rhodophyta) have been studied with particular reference to their taxonomy, relationships and phylogeny; in all cases the type specimens have been examined.

Three tribes Crouanieae, Antithamnieae and Heterothamnieae are recognized for southern Australian taxa and include sixteen genera (of which five are newly-described) and forty-eight species (twenty-six newly-described). Recognition of the sub-families Crouanioideae and Ceramioideae as defined by Hommersand (1963), is not supported by these studies.

Features of greatest taxonomic significance are those indicative also of phylogenetic trends and hence the classification is based upon concepts of phylogeny. Evolutionary advance in both morphological and reproductive features involves specialization particularly towards adaptations in form with relation to function.

Prominent trends within Crouanieae, Antithamnieae and Heterothamnieae are toward,

(i) development of erect axes, often with rhizoidal cortication and discrete holdfasts, from prostrate non-corticated axes attached by scattered rhizoids.

(ii) whorl-branchlets showing specialization in form and position in each whorl.

(iii) regular, in place of irregular, arrangement of lateral branches.

(iv) greater organization in carposporophyte development with reduction in the number of procarps formed at much-reduced branch apices.

Relationships are discussed also with particular reference to phylogeny. The Crouanieae, Antithamnieae and Heterothamnieae together represent a probably primitive group of the Ceramiaceae. Antithamnieae and Heterothamnieae are closely related and have probably arisen from the same evolutionary line, while Crouanieae has evolved independently. Thallus forms in Heterothamnieae are smaller and less specialized than those of Antithamnieae and it is likely that the Heterothamnieae arose as a branch from the Antithamnieae line of development through specialization in carposporophyte production. The development and form of both thallus and reproductive organs are also discussed together with reasons for the choice of the terminology adopted.

Finally, the geographic distribution of the species within southern Australia is analysed. Records are, however, from scattered localities and few useful conclusions can be drawn from the data available.

II. INTRODUCTION

The tribe Crouanieae Schmitz is considered a primitive tribe of the Ceramiaceae (Ceramiales, Rhodophyta) and includes species similar in form to phylogenetically less advanced members of the Rhodophyta. Crouania, Gattya and Gulsonia were, for example, originally placed close to genera such as Nemalion, Mesogloia (Phaeophyta), Batrachospermum and ~~other~~ species of the Cryptonemiaceae on the basis of thallus structure, since each axial cell bears a whorl of short branchlets. In reproduction, however, the Crouanieae are clearly related to other genera of the Ceramiales. Schmitz (1889) included in the Crouanieae the genera Ballia, Antithamnion, Crouania, Gulsonia, Gattya and Ptilocladia. Later Kylin (1956) also included Heterothamnion, Antithamnionella, Grallatoria, Platythamnion, Acrothamnion and Warrenia -- a total of twelve genera, all (except Grallatoria) occurring in southern Australia. Several other genera, mainly non-Australian, were added and removed by various authors between Schmitz's description of the tribe and Kylin's recent revision. (These are outlined in Section VI, p328 of this study).

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Kylin (1956) included in the Crouanieae genera having whorls of 2-5 whorl-branchlets from each axial cell and bearing procarps on the basal cells of the whorl-branchlets. Axial growth is basically monopodial and occurs typically by transverse divisions of a dome-shaped apical cell. Hommersand (1963) examined the relationships of the Crouanieae in comparison to other tribes of Ceramiaceae and separated a new tribe Antithamnieae to include the genera *Acrothamnion*, *Antithamnion*, *Antithamnionella*, *Ballia*, *Bracebridgea*, *Grallatoria*, *Heterothamnion*, *Platythamnion*, *Ptilocladia* and *Warrenia*. He defined this tribe to include genera having rod-shaped axial cells each bearing a whorl of 2-4 branchlets and procarps borne at intervals along the branches of unlimited growth, or, in a few advanced genera such as *Ballia* and *Warrenia*, on small fertile side-branches. Sterile groups associated with procarp development could be in the form of a well-developed vegetative branch or may be short, with growth suppressed at time of formation of the carpogonial branch. The position of spermatangia and tetrasporangia is variable in the tribe.

From detailed study of the southern Australian species of Crouanieae Schmitz, three tribes Crouanieae, Antithamnieae and Heterothamnieae are defined. These are separated on both morphological and reproductive features (particularly on position and development of procarp and carposporophyte). Details of this classification are discussed and set out in Section VI. As a result of these investigations it has been necessary to modify Hommersand's definition of Antithamnieae, particularly in reference to procarp development. Carposporophytes are produced (except in *Ptilocladia australis*) near branch apices in all species and axial elongation typically ceases with initiation of procarps. Unfortunately fertile material of *Ballia* is rare and has not been available for study.

These studies of southern Australian species reveal probable phylogenetic lines which form useful bases for comparison of morphological and reproductive features and provide also a logical approach to the taxonomy of the group.

III. MATERIALS AND METHODS

Investigations have been made as far as possible on liquid-preserved material. Field collections are stored initially in 4% formaldehyde in sea-water and later transferred to 70% alcohol and 5% glycerine. Only very few determinations (indicated in the text) have been based on dried material. Type material on herbarium sheets has been softened by soaking in water with a few drops of detergent added.

Staining has been in 1% aqueous aniline blue, fixed by acidifying with HCl, washed, and mounted in 50-80% solution of Karo syrup in distilled water. This mounting medium is convenient to use and sets to a firm, clear mount. Most species can be placed directly in a 20% solution of Karo and brought up to 50-80% for final mounting. This can be effected either by evaporation of the Karo solution or by transferring the material through a series of solutions of increasing concentration. The method of evaporation is particularly useful for delicate material or small fragments. The time required for staining in aniline blue varies from about half an hour (e.g. most species of Crouanieae) to two (or more) days (e.g. species of Ballia) and is usually less for young parts of the thallus. Most observations were made on lightly-squashed dissections and recorded by free-hand drawings.

<u>Measurements</u>: — All measurements, unless otherwise indicated, are taken within the gelatinous sheath which covers the thallus and represent average, mature dimensions. In some cases, where gross variations occur (as in height of thallus) only the maximum measurement is given (e.g. to 5 cms.).

<u>Herbaria quoted</u>: —

AD	—	Department of Botany, University of Adelaide, South Australia.
B	—	Botanisches Museum, Berlin - Dahlem, Germany.
BM	—	British Museum (Natural History), London, England.
LD	—	Botanical Museum and Herbarium, Lund, Sweden.
MEL	—	National Herbarium of Victoria, Melbourne, Australia.
TCD	—	School of Botany, Trinity College, Dublin, Eire.
W	—	Naturhistorisches Museum, Wien, Austria.

(Note — Abbreviations are taken from Lanjouw, J. and Stafleu, F.A. (1964)).

IV. FEATURES USED IN CLASSIFICATION AND THEIR RELATIVE TAXONOMIC SIGNIFICANCE

The tribes Crouanieae, Antithamnieae and Heterothamnieae are separated firstly on reproductive features and secondly on characters of plant form. Naegeli (1861) used characters of reproduction as taxonomic features when he proposed division of the Callithamnieae into ten genera and since that time the position and development of tetrasporangia, procarp and carposporophyte have been widely used in classification. The importance of an understanding of reproductive features in relation to classification has been stressed by Drew (1954). Schussnig (1955) briefly traces the development of classification of the Rhodophyta and points out the use made of female reproductive organs in Feldmann-Mazoyer's (1940) revision of the groups of Ceramiaceae. Kylin (1956) uses the position of procarp in his first major groupings of the Ceramiaceae and thereafter uses features of thallus structure to separate individual tribes.

A. Thallus features of the Crouanieae, Antithamnieae and Heterothamnieae.

I. Development of Axes and Branches.

1. Classification and Terminology applied to types of branching: —

Thalli are basically built up of similar combinations of branch forms in the three groups. Variations such as presence or absence of a prostrate part of the thallus and position and form of individual branches give distinctions between species. The terminology adopted and discussed below, includes:

(a) Main axes which may form prostrate axes and/or erect axes.

(b) Axial branches which take the place of main axes and occur mainly in female plants and in sympodially-developed genera of the Crouanieae. In *Gattya pinella* where these branches are produced regularly to form a pinnate segment the term pinnate branch is used.

(c) Lateral branches which may be either indeterminate or determinate in growth and are hence referred to respectively as indeterminate branches or determinate branches.

(d) Whorl-branchlets which occur in whorls of 2, 3, 4 or 5 (except in *Ballia scoparia* and *B. hirsuta*) from the upper end of each axial cell. The term pinna is used for the special form of whorl-branchlet consisting of a central rachis bearing distichously arranged pinnules, as occurs in most species of Antithamnieae.

(a) Main Axes: — Characteristically main axes are monopodially developed with growth occurring by transverse divisions of a dome-shaped apical cell. They consist mainly of larger cells than those occurring in other parts of the thallus and form a central axis from which lateral branches arise. When parts of the thallus are corticated by rhizoidal filaments the densest cover is always developed over main axes. Some thalli with prostrate axes occur in each tribe, in genera which are probably more primitive than those having only erect axes. In the Antithamnieae, for example, species of *Antithamnion* usually have a main prostrate axis with erect portions formed from young unattached apices of this axis.

In *Acrothamnion* there are distinct prostrate, creeping axes and erect axes which arise as lateral branches from the prostrate thallus and which do not themselves become prostrate. *Ballia* has only well-developed erect axes attached by distinct holdfasts and is probably more highly advanced in form than either *Antithamnion* or *Acrothamnion*.

(b) *Axial branches* are branches which take the place of a previous main axis. They occur in sympodially branched genera, and are strongly developed in *Gattya*. They occur frequently in *Crouania* where they are distinct from other lateral branches in arising directly from the axial cell and not from the basal cell of a whorl-branchlet (e.g. *Crouania mucosa*). In several genera (e.g. *Tetrathamnion*) thallus growth in the female plant is continued after initiation of procarps at the apex of the main axes, by branches which develop immediately below the procarps. Axial branches of this type occur only in female plants.

(c) *Lateral branches* develop as secondary branches from main axes. They are usually borne on the basal cells of the whorl-branchlets and develop similarly to main axes. They may occur at regular or irregular intervals from main axes or other lateral branches, but are usually shorter with smaller cells than the axes from which they develop. *Indeterminate branches* continue to grow and branch indefinitely while *determinate branches* elongate at first, similarly to indeterminate branches, but growth is limited and they remain short. Branches of this form occur for example in species of *Ptilocladia* and *Euptilocladia*. In most species axial growth in branches of the female thallus ceases with the development of procarps near branch apices and lateral branches which may normally be indeterminate thus become determinate in growth. Hommersand (1963) used the terms " adventitious branches", "dwarf branches" and "dwarf shoots" to describe determinate branches in Gulsoniopsis. The descriptive term "determinate branch" seems, however, to best imply the form and origin of these branches and is used in this survey only in the above sense.

(d) Whorl-branchlets. All species of the Crouanieae, Antithamnieae and Heterothamnieae characteristically have a whorl of short branchlets developed from the upper part of each axial cell of both main and lateral branch axes. The term "branchlet" infers the modified form of these short branches, which, unlike determinate branches, are consistent in form, arrangement and number per whorl for each species. Form varies with the species and, again unlike determinate branches, usually bears no resemblance to normal lateral branches. The simplest whorl-branchlets consist of unbranched chains of cells while in other species they may have several orders of branching.

Previous authors have used various terms for these branchlets, e.g.

Ramulus — (Harvey 1860. e.g. for Ballia scoparia pl. 168).

Pinna — (Harvey 1862. e.g. for Callithamnion dispar, pl. 227 and C. simile pl. 207. J. Agardh 1876, for C. hanowioides).

Plumule — (Harvey 1858 and 1859 e.g. for B. robertiana, pl. 36 and B. mariana, pl. 112).

Short branch — ("rameau court") — (Feldmann-Mazoyer 1940, as an abbreviation of "rameau a croissance limitée" for

Crouania attenuata, Crouaniopsis annulata and species of Antithamnion.

Daines 1913, for Antithamnion floccosum).

Branchlet — (Kylin 1925, for species of Antithamnion and Platythamnion.

Capt 1930, also for Antithamnion.

Balakrishnan 1958, for Antithamnion floccosum).

Determinate ramulus —
Determinate branch —
Branchlet (applied also to branches of the second order)
Determinate branchlet -
(Dawson 1962c, for species of Antithamnion).

Pleuridium — (Chadefaud 1952, 1954 for general plant structure.

Hommersand 1963, for plants of the Crouania and Antithamnion form).

Short branches of limited growth
Whorled lateral branch (or whorled branch)
Lateral whorl branch
(Wollaston and Womersley 1959, for Gulsonia annulata)

Verticillate filament
Verticillate branch
Determinate branch
(Hommersand 1963, p. 170 and throughout text for Gulsoniopsis insignis).

The number and diversity of terms used, especially when interchanged one with another as in Dawson (1962c) and Hommersand (1963), suggest the need for one acceptable term to describe this form of branch.

Whorl-branchlet is chosen in this text as a comparatively simple term indicating the whorled arrangement and the short branch-like form of the structures. The term branchlet allows for a diversity of form and at the same time indicates a distinction between this structure and a typical branch having a central axis, production of laterals, and an apical growing point. Terms involving plumule, ramulus, and branch are rejected due to possible confusion associated with wide usage of these terms. Pinna indicates a leaf-like form and may only be applied to certain forms of whorl-branchlets which are distichous in structure — such as commonly occur in Antithamnieae. It is used here in this sense only. Pleuridium suggested by Chadefaud and adopted by Hommersand, is unsatisfactory because:

(i) it was originally applied by Chadefaud to one part of a branch system (cladome) used specifically in his application of the Telome theory to all phyla of the plant kingdom. Use of this term out of its original context could imply acceptance of Chadefaud's interpretation of the Telome Theory for the Algal phyla.

(ii) In application of the Telome Theory as interpreted by Chadefaud, whorl-branchlets arranged upon a central axis would be equivalent to the leaves of a leafy shoot in higher plants. The Telome theory suggests that leaves of the higher plants were derived from simple branch systems. In algae of the Crouanieae, Antithamnieae and Heterothamnieae whorl-branchlets more closely resemble branches than leaves in their form and in their function of bearing lateral branches , cortical rhizoids and sex organs.

If taken as comparable to a leaf in form, these structures would arise from positions comparable to the veins and petiole of the leaf. Modification of whorl-branchlets bearing procarps usually involves loss of vegetative cells (e.g. in Crouanieae the procarp develops in place of a whorl-branchlet, and the supporting cell is probably representative of the basal cell of the whorl branchlet). In contrast, modification in higher plants of leafy structures to bear sexual organs as explained by the Telome Theory, usually involves a change in form rather than simply the loss of vegetative cells (e.g. sporophylls composing the cones of gymnosperms and the flowers of angiosperms). Naegeli (1847), in discussing the habit of *Antithamnion*, suggested a similarity between the whorl-branchlets of *A. cruciatum* and the leaf-form of a leafy liverwort. He did not realise, however, that lateral branches of *Antithamnion* are borne on the basal cells of the whorl-branchlets which, for this reason, must be more closely allied to branches than to leaves.

2. Origin and form of Indeterminate Lateral Branches.

Indeterminate lateral branches are borne in most species on the basal cells of whorl-branchlets and may be initiated either in regular sequence as the axes elongate, or may occur irregularly from any part of the thallus at any time. In the Crouanieae lateral branches are initiated on basal cells of whorl-branchlets in all monopodially formed genera; in Crouania further axial branches are also produced. Lateral branches may appear to be initiated directly from axial cells (usually in place of a whorl-branchlet) due to loss of the whorl-branchlet. Whorl-branchlets are sometimes lost during growth of the lateral branch or the condition may be developed in which the whorl-branchlet is never formed.

In Gattya the lateral branches as well as the axial (pinnate) branches are formed directly on axial cells and, as Gattya is probably phylogenetically advanced, this condition may denote a more specialized form of branch initiation. Lateral branch initials may develop chains of up to 20 cells before whorl-branches are initiated (Crouania, Gattya, Gulsonia), but commonly the whorl-branchlets are initiated while the young lateral branch is only a few cells long (monopodial species of Crouanieae, Antithamnieae and Heterothamnieae). The arrangement, position and initial development of lateral branches is useful as a supplementary character in definition of genera or species but, in most cases, branching features are too variable to be of much taxonomic use.

3. Determinate Lateral Branches: — Determinate lateral branches are initiated similarly to indeterminate laterals on the basal cells of whorl-branchlets. They do not occur in Gattya, although growth of laterals may at times be temporarily interrupted thus forming occasional constrictions along the branches. Determinate laterals are most prominent in Ptilocladia and Euptilocladia where they remain short and unbranched; they occur irregularly between the indeterminate lateral branches. Lateral branches in female plants of Antithamnieae and Heterothamnieae cease growth with the development of procarps, but do not otherwise become determinate. Branching in some species of Ballia (e.g. B. callitricha) is specialised so that determinate branches may occur in place of whorl-branchlets. The determinate branches of B. hirsuta, which arise from cells of the corticating rhizoids, may be comparable to determinate branches arising from cells of whorl-branchlets, and those of B. scoparia which occur directly on axial cells may represent a higher stage of evolution as is indicated in Gattya in the Crouanieae.

4. Origin and Arrangement of Whorl-branchlets: — In all species of the Crouanieae, Antithamnieae and Heterothamnieae whorl-branchlets are initiated from immature axial cells. The branchlets of each whorl arise successively and, in whorls of four branchlets, an opposite pair is formed first followed by the pair between. This order of initiation was described first for Antithamnion (Naegeli 1861) and occurs in all monopodial Crouanieae having four whorl-branchlets (see notes on tribe). This order of formation differs from that of Rhodomelaceae in

which the pericentrals on either side of the first-formed initial develop before the one opposite. The order of initiation in the Heterothamnieae agrees with that of Crouanieae and species of Antithamnieae bearing four whorl-branchlets.

The position of initiation of the first initial is spirally rotated on adjacent axial cells in the Crouanieae. Rotation may be to the right or to the left and usually results in whorls being superimposed on each 4th or 2nd axial cell — i.e. a rotation of 40° between whorls on adjacent axial cells in species having three branchlets per whorl (Crouania, Gattya) and a rotation of 45° in species with four branchlets per whorl. In Antithamnieae there is a distinct tendency toward distichous arrangement of whorl-branchlets and often a whorl consists of only two branchlets (Antithamnion, Ballia). Where four branchlets occur (e.g. Platythamnion) two are reduced in form and occur as an opposite pair between the two major branchlets. Acrothamnion shows a tendency towards dorsiventrality with two minor branchlets placed on the one side between the opposite pair of major branchlets. These features are useful basic characters in determination of species.

The position of whorls in relation to one another is often difficult to determine due to rotation between axial cells. This is marked in some species of Antithamnion where distichous and decussate branchlet arrangement cannot easily be distinguished except at the point of initiation. Similarly rotation between axial cells in species of Heterothamnieae make it difficult to determine the basic rotation of whorls on adjacent axial cells. This feature is hence unsatisfactory as a taxonomic character. Orthostichous arrangement of whorl-branchlets can kccur with a rotation of 90° or 180° between whorls as occurs in Euptilocladia, and is not necessarily the result of a Rhodomelacean order of initiation. Euptilocladia is thus included in the Crouanieae (see notes on the Crouanieae).

5. Branching of Whorl-Branchlets: — Whorl-branchlets may be one of two types: —

(a) those which have a distinct central rachis either with or without side branches (e.g. as in Antithamnieae),

(b) those which have no central rachis, but each successive cell produces 2-4 cells from its outer end (e.g. as in Crouanieae and in most species of Heterothamnieae).

In type (a) the rachis consists of a chain of cells often with a smaller basal cell (e.g. Antithamnion, Acrothamnion). Branching of this rachis is usually distichous and the branches may be simple or again branched. This flattened distichous form of branchlet occurs in most species of Antithamnieae and may appropriately be referred to as a pinna. The rachis develops from the initial of the whorl-branchlet and usually grows almost to its mature length before initiation of side branches which, in this form of branchlet, represent the pinnules. In type (b) each successive group of cells when mature appears as a di-, tri- or quadri-chotomy. The cells are, however, produced successively (as described for Ptilocladia pulchra) and are not truly di- (or tri- or quadri-) chotomous. Possible phylogenetic significance of these forms of whorl-branchlets is discussed elsewhere (Sections IX and X). The form of whorl branchlets and number per whorl is consistent for a species (except where reductions and modifications occur towards the base of axes in species of Heterothamnieae) and these features form reliable and useful taxonomic characters.

II. Gland-Cells: — Gland-cells are widely distributed in species of the Ceramiaceae and occur particularly in the tribes Antithamnieae and Heterothamnieae (in all species except Ballia spp. and Trichothamnion planktonica). Pyriform gland-cells different in form from those of Antithamnieae and Heterothamnieae occur in several species of Crouanieae. These were described for Gulsonia annulata (Wollaston and Womersley 1959), and also occur in Ptilocladia australis and P. vestita (Section V). They bear a resemblance to the protein-containing gland-cells of Ceramium tenuissimum figured by Kylin (1915 p. 9) and always contain crystal-like inclusions similar in form to the "protein-crystals" described by Feldmann-Mazoyer (1940, p. 64) and reported to be commonly present in cells of some species of Ceramiaceae. Similar "crystals" also occur in axial cells of Ptilocladia agardhiana and P. pulchra.

Gland-cells of the type occurring in Antithamnieae and Heterothamnieae have been widely studied, but their composition and function is not well understood. Naegeli (1847) described "aborted spore-mother-cells" developed on the first (or second) cell of short secondary or tertiary branches in Antithamnion cruciatum. His figures are almost certainly of gland-cells which he did not otherwise describe for the genus. Again (1861) he referred to them as being "without doubt aborted spore-mother-cells." Other authors have described these structures in A. plumula as galls produced by a parasite (Cohn 1867), as organs associated with nutrition (Berthold, 1882; Nestler 1899), for regulation of light (Bruns 1894), as aids to flotation (Schussnig 1914), as excretory organs (Schussnig 1927) and as a protection against animals e.g. herbivorous molluscs (Kylin 1927).

The function of these cells remains doubtful although they are known to contain proteins (Nestler 1899; Kylin 1915, 1927; Feldmann-Mazoyer 1940) or possibly phenol-containing substances (Feldmann-Mazoyer 1940 p. 90). Sauvageau (1926, 1928) reported the presence of free bromine, but this was denied by Kylin (1927, 1930) and Feldmann-Mazoyer (1940).

As so little is known of the structure and function of these cells, the term gland-cell, now in common usage, is retained here.

All species of Antithamnieae and Heterothamnieae have gland-cells similar in origin and form. They vary, however, in position and this is found to be a useful taxonomic feature in distinguishing genera.

(i) Development and structure of gland-cells of Antithamnieae and Heterothamnieae:-

Gland-cells are initiated in most species before the whorl-branchlets are fully formed and they occur most abundantly near branch apices and in young parts of the thallus. This is particularly marked in *Antithamnion* and *Macrothamnion*, while in a few species (e.g. *Antithamnionella glandifera*) gland-cells are sparse in the upper part of the thallus and numerous on the lower branchlets.

Nestler (1899) recognized two forms of development of gland-cells in *Antithamnion plumula* and *Antithamnion cruciatum* respectively. These types are now known to be distributed in genera of the Antithamnieae and Heterothamnieae (as described in Section V) and are differentiated thus: —

(a) Gland-cells cut off laterally (except in *Acrothamnion*) from cells of the whorl-branchlets, and which remain sessile upon the parent cell. They are formed on young cells (See *Antithamnionella tasmanica*, Fig. 28B) and at first the gland-cell initial is similar in staining properties and appearance to a normal vegetative cell.

(b) Gland-cells cut off laterally or obliquely from the upper outer part of the basal cell of a special branch. This form only occurs in Antithamnieae and the special branch often takes the place of a normal branch (pinnule) of a whorl-branchlet (pinna). The gland-cell initial is cut off from the basal cell before further cells of the special branch are formed. During development it remains attached to this basal cell (see figures for *Macrothamnion secundum* and *Antithamnion armatum*, Figs. 27A, 18C) while the lower outer part of the cell elongates and cuts off a second and sometimes a third small vegetative cell. These cells form the special branch and the mature gland-cell appears to be supported by these cells. Occasionally the special branch may be 4 (-5) cells long and the gland-cell may be formed from the second (and not the basal) cell. A possible origin of this gland-bearing branch is described for *Antithamnion pinnafolium* (Section V). Occasionally the special gland-bearing branch is extended and further branched as in *Macrothamnion mucronatum* and *M. secundum*.

Mature gland-cells consist of a densely staining homogenous refringent substance and often appear to be pitted by numerous minute pores (see *Antithamnionella glandifera*, Fig. 30 J). They are usually ovoid in form, rounded on the outer side and on the inner side fit against the parent cell. A thickened longitudinal band occurs on the outer part in some species e.g. in Macrothamnion. When mature they are not attached to the branch cell and are enveloped by the gelatinous sheath which covers the thallus. Occasionally new gland-cells develop in older parts of the thallus and the first-formed gland-cells degenerate (e.g. see species of Heterothamnion and Macrothamnion). The usual size is (10-) 15-30µ long with a variation of only 2-5µ within a species. The smallest (8-10µ) occur in Trichothamnion minimum and the largest (40-45µ) in Platythamnion nodiferum.

(ii) Position of gland-cells: — The position of gland-cells is used in the separation of genera although it is recognized that in some (probably the more primitive genera e.g. Antithamnionella) the ppsition is not always constant. Position of gland cells falls broadly into three main groups:

(a) gland-cells borne on special short branches (e.g. Antithamnion, Macrothamnion),

(b) gland-cells sessile on the rachis and sometimes the pinnules, of a pinna-like branchlet (e.g. Antithamnionella, Platythamnion, Heterothamnion),

(c) gland-cells borne on the outer cells of whorl-branchlets (e.g. Perithamnion, Tetrathamnion).

Types (a) and (b) occur in Antithamnieae and types (b) and (c) in Heterothamnieae. Type (b) is subject to most variation in position, but this variation is not more than is found in other features in separate species and even in individual plants e.g. in numbers of cells composing the rachis of a whorl-branchlet. Gland-cells occurring near the central region of a branchlet may vary for example from 3rd - 5th cell of the rachis in Platythamnion nodiferum, Antithamnionella tasmanica and Heterothamnion muelleri, or from 2nd - 3rd cell in Antithamnionella spirographidis. However the position is in general remarkably consistent.

III. Axial Cortication.

Cortication of axes occurs in species having comparatively large thalli consisting of erect axes and attached by fibrous holdfasts (e.g. most species of Ptilocladia, Euptilocladia, Ballia and Macrothamnion). The cortication, which is always of interwoven rhizoidal filaments, provides some support to the axial cells. The rhizoidal filaments, arise from the lower side of the basal cells of whorl-branchlets, are usually branched, and consist of elongate cells which form intertwining filaments densely covering the lower parts of the axes. They are most densely developed on the lower parts of main axes which are often spongy with the thick covering of matted filaments. Specialization in the form of axial cortication occurs in some species, such as

(a) formation of distinct layers with larger inner cells and smaller more densely pigmented outer cells (e.g. Ptilocladia pulchra, P. agardhiana).

(b) rhizoids interwoven with longitudinal extensions of whorl-branchlets which run parallel to the axis and bear short outwardly-projecting branches (e.g. Ptilocladia vestita, Euptilocladia spp.)

(c) Rhizoids which bear short, unbranched, often densely pigmented, outward projections (e.g. *Ptilocladia pulchra*, *Ballia pennoides*). Similar branched projections sometimes occur (e.g. *Ballia callitricha*, *B. mariana*).

(d) Rhizoids which occur in place of whorl-branchlets (*Ballia scoparia*), or which bear determinate branches from their cells (*B. hirsuta*).

Presence or absence of axial cortication has been widely used in classification of the Crouanieae and the form of cortication has served as a distinguishing feature for tribes of the Ceramiaceae. The forms of rhizoidal axial cortication outlined above are useful in separation of species of the Crouanieae, Antithamnieae and Heterothamnieae and are probably useful also as phylogenetic indicators, (see notes on Phylogeny for respective groups - Sections IX and X).

IV. Attachment Organs.

All species, including those of the Heterothamnieae which penetrate host tissues, are attached by rhizoidal structures. These develop (except in species in which they penetrate the host) as do the filaments which corticate the axes, from the lower side of the basal cells (and occasionally other cells e.g. *Euptilocladia spongiosa*) of whorl-branchlets. They may be branched or unbranched and may or may not develop a terminal digitate attachment organ. Details of different forms developed are described for individual species and include,

(a) Sparingly-branched rhizoids of elongate cells (e.g. Crouania shepleyana.).

(b) Unbranched (or occasionally branched) rhizoids which develop a digitate attachment organ on contact with the host. These often occur in groups from the basal cells of the whorl-branchlets, particularly from prostrate axes (e.g. Antithamnion divergens, A. hanowioides). Many of the rhizoids originally formed in each cluster may later be lost and those which attach to the host contract and become shorter and stouter in form (see A. hanowioides).

(c) Development of a discrete holdfast. This is usually associated with rhizoidal cortication of axes and the holdfast is probably formed from the extension and dense interweaving of the corticating filaments. An intermediate form occurs in Macrothamnion pectenellum in which sparsely developed rhizoidal filaments become concentrated towards the base of the plant and form a small holdfast-like structure in which the rhizoids usually attach individually.

In Heterothamnieae many species attach by penetration of rhizoids between cells of the host tissue. These rhizoids are formed by extension and modification of the base of the erect axes and branches arising from the lower part of the basal axial cells (e.g. Heterothamnion spp., Tetrathamnion spp.). Axial cortication does not occur in this tribe and rhizoidal attachment filaments which penetrate host tissues are distinct in origin from those of Crouanieae and Antithamnieae and those species of Heterothamnieae having non-penetrating attachment rhizoids (e.g.

Antithamnionella spp.). Taxonomically the form of attachment organ has only been found useful in a few cases (e.g. in the separation of *Antithamnion divergens* from *A. gracilentum* and broadly, in definition of the Heterothamnieae). In general there is similarity in form of rhizoids bearing digitate attachment processes and in the development of fibrous holdfasts. These features may be correlated with axial cortication and, hence, in a wide sense, with phylogenetic features.

V. Hairs.

The development of hairs terminally on the outermost cells of whorl-branchlets occurs commonly but by no means consistently. They occur most prolifically in some species of Crouanieae (e.g. *Crouania mucosa*, *Gulsonia annulata*) and are also present in species of Heterothamnieae (e.g. *Perithamnion ceramioides* and *Tetrathamnion lineatum*). In *Trichothamnion* they are distinguished by having a short stalk cell and in *Trithamnion* often occur in pairs.

Hairs of all species are elongate with a slightly enlarged base and a gradually expanded tip. They are formed in young parts of the plant and may persist or fall off as the thallus matures.

Hairs are not known for species of Antithamnieae where the pinna-form of whorl-branchlet is strongly developed.

VI. Features of cell structure.

Thallus cells of Crouanieae, Antithamnieae and Heterothamnieae are characteristically cylindrical in form, or sometimes tapered towards the ends and have prominent pit-connections at cell junctions.

(i) Pit connections are marked by thickened, transverse plate-like structures between cells. Occasionally a pair of parallel plates occurs (e.g. *Heterothamnion muelleri*) while species of *Ballia* are particularly specialized in having pit-connections capped on either side by dome-like structures. Detail of pit-connection structure for the Crouanieae has been described by Feldmann-Mazoyer (1940).

(ii) Nuclei: — In Crouanieae, Antithamnieae and Heterothamnieae cells of the thallus are uninucleate. This feature may be used as a taxonomic character only in separating species of other groups with more than one nucleus per cell (e.g. *Callithamnion* spp.) from species having a single nucleus in each cell. The single nucleus of species of Crouanieae, Antithamnieae and Heterothamnieae is rounded, stains densely and is often laterally suspended in the cytoplasm.

(iii) Chromoplasts: — The form of chromoplasts may be a useful taxonomic feature in broader plant grouping. There is, however, marked consistency in form of chromoplasts in Crouanieae, Antithamnieae and Heterothamnieae. In young cells they are rounded but gradually become elongate as the cells mature and finally are often branched, irregularly narrow and almost equal to the cell in length. In some species (e.g. *Trichothamnion planktonicum*) they always remain proportionately shorter and rounder but variations which occur are not sufficient to be of taxonomic significance.

VII. Calcification of the Thallus.

Some degree of thallus calcification occurs in most species of Crouanieae but is not known in Antithamnieae and Heterothamnieae. Ptilocladia australis and P. vestita effervesce strongly with the addition of weak acid and are probably the most highly calcified species in the group. The thallus of these species may be dull red in colour probably due to the presence of calcium compounds. Other species which are definitely calcified are Ptilocladia pulchra, P. agardhiana and Crouania shepleyana. Gattya is variable in degree of calcification and Crouania mucosa gives only a slight reaction to acid. Species of Euptilocladia may or may not be calcified and when present calcification is only slight. No calcification occurs in Gulsonia annulata. Due to the structure of the thallus, species growing in calm water conditions tend to accumulate fragments of debris between the whorl-branchlets (e.g. Ptilocladia australis, Crouania shepleyana) and it is sometimes difficult to determine whether effervescence comes from the cells of the thallus or from minute particles of shells etc. Because of its unreliability in most species calcification is not a useful taxonomic character.

B. <u>Reproductive Features of the Crouanieae, Antithamnieae and Heterothamnieae</u>.

I. <u>Procarp and Carposporophyte</u>.

1. <u>Position and form of Procarp</u>: — The carpogonial branch in Ceramiaceae is 4-celled and borne on a supporting cell which in Crouanieae, Antithamnieae and Heterothamnieae is borne directly on an axial cell near the branch apex. In Antithamnieae and Heterothamnieae the supporting cell is the basal cell of a whorl-branchlet which, in Heterothamnieae, is much reduced in length. In Crouanieae no vegetative cells are formed and the fertile branch consists only of the supporting cell and carpogonial branch. This structure may be analogous to that of Antithamnieae and Heterothamnieae, but with complete reduction of vegetative cells of the whorl-branchlet. These tribes could then be considered similar in having the carpogonial branch produced on a cell equivalent to the basal cell of a branchlet, and differing only in the number of vegetative cells developed.

A 4-celled carpogonial branch is characteristic of Ceramiales but differs in position, form and development in individual tribes. Details of these features are described for individual species of the Crouanieae, Antithamnieae and Heterothamnieae, and are here summarized for each tribe.

(a) <u>Crouanieae</u>: The carpogonial branch initial is cut off from the outer side of the supporting cell and enlarges before division to ~~form an initial cell~~ to a size about equal ~~in size~~ to the remaining supporting cell. Divisions of this cell to form the 4 cells of the carpogonial branch occur almost simultaneously and before the carpogonial branch commences to straighten. When mature it is upwardly curved. Cells of the carpogonial branch are rounded (e.g. Crouania mucosa, and Ptilocladia pulchra).

(b) Antithamnieae: The carpogonial branch initial forms from the lower part of the supporting cell and divisions occur successively as the initial elongates upward. The first two divisions are transverse and the third is usually oblique. Thus the lower two cells of the mature carpogonial branch are rounded in form, the third is rather more cone shaped with the carpogonium cut off obliquely from it (e.g. Antithamnion gracilentum).

(c) Heterothamnieae: Cells of the carpogonial branch are formed as in Antithamnieae and are similar in form. The third cell is usually shorter than it is in Antithamnieae and hence is more rounded in appearance (see Antithamnionella spirographidis).

2. Development of Carposporophyte.

After disintegration of the trichogyne a small cell-like structure (capping cell) remains above the carpogonium (see Crouania mucosa, Acrothamnion preissii). Balakrishnan (1958) has described this cell as cut off from the carpogonium after fertilization in Antithamnion floccosum (Mull.) Kleen. It has been similarly described by Feldmann-Mazoyer (1940) for Crouaniopsis annulata, by Capt (1930) for species of Antithamnion and by Segawa (1949) in Antithamnion plumula (Ellis) Thuret, and suggested by Wollaston and Womersley (1959) in Gulsonia annulata. A more accurate derivation for this cell is given by Hommersand (1963) for Gulsoniopsis insignis, where he describes it as a "fragment" of the partly broken down trichogyne. This cell is formed in all species of Crouanieae, Antithamnieae, and Heterothamnieae from the basal part of the trichogyne which remains separate from the carpogonium. It is distinctly cell-like in form although there is no evidence that it is nucleated as Hommersand (1963) suggests.

Following fertilization the upper part of the supporting cell enlarges prior to formation of an auxiliary cell and, at the same time the lower part of the carpogonium grows out toward the developing auxiliary cell (e.g. Crouania mucosa, Fig. 5K; Antithamnionella tasmanica, Fig.28L; Tetrathamnion ramosum Fig.32 Tb). A small connecting cell is cut off from this projection of the carpogonium and fuses with the lower part of the auxiliary cell almost at the same time as the auxiliary cell is separated from the supporting cell. These events occur rapidly and it is difficult to determine their exact sequence (e.g. Antithamnionella tasmanica Fig.28M; A. spirographidis Fig.29L; Ptilocladia pulchra Fig. 12 G.H; Crouania shepleyana Fig. 7G; Antithamnion hanowioides Fig.19N,O). Fusion of the male and female nuclei takes place in the carpogonium (Drew, 1954) and presumably the diploid nucleus is transferred to the auxiliary cell via this connecting cell. Dixon (1964) describes for Antithamnion spirographidis a condition in which supporting cells act as auxiliary cells without separation into two distinct cells. The fate of the connecting cell after fusion is not clearly understood. In Crouania mucosa and Ptilocladia pulchra it becomes fused to the auxiliary cell and can be distinguished for a short time after fusion (Crouania mucosa Fig. 5L; Ptilocladia pulchra Fig. 12H). This also occurs in

<u>Gulsonia annulata</u> (Wollaston and Womersley 1959). In some species of Antithamnieae and Heterothamnieae the connecting cell remains as a separate entity (e.g. <u>Antithamnion divergens</u>, Fig.15G; <u>Trichothamnion elongatum</u>, Fig36 P; <u>Antithamnionella tasmanica</u>, Fig.28 M). It is possible that the connecting cell usually fuses completely with the auxiliary cell in Crouanieae, but remains distinct after fusion in the Antithamnieae and Heterothamnieae.

After fusion with the connecting cell, the auxiliary cell divides transversely to form a lower foot-cell and an upper central cell which gives rise to the gonimolobe initials. In <u>Ptilocladia</u>, <u>Euptilocladia</u> and <u>Gulsonia</u> (Crouanieae) the first formed gonimolobes develop laterally from an elongate central cell. In <u>Crouania</u> and <u>Gattya</u> (Crouanieae) and in all species of Antithamnieae and Heterothamnieae a terminal initial develops first. It is thus clear that this feature can only be used in association with other features in distinguishing genera. The number of carpospore groups ultimately developed is of similar use in distinguishing genera. During development cells of the carposporophyte may fuse, the fusions being more pronounced in some genera than in others. For example, there is strong fusion between the axial cell, residual supporting cell and foot-cell in <u>Antithamnion</u>, <u>Acrothamnion</u> and <u>Ptilocladia</u> while in <u>Gattya</u>, <u>Crouania</u> and <u>Perithamnion</u> fusions are much less marked. The number and form of sterile cells between the central cell and fertile carposporangia is also variable, and as with degree of fusion between cells of the carposporophytes does not constitute a dependable taxonomic feature. These characters are described for individual species and in comparisons of tribes and genera.

No special involucre is formed around the carposporophyte in species of Crouanieae, Antithamnieae and Heterothamnieae. In some genera, however, upward and occasionally increased growth of surrounding whorl-branchlets gives protection to the carposporangial groups. This is best developed in Crouanieae (e.g. in Gattya, Crouania and some species of Ptilocladia) while species of Heterothamnieae often have carposporophytes almost completely exposed.

In all three tribes only one carposporophyte normally matures at each branch apex, even when up to twenty procarps are formed. It is not known whether the inhibitory factor responsible for this is the same as that which, in most species, inhibits further axial elongation in a branch bearing procarps. This inhibition does, however, help to define two phylogenetic lines.

(a) Species (e.g. Ptilocladia australis) in which inhibition of axial elongation does not occur. These are considered more primitive than species where axial growth ceases with procarp development.

(b) Species which produce a large number of procarps at each branch apex, of which only one matures, and which are considered more primitive than those which produce only a limited number (e.g. 1-3 as occurs in Heterothamnieae) at each apex. This follows the commonly accepted hypothesis that reductions of this type are often correlated with greater efficiency and hence may represent more advanced stages of evolution.

3. Terminology: — Terminology used in reference to reproductive systems has been adopted on the basis of common usage, and with the aid of accompanying diagrams for specific descriptions, should in most cases be self-explanatory.

Supporting cell is used to describe the cell bearing the carpogonial branch before development of the carposporophyte. The remaining lower part of this cell, after separation of the auxiliary cell, is termed the residual supporting cell. The auxiliary cell on division forms a lower foot-cell and an upper central cell which, in turn, bears the rounded groups of carposporangia. Initials of these are termed gonimolobes, and gonimoblast is used to include the central cell plus its derivatives.

The term fertile branch has been used with caution on account of possible confusion and, where used, applies strictly to a whorl branchlet bearing procarp or carposporophyte.

II. Spermatangia.

Spermatangial mother cells occur in terminal whorls from the outer cells of whorl-branchlets (Crouanieae) or of especially adapted short branches, usually in the place of branches (or pinnules) of whorl-branchlets (Antithamnieae and Heterothamnieae).

Typical spermatangia for Crouanieae are described for *Crouania mucosa*, *Gattya pinnella* and *Gulsonia annulata* (Wollaston and Womersley 1959). In each case the spermatangial mother cells are borne as whorls of 2-4 cells, which develop successively, from the final branchings of the whorl-branchlets and in position and form are consistent for the tribe.

In Antithamnieae and Heterothamnieae there is much more variation although usually the spermatangia are formed in clusters confined to special small branches. These clusters usually occur on the upper side of cells in the lower part of whorl-branchlets and are usually most prolifically developed in the upper parts of the thallus. Variation in the form of these branched clusters is shown in Antithamnion divergens, Acrothamnion preissii, Platythamnion nodiferum and Macrothamnion mucronatum in the Antithamnieae and may at times be a helpful feature in separation of genera. For example, in Antithamnion the clusters occur on the lower part of the whorl branchlets and consist of a central axis several cells in length, each cell of which bears one or more successive whorls of cells terminated by whorls of spermatangial mother cells. In Macrothamnion the male clusters are developed on extensions of the special branches which bear gland-cells; in Acrothamnion they occur near the apices of the pinnules on the pinna-like branchlets, and in Platythamnion nodiferum the spermatangial mother-cells are terminal on protrusions from the sterile cell which bears them.

Male organs are not as well known for the Heterothamnieae. Clusters of spermatangial mother cells occurring in Antithamnionella, Heterothamnion and Trichothamnion are similar to those of Antithamnion. These genera have whorl-branchlets with a central rachis as in the pinna-like branchlets of Antithamnion and are probably phylogenetically not far removed from this genus. The position and form of male clusters in genera having whorl-branchlets branched by whorls is not known except for Perithamnion densa. In this species they occur on special small densely-branched branches borne on the upper side of the basal cell of each whorl-branchlet. As the position of tetrasporangia is rather specialized in this species, it is possible that male organs may also differ from other species and genera.

These observations agree with the general opinion of Abbott (given at the Tenth Pacific Science Congress, Honolulu, 1961) that the nature of spermatangial plants can be used to some extent to separate genera, but are of only limited use at the species level. Grubb (1925) attempted to classify about forty species of Rhodophyta on spermatangial characters, but concluded that methods of spermatangial production were of little importance as a taxonomic character. There was, however, a fundamental similarity underlying the development in all species which, she suggested, points to a common origin for all types.

The similarity in form and development of spermatangial mother-cells is very marked in Crouanieae, Antithamnieae and Heterothamnieae. In all species a whorl of spermatangial mother cells is formed by successive cutting off of protrusions from the outer end of a sterile cell and the whorls are constantly of 2-4 cells. Each spermatangial mother-cell is richly protoplasmic and stains densely at first. The protoplast then gradually becomes concentrated, usually at the upper end, but occasionally in the central region (Crouania mucosa) of the cell. The spermatium is usually liberated through an apical pore or split leaving the empty gelatinous cell wall. When fully developed, spermatangial mother cells are usually less than 5μ long (5-7 μ in Perithamnion densa), and ovoid in form.

III. Tetrasporangia.

The development of tetrasporangia has been studied in most species of Crouanieae, Antithamnieae and Heterothamnieae and in all cases the development of the spore-mother-cell and the ultimate production of four sporangia from each mother-cell is consistent. Bispores and monospores have not been observed for any species, although these are recorded for

Crouania attenuata f. bispora and for _Antithamnion tenuissimum_ and _A. plumula_ in the Mediterranean (Feldmann-Mazoyer, 1940, p. 215). The sequence of divisions to form the tetrad of sporangia is, however, variable between species.

(i) _Position of tetrasporangia_: — Tetrasporangia usually occur on the younger parts of the thallus and are formed directly from cells of the whorl-branchlets or their branches. The position of tetrasporangia is of limited use in classification. It can sometimes be used at the generic level and occasionally at the species level (e.g. _Perithamnion densa_). In the Crouanieae, for example, tetrasporangia are borne on the basal cell of whorl-branchlets in _Crouania_ and _Gattya_, on the basal and second cells in _Ptilocladia australis_ and _P. vestita_ and on the second and third cells in _P. agardhiana_ and _P. pulchra_. Position is more significant in the Antithamnieae, where it can be correlated with form of the whorl-branchlet in _Antithamnion_, and is of generic significance in _Macrothamnion_ (formed on extensions of the small gland-cell-bearing branches) and _Ballia_ (borne on special small branches at the base of the whorl-branchlets). In Heterothamnieae also the position of tetrasporangia is of most use in association with the form of whorl-branchlet (e.g. on the inner or outer orders of branching of whorl-branchlets). Position of tetrasporangia is thus best used as an accessory feature of classification within these tribes.

(ii) Development of Tetrasporangia: — This is described and figured in detail for Ptilocladia australis and Euptilocladia villosa (Crouanieae), for Antithamnion divergens, Macrothamnion secundum and Platythamnion nodiferum (Antithamnieae) and for Trichothamnion elongatum, Heterothamnion muelleri and Antithamnionella spirographidis in Heterothamnieae. The initial of the tetrasporangial mother-cell is formed in most species as a protrusion, usually on the upper side, of a vegetative cell of a whorl-branchlet. It is richly protoplasmic, stains densely and is usually ovoid, often becoming pear-shaped, in form. Finally it may be either ovoid or spherical but is consistent in form for each species. In Antithamnieae tetrasporangial mother-cells are usually ovoid and in Heterothamnieae and Crouanieae they are more often spherical. In a few species the tetrasporangium is stalked and may be:

(a) borne on an elongate protrusion which is not divided as a separate cell from the vegetative parent cell (e.g. Acrothamnion preissii and Trichothamnion elongatum).

(b) Developed from the outer part of an initial which has divided transversely so that a small stalk-cell is formed which bears the tetrasporangium (Heterothamnion muelleri).

One or more tetrasporangia may occur on a single parent cell. When more than one develops they are usually produced successively and sometimes up to ten may occur on a cell at one time (e.g. Crouania mucosa). In some species two or three sporangia appear to be formed successively from the same position. This is indicated by the presence of a double (or triple) sheath around some sporangia (e.g. Macrothamnion secundum, Heterothamnion sessile).

The development of tetrasporangia in Ballia is rather more specialised than in other genera. In all species they are borne on special small branches near the base of whorl-branchlets and in B. scoparia are more specialized than in other species.

(iii) Division of Tetrasporangia: — Divisions, resulting in the formation of four spores, may be fundamentally of two types: —

(a) cruciate, in which a transverse division of the mother-cell is followed by longitudinal divisions to produce four daughter sporangia.

(b) Tetrahedral, in which the four daughter sporangia are formed simultaneously by divisions which commence at the periphery of the protoplast of the mother cell, extend inward and finally unite near the centre.

Type (a) as expressed in the Antithamnieae is clear cut and provides a comparatively consistent feature within the tribe. The transverse division always occurs obviously before longitudinal divisions and the resultant tetrad appears divided by three planes of division each at right angles to the other two (see figures for Antithamnion gracilentum and A. hanowioides). Tetrasporangia divided in this way are often ovoid in form and are more easily distinguished when of this shape. Occasionally the two longitudinal divisions are in the same plane and all four sporangia may be seen. Feldmann-Mazoyer (1940) defines the former type as decussate cruciate division. Type (b) is more difficult to define and much more difficult to distinguish as observations on timing of divisions is dependent on finding stages in which division is almost complete. Very often peripheral divisions may commence together, but are not completed simultaneously. This results in the mother-cell being divided first into two parts as occurs in cruciate division — (see figures for Trichothamnion minimum). The resultant tetrad is however composed of sporangia in which the planes of division are oblique to one another, rather than in the form of a cross.

It is doubtful whether any species of the Heterothamnieae have consistent true tetrahedral division of tetrasporangia. Observations indicate that, although the divisions may occur obliquely to one another they are seldom truly simultaneous. This type of division is cruciate, although ~~apparently~~ seemingly tetrahedral from the arrangement of the mature sporangia. Tetrasporangia of both cruciate and tetrahedral form (usually cruciately divided) occur in Antithamnionella. This genus probably represents an intermediate form in the evolution of Heterothamnieae from an Antithamnieae - type ancestor (see notes on phylogeny - Section X).

Division of tetrasporangia in Crouanieae is more consistently tetrahedral and stages of simultaneous division occur more frequently.

In summary, tetrasporangia as occur in Crouanieae, Antithamnieae and Heterothamnieae may be described as:

(a) Tetrahedral division producing sporangia tetrahedral in form (Crouanieae).

(b) Cruciate division producing sporangia cruciate in form (Antithamnieae).

(c) Cruciate division producing sporangia tetrahedral in form (Heterothamnieae).

IV. Vegetative Reproduction.

Vegetative reproduction probably occurs fairly commonly. Several forms of thallus reproduction have been encountered during this investigation.

(i) Simple breaking of prostrate axes. This involves the breaking of living axes or the breakdown of aged axes so that the young branches become separated and form individual plants (e.g. most species having prostrate axes, such as *Antithamnion*, *Antithamnionella* and *Acrothamnion*).

(ii) Layering, which occurs by the development of rhizoids from branches of an erect thallus on contact with the substratum or host plant (e.g. *Crouania shepleyana*).

(iii) Development of new erect axes from the digitate attachment processes (e.g. *Antithamnionella spirographidis* (Fig 29G)).

(iv) ~~Liberation~~ Separation of short branches from the upper parts of the thallus (e.g. *Trichothamnion planktonicum*, *Trithamnion vulgare*).

It is well known that living portions of thalli can be transferred to culture and will attach and grow into new plants. It is thus probable that ~~liberated~~ detached fragments of plants may develop into new individuals provided they are able to find a suitable attachment in favourable conditions. Sundene (1962) records that fragments may be kept alive in sealed jars in sea water for several months before transfer to culture media. It is thus possible that fragments under natural conditions can exist for considerable periods before attachment and regrowth occurs.

Summary of useful Taxonomic Features of Crouanieae, Antithamnieae and Heterothamnieae.

Features found to be of greatest taxonomic use in Crouanieae, Antithamnieae and Heterothamnieae may be summarized thus.

At Tribe level: —

1. Number and position of procarps developed at each branch apex.
2. Form of carpogonial branch.
3. Division and form of tetrasporangia.
4. Form and branching pattern of thallus.

At Generic level: —

1. Position, number and form of procarps, form of carposporophyte (e.g. degree of fusion between cells, number form and position of carposporangial groups).
2. Arrangement of lateral branches.
3. Number and form of whorl-branchlets.
4. Form of axial cortication.
5. Position and form of gland-cells.

At Species level: —

1. Form and arrangement of whorl-branchlets.
2. Form of attachment organ.
3. Degree of axial cortication.

These features are, in general, consistent and clearly defined for the level at which they have been found most useful. Other features which have been found useful in certain instances, particularly at the species level, are those which occur only in certain individuals e.g. stalk cells on tetrasporangia in Acrothamnion preissii, branching habit of Ballia scoparia, instability of form and number of whorl-branchlets in Antithamnionella. Further characteristics are summarized in each generic and specific description, but in all cases accurate definition of a tribe, genus or species is dependant upon the combination of a number of features. Harris (1962) has illustrated this in a table prepared to delineate species of Callithamnion and by which he also shows some of the characters usable in the taxonomy of the genus. He considers features of male reproductive organs, length of cells, shape of chromoplasts and relative growth rate of laterals also to be useful features. None of these have been found useful in the tribes studied.

Length of cells, or other cell dimensions, can only be used with caution and when taking account of variations occurring with environmental conditions. Even the relative proportions of cells may vary under different conditions e.g. axial cells may be long and slender or comparatively short and broad while cells of branchlets may remain closely similar. It is well recognized that certain species, e.g. Antithamnion cruciatum and A. plumula, vary considerably in form with depth, light intensity, temperature and so on, while Sundene (1959, 1962b) has demonstrated some of the variations which occur in strains of A. plumula and A. boreale. Other vegetative features may also be variable, as, for example, position of whorl-branchlets. Variation due to rotation between axial cells has already been discussed, but other changes due to environmental factors may occur, such as the position of branching of whorl-branchlets with light or salinity (Berthold 1882, Rosenvinge 1923-24).

V. DESCRIPTIONS OF TAXA

GATTYA Harvey 1854.

Gattya is a monotypic genus first described by Harvey in 1854 from sterile specimens collected at Rottnest Island, Western Australia and placed tentatively in the Cryptonemiaceae. J. Agardh (1876) placed it, with Endocladia, in the Hypneaceae, tribe Endocladieae, but noted its structural similarity to Ptilocladia of the Ceramiaceae. Later (1885) he transferred it to the Ceramiaceae on the basis of triangularly-divided tetrasporangia as distinct from the zonate or cruciately - divided tetrasporangia of Catanella, Caulocanthus and Gloiopeltis with which it had previously been associated. The development of cystocarps, in the club or flask-shaped thickened end of a branch, were first noted by Schmitz and Hauptfleish (1897) who considered that on this basis it should remain in the Ceramiaceae and hence placed it with Ptilocladia in the Crouanieae.

TYPE: — Gattya pinnella Harvey 1854, from Rottnest Island, Western Australia

GATTYA PINNELLA Harvey 1854: 555

Agardh, J.G. 1876: 559; 1885: 9. De Toni 1897: 1422; 1924: 501. Harvey 1854: 555; 1859: pl. 93. Kützing 1866: pl. 57. Kylin 1956: 373. Lucas 1909: 52. Lucas and Perrin 1947: 359. Wilson 1892: 172.

TYPE LOCALITY: — Rottnest Island, Western Australia.

TYPE: — TCD. Herbarium of Harvey. No. 223.

DISTRIBUTION: — Southern Australia, widely distributed from Rottnest Island, Western Australia to Port Phillip Heads, Victoria.

(Figs. 1 - 3).

General Features: — Plants are commonly 2-4 cm . in height although larger ones are recorded e.g. A9237 b and c in AD. and MEL 8440 and 8442 are 6-8 cm . high. They attach to a variety of algae and marine angiosperms by means of multicellular rhizoids which arise from the lower cells of the thallus so that a creeping prostrate portion often occurs at the base of the plant (Fig. 1D). Plants are soft and firm and in no way slimy nor mucous. The thallus is built up of branched segments (Fig. 1A, a, b and c). Each segment is distichously, pinnately branched and flattened in the plane of branching (Fig. 1 A,D). Individual segments are separated by constrictions in the thallus and result from new phases of growth which may be

(1) apical from the pinnate branch (in future referred to as "pinna") of a segment,

(2) developed from any lateral branch which may arise from any part of the thallus,

(3) new growth stimulated by injury to an existing segment and initiated as a lateral branch from an axial cell near the point of injury.

Although new branches may be produced quite irregularly at any time from any part of the thallus, there is a marked tendency for new growth to be associated with apices and to occur in definite growth phases (Fig. 1A).

A whorl of three horizontal whorl - branchlets of determinate growth is borne on the upper part of each cell of the articulate, central axis. Previous authors, following Harvey (1858) and Kützing (1866) have recorded up to six whorl-branchlets per whorl but this has not been seen in this investigation. Each whorl-branchlet is di- or tri-chotomously branched several times. All cells of the thallus are enveloped by a colourless, gelatinous sheath and the outermost cells of the whorl-branchlets cohere together by means of this gelatinous sheath so that a complete membranous cover is formed over the thallus surface (Fig. 1C).

A phase of growth may occur, however, in which apical growth from the pinnae of the segments is terete and non-distichously branched with whorls of 3 (occasionally 4) short, lax, open whorl-branchlets from each axial cell (Fig. 1B). From this loose structure new lateral branches of the usual flattened form are developed. One or two axial cells bearing loosely formed short whorl-branchlets often occur at constrictions of the thallus between segments. This suggests that new segments may arise from lateral branches (Fig 1B, a), and that the upper part of the loose growth may finally be lost.

The complete thallus may thus be formed by a series of growth phases with "sets" of segments being developed from the apices of the pinnae formed during a previous phase of growth. Possibly a phase of lax apical growth alternates with a phase in which the distichous segments are formed. The lax thallus form has only been seen to develop from the apices of the pinnate segments of the thallus.

Growth phases are represented (Fig. 1A) where the upright segment may be considered as representative of one phase of growth while the semi-horizontal segments developed from the apices of the pinnae represent another growth phase. In addition, small lateral branches are scattered on the thallus, particularly near branch apices.

Structure and development of the thallus: —

(1) Cell Form and Thallus Development: — The thallus is composed of cells which vary from 2-8 times as long as broad. Mature axial cells average about 145 x 35µ, while basal cells of whorl-branchlets are comparatively short. Chromoplasts in mature axial cells are numerous and irregularly elongate but in young cells and in cells of the whorl-branchlets they are small and discoid to spherical or somewhat ovoid to shortly elongate. A densely staining plate-like structure is prominent in the pit connections between cells.

Growth takes place by transverse divisions of a dome-shaped apical cell. On the initiation of a new branch a short chain of three to nine horizontally-elongate axial cells develops before the first whorl-branchlet initials are formed as lateral protuberances on cells several below the apex. In the young actively growing branch a short terminal chain of several undivided cells persists (Fig. 2 A,B,C,D) but after the initial of a new branch has been formed below the growing apex, the activity of the original apical cell decreases. Enlargement and divisions occur less rapidly and the apical cell usually appears smaller and stains less densely. Lateral initials of whorl-branchlets occur even up to the sub-apical cell and slow elongation of the axis continues for a limited time.

Lateral branches may be initiated from any part of the thallus at any time. They occur most commonly in the younger parts of the thallus or as a response to injury or breakage of the axis in which case regeneration occurs by the production of a new lateral branch from the apex of the apical cell (Fig. 1E). As with the branches which form each unit of the sympodium they are initiated from the upper part of the axial cell above the whorl-branchlets. Commonly they are of the distichous form but where lax, terete, apical growth occurs both axial and lateral development of similar form is developed.

(2) Development of Whorl-branchlets: — Whorls of 3 evenly-spaced branchlets are cut off laterally from the upper part of each axial cell. Occasionally 4 branchlets make up a whorl where the thallus is terete and lax in structure.

Whorl-branchlets are usually developed in a spiral sequence on adjacent axial cells with the direction of spiral to either the right or left. This sequence is not consistent however and whorl-branchlets sometimes appear to be initiated irregularly. Mature whorls are, however, spirally arranged on successive axial cells and a rotation of 40° occurs in the positions of whorl-branchlets on adjacent cells. Thus, with a consistent rotation in one direction, the whorl-branchlets are superimposed on every 4th cell of the axis, and one complete rotation of the spiral is completed in 9 axial cells.

Four consecutive cells of the thallus are represented by a, b, c and d (Fig. 2M); further consecutive cells are shown by further concentric circles. For descriptive purposes let "a" be the uppermost and "d" the lowest in axial sequence, although a similar sequence could apply equally well where "a" represents a cell four cells below "d". Numbers 1,2, and 3 represent the whorl-branchlets of each cell. Branch (1) with a 40° divergence from cell to cell, will become superimposed over branch (2) (on cell "a") three cells below i.e. on cell "d". Similarly with a continuation of the spiral insertion (1) will superimpose with (3) (of cell "a") another 3 cells below and will complete one spiral 9 cells below the original position on cell a. A similar spiral rotation occurs for (2) and (3), so that each 4th axial cell will bear whorl-branchlets in similar positions, but each complete spiral will occur only once in 9 cells.

Whorl-branchlets are about 350µ in length and are tri-(occasionally di-) chotomously branched from the outer end of each successive cell. The basal cell of each whorl-branchlet is 1-2 times as long as broad. Cells of the first trichotomy have a length approximately 5-6 times their breadth, but cells of the subsequent 3-5 orders of branching become proportionally shorter. The small outermost cells, < 10µ diameter, are almost spherical and are embedded firmly in the continuous colourless membrane formed from the cohering sheaths which form the complete thin cover over the thallus.

All whorl-branchlets are similar in form and accommodate themselves to the short and long diameters of the flattened thallus by respectively more or less spreading of their branches.

(3) Development of Segments: — The development of each segment is primarily sympodial (Fig. 1F). The pattern of growth is, however, often difficult to determine because of the irregular and often prolific development of lateral branches which develop into further sympodial segments.

The lower four axial cells of branch (4) form part of the main axis of the segment and the upper cells (above the initial of the new branch(5)) provide a pinnate branch of the sympodium directed to the left. Thus the branch (4) has contributed to a continuation of the axis provided by the lower cells of branch 3. Similarly (3) has superceded branch (2) and so on . The newly initiated branch (5) can be expected to contribute to the continuation of the axis from its lower part, while its upper part will form the next pinna on the right.

In this way the main axis of the segment is built up from the lower cells of each successive branch, while the pinnae are formed from the upper cells which become laterally inclined to the right and to the left alternately.

Each branch of the sympodium is initiated above the whorl of branchlets and near the apex of the 4th axial cell (or occasionally the 3rd, 5th or 6th axial cell) of the previous branch and on the same side as the pinnate branch immediately below it. This position of origin directly on the axial cell is not found in genera of the Crouanieae which have a monopodial form of development and the production of the new initial consistently on the same side of the axis as the pinnate branch below is evidence for a sympodial system of development.

Initial elongation of the main axis of a segment may proceed beyond the usual 3-6 cells found between new branch initials once sympodial development commences. After initiation of the first pinnate branch of the segment the sympodial pattern is however, maintained throughout further development.

The irregular production of lateral branches and the development of segments separated by constrictions in the thallus produce changes in the plane of flattening between individual segments.

Axial Cortication and Organs of Attachment: — Axial cortication is entirely lacking in the upper parts of the plant but attachment rhizoids are produced from the lower side of basal cells of whorl-branchlets in the lower parts of the plant and the ~~rhizoids which~~ axes may consequently become prostrate. Rhizoids are initiated as small, densely-protoplasmic buds which elongate and divide transversely to form multicellular, branched, rhizoidal structures terminating in digitate attachment organs (up to 100 µ diam.) which ~~is~~ are built up of short cell-branches and ~~which~~ adhere~~s~~ to the surface of the host (Fig. 2 E-J).

Several buds may be developed successively from any one basal cell and the rhizoids produced may interweave between the whorl-branchlets of the thallus in the lower part of the plant, but they always tend to (1) protrude towards the host and (2) to be produced only in parts of the thallus reasonably close to the host surface.

Tetrasporangia: — Tetrasporangia are confined to the whorl-branchlets in the upper parts of the latest-formed segments (Fig. 2K) and are produced successively from the basal cells of the whorl-branchlets. The sporangia are initiated as pear-shaped to ovoid protuberances which enlarge and develop when mature to form sessile, spherical, tetrahedrally-divided tetrasporangia, 45-60µ in diameter (Fig. 2L). The first initials usually develop on the upper, outer end of the cell, but later-formed sporangia are produced from any part of the cell. Several stages of sporangial development may be seen on a single cell at one time.

The spores are liberated from between the whorls of branchlets which are often loosely constructed and separate as the tetrasporangia mature.

When stained with iodine a red colouration of the protoplast, which is very dense in some spores, indicates the presence of Floridean starch.

Spermatangia: — Spermatangial mother cells (4-6μ diam.) are borne in whorls of 2-4 outwardly on the 1- to 2-celled short branches which terminate the whorl-branchlets. The spermatangial mother cells thus occur on the outer surface of the thallus (Fig. 3H).

Development of the Procarp and Carposporophyte: — The pattern of carpogonial branch and carposporophyte development is essentially similar to that found in Crouania. The procarp is initiated several cells below the branch apex in place of a whorl-branchlet, the carpogonial branch is 4-celled and upwardly curved, some fusions may occur between cells of the carposporophyte and the first gonimolobe is produced terminally from a rounded central gonimoblast cell. Similarly also the carposporophyte is protected by the upward elongation of whorl-branchlets to form a club-shaped branch apex (Fig. 3A) with an apical depression through which the mature carpospores escape.

Several procarps may be produced at one branch apex and may occur on adjacent or closely situated axial cells, or two may be initiated on the one axial cell. In this case only one produces carpospores.

A large supporting cell replaces a whorl-branchlet and bears the carpogonial branch on its outer (abaxial) side (Fig. 3B). All cells of the procarp are large in comparison to the young vegetative cells of the thallus and stain densely. Limited elongation of the axis continues after the initiation of the procarp, so that the carposporophyte at maturity is completely surrounded by mature whorl-branchlets (Fig. 3G). A trichogyne is developed from the carpogonial cell and protrudes through the developing whorl-branchlets of the branch apex. Few stages of trichogyne development were seen in the many young carpogonial branches examined. This suggests that trichogyne development may be rapid and that the trichogyne may disappear soon after fertilisation. A small capping-cell is cut off from the carpogonium at the base of the trichogyne (Fig. 3C). Wollaston and Womersley (1959) described for Gulsonia annulata transverse division of the carpogonium after fertilization to form a small superior cell. In Gattya this cell seems to be formed at the time of initial elongation of the trichogyne and remains after the trichogyne disintegrates. Stages of actual fusion, immediately following fertilization, have not been seen. An auxiliary cell is, however, cut off from the upper side of the supporting cell and presumably fusion occurs between this cell and the carpogonium by means of a connecting cell as in species of Crouania. The central cell develops as an upwardly-elongate protrusion from the upper side of the auxiliary cell (Fig. 3D) and finally becomes separated to form a distinct, densely protoplasmic cell from which the gonimolobes develop (Fig. 3 E and F). The old auxiliary cell becomes depleted in form and sometimes appears closely associated with the residual supporting cell (Fig. 3F).

A terminal gonimolobe bud is initiated first and is followed by several successively formed buds cut off laterally. Each bud expands and divides to form a rounded mass of carpospores.

As the carposporophyte develops elongation of the main branch axis ceases and the whorls of branchlets on adjacent axial cells mature and elongate upward. Basal cells of the whorl-branchlets often stain densely possibly indicating a nutritive function. The carposporophyte thus develops in the club-shaped apex of a pinna, and further axial growth takes place from a branch developed laterally on the axis below the carposporophyte. This position of carposporophyte is characteristic of both Gattya and Crouania.

Discussion.

The species, although widely distributed in southern Australia, is not common and only limited fertile material has been available for this study. Harvey's original description (1854) was based upon sterile plants and there have been few records of fertile material since. Most records of the plant are from drift material and it probably occur in comparatively deep water. One collection (AD, A 24,861, Port Malcolm, Semaphore, S.Aus.) was dredged from a depth of 30 ft. This study has been based on recent collections of drift material from Marino, South Australia.

The plant is similar to Crouania in having:

(a) Whorls of three branchlets on each axial cell.

(b) Sympodial development of main axes (not regularly occurring in Crouania).

(c) The carposporophyte developed in the club-shaped branch tip, with further axial elongation taking place from a lateral branch produced from an axial cell below the carposporophyte.

(d) Terminal position of the first developed carpospore group on a rounded central gonimoblast cell.

Gattya is, however, sufficiently distinct from Crouania to be retained as a separate genus. The main differences are vegetative and include:

(1) A flattened thallus of pinnately-branched, distichous segments.

(2) Consistent sympodial development of thallus segments.

(3) An external, membranous outer sheath over the thallus formed from the cohering terminal cells of the whorl-branchlets.

(4) Absence of hairs such as occur terminally on cells of the final order of cells in whorl-branchlets of Crouania mucosa.

These points could be considered phylogenetically to represent a higher degree of thallus organisation in Gattya than is seen in Crouania. This is emphasized in the consistency of the sympodial branching pattern, the flattened thallus segments and the firm cohering sheath covering the thallus.

CROUANIA J. Agardh 1842

J. Agardh described the genus Crouania based upon Crouania attenuata and placed it in the Cryptonemeae. The genus included mucilaginous plants bearing whorls of branchlets from each axial cell. Later (1876) he extended his definition to include non-gelatinous (spongiose) species particularly from Australia. Critical examination of these species now shows that most of Agardh's Australian species rightly belong to Ptilocladia Sonder and that the genus Crouania includes plants having:

(i) Whorls of 3 whorl-branchlets per axial cell.

(ii) Both axial and true lateral branches (borne respectively directly on the axis and on the basal cell of a whorl-branchlet).

(iii) Tendency to sympodial branching.

(iv) Spherical tetrasporangia, tetrahedrally divided and borne on basal cells of whorl-branchlets.

(v) Procarps borne in place of whorl-branchlets near the branch apex and carposporophytes developed in club-shaped branch apices. Terminal groups of carposporangia develop first.

These features are more fully discussed in Section IX.

TYPE species: Crouania attenuata (Ag.) J. Ag. (European).

Key to the Southern Australian species of *Crouania*

1. Plant slimy-mucilaginous. Rhizoidal axial cortication in lower part of thallus... ... ... *C. mucosa*

1. Plant not slimy-mucilaginous. With or without axial cortication of rhizoids.... 2

2. Erect thallus to 2 cm high with creeping base. Branches slender with tapered apices. Axis without rhizoidal cortication and exposed between whorls of whorl-branchlets.... *C. shepleyana.*

2. Plant small (1 cm high), not creeping. Branch apices rounded. Axis lightly corticated with rhizoids in lower parts of plant and not exposed between whorls of whorl-branchlets... ... ... *C. destriana*

CROUANIA MUCOSA n.sp.

Thallus usque ad 7 cm. altus. Axes teretes gelatinosi, interdum annulares, inferne filamentis rhizoideis corticati; quaeque cellula 3 vortico-ramulis instructa. Ramificatio irregularis ramis lateralibus axialibusque. Tetrasporangia tetrahedralia in thallo superiore sessilia in cellulis infimis vortico-ramulorum. Spermatangia in vortico-ramulis terminalia. Carposporophyti in cacuminibus clavatis ramorum positi.

TYPE locality: Robe, S. Aust.

HOLOTYPE: AD, A 11,088.

DISTRIBUTION Pearson Is., Elliston, Cape Carnot and Robe, also Pennington Bay and Sou'west River, Kangaroo Is., in South Australia to Port Phillip, Victoria (J.B. Wilson, Herb. Agardh, LD, as C. australis) and also Low Head (Georgetown), Penguin and Rocky Cape, Tas.

(Figs. 4-6; Plate 1).

General Features: - The plant grows to 7 cm in height, often with several, erect branches arising from the base (Fig. 4A). The thallus is terete, soft, very gelatinous and slimy and consists of an articulate axis each cell of which bears a whorl of three branchlets from its upper part. The whorl-branchlets are embedded in a colourless mucilaginous matrix and completely obscure the axis. Branches are sometimes annular in appearance due to the position of the whorls or, in the basal parts of the thallus, the individual whorl-branchlets may become rather more separated and give an undulating thallus surface. Terminal cells of the whorl-branchlets may bear elongate hairs(250 µ long) with slightly expanded tips (Fig. 4B).

The axis toward the base of the plant is loosely corticated with multicellular rhizoids.

Carposporangial plants are readily recognized by their shorter, more branched form and the club-shaped apices of the branches which bear the carposporophytes (Fig. 5A).

Structure of the thallus.

1. Form and Development of Main Branches: — Axial growth occurs by transverse divisions of a dome-shaped apical cell to form a chain of cells. In young, newly developing branches this chain is 10-20 cells long and 50 - 80µ in length before initiation of whorl-branchlets commences (Fig. 4 D,E.) in the central region. Axial cells when mature vary in dimensions but usually are about twice as long as broad and measure up to 600 x 350µ. The pit-connections between cells are characterized by a thickened plate-like structure set obliquely to the branch axes. Numerous chromoplasts occur in each cell. They are rounded in small exterior cells and in young cells and irregularly elongate in mature cells and axial cells.

Early development of the thallus is monopodial. On the upper part of each branch, however, one to several (usually 2-3) new branches (here termed axial branches) are initiated which grow upward and contribute to further axis elongation, while growth of the primary axis slows down and finally ceases. Each new axial branch arises directly from the upper part of an axial cell (above the whorl of branchlets) and, when more than one is developed, they are borne on the same side of the axis and separated by 2-5 axial cells (Fig. 4F, G). A bending of the upper part of the previous axis allows these branches to assume a more or less erect position (Fig. 4A). A shift of dominance from an old axis to one or more new ones occurs several times in the development of each main branch of the thallus (Fig. 4A and B). Although this branching pattern is not regularly developed it suggests a primitive form of sympodial branching in the cessation of elongation of one axis and the development of a new axis (in this case, several) developed from a lateral position. This is a more primitive form of sympodial branching than that seen in Gattya pinnella where a well-defined sympodium is formed. Lateral branches occur irregularly from any part of the thallus and are borne on the outer end of the basal cell of a whorl-branchlet (Fig. 4D,E). Thus they are distinct in origin from axial branches.

2. The Development and Structure of Whorl-branchlets: — Whorl branchlets are initiated several cells below the apex and at this stage the young axial cells are about twice as broad as long. The axis of the new branch is well covered by whorl-branchlets before it protrudes beyond the whorl-branchlets of the parent branch. Each initial of a whorl-branchlet is formed from a lateral elongation of an axial cell and is cut off from the axis by a longitudinal division.

Initiation of whorl-branchlets occurs in spiral sequence from adjacent axial cells (Fig. 4E) and may be directed either toward the right or the left. This results in a rotation of 40° between whorl-branchlets on adjacent cells so that, in mature whorls, the branchlets borne on each 4th axial cell are superimposed (Fig. 4C).

Each mature whorl-branchlet consists of a series of 5-8 orders of apparent quadrichotomies (sometimes trichotomies), the cells of which ~~become~~ are successively smaller towards the exterior. The basal cell of the whorl-branchlet is about 100 x 75µ and bears the first quadrichotomy on its outer end. Each of these cells bears a further quadrichotomy of cells, with rounded terminal cells 10-12µ diam. Mature whorl-branchlets measure about 380µ in length, but are always shorter towards the base of branches so that all branches appear basally constricted.

<u>Axial Cortication:</u> — Multicellular rhizoids arise from the lower side of the basal cell of each whorl-branchlet in the lower parts of the plant. Several may be produced successively from each basal cell. Rhizoids consist of elongate cells (200 x 10µ) and are usually unbranched, although occasionally they may be once or twice branched. They grow downwards and interlace to loosely clothe the axis (Fig. 4B).

<u>Tetrasporangia</u> are borne on the upper side of the basal cells of the whorl-branchlets in the upper parts of the plant (Fig. 6F,G). They are sessile, produced successively with as many as ten buds at various stages of development on one cell (Fig. 6G). Mature tetrasporangia are almost spherical, ~~and~~ about 60-80µ in diam., and divide tetrahedrally.

<u>Spermatangia:</u> — Spermatangial mother cells are borne terminally in whorls, usually of three, on the whorl-branchlets in the upper part of the plant. Each spermatangial mother-cell is dumb-bell-shaped, 4-5 µ long, with a band of

dense protoplasm concentrated in the region of the median constriction. The three spermatangial cells of the whorl do not always mature at the same time, and sometimes smaller, completely protoplasmic cells make up part of the group (Fig. 4H, I).

Development of the Procarp and Carposporophyte.

Plants bearing carposporophytes are usually shorter and more prolifically branched. Axial elongation ceases soon after the initiation of carpogonial branches near branch-apices and further growth takes place from new branches produced lower down on the axis. Branch ends become club-shaped and expanded with the enlarging carposporophyte which is protected by the mature surrounding whorl-branchlets.

Carpogonial branches are initiated near the apex of young lateral branches or main axes. The supporting cell, which may, in a lateral branch, be developed before the branch protrudes through the covering whorl-branchlets/ of the axis is produced in place of a whorl-branchlet, and is readily recognized by its densely-staining protoplasm and comparatively large size (about 12µ diam. and equal in size to the young axial cell) (Fig. 5B). Several axial cells are developed beyond the carpogonial branch initials (Fig. 5B); further axial elongation ceases, however, and carposporophytes always occur at branch tips.

Several carpogonial branches may occur ~~on~~ at one branch apex and two or three of these may ~~produce~~ develop carpospor~~angia~~ophytes. Occasionally two procarps are formed on a single axial cell.

The carpogonial branch is initiated from the outer side of the supporting cell and seems to develop rapidly as very few stages in its formation have been seen. From these few observations it appears, however, that a protrusion develops from the supporting cell (Fig. 5C) which gives rise to an almost spherical cell (the carpogonial branch mother-cell) equal in size to the supporting cell. The 4 cells of the carpogonial branch form by almost simultaneous divisions of this cell (Fig. 5D) and straighten out to give a slightly curved carpogonial branch about 20μ in length (Fig. 5E-I). The trichogyne is formed as an elongate process from the carpogonium (Fig. 5G-I) and may be up to 90 μ long when mature (Fig. 5I). The receptive tip of the mature trichogyne is slightly swollen and a strand of protoplasm is continuous throughout its length. Each cell of the carpogonial branch is characteristic in form. A small terminal capping-cell is cut off from the carpogonium and is incorporated in the development of the trichogyne. Only a few stages showing elongation of the trichogyne have been observed indicating that it is probably rapidly formed.

Spermatia adhere to the thickened tip of the trichogyne and fusion occurs by means of a tubular connection with a spermatium (Fig.5J). After fertilisation the trichogyne is completely lost. A small cell remains corresponding to the capping-cell involved in its development. A protrusion develops from the carpogonium towards the supporting cell, which now enlarges and stains densely in the upper part prior to transverse separation of the auxiliary cell.

The protrusion from the carpogonial cell is surrounded by a lightly-staining and yet distinct mucilaginous sheath which may serve both as a protection and to make contact with the tubular protrusion developed from the auxiliary cell toward the carpogonium (Fig. 5K). Immediately after fusion the small connecting cell, cut off from the carpogonium during the process, may be seen attached to the extension of the auxiliary cell (Fig. 5L). The stages seen indicate that the auxiliary cell must be separated from the supporting cell very close to the time of actual fusion with the connecting-cell from the carpogonium.

A distinct pit-connection occurs between the third cell of the carpogonial branch and the carpogonium.

Following fusion the old carpogonial branch becomes detached and takes no part in further developments.

No nuclei have been observed with certainty and it is not known where the actual fusion of male and female nuclei occurs.

The axial cell bearing the fertile branch becomes depleted in size and stains densely during these developments. It probably acts as a source and conveyer of nutriment during the rapid changes leading to development of the carposporophyte.

After receiving the diploid nucleus from the carpogonium the auxiliary cell (at this stage referred to by some authors as the "fusion cell"), elongates upward (Fig. 5M). The upper part enlarges and is cut off to form the rounded central cell from which several successive gonimolobes (carpospore buds) develop, while the lower part remains as the foot-cell. A terminal bud develops first and lateral ones later (Figs. 5N; 6A,B).

Each gonimolobe cuts off several cells (Fig. 6A) each of which divides repeatedly (Fig. 6 B,C) to form the cells which mature into carposporangia. A mature group of carposporangia is globose and may be 200µ or more in diameter (Fig. 6D). Each carposporangium is somewhat angular and measures about (15-20) x 30µ (Fig. 6E).

There may be a widening of the connections, particularly between axial cell and residual-supporting-cell as the carposporophyte matures, but it is doubtful as to what extent actual fusion occurs. No special involucre is formed. The groups of carposporangia are protected during development by the whorl-branchlets of the surrounding axial cells. When axial elongation ceases, the initials of the whorl-branchlets near the branch apex mature to form the club-shaped tip characteristic of the fertile branches (Fig. 5A). Carposporangia are liberated terminally through a pore in the mucilaginous sheath which covers the plant.

Discussion: —

The material used for this investigation was collected from sheltered areas on the reefs in South Australia at Pennington Bay, Kangaroo Island, and at Robe. A third collection made by A.B. Cribb at Low Head, Georgetown on the north coast of Tasmania was used for comparison. The plant is found most commonly in sheltered areas such as pools, channels and in the shelter of larger rocks on open reefs in the upper-sub-littoral to littoral zone. Although comparatively widely distributed it has not previously been described.

In both vegetative and reproductive features the plant agrees well with the genus Crouania as first described by J. Agardh (1842: 83), but differs from other known species of the genus. The nature of these differences in relation to other southern Australian species of Crouania will be discussed later. Of other known species of Crouania it most closely resembles C. attenuata but is distinct in having shorter terminal cells to the whorl-branchlets and axial cortication of rhizoids in the lower part of the thallus.

CROUANIA SHEPLEYANA n.sp.

Thallus 1-1½ cm altus in basi prostrata positus. Axes teretes, flexuosi, non gelatinosi, sine corticatione, annulares; quaequecellula 3 vortico-ramulis instructa. Ramificatio irregularis ramis lateralibus axialibusque. Tetrasporangia tetrahedralia in cellulis basalibus vortico-ramulorum sessilia. Spermatangia ignota. Carposporophyti in cacuminibus rotundatis ramorum positi.

TYPE locality: — Port Willunga, S. Aust.

HOLOTYPE: — AD, A 28,382.

DISTRIBUTION: — Port Willunga, S. Aust. and Ulverstone, Tasmania.

In shaded rock pools and drainage channels on reef.

(Fig. 7; Plate 2)

General Features: — The plant is 1-1½ cm high, with creeping prostrate base attached by sparingly branched multicellular rhizoids which arise from the basal cells of the whorl-branchlets. The thallus is terete, flexuous and neither slimy nor axially corticated with rhizoids.

Each axial cell bears a whorl of three whorl-branchlets which are almost horizontal and allow the larger axial cells, particularly in the lower parts of the plant, to be exposed between whorls. The plant is distinctly banded in appearance (Fig. 7A).

Structure of the Thallus: —

(1) Development and Form of Main Branches: - Growth takes place by transverse divisions of a dome-shaped apical cell to give articulate axes with mature cells about 1½-2½ times as long as broad and measuring about 120-170µ x 60-120µ. All branches of the thallus develop from an initial elongate chain of cells. Axes are monopodial, but occasionally new axial branches as in *C. mucosa* are produced near apices. These become dominant and continue to grow upwards, while the original axis ceases further

elongation (Fig. 7A, a and a_1). As in other species of Crouania, branching is thus of two types:

(i) New axial branches are borne directly on cells of the main axes slightly above the whorl of whorl-branchlets. After initiation of these branches (Fig. 7A, b_1 & b_2), suppression of growth in the previous axis is sometimes delayed and the main axis (Fig 7A, a_2) continues to grow indefinitely. Hence the tendency toward the development of a sympodium is not as marked as in C. mucosa.

(ii) Lateral branches, typical of the genus, may occur on any part of the thallus. These arise from the upper part of the outer end of the basal cell of a whorl-branchlet and are thus distinct in origin from axial branches.

(2) Development and Structure of Whorl-branchlets: — Each mature axial cell bears a whorl of three whorl-branchlets each about 100µ long and each of which is itself branched by 4-6 successive whorls from the outer end of each cell. The small terminal cells are spherical and about 6µ in diameter. Initiation of whorl-branchlets is in spiral sequence as described for C. mucosa and the whorls are similarly rotated by 40° on adjacent axial cells. No hairs occur on the terminal cells of the whorl-branchlets.

Tetrasporangia.

Tetrasporangia are borne successively from basal cells of whorl-branchlets in the young parts of the thallus. The sporangia are conspicuous (50µ diameter) on the comparatively short whorl-branchlets. They are sessile and divide tetrahedrally (Fig. 7J).

Spermatangia — unrecorded.

Development of the Procarp and Carposporophyte: — The development of the procarp follows the same pattern as described for C. mucosa. Supporting cells are borne on axial aells near the apices of young branches and each is initiated from a lateral protuberance of an axial cell (Fig. 7C). Each carpogonial branch develops from the outer part of a supporting cell. Axial elongation ceases after the procarps are formed and a new axial branch, which arises below the fertile branch apex may continue upward growth of the axis (Fig. 7B).

Cells of the procarp are much larger than surrounding vegetative cells of the thallus (Fig. 7C,D). The trichogyne forms from a densely-staining cell-like cap cut off from the summit of the carpogonium (Fig. 7E). A mature trichogyne is about 80μ long with a receptive tip to which the spermatia adhere (Fig. 7F).

After fertilization the trichogyne disintegrates and a connecting cell is cut off from the carpogonium in the direction of the supporting cell. An auxiliary cell is cut off from the upper part of the supporting cell and presumably makes connection with the carpogonium via the connecting cell (Fig. 7G).

A rounded central cell is cut off from the upper part of the auxiliary cell leaving a narrow lower foot-cell (Fig. 7H).

The first gonimolobe develops terminally and further buds are cut off laterally later (Fig. 7I).

Whorl-branchlets surrounding the carposporophyte are directed upward and form a protection around the maturing carposporangia (Fig. 7B).

This results in a club-shaped branch apex enclosing the carposporophyte as found in other species of *Crouania*.

Discussion:

Some plants carry dense growths of epiphytes and these appear much shorter, stiffer and tuftier in form than the usual plants and suggest superficially a different species.

This species has the smallest plant form of any *Crouania* so far recorded in southern Australia. It ~~This plant~~ most closely resembles *Ptilocladia australis* (Harv.) J. Ag. but is quite distinct in size ~~of plant~~ (*P. australis* grows to 6 cm.), in having whorls of three, and not four, branchlets, in lacking gland-cells as occur in *P. australis* and in position of the carposporophyte.

CROUANIA DESTRIANA n.sp.

Thallus ca. 1 cm altus. Axes teretes, non gelatinosi, inferne filamentis rhizoideis corticati; quaeque cellula 3 vortico-ramulis instructa. Ramificatio irregularis ramis lateralibus axialibusque. Tetrasporangia et spermatangia ignota. Carposporophyti ad apices clavatos ramorum positi.

TYPE locality: — D'Estree Bay, Kangaroo Is., S. Aust.

HOLOTYPE: — AD, A 27,035.

DISTRIBUTION: — Recorded only from the type locality.

(Fig. 8, A - D).

General Features: — The plant is about 1 cm. high with several branches from the base. The thallus is terete, axially corticated with rhizoids in the lower parts, and is not gelatinous nor slimy. Branching is irregular and the articulate axis is clearly seen through the whorls of whorl-branchlets.

Structure of Thallus.

(1) Development and form of Main Branches: — Growth occurs as in C. mucosa by the transverse divisions of a dome-shaped apical cell, and an elongate chain of cells is formed before whorl-branchlets commence to form. Mature axial cells measure about 160-200 x 80-100μ. Two kinds of branches are produced:

(i) Axial branches, which arise directly from the axial cells, above the whorls of branchlets and contribute to axis elongation. These are usually produced in pairs near the apices of branches which, shortly afterwards, cease further elongation.

(ii) Lateral branches which arise from the outer upper part of the basal cell of a whorl-branchlet, and occur irregularly from any part of the thallus.

(2) Development and form of Whorl-branchlets: — Each cell of the axis bears a whorl of three whorl-branchlets which are initiated as in C. mucosa and when mature measure 200-300μ in length. Each branch is itself branched by 6-7 successive whorls (each of 3-4 cells)

from the outer end of each cell. The terminal cells are small and ovoid, measuring about 4-6 x 6-9µ. Whorl-branchlets of adjacent whorls just meet to give a nodulose banded thallus (Fig. 8D).

Axial Cortication: — In the lower parts of the plant, multicellular rhizoids arise from the lower side of the basal cells of whorl-branchlets and loosely clothe the axis. They are composed of elongate cells and may occasionally be branched. Attachment is by means of rhizoids developed from the basal part of the plant.

Tetrasporangia and Spermatangia: — Unrecorded.

Development of the Procarp and Carposporophyte: — Procarps are developed in place of whorl-branchlets on axial cells several below the branch apex. Axial elongation ceases and, as in all species of Crouania, further growth takes place from a new axial branch initiated below the developing carposporophyte. After fertilization a small connecting cell develops from the lower adaxial part of the carpogonium before the auxiliary cell is separated from the supporting cell (Fig. 8A). Separation of the auxiliary cell from the supporting cell probably occurs rapidly and close to the time of fusion with the connecting cell. Further development of the carposporophyte occurs as in C. mucosa with the first carposporangial bud developed terminally (Fig. 8C). The first gonimolobe initial may begin to form before the central cell is cut off from the auxiliary cell (Fig. 8B).

Further gonimolobes develop laterally. Occasional widening of the connections, with possible fusion, occurs between the axial cell and the residual supporting cell and at times between other cells of the carposporophyte.

Discussion: —

Only one plant (carposporangial) has been collected and it seems doubtfully wise to propose a new species based on one specimen. The plant is, however, sufficiently distinct from other known species to deserve comment. It differs from *Crouania shepleyana*, the only other non-slimy southern Australian species, in having a more robust plant form, rhizoidal cortication of the axis in the lower part of the plant and whorl-branchlets covering but not obscuring the axis.

This species completely lacks the very slimy texture of *C. mucosa* and differs from that species also in having shorter, broader axial cells and more loosely constructed whorl-branchlets which do not obscure the central axis.

The rounded branch apices bearing the carposporophytes and the development of axial branches which suggest a sympodial form of branching are generic characters well developed in this plant.

DOUBTFUL SPECIES OF CROUANIA

1. *CROUANIA GRACILIS* J. Ag. (1876).

Agardh, J. 1876: 85; 1879. t II. f 1-7; De Toni 1897: 1418.

Lucas 1909: 51; 1929a: 25.

TYPE Locality: — Tasmania (Gunn).

TYPE: — LD., Bot. Museum., Herbarium J. Agardh, No. 20269.

DISTRIBUTION: — Tasmania. The only record is the type collection of R. Gunn (without date or locality data) and of which there is a probable isotype, MEL. 8438.

The species was first described by J. Agardh (1876) and figured by him (1879). He ascribed it to the genus Crouania as the only gelatinous species having rhizoidal axial cortication developed in the lower part of the plant, and recognized it as distinct in its slender, elongate form, its large tetrasporangia and articulations of the main axis longer than in other species.

The material from MEL agrees well with J. Agardh's figures, and sometimes several cells occur between successive branchings of whorl-branchlets(J.Agardh 1897, t. II, figs. 2,3). The specimen examined is tetrasporic and has:

(1) whorls of 4 or 5 whorl-branchlets,

(2) axes corticated by rhizoids bearing short projections outwardly.

(3) tetrasporangia, sessile on cells of whorl-branchlets, spherical, about 80µ diam., probably tetrahedrally divided.

These features indicate that the species does not belong to Crouania, but material is inadequate to place it correctly.

The type of Dasya crouanioides Sonder (1852) (MEL 8458) is probably the same species, but again too fragmentary to determine.

2. <u>CROUANIA MUELLERI</u> Harvey 1863, synop: 638.

J. Agardh 1876: 85. De Toni 1897: 1419. Lucas 1909: 51. Lucas & Perrin 1947: 356. Wilson 1892: 85.

<u>TYPE Locality</u>: — Phillip Is., Victoria. F.v.M.

<u>TYPE</u>: — TCD. Herbarium of Harvey.

<u>DISTRIBUTION</u>:— From Pt. Sinclair, S. Aust. to Sealer's Cove, Wilson's Promontory, Victoria.

The plant is rare and inadequate material has been available for detailed investigation, particularly of reproduction. The following features show that, almost certainly, it is not a species of <u>Crouania</u>. It has:

(1) Whorl-branchlets in whorls of 5 (4). <u>Crouania</u> in 3's.

(2) Branching without sympodial tendency produced by axial branches as occurs in <u>Crouania</u>.

(3) Gland cells, similar to those occurring in Antithamnieae and Heterothamnieae, borne on final branchings of whorl-branchlets. Gland-cells are absent in <u>Crouania</u>.

(4) Attachment by branched rhizoids and lateral branches which coil around a support. A holdfast occurs in <u>Crouania</u>.

(5) Carposporophyte produced at reduced apices (as in Heterothamnieae) of short lateral branches.

These features suggest that the species probably belongs to <u>Perithamnion</u>. Fresh material, particularly female, is necessary to confirm its identity. The only female plants available are dried material from the type collection and are difficult to restore. Stages showing procarp and early carposporophyte development are lacking. The plant differs from other species of Perithamnion chiefly in having fewer lateral branches. Whorl-branchlets, in whorls of 5, indicate similarity with P. dispar in which 4-5 branchlets of varying lengths occur in each whorl. Phylogenetically the two species may be closely related to one another.

PTILOCLADIA Sonder 1845.

Examination of the type material of Ptilocladia pulchra has shown that this plant is synonomous with Gulsoniopsis insignis Hommersand and on the basis of priority this binomial must replace all later synonyms. Ptilocladia includes plants having:

(i) terete, non-mucilaginous axes bearing whorls of 4 equal whorl-branchlets from each axial cell.

(ii) Dense axial cortication of rhizoidal filaments.

(iii) Axes, monopodial and bearing lateral branches which are irregular to alternate-distichous in arrangement. Determinate laterals may also occur.

(iv) Carposporophyte borne near the apices of short determinate lateral branches (except in P. australis in which the branch axis continues to elongate after initiation of the carposporophyte).

A new genus, Euptilocladia is proposed for plants having flattened axes and differing from Ptilocladia in other structural details. Further discussion on the characteristics and phylogeny of these genera is given in Section IX.

Schmitz (1889) placed Ptilocladia in the Crouanieae because of its structural similarity to Crouania.

TYPE species: Ptilocladia pulchra Sonder.

Key to the southern Australian species of Ptilocladia

1. Plant lax, irregularly branched without short determinate lateral branches. Axes with or without rhizoidal cortication in lower parts of thallus. Carposporophytes borne at intervals along the axis... 2

1. Plant more or less alternately-distichously branched with short determinate lateral branches. Axes corticated with rhizoids except at branch apices. Carposporophyte borne on the determinate branches... 3

 2. Axis, without rhizoidal cortication, exposed between whorls of branchlets.... ... ... *P. australis*

 2. Axis with rhizoidal cortication in lower parts of thallus, exposed in uncorticated upper parts. *P. australis* (var. *cortica*)

3. Additional cortication of axis by elongation of whorl-branchlets upwardly and downwardly, parallel to the axis, in lower parts of plant. Axis not cartilaginous nor exposed between whorls of branchlets... ... ... *P. vestita*

3. Axial cortication of rhizoids modified to form inner layer of large cells and outer layer of small cells in lower parts of thallus. Axis cartilaginous and exposed between whorl-branchlets towards base of plant 4

4. Thallus with branched segments, pyramidal in outline, formed from the alternate-distichous branching of indeterminate branch-axes. Carposporophytes borne on short determinate branches usually with rounded apices... ... ... P. pulchra

4. Thallus without pyramidal segments. Carposporophytes borne on short determinate branches with bluntly tapered apices ... ... P. agardhiana

PTILOCLADIA AUSTRALIS (Harv.) comb. nov.

Crouania attenuata var. australis Harvey alg. Aust. exs. No. 485; 1854: 558; 1860: 330.

Crouania australis (Harvey) J. Agardh 1876: 85. De Toni 1897: 1418. Lucas 1909: 51; 1929a: 25; Wilson 1892: 185.

TYPE Locality: — King George's Sound, Western Australia (Harvey).

TYPE: — TCD. Herbarium of Harvey. No. 485.

DISTRIBUTION: -- From King George's Sound, Western Australia to Kangaroo Is., South Australia, and Tasmania.

(Figs. 8 E - J, 9).

General Features.

Plants usually 3-8 cm. high and neither gelatinous nor slimy. The thallus is soft, irregularly branched and banded due to the whorls of whorl-branchlets developed from each axial cell. The whorls become widely separated in the older parts of the uncorticated plants so that the banded, nodose effect becomes very prominent (Fig. 8E).

Plants are lightly calcified and attached by rhizoids which develop from the basal cells of whorl-branchlets in the lower part of the plant. There is no axial cortication of rhizoids, even in large plants of the typical form. Development of cortical rhizoids covering the axis in the central to lower parts of the thallus is, however, a distinguishing feature of forma cortica (see later).

Pyriform gland-cells occur near branch apices, replacing some of the terminal cells of the whorl-branchlets (Fig. 9F). They have not been seen on older parts of the thallus and may, therefore, be deciduous. In form they are similar to those described for Gulsonia annulata Harvey by Wollaston and Womersley (1959) and contain similar crystal-like inclusions.

Structure of thallus.

(1) Development and form of main branches: — Growth takes place by transverse divisions of a dome-shaped apical cell to form a short chain of 3-5 cells before the initiation of whorl-branchlets (Fig. 9F). Axial cells when mature are about 3-4 times as long as broad with prominent pit-connections and measure about (150-200) x (50-60)µ. Cells near the base of the plant may be much larger and thoxe of the younger branches

proportionally smaller. All lateral branches are indeterminate in growth and arise from the upper outer end of a basal cell of a whorl-branchlet (Fig. 9A-C). There is no development of axial branches as described for species of Crouania and growth is consistently monopodial.

(2) Whorl-branchlets: — Each axial cell bears a whorl of four branchlets each of which is branched by 3-5 successive whorls of cells from the outer end of each cell. The cells of the whorl-branchlets are elongate but become progressively smaller toward the exterior. Terminal cells average (12-16) x 5μ and often divide to give short 2-3-celled chains. The base of each whorl-branchlet is at right angles to the axis while the outer part turns upward parallel to the axis (Fig. 8E). There is a rotation of 45° between whorls on adjacent axial cells and a spiral sequence of initiation of whorl-branchlets at branch apices (Fig. 9C).

Development of Tetrasporangia.

Tetrasporangia are borne on the upper, outer end of the first (basal) and second cells of whorl-branchlets and are scattered over the plant, usually more densely on the younger branches.

Each sporangium is spherical, sessile, 55-70 μ in diameter within a thick gelatinous sheath and divides tetrahedrally (Fig. 8 F-J). At least a second tetrasporangium may develop successively from ~~one~~ each cell.

Development of Procarp and Carposporophyte.

The procarp replaces a whorl-branchlet on an axial cell near the branch apex (Fig. 9D). A supporting cell develops directly from an axial cell of the branch and bears a curved 4-celled carpogonial branch on its outer side. Usually only one carpogonial branch is produced near the branch apex at one time. The supporting cell is somewhat smaller (12μ diameter) than that found in species of Crouania, but retains the characteristic appearance in its form and densely-staining protoplasmic contents. Other cells of the carpogonial branch are as big or bigger than the supporting cell. After initiation of the procarp axial growth continues and further procarps initiated are widely spaced along the axis (Fig. 8E). By the time one carposporophyte is mature, one to three further carpogonial branches have been initiated.

The densely-staining carpogonial branch initial is cut off from the outer side of the supporting cell (Fig. 9D) and enlarges and divides rapidly to form the carpogonial branch with terminal carpogonium and an elongate trichogyne (up to 200μ) (Figs. 9E-G). No stages showing incomplete divisions in the formation of the carpogonial branch have been seen, but a young carpogonial branch soon after formation (Fig. 9E) indicates near-simultaneous divisions of the initial cell as in Crouania mucosa, and probable planes of the divisions leading to the development of the four cells of the carpogonial branch are still clear. The carpogonium appears to be cut off from the 3rd cell of the carpogonial branch by a division at right angles to the division separating the 2nd and 3rd cells (Fig. 9G), while in Crouania mucosa and Gattya pinnella this division occurs parallel to that dividing the 2nd and 3rd cells. In many cases the carpogonium did not stain densely until the trichogyne was mature although other cells showed very dense protoplasts. Possibly trichogyne development rapidly absorbs nutriment from the carpogonium and this is replenished via other cells of the carpogonial branch.

After fertilization the trichogyne is rapidly lost and an auxiliary cell is cut off from the upper part of the supporting cell to leave a laterally-elongate residual supporting cell. An elongate process, in place of the attachment of the carpogonial branch, remains on the outer side of the residual supporting cell (Fig. 9, H,I). The auxiliary cell divides transversely to give a narrow foot cell (the lower part) and a large rounded central cell (the upper part). The first gonimolobes are cut off laterally (Fig. 9H). At about this stage widening of connections with probable fusions between the cells of the carposporophyte become evident and, as the carposporangia mature, become further enlarged. Finally the residual supporting cell and the central cell become linked by a wide densely-staining connection without apparently involving the foot cell which at this stage usually stains less densely and does not appear functional. The cells of the carposporophyte become rigid and reduced in size as the carposporangia mature (Fig. 9I).

As the carposporophyte develops, the basal cells of the whorl-branchlets both above and below the carposporophyte, develop protrusions toward the carposporophyte (Fig. 9I). Occasionally similar protrusions are developed from other cells of surrounding whorl-branchlets. Rhizoidal filaments may also be produced from cells of the whorl-branchlets from adjacent axial cells and appear sometimes to connect with other vegetative cells below or above the carposporophyte (Fig. 9I). These filaments may possibly form a nutritional bridge connecting the upper and lower parts of the plant around the carposporophyte. The development of such filaments seems, however, to be inconsistent. The cells of the whorl-branchlets surrounding the carposporophyte enlarge to form a dense protection around the carposporophyte.

Discussion: —

In his original description of Crouania attenuata var. australis Harvey (1854) noted that the plant was much larger and less gelatinous than the British plant of Crouania attenuata. The Australian plant was later given specific status by J. Agardh (1876). Harvey's type material from TCD has been examined and agrees well with plants collected from American River Inlet, Kangaroo Is., South Australia which include both tetrasporic and carposporic plants.

Features in which this plant differs from the European C. attenuata are:

(1) Whorls of 4 whorl-branchlets (3 in C. attenuata).

(2) Presence of gland-cells (not recorded for C. attenuata).

(3) Lateral branches borne on basal cell of whorl-branchlet (C. attenuata reported as direct on axial cell (Feldmann-Mazoyer 1940)).

(4) Axial elongation continuing indefinitely after the initiation of the first procarp, and further procarps [illegible] initiated later.

(5) Extensive fusions between cells of the carposporophyte.

(6) Development of "bridge" filaments and protrusions from vegetative cells near the carposporophyte.

(7) Lateral gonimolobes developed first.

(8) Tetrasporangia tetrahedrally divided.(Feldmann-Mazoyer (1940) reports cruciate division in C. attenuata, but Harvey (1846-51) describes triangular division).

(9) Tetrasporangia borne on first and second cells of whorl-branchlets (first (basal) cell only in C. attenuata).

Two distinct plant forms are included as Ptilocladia australis. These characteristically are:

(1) Plants which are banded throughout in appearance and almost completely without axial rhizoidal cortication. This is the form represented in the original type material (Crouania australis (Harvey) J. Ag.).

(2) A denser form in which, in the lower parts of the plant, the banded appearance is lost through the development of an axial rhizoidal cortication. The rhizoidal filaments are borne from the basal cells of whorl-branchlets and loosely clothe the axis. Each filament is composed of elongate cells and outer filaments may bear short, horizontal projections towards the exterior.

Unfortunately no cystocarpic plants of the axially corticated form have been collected and, for the present, its classification must depend on vegetative features. Until details of its reproduction are known it seems best to regard it as a corticated variety (var. cortica) of Ptilocladia australis which species it resembles most closely.

The presence of axial cortication suggests relationship with P. vestita, but it differs from this species in having a lax habit without tendency to alternate distichous branching and whorl-branchlets which are basally horizontal to the axial cells while those of P. vestita are inserted at about 45° to the axis.

P. australis is recorded from calm-water areas, while P. vestita is more frequently found on rough coasts. Both forms of P. australis are recorded from Saunders Beach and American River Inlet, Kangaroo Is., South Australia. Individual collections have been of either one form or the other and may indicate response to local conditions at any one time.

PTILOCLADIA VESTITA (Harv,) comb. nov.

Crouania vestita Harvey 1854: 558; 1860: pl. 140. J.G. Agardh 1876: 86; 1879. t. II, figs. 8-9. De Toni 1897: 1419; De Toni and Forti 1922: 56. Lucas 1909: 51.

TYPE Locality: — Rottnest Is., Western Australia (Harvey, on Zostera).

HOLOTYPE: — TCD. Herbarium of Harvey, No. 338.

Harvey's specimens 486-B (TCD) also compares well with the type.

DISTRIBUTION: — Southern Australian — from Rottnest Is., Western Australia to Robe, South Australia and Tasmania.

(Fig. 10).

General Features: — Plant 2-5 (-8) cm in height, attached by a small holdfast. The thallus is terete, spongiose, completely non-slimy and pyramidal in outline. Branching may be irregular, but often is alternate-distichous with lateral branches arising from about every 4th cell of the axis. Occasionally branches occur in twos from the one side (Fig. 10A). Short lateral branches which are restricted in growth, occur between the major laterals.

Pyriform gland-cells containing various crystal-like inclusions are scattered, usually densely, over the thallus. They arise from the cells of the final branching order of whorl-branchlets and are thus terminal on the whorl-branchlets.

Structure of the Thallus.

(1) Form and Development of Main Branches: — Axial growth is monopodial and takes place by transverse divisions of a dome-shaped apical cell. Mature axial cells are about 1½ to twice as long as broad and measure about 80-100 x 50µ.

All lateral branches arise from the upper, outer end of the basal cells of whorl-branchlets (as in *P. australis*) and develop into a short chain of several axial cells before the development of whorl-branchlets commences.

(2) The Development and Structure of Whorl-branchlets: — Each axial cell bears a whorl of 4 whorl-branchlets which are themselves branched by successive whorls of cells as in *Ptilocladia australis*. They are, however, directed obliquely upward at an angle of about 45° to the axis, in contrast to those of *P. australis* which are horizontal at their base and upwardly projected at the tip.

Whorl-branchlets are spirally initiated from adjacent axial cells and develop as described for *P. australis*. When mature a whorl-branchlet measures about 200-300µ in length but may be longer or shorter in the basal and younger parts of the plant respectively. Cells of the whorl-branchlets become progressively smaller towards the exterior, and a short chain of 2-4 small cells (each about 10 x 5µ) terminates the final order of branching.

Axial Cortication: —

Rhizoidal cortication of the axis extends throughout all except the youngest parts of the thallus. The rhizoids arise from the lower side of the basal cell of the whorl-branchlets and project downward densely clothing the axis. In the lower part of the plant the rhizoids interweave with the whorl-branchlets which extend upward and downward parallel to the central axis (Fig. 10B). Each cell of the extensions of the whorl-branchlets bears a horizontal branch directed toward the exterior. The gelatinous sheath, which surrounds all cells of the thallus, becomes very thick in the lower parts of the plant.

The axial cortication is thus densely and firmly developed and gives rigidity to the thallus structure.

Tetrasporangia are borne, as in P. australis, from the outer end of the basal and second cells of the whorl-branchlets in the upper parts of the plant. Each tetrasporangium is sessile, spherical, 55-65µ diameter within a thick colourless sheath and divides tetrahedrally. Development of tetrasporangia is usually successive from each cell, although some cells appear to produce only one tetrasporangium.

Spermatangia: — Not recorded.

Development of Procarp and Carposporophyte: — Development of the procarp and carposporophyte is very similar to that in P. australis but differs in:

(1) Position of Procarp and carposporophyte: — After initiation of the procarp in place of a whorl-branchlet near the apex of a young lateral branch, only limited elongation of the branch axis takes place. Mature carposporophytes occur on short lateral branches which have an elongated apex developed beyond the mature carposporophyte (Fig. 10A, F). Usually only one procarp is formed but two, on non-adjacent axial cells (usually separated by one cell) are occasionally seen (Fig. 10C). Only one

carposporophyte occurs on each branch. At times further procarps are produced at wide intervals as the branch axis elongates (Fig. 10F) but in all cases observed these are abnormal in position in developing in place of the lower branch of the two developing from the outer end of the basal cell of a whorl-branchlet (Fig. 10G). Such procarps do not develop beyond a 4-celled carpogonial branch. This arrangement may indicate an intermediate phylogenetic stage between *Ptilocladia australis*, where carposporophytes are matured successively along an indeterminate branch, and *Ptilocladia pulchra* where the carposporophyte develops near the apex of a determinate branch.

(2) *Form of cells of carposporophyte*: -- As in *P. australis* complete fusions occur between all cells of the carposporophyte and the rounded axial cell. The process, which in *P. australis* marks the point of attachment of carpogonial branch to the residual-supporting cell, is seldom seen in this species.

(3) *Form of surrounding thallus cells*: — The basal cells of the whorl-branchlets borne on adjacent axial cells always form projections toward the carposporophyte, but no indication of their function is evident (Fig. 10E). An elongate filament grows down from the lower part of the axial cell immediately above that bearing the carposporophyte. This filament is made up of elongate cells and is occasionally branched. Its function is not known (Fig. 10E, F).

The maturing carposporophyte is protected by the surrounding whorl-branchlets, the cells of which elongate and curve to envelop the enlarging carposporangial groups.

Discussion: —

The plant closely resembles P. australis var. cortica in form but is distinct in certain reproductive as well as vegetative features. These differences are as follows: —

1. The thallus is firmer in form than is P. australis due in large part to the dense interwoven axial cortication of rhizoids and special extensions of the whorl-branchlets.

2. Shorter axial cells, approximately 2-2½ times as long as broad e.g. 350 x 180µ, so that whorls of branchlets are comparatively close together and completely cover the axis. There is no nodose or banded effect.

3. Branching commonly alternate-distichous with laterals from about every 4th cell of the axis. This character is usually clearly defined in some part of each plant, and the added rigidity of the plant form due to the specialization of the whorl-branchlets in the lower parts of the plant, tends to emphasize this feature. This branching habit is clearly shown in Harvey's type specimen.

4. Gland-cells scattered over the plant. In P. australis they have been found only at branch apices. This feature may vary with local conditions or seasonally, and insufficient observations have been made to clarify this point.

5. The carposporophyte matures on a branch of limited growth. In P. australis var. cortica all branches are indeterminate.

6. Lack of an elongate process on the outer end of the residual supporting cell at the point of attachment of the old carpogonial branch.

7. Projections from basal cells of surrounding whorl-branchlets toward the carposporophyte and an elongate filament from the lower part of the axial cell above that bearing the carposporophyte.

Short lateral branches of limited growth are also found in P. pulchra and P. agardhiana and also in Euptilocladia spp.

The axial cortication in Euptilocladia also includes a specialised arrangement of whorl-branchlets in the lower and central parts of the plant but, unlike P. vestita, there is no modification in the growth pattern of the whorl-branchlets involved, and elongation parallel to the axis is due to changes in orientation of the cells of the whorl-branchlets.

PTILOCLADIA AGARDHIANA (Harv.) comb. nov.

Wrangelia agardhiana Harvey 1854: 545.

Crouania agardhiana (Harv.) Harvey 1863: pl. 256, J. Agardh 1876: 87. J.B. Wilson 1892: 185.

Muellerena agardhiana (Harv.) De Toni 1897: 1389; 1924: 490. Lucas 1909: 50. Lucas and Perrin 1947: 345.

TYPE Locality: — King George's Sound, Western Aus. Dredged from 6-7 fathoms.

TYPE: — TCD, Herbarium of Harvey, No. 487 (Lectotype No. 40, TCD, replaces the original specimen).

<u>DISTRIBUTION</u>: — From King George's Sound, Western Australia to Port Phillip Heads, Victoria.

(Fig. 11 A - E).

<u>General Features</u>: —

<u>Ptilocladia agardhiana</u> is very similar to <u>P. pulchra</u> and can only be separated on details of thallus structure. The plant will therefore be described by comparison with <u>P. pulchra</u>. In general appearance <u>P. agardhiana</u> is a smaller plant lacking the distichous branching habit often seen in <u>P. pulchra</u>. Short, simple, horizontal lateral branches which are limited in growth are scattered irregularly over the thallus and give the plant a softly spiny appearance. In herbarium specimens apparent distichous arrangement of lateral branches is usually due to flattening of the plant in mounting.

The development of tetrasporangia (Fig. 11E) and carposporangia is similar in both species. In <u>P. agardhiana</u> the short branches which bear the carposporophytes are, however, often a little longer with more pointed apices than those of <u>P. pulchra</u>, indicating that axial elongation after initiation of the carposporophyte may continue slightly longer in <u>P. agardhiana</u>. Terminal hairs on whorl-branchlets have not been found in <u>P. agardhiana</u>. Gland-cells are lacking in both species, but hexagonal and diamond-shaped crystal-like inclusions occur in cells of the axes of young branches (Fig. 11A).

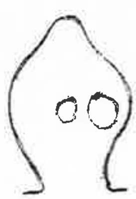
The main differences which separate the two species may be summarised as follows: -

Ptilocladia pulchra.	Ptilocladia agardhiana.
1. Plant habit -	
(a) Plant large (10-30 cm. high) and robust.	Plant usually smaller (5-20 cms.) and less robust.
(b) Axes terete, cartilaginous and firm in most parts due to well developed axial cortication of rhizoids embedded in a gelatinous matrix.	Similar, but laxer in habit, with similar but less strongly developed axial cortication.
(c) Terminal hairs on whorl-branchlets usually abundant.	Terminal hairs on whorl-branchlets lacking.
2. Branching -	
(a) Main axes with alternate-distichous development of unlimited laterals from every 4th cell to give a pyramidal form.	All unlimited laterals irregularly placed, lax and elongate. No pyramidal form.
(b) Short lateral branches of limited growth with tendency to distichous arrangement.	Numerous short, lateral branches of limited growth, irregularly scattered, not distichous, and horizontal to axis giving spiky appearance to plant.
(c) Whorl-branchlets in whorls of 4 from each axial cell. Each whorl-branchlet itself branched by apparent di- (or tri-) chotomies of cells from the outer end of each cell.	Whorl-branchlets similar but with cells of the apparent di- (or tri-) chotomies more widely diverging.

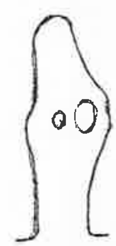
Ptilocladia pulchra.	Ptilocladia agardhiana.

3. Branches bearing Carposporophytes -

(a) **Ptilocladia pulchra.** Short branch usually with rounded apex and very short section of unexpanded branch below the carposporophyte.



Ptilocladia agardhiana. Comparatively longer branch with more elongate apex and often with a longer section of unexpanded branch below the carposporophyte.



(b) **Ptilocladia pulchra.** Line of axis of short branch bearing carposporophyte only slightly bent to one side as carposporophyte matures.

Ptilocladia agardhiana. Axis of short branch bearing carposporophyte distinctly bent with development of carposporophyte.

Spermatangia have been recorded for P. agardhiana. Groups of four spermatangial mother-cells are borne on the outer end of the terminal cells of whorl-branchlets which in this case do not develop a terminal chain of cells (Fig. 11C). Spermatangial cells are 5-6μ in length, and all those observed stained densely without apparent concentration of the protoplast in any one region of the cell.

Discussion: —

The close similarity of thallus structure in P. agardhiana and P. pulchra indicates a probable close phylogenetic relationship. This will be discussed in detail later. It seems probable, however, that the lack of distichous branching and the more elongate short lateral fertile branch in which growth is continued longer than in P. pulchra, are indications of a slightly more primitive thallus form. It is clear that this species must remain taxonomically close to P. pulchra and must be placed in the genus Ptilocladia.

PTILOCLADIA PULCHRA Sonder 1845: 52; 1846: 170.

Crouania insignis Harvey 1860: 331, pl. 193B. J. Agardh 1876: 87. Wilson 1892: 185.

Muellerena ? insignis De Toni 1897: 1389; 1924: 490. Lucas 1909: 50; 1929a: 25. Lucas and Perrin 1947: 346.

Gulsoniopsis insignis (Harv.) Hommersand 1963: 167.

TYPE Locality: — Swan River (near Fremantle), Western Australia.

HOLOTYPE: — MEL, 8445. Preiss 2549.

DISTRIBUTION: — Widely distributed along southern Australian coasts from Esperance, W.A., to Queenscliff, Victoria, and on the northern coast of Tasmania.

(Figs. 11. F-S, 12).

General Features: — The plant is usually about 10-15 cm. high but may occasionally reach 30 cm. It often has blue-green algae such as Calothrix spp. epiphytic upon it. The thallus is spongiose, with a terete axis and is more or less distichously and alternately branched, but occasionally with pairs of lateral branches developed on the same side. Sometimes short alternately-arranged lateral branches of limited growth occur between the longer laterals, and further irregularly placed indeterminate laterals may develop at any time and may to some extent mask the alternate-distichous branching pattern. Long main axes often arise from near the base of the plant and with the development of lateral branches form a somewhat pyramidal branch system.

Whorl-branchlets are produced in whorls from each cell of the axis and completely cover the upper branches. In lower parts of the plant a rather cartilaginous axis, corticated with rhizoids, is exposed between the whorl-branchlets.

Gland-cells such as are found in P. vestita and P. australis are not developed. Occasional terminal cells of the whorl-branchlets are, however, somewhat larger and more rounded than others. These cells do not bear hairs and are reminiscent in form of the gland-cells of other species of Ptilocladia (Fig. 11M).

Crystal-like inclusions, similar to those found in the gland-cells of P. vestita and P. australis occur in the mature axial cells of the younger parts of the thallus. These occur also in P. agardhiana and possibly represent a form of either storage or waste disposal. Protein-crystals similar in form to these inclusions are described by Feldmann-Mazoyer (1940, p. 64) for several species of Ceramiaceae.

Structure of Thallus: —

(1) Form and Development of Main Branches: — Elongation of the axes takes place by transverse divisions of a dome-shaped apical cell and a short chain of several cells is formed before the initiation of whorl-branchlets.

Lateral branches, both limited and unlimited in growth, are borne on the outer ends of the basal cells of whorl-branchlets (Fig. 11G-I). Hommersand (1963, p. 171, fig. 1a) has shown that lateral branches arise from the basal cell of the first-formed branchlet of a whorl on each 4th axial cell. Thus, if initiation of whorl-branchlets follows a spiral rotation of 45° on adjacent axial cells, an alternate-distichous arrangement of lateral branches will result. The resultant pattern of branching is not consistent and suggests that variations often occur in the basic pattern of initiation suggested by Hommersand. Later irregularly placed indeterminate lateral branches are apparently formed from the basal cell of any whorl-branchlet, as also occurs with the short determinate lateral branches, and in particular, those which bear the carposporophtes in female plants.

(2) Development and structure of Whorl-branchlets: — Each cell of the axis bears from its upper part a whorl of 4, evenly-spaced, horizontal whorl-branchlets (400µ in length).

The initiation of whorl-branchlets has been described by Hommersand (1963, p. 170) and follows the same pattern in apices of both main and lateral branch axes. When the branch is actively growing, initiation of whorl-branchlets occurs several cells below the apical cell, but if growth is slowed down, they may occur on the second or third cell. Development of the whorl-branchlets is however rapid and the growing apex of the axis is covered and protected by the young immature whorl-branchlets. The second whorl-branchlet is initiated opposite the first, the third is formed between the first and second, and the fourth is produced opposite the third. A 45° rotation occurs in arrangement of the whorls on adjacent cells. This rotation may occur to the right or to the left but is consistent in each branch and results in the mature whorls appearing superimposed on alternate cells. This arrangement is marked in lower parts of the plant, where axial cells are comparatively enlarged and the whorls sufficiently separated to give an annular appearance to the thallus. In still older parts, each individual branchlet of the whorl is identifiable as a discrete, bushy tuft, clearly showing the relative arrangement of the whorls (Fig. 12B).

Each whorl-branchlet is itself branched apparently di- or tri-chotomously from the distal end of each cell for 5-7 orders.

The development of the branching is not, however, strictly di-(or tri-) chotomous as the cells are formed successively (Fig. 11 N-S).

The cells of the whorl-branchlets become progressively smaller toward the exterior, terminating in a short chain several cells in length. There is often a terminal hair, 100-600µ in length, which has a small basal nodule and an elongate swollen tip (Fig. 11M). Hommersand (1963, p. 171) stated that hairs were deciduous in the lower parts of the plant. No evidence has been seen for this, as observations on fresh material of this species show that hairs are either present in all parts of the plant, or completely lacking. This suggests that hairs may be deciduous from the whole plant at certain periods, or, which seems more likely, that some plants do not develop hairs.

Axial Cortication: — Axial cortication occurs by means of branched rhizoids which arise from the lower side of the basal cells of whorl-branchlets and grow downward densely covering the axes in the lower parts of the plant. Only the young branch tips are completely without axial cortication.

A cross-section of the older thallus shows two layers of axial cortication, (a) an inner single layer of larger cells, and (b) an outer layer (or layers) of small rhizoidal cells with scattered, horizontal, simple or branched, outward projections arising from them (Fig. 11L). These layers are formed from elongation and branching of the rhizoidal filaments. The first cell of the filament bears three branches (Figs. 11 J,K) each of which grows downward and bears further outwardly placed branches of smaller elongate cells (Fig. 11K). The upper larger cells from the inner layer of cortication and the outer, finer filament-like branches intertwine and form the outer cortical layer.

The cortical cells, particularly those of the inner layer together with the basal cells of the whorl-branchlets become embedded in a firm gelatinous matrix which contributes to the apparent cellular structure of the inner layer and also gives the mature thallus a cartilaginous texture. This form of axial cortication is also found in Muellerena wattsii and Dasyphila preissii of the Dasyphileae.

Tetrasporangia: — Tetrasporangia are scattered over the plant but occur more abundantly on the younger branches (Fig. 12B). Tetrasporangia are initiated as described by Hommersand (1963, p. 175) and are produced successively on the 2nd, 3rd and sometimes other outer cells of the whorl-branchlets. Mature sporangia are spherical or slightly ovoid and have a diameter of 60-70µ within the thick gelatinous sheath (Fig. 12A). All are distinctly tetrahedrally divided and arranged and there seems no evidence for Hommersand's statement (1963, p. 175) that, although simultaneously formed, the tetraspores are cruciately arranged.

Spermatangia: — Not recorded.

Development of the Procarp and Carposporophyte: — Carpogonial branches are borne 3-7 cells below the apex of short lateral branches of limited growth which are scattered irregularly (not distichously) over the thallus (Fig. 11F) as are the short lateral branches in non-carposporic plants. None of these branches has been seen to arise from a "supra-basal segment" as recorded by Hommersand (1963, p. 173), but are formed in the usual position for a lateral branch on the outer end of the basal cell of a whorl-branchlet. The basal cell of a whorl-branchlet may occasionally bear a trichotomy (as usually borne from the second cell) rather than the usual dichotomy of cells and it is probable that this condition was taken by Hommersand to represent a supra-basal cell.

Initiation of the carpogonial branch results in an immediate decrease in axial development, as the cell immediately above that bearing the carpogonial branch is always comparatively small (Fig. 12D,E). Axial growth must continue, however, for some time as the mature carposporophytes are produced some distance below the apex and a series of several carpogonial branches may occur along the axis. Some of these may be abnormal in structure. Only one carposporophyte matures on each of the branches which are much shorter and with a more rounded apex than comparable fertile branches in Ptilocladia vestita (Fig. 11F). Carposporangial plants may be readily recognised by their nodose appearance due to the prolific production of short fertile branches. No justification has been found for Hommersand's statement (1963, p. 173) that the formation of these branches tends to spread progressively downward toward the main axes and the base of the plant.

Development of the procarp is essentially similar to that in P. vestita. A rounded supporting cell is formed in place of the initial of a whorl-branchlet. It is densely protoplasmic and is readily recognised by its larger size and almost spherical form (Fig. 12C). The carpogonial branch initial is cut off from the outer side of the supporting cell (Fig. 12D) and divides rapidly by almost simultaneous divisions to give the four cells of the carpogonial branch (Fig. 12E). The cells so formed expand into a curved carpogonial branch (Fig. 12F). As in P. vestita the division between the third cell of the carpogonial branch and the carpogonium is normally at right angles to the transverse divisions dividing the other cells of the carpogonial branch. The trichogyne develops terminally from the carpogonium. It is very long (to 350µ) and has a slightly expanded tip (Fig. 12F). The sequence of cell development of the carpogonial branch and the diagrams given by Hommersand (1963, p. 173, Figs. 2d, e, f & g) do not agree with observations made on freshly collected material e.g. the trichogyne development shown by him (Figure 2 g) suggests a form representative of an abnormal carpogonial branch destined never to mature; his figure (Fig. 2i) of a "senescent carpogonial branch" is actually much closer to what is seen during the normal expansion of a young carpogonial branch.

After fertilization the trichogyne disappears rapidly, an auxiliary cell is cut off from the upper side of the supporting cell and a protrusion develops toward it from the lower inner part of the carpogonium (Fig. 12G). A division occurs separating this protuberance to form a connecting cell (Fig. 12G). Fusion between the carpogonium and auxiliary cell apparently occurs by means of this connecting cell, and is immediately followed by transverse division of the auxiliary cell to form a lower foot-cell and an upper central cell (Fig. 12H). A small protuberance on the outer end of the foot-cell indicates the position of fusion with the connecting cell.

Broadening of the connections between the 3rd and 4th cells of the carpogonial branch with subsequent fusion between the 3rd cell and the auxiliary cell, as presumed by Hommersand (1963, p. 175) have not been observed. Break down of the lower cells of the carpogonial branch commences soon after fertilization and it is probable that an early stage of dis-integration of the protoplasm of the first cell of the carpogonial branch accounts for the "spine-like emergences" reported by Hommersand (1963, p. 174) for this cell.

The central cell elongates transversely and produces two lateral gonimolobes, one after the other. As the first gonimolobe develops, fusions between the axial cell and basal cells of the carposporophyte become evident (Fig. 12I). Finally the residual supporting cell forms a broad connection between the axial cell and the central cell of the carposporophyte, while the foot cell loses its structure and becomes insignificant (Fig. 12J).

Subsequently, as the two lateral groups of carposporangia near maturity, the protoplast of the old supporting cell often appears to break down, and possibly in such cases no further carposporangial buds are able to mature. Transverse and later longitudinal divisions of initials form chains of carposporangia (Fig. 12 K-M).

No special involucre is formed but the cells of the surrounding whorl-branchlets become somewhat elongated and form a protection around the developing carposporophyte.

Discussion: —

Abundant fresh material, both growing and drift, has been available for this study and has allowed revision and extension of Hommersand's recent work (1963). Sonder's type specimen of Ptilocladia pulchra (MEL) has been found to represent this species and being of an earlier collection, must replace all later synonomy.

Sonder's specimen of Dasya crouanioides, MEL, has also been examined and it is quite clear that the two species are distinct. Dasya crouanioides is probably synonomous with the poorly known species Crouania gracilis. In first describing the plant Sonder (1845) referred to anastomising of the ramelli in the central cortical region; J. Agardh (1851) also mentioned this feature. Harvey emphasized the close resemblance of the plant to the genus Crouania and considered that it probably differed from C. vestita in specific characters only. He left it, however, as a distinct genus on the basis of the anastomising ramelli recorded by both Sonder and J. Agardh, although he himself had not observed the character. Axial cortication of the plants has now been carefully examined and, although the whorl-branchlets and the axial rhizoids become closely pressed together no true anastomising has been observed.

J. Agardh (1876) also mentions the outer cortical region of horizontal free filaments which he considers an indication that the plant may be intermediate in position between Dasyphila and Haloplegma. In this instance he probably refers to Euptilocladia spongiosa which has been confused with Ptilocladia pulchra. In this species the free filaments referred to by Agardh are doubtlessly the terminal filaments of the whorl-branchlets. In Dasyphila the horizontal projecting filaments are outgrowths from the rhizoidal cortication of the axis and are thus distinct in origin and do not indicate any relationship between the species.

The taxonomic position and phylogenetic relationships of this plant will be further discussed later.

EUPTILOCLADIA nov. gen.

Thallus erectus, ad 15 cm. altus. Axes planati, filamentis rhizoideis dense corticata. E quoque cellula 4 vortico-ramuli, vorticibus sequentibus cellularum ramosi, filamentis 2-10 cellulae longis terminati. Ramificatio alternato-disticha ramis et indeterminatis et determinatis. Tetrasporangia tetrahedralia in thallo superiore sessilia in cellulis et centralibus et exterioribus vortico-ramulorum. Spermatangia ignoti. Carposporophyti ad cacumina ramorum brevium lateralium positi.

The genus Euptilocladia is distinct in having a flattened, highly organized thallus structure. The genus is defined by:

(i) A monopodial axis bearing whorls of 4 branchlets from each axial cell.

(ii) Whorl-branchlets in opposite pairs and, when mature, with one pair longer than the other thus forming the flattened thallus.

(iii) Branching alternate-distichous from the edges of the flattened thallus. Numerous short determinate laterals occur between the indeterminate lateral branches.

(iv) Axes densely corticated with rhizoidal filaments arising from inner to central cells of the whorl-branchlets.

(v) Carposporophytes produced near the apices of short determinate lateral branches.

The organized thallus structure is probably more highly-advanced than that of other genera of the Crouanieae. Its possible phylogenetic relationships are discussed in Section IX.

TYPE species: — Euptilocladia spongiosa n. sp.

Key to southern Australian species of Euptilocladia

(2 species only)

1. Axes enclosed by closely packed apices of terminal filaments of whorl-branchlets. Annular banding not obvious. Mature tetrasporangia 45-60µ... ... ... E. spongiosa

1. Axes covered by upwardly directed partly overlapping terminal filaments of whorl-branchlets. Annular banding at nodes. Mature tetrasporangia 80-100µ diam... ... ...E. villosa

EUPTILOCLADIA SPONGIOSA n. sp.

Ptilocladia pulchra sensu J. Agardh 1851: 112; 1876: 89. De Toni 1897-1903: 1424; 1924: 501. Harvey 1854: 557; 1862: pl. 209. Kutzing 1849: 674; 1862: pl. 65. Lucas 1909: 52; 1929: 52. Reinbold 1897: 61. Wilson 1892: 185 (non Sonder).

Thallus usque ad 15 cm. altus. Axes planati, 1-4 mm. latus, filamentis rhizoideis dense corticati; quaeque cellula 4 vortico-ramulis instructa. Vertico-ramuli filamentis 3-8 cellulae longis terminati. Ramificatio alternate-disticha ramis et indeterminatis et determinatis. Tetrasporangia, 45-55μ diametro, tetrahedralia in thallo superiore sessilia in cellulis et centralibus et exterioribus vortico-ramulorum. Spermatangia ignoti. Carposporophyti ad cacumina ramorum brevium lateralium positi.

TYPE Locality: — Robe, South Aust.

HOLOTYPE: — AD, A 27,925.

DISTRIBUTION: — Common on southern Australian coasts from Fremantle, Western Australia, to Port Phillip Heads, Victoria. Records are of drift material presumably washed up from deeper waters.

(Fig. 13B-J; 14 A-H; Plate 3).

General Features: — The plant is attached by a small holdfast and grows to about 15 cm. high. The thallus is spongy in texture with flattened axes which vary in width from about 1-4 mm in the central region of the thallus. Branching is markedly alternate-distichous from the edges of the axis, with numerous short often simple branches occurring between the longer laterals, and which, in the female plants, bear the carposporophytes (Fig. 13B). The axis is completely obscured by a dense, rhizoidal cortication except in the extreme apices of the branches, and by the whorls of branchlets developed from each axial cell. In the lower parts of the plant these whorl-branchlets elongate parallel to the axis and further contribute to the felt-like axial cortication. All cells of the thallus are enveloped in a thick, firm colourless, gelatinous sheath.

Structure of the thallus: —

(1) Form and Development of Main Branches — Each branch consists of an articulate central axis made up of cells 1-2 times as long as broad, each of which bears a whorl of four branchlets. Elongation of the axis takes place by successive transverse divisions of a dome-shaped apical cell and cell formation is followed almost immediately by initiation of the whorl-branchlets, which may sometimes occur even on the sub-apical cell (Fig. 13E). The growing apex is covered and protected by the developing whorls.

Branch tips above the region of rhizoidal cortication are terete, and the short, simple lateral branches which occur between the fully-developed laterals, always remain terete without rhizoidal cortication. These short laterals are limited in growth but vary in length from about 1-5 mm. even upon the same plant. Each cell of the axis may produce a branch to the right or left alternately and short branches may occur from any cell which does not bear a long, indeterminate branch. Development of the short branches is, however, very variable and in some plants they are much more abundant than in others. Their initiation will be described with reference to the form of the whorl-branchlets.

(2) The Development and Structure of Whorl-branchlets: — Whorl-branchlets of each whorl are initiated successively on the axial cell with the second branch formed opposite the first. The apparent tri- and di-chotomies, which make up the orders of branching of each whorl-branchlet, are formed by successive development and cutting off of elongate protrusions from the distal end of each cell. Hence each order of branching is not a true di- (or tri-) chotomy in origin. The order of formation of cells of the branch is not consistent, and once a cell is formed it may continue to cut off further outward cells before the apparent di- or tri-chotomies of previous cell orders are complete.

The structure of a single whorl-branchlet taken from the terete upper part of a branch (Fig. 13G) is diagrammatically represented in Fig. 13F. The basal cell (1), attached to the axial cell (A), is almost as long as it is broad and bears on its outer end an apparent dichotomy of two cells (2). Each of these bears an apparent trichotomy (cells 3) followed by 3-6 further apparent dichotomies from the outer end of each successive cell (4, 5, 6). Occasionally trichotomies occur in place of one or more of these outer dichotomies. Each cell of the terminal dichotomy divides transversely to form a short chain (about 100µ in length) of 3-8 cells which are more densely pigmented than the inner cells. Each cell of the chain is 4-7µ in diameter and the short filament so formed is curved slightly upward toward the branch apex. These outer filaments form a dense covering over the thallus. No hairs on the terminal cells of the whorl-branchlets have been observed in this species.

The whorl-branchlets are arranged with one directly above another on adjacent axial cells and flattening of the thallus is due to the elongation of two opposite whorl-branchlets in the same plane (Fig. 13H, branches 1 and 2). Fig. 13I represents a transverse section of a whorl of branchlets developed on one axial cell of a flattened branch. "A" represents the axial cell which bears the evenly-spaced whorl of four whorl-branchlets (1, 2, 3, 4), each having a basal cell, "B." Other cells have been shown by dashes and, in most cases, further branching of only one member of each tri- or di-chotomy has been shown.

The two opposite branches, 3 & 4, form the shorter axis and are branched as in the terete axis (Fig. 13, F,G). Apart from a general enlargement of the inner cells of the branch and an increase in thickness of the gelatinous sheath, these two branches retain their early form. Branches 1 & 2 however become specialized in form and alternate in position on successive axial cells. The alternating sequence in position of branch 2, which bears the lateral branch initial, accounts for the alternately-distichous arrangement of all lateral branches. These lateral branches, although usually initiated, may be inhibited in development (limited in growth) and do not always protrude as visible external branches.

Branch 1 differs from branches 3 & 4 by the insertion of one (occasionally 2) additional trichotomies of cells (e.g. cells, 4) from the outer ends of cells of the first trichotomy (cell 3). One cell of each trichotomy (cells 3, 4) becomes directed outwards parallel to the plane of branch elongation (and thallus flattening) while the other two cells become laterally orientated. Further orders of branching follow the pattern of dichotomies (or trichotomies) as in branches 3 & 4 and terminate similarly in a short curved filament.

The structure of branch 2 bearing a lateral branch, is shown in Fig. 13J. The basal cell, corresponding to cell 1 is more elongate than basal cells of other whorl-branchlets and bears a trichotomy of 3 normally branched segments. A further cell (2) is borne on the upper outer end of cell 1, and is probably the initial cell of the new branch. This cell bears a trichotomy, similar to cell 1, and again a further cell (3) from the apex. The following cells (3, 4, 5,.....) are similar to axial cells in being joined end to end and each bearing a whorl of 4 whorl-branchlets.

It has not been possible to account for the formation of a branch of the form described in Fig. 13H (2) and Fig. 13J, directly from the simple form of whorl-branchlet shown in Figs. 13, F and G.

Further examination of freshly growing branch apices is necessary to clarify this structure and to check whether there is any difference in the initiation and development of long lateral branches and those of limited growth which remain terete.

Axial cortication: — A dense rhizoidal cortication clothes the axes in all parts of the plant except the branch apices and short determinate lateral branches.

Rhizoidal filaments arise from the lower side of the inner and central cells of whorl-branchlets with the first filaments developing on the basal cells (Fig. 14, A-C).

Mature rhizoids are very long, sparingly branched and composed of elongate cells of somewhat varying lengths. The inner-most rhizoids may be 70μ in diameter, (Fig. 14C). The rhizoids penetrate between the cells of the whorl-branchlets which are thus held firmly in position, and form a dense interlacing mat around the axis.

In mature parts of the thallus whorl-branchlets contribute considerably to the density of the felt-like covering of the thallus. One cell of each inner apparent di- or tri-chotomy becomes aligned more or less parallel to the central axis (Fig. 14C) so that the whorl-branchlets extend both upward and downward and overlap one with another. Other cells of the di- and tri-chotomies involved are directed outward and maintain the apparent whorls of branchlets.

Development of Tetrasporangia: — Tetrasporangia at various stages of maturity are scattered on the upper branches of the plant but are not restricted to younger apices only (Fig. 13D). They are borne on the several outer cells of the central region of the whorl-branchlets (Fig. 13C) and are initiated as protrusions usually from the outer, upper part of the cell. Each tetrasporangium is sessile, and when mature is spherical and comparatively small, 45-55μ diam. within the thick gelatinous sheath (about 20μ in thickness) and divides tetrahedrally. More than one tetrasporangium has not been seen on any one cell at one time.

Development of Procarp and Carposporophyte: — Carposporophytes are developed in short, terete lateral branches which occur along the edges of the flattened branches (Fig. 13B) and the development of both carpogonial bbanches and of the carposporophyte follows the general pattern found in genera of the Crouanieae. Although several carpogonial branches may be initiated near the apex of a branch only one produces a carposporophyte and mature carposporangia.

The carpogonial branch is produced on the outer part of a supporting cell which replaces the initial of a whorl-branchlet on an axial cell several cells below the branch apex. Only one occurs on any one axial cell (Fig. 14D). The carpogonial branch is 4-celled and curved upward (Fig. 14 E-G).

After fertilization an auxiliary cell, cut off from the enlarged upper portion of the supporting cell, divides, presumably after receiving the diploid nucleus from the carpogonium, into a lower foot cell and a large laterally elongate central cell (Fig. 14H). The first gonimolobes are lateral and develop one after the other from opposite ends of the central cell. These gonimolobe initials are large and each cuts off several cells all of which remain sterile and somewhat larger than the carposporangia which develop from them (Fig. 14H). Several further gonimolobes may be initiated nearer the summit of the central cell and several carpospore groups may finally mature.

Mature carpospores are angular and usually somewhat elongate (30-45μ x 20-30μ). During development the spores tend to be orientated with this longer axis parallel to the long axis of the initial bud from which the group develops.

No special involucre is formed and the maturing carposporophyte is protected by the surrounding whorl-branchlets which elongate to cover the enlarging carpospore groups.

<u>Spermatangia</u>: — Not recorded.

Discussion: —

Tetrasporic plants are occasionally found, but, although the plant occurs commonly, carposporangial plants are rare and no collection of spermatangial plants has been recorded.

Sonder's type ~~specimen~~ of Ptilocladia pulchra (MEL) has been examined. It is a carposporangial plant although this fact was not noted by Sonder in his original description (1845). No further material of Sonder's type has been located in any other herbarium.

The specimen is without doubt a plant of Gulsoniopsis insignis Hommersand (1963) and the two epiphets ~~must~~ are therefore ~~be~~ synonymous. Ptilocladia pulchra (1845) ~~must have~~ has priority. ~~over, and must replace, the newer binomial Gulsoniopsis insignis (1963).~~

The plant herein described ~~must~~ therefore becomes the type ~~species~~ of a new genus (Euptilocladia).

One plant of Euptilocladia spongiosa (MEL 8448) collected from Pt. Phillip Heads by J.B. Wilson bears the label "Ptilocladia pulchra, forma teretiuscula J. Agardh" indicating that Agardh may have recognized two plant forms and was aware that Sonder's type was not identical with this plant.

EUPTILOCLADIA VILLOSA n. sp.

Thallus usque ad 15 cm altus. Axes planati, filamentis rhizoideis dense corticati; quaeque cellula 4 vortico-ramulis instructa. Vortico-ramuli filamentis curavto-adscendentibus 2-10 cellulae longis terminati. Ramificatio alternato-disticha ramis et indeterminatis et determinatis. Tetrasporangia tetrahedralia in thallo superiore sessilia in cellulis et centralibus et exterioribus vertico-ramulorum. Spermatangia et carposporophyti ignoti.

TYPE Locality: — Robe, South Aust.

// HOLOTYPE: — AD, A 29,282. date ?

DISTRIBUTION: — Southern and western coasts of Kangaroo Island, Middleton and Robe, South Australia.

(Fig. 14 I - P; Plate 4)

General Features: — The plant is about 15 cm high and is attached by a small holdfast. The thallus is spongy in texture with flattened branches and a dense rhizoidal cortication covering the central axis. Branching of the thallus is alternate-distichous from the edges of the axes with both long, flattened laterals which are themselves branched, and short, usually unbranched, terete laterals between them. These short branches can be produced alternately to the right or left from each axial cell (except those which bear long laterals) and are usually most abundant in the central part of the plant. Terminal filaments developed on the whorl-branchlets are curved upward and form a loose outer filamentous cover to the thallus (Fig. 14I). All cells of the thallus are enveloped by a thick colourless gelatinous sheath.

Structure of Thallus: --

(1) Form of Main branches: — The central axis is articulate with cells about twice as long as broad and each bearing an evenly-spaced whorl of four whorl-branchlets from the upper part of the cell. Axial elongation takes place by means of transverse divisions of a dome-shaped apical cell and follows the same pattern as described for Euptilocladia spongiosa. Initials of whorl-branchlets develop quickly and the young branchlets cover and protect the growing apex.

(2) Organization of Whorl-branchlets: — Whorl-branchlets of this species are similar in form and development to those previously described for E. spongiosa. In the upper, terete parts of the thallus, each axial cell bears a whorl of 4 equal branchlets (Fig. 14J). Flattening of the thallus occurs exactly as in E. spongiosa by the modification in form of two opposite whorl-branchlets. The apparent di- and tri-chotomies which form the orders of branching of these whorl-branchlets are developed from successive protrusions from the upper part of each cell which becomes cut off to form a cell of the next order. Lateral branches as in E. spongiosa, are borne on the basal cells of the longer whorl-branchlets (Fig. 14J - lateral branch developed at commencement of thallus flattening). Terminal filaments on whorl-branchlets vary considerably in length. In the upper parts of the plant they are usually 2-5 cells long and 60-100μ in length, but in more mature parts of the thallus they may be 6-10 cells long. Each cell is longer than broad and measures about 6-12 x 10-18μ. Occasional terminal hairs are borne on the final cell of the filament.

Axial Cortication: — Rhizoidal filaments commence to develop near the branch apices and elongate to form a dense mat interlacing between the whorl-branchlets and covering most parts of the thallus. Rhizoids are multicellular, formed of elongate cells and simply (sometimes appearing dichotomously) branched. They arise from the lower surface of the inner cells of the whorl-branchlets and develop first on the basal cell.

Whorl-branchlets elongate upward and downward in a plane parallel to the central axis as shown for E. spongiosa and contribute to the density of axial covering and to the firm sponginess of the thallus.

All terete parts of the plant (short lateral branches and apices of the long laterals) are almost without rhizoidal cortication so that the whorls of branchlets are evident.

Tetrasporangia: — Tetrasporangia are borne on the central and outer cells of whorl-branchlets and are scattered, at various stages of development, irregularly over the upper parts of the plant. They are most abundant in the younger branches (Fig. 14I). Young tetrasporangia are sessile and pear-shaped but become spherical and finally large (80-100μ diam) within a thick gelatinous sheath and divide tetrahedrally (Fig. 14K-P).

Several sporangia may be developed successively from each cell and often a second (Fig. 14L-O), or even a third (Fig. 14P), bud appears to develop within an old tetrasporangial sheath (or sheathes). When this occurs the first formed sheath is the largest and may indicate that the later formed tetrasporangia are smaller than those previously developed.

Carposporangial and Spermatangial Plants: — Not recorded.

Discussion: —

The plant is known only from the rough south and west coasts of Kangaroo Island, and from Robe, South Australia, and has been collected only as drift material presumably from deeper water. Until the present time it has been included with *Euptilocladia spongiosa* n. sp, but is clearly distinct from this species in thallus form and size of sporangia.

by whom?

Euptilocladia spongiosa and E. villosa agree in generic characters. These include in particular, the flattened, spongiose form of the thallus, arrangement and development of both lateral branches and whorl-branchlets, axial cortication and position of tetrasporangia. Carpospore development cannot be compared until fertile material of E. villosa has been investigated. E. villosa differs, however, from E. spongiosa in the following features:

(1) There is commonly a more prolific development of short terete lateral branches between the long laterals particularly in the central parts of the plant.

(2) Terminal filaments of whorl-branchlets are comparatively longer and composed of larger cells more loosely arranged allowing a more obvious upward curvature. In E. spongiosa the thallus is covered by a cellular-like sheath formed from the closely-fitting terminal cells of the filaments whereas in E. villosa the filamentous structure is clearly distinguishable in the lax, upwardly curved arrangement. Short branches and apices show a nodal banded appearance marking the position of the whorl-branchlets.

(3) Rhizoids, which form the axial cortication, are rather shorter and more branched than in E. spongiosa. Fewer are developed in terete parts of the plant again allowing the individual whorls of branchlets to be seen more clearly.

(4) Terminal hairs on the whorl-branchlets may occur in E. villosa. These have not been observed in E. spongiosa, although many more plants have been examined.

(5) There is a distinct difference in size of mature tetrasporangia between the two species. In E. spongiosa they are small, 45-55µ, diameter while in E. villosa they are comparatively large 80-100µ diameter. In E. villosa the sporangia are more concentrated on the young lateral branches in which the whorls become separated as they mature. In E. spongiosa, however, the sporangia tend to occur more prolifically on the flattened parts of the branch tips where they appear embedded in the outer thallus structure.

The form and arrangement of terminal filaments of the whorl-branchlets and the larger size of the tetrasporangia are consistent features which readily distinguish the two plants as separate species.

GULSONIA Harvey.

Gulsonia was described by Harvey (1855) as a monotypic genus based on Gulsonia annulata from Phillip Is., Victoria. Harvey placed it in Cryptonemiaceae where it remained until J. Agardh (1876) transferred it to Ceramiaceae because he recognized similarities with Crouania. Schmitz (1889) placed it in the tribe Crouanieae of the Ceramiaceae. After examining cystocarps J. Agardh (1894, 1897) considered it to have affinities with Wrangelia while Schmitz and Hauptfleisch (1897) and Fritsch (1945) placed it close to Batrachospermaceae. It was finally described in the Ceramiaceae, tribe Crouanieae, by Wollaston and Womersley (1959). Its classification and phylogenetic relationships are further discussed in Section VIII.

TYPE species: — Gulsonia annulata Harvey.

GULSONIA ANNULATA. Harvey.

Harvey 1855: 334; 1860: 320 , pl. 193A; 1863: Synop: 614. Agardh, J.G., 1876: 88; 1894: 122, pl. 2, fig. 13; 1897: 56. De Toni, ~~G.B.~~, 1897: IV, 66; 1924, VI: 151. Feldmann-Mazoyer 1940: 279. Kuetzing 1866: pl. 66. Kylin 1956: 372. Lucas 1909: 21, 1929a; 15. Schmitz 1889: 451. Schmitz and Hauptfleisch 1897: 331. Wollaston and Womersley 1959: 55-62. Womersley 1948: 161; 1950: 178.

TYPE Locality: — Phillip Island, Western Port, Victoria.

TYPE: — TCD, Herbarium of Harvey, No. 423i (Lectotype from Georgetown, Tasmania).

DISTRIBUTION: — From Eucla on Western Australian border to Western Port, Victoria, and Tasmania (Georgetown).

(Fig. 13 A)

General Features and Discussion: — Gulsonia annulata was described in detail by Wollaston and Womersley (1959), based on a rich collection of drift material from Pennington Bay, Kangaroo Is., South Australia, during February 1956. Kylin (1956) recognised the identity of Gulsonia Harvey and the mediterranean genus Crouaniopsis (Berthold) J. & G. Feldmann which he referred to the former genus as Gulsonia mediterranea Kylin. Feldmann-Mazoyer (1940) had pointed out the vegetative similarity of the two species, but, on the basis of the description of carpospore development given by J.G. Agardh (1894), left the two genera distinct. The detailed study by Wollaston and Womersley of the carposporophyte development of Gulsonia annulata confirmed Kylin's recognition of the identity of the two genera.

In the present study Gulsonia annulata Harvey has been examined with special reference to its relationship with other genera of the Crouanieae and the study of Wollaston and Womersley (1959) has been extended to embrace more fully generic and specific features found to be useful in the classification of the group.

The plant is comparatively large, to 30 cm. high, with terete monosiphonous, articulate axes arising from the base and marked in all but the very young branches by conspicuous bands formed from the whorls of branchlets (Fig. 13A). The texture is somewhat cartilaginous in the older axes and the whole plant is enveloped in an extremely slimy gelatinous matrix. Growth is essentially monopodial with long lateral branches formed at more or less regular intervals along the axes. Short upwardly curved branches occur irregularly over the thallus, but are most abundant in the upper parts of the plant. These correspond in origin and form with young parts of long lateral branches and probably indicate that lateral branch initiation can occur at any time from any part of the thallus. These short laterals can, as they develop, become themselves laterally branched and seem, therefore, not to be homologous with the short laterals of limited growth found in Ptilocladia pulchra and Euptilocladia. Also, carposporophytes are produced on both long lateral branches and on these shorter laterals.

Apical growth is by transverse division of a dome-shaped apical cell. Lateral branch initials are produced from the upper, outer part of the basal cells of whorl-branchlets and an elongate chain of 16-20 cells is formed (as in Crouania attenuata, Feldmann-Mazoyer 1940, p. 126) before the initiation of whorl-branchlets. These are cut off by longitudinal divisions from lateral protrusions of the transversely-elongate cells of the chain and are initiated in a spiral sequence with a rotation of 45° between initials on adjacent axial cells. Four branchlets are developed in each whorl so that, in the mature branch, the whorls are superimposed on alternate axial cells as in Ptilocladia pulchra Each whorl-branchlet branches by successive di- and tri-chotomies of cells which become progressively smaller towards the exterior. The final cells are usually single about 20 x 6µ and are often terminated by an elongate hair (300µ long) with an expanded tip (Wollaston & Womersley 1959, fig. 2 a, b, f).

Cortication of the axis by simple or sparingly branched rhizoidal filaments occurs in mature branches. Several rhizoids are produced downwardly from the lower part of the basal cells of whorl-branchlets. These form a dense cover to the axes in the lower parts of the plant and may in the oldest parts completely envelop the whorl-branchlets.

Pyriform "gland-cells", similar to those found in Ptilocladia australis and P. vestita which contain inclusions of definite crystal-like forms, occur from the outer ends of any cells of the whorl-branchlets. In both P. australis and P. vestita gland-cells are, however, borne only in a terminal position on the whorl-branchlets.

Tetrasporangia are borne on the third cell of the whorl-branchlets in the younger upper parts of the thallus. Each sporangium is initiated as a protrusion usually from the outward upper part of the cell. The mature sporangium is sessile, spherical-ovoid measuring about 75-100µ in diameter within the gelatinous sheath and divides tetrahedrally.

Carposporophyte development: — The development of the carposporophyte has been described in detail by Wollaston and Womersley (1959 p. 38 and 39, Fig. 2g, 3 & 4). The short, special branch which bears the carpogonial branches is initiated in the position of a lateral branch. It is determinate in growth and elongation and production of initials of whorl-branchlets ceases with the development of carpogonial branches. No whorl-branchlets develop in the reduced branch apex above the cells bearing the carpogonial branches. In other species e.g. Ptilocladia pulchra and Euptilocladia spongiosa where the carposporophyte is borne on a branch of determinate growth, whorl-branchlets always occur on all cells to within two or three of the branch apex. Possible phylogenetic significance of this feature will be discussed later.

As in other closely related species, only one carposporophyte per branch has been seen to mature when the procarps are formed on special determinate branches. During development of the carposporophyte, after fusion of the auxiliary cell and carpogonium, the connections between axial and residual supporting cell and between supporting cell and foot cell widen.

The central cell, formed from the upper part of the auxiliary cell elongates laterally and the first gonimolobes are cut off one after the other from opposite ends. Fig. 3 j and k in Wollaston and Womersley (1959) probably represent the formation of later gonimolobes towards the summit of the cell, while Fig 3, b illustrates the typical lateral position of the first-formed gonimolobes.

Carposporangia are large (75-80μ x 100-120μ) and protected during development by surrounding whorl-branchlets, produced on the axial cells below. The cells of these whorl-branchlets elongate so that the branches lengthen and are directed upward and envelop the carposporophyte.

ANTITHAMNION Naegeli 1847: 200

Naegeli (1847) based the genus Antithamnion on Callithamnion cruciatum Agardh 1827 and described the genus as having a strongly developed monosiphonous main axis of unlimited growth bearing from each cell two equal opposite short branchlets of determinate growth. These in C. cruciatum were arranged decussately thus forming 4 rows of branchlets along the axis. Later authors including Naegeli (1861) extended this to include species having individual whorls of four short whorl-branchlets. Due to their distichous usually leaf-like form it is appropriate to refer to the whorl-branchlets as pinnae and to their branches as pinnules. Lateral branches develop into main axes and become attached to the host in their basal part while the apex continues to elongate indefinitely. In contrast to this, a prostrate main axis may give rise to distinct unattached, erect branches as occur, for example, in Acrothamnion.

In the diagrams accompanying his original description Naegeli shows a small basal cell, lacking pinnules, on each whorl-branchlet and gland-cells (believed by him to be "aborted spores") borne on special short branches. Both these features, and the cruciate division of tetrasporangia, he incorporates in his later description of the genus (1861). Here also he mentions the occasional development of rhizoids from the basal cells of whorl-branchlets. Rhizoids may occur on the basal cell of any whorl-branchlet whereas in species having distinct prostrate and erect parts of the thallus, rhizoids develop only from whorl-branchlets of the prostrate axis. Sexual reproductive organs for the genus Antithamnion were first recorded by Hauck (1885). He described antheridial clusters on the upper whorl-branchlets of male plants, and female plants bearing 2-4, rounded, naked groups of carposporangia, situated on the upper part of branches. He describes only tetrasporangia for A. cruciatum. The position of carpogonial branches on the basal cells of whorl-branchlets usually with several occurring on a single reduced branch apex, was described first by Schmitz and Hauptfleish (1897), again for the genus Antithamnion. Unfortunately no plants showing sexual reproduction of A. cruciatum have been available for comparison with southern Australian species, and sexual plants of this, the type species, seem to be extremely rare. Since these early descriptions the genus has been expanded to include species showing one or more of the following variations:

(1) Distinct prostrate and erect parts of the thallus.

(2) Tetrahedrally divided tetrasporangia.

(3) Gland-cells sessile on the cells of the pinnae and pinnules.

(4) Pinnae of unequal lengths or arranged in whorls of two to five on each axial cell.

In this study the genus has been limited strictly to include only those species showing features consistent with those of A. cruciatum. Features which have emerged as useful generic characters are: -

(1) Prostrate axes having erect parts formed from unattached ends of indefinite branches (as distinct from an attached prostrate axis bearing erect laterals which do not become attached and are limited in length or in rate of elongation).

(2) Axes completely lacking rhizoidal cortication.

(3) Pinnae all similar and arranged in opposite pairs, either distichous or decussate on the axis; each pinna has a small basal cell which does not bear pinnules. Pinnules are distichous on the rachis of the pinna and may be either opposite, alternate or secund.

(4) Each gland-cell is borne on a special short 2-4 celled branch.

(5) Tetrasporangia are cruciately divided and usually ovoid when mature.

(6) Carpogonial branches are borne on the basal cells of pinnae which are at least several cells in length. A series of (4-) 8-20 procarps are developed successively on each fertile branch apex. Only one carposporophyte matures on each branch.

Based on these features, a group of seven species of Antithamnion occur in southern Australia. All are small delicate epiphytic plants and most have pinnae bearing alternate pinnules with, occasionally, opposite pairs in the lower part of the pinna.

The Phylogeny of Southern Australian species of Antithamnion.

The species of Antithamnion in southern Australia show distinct trends from a probably more primitive form towards a more highly organized thallus and reproductive system.

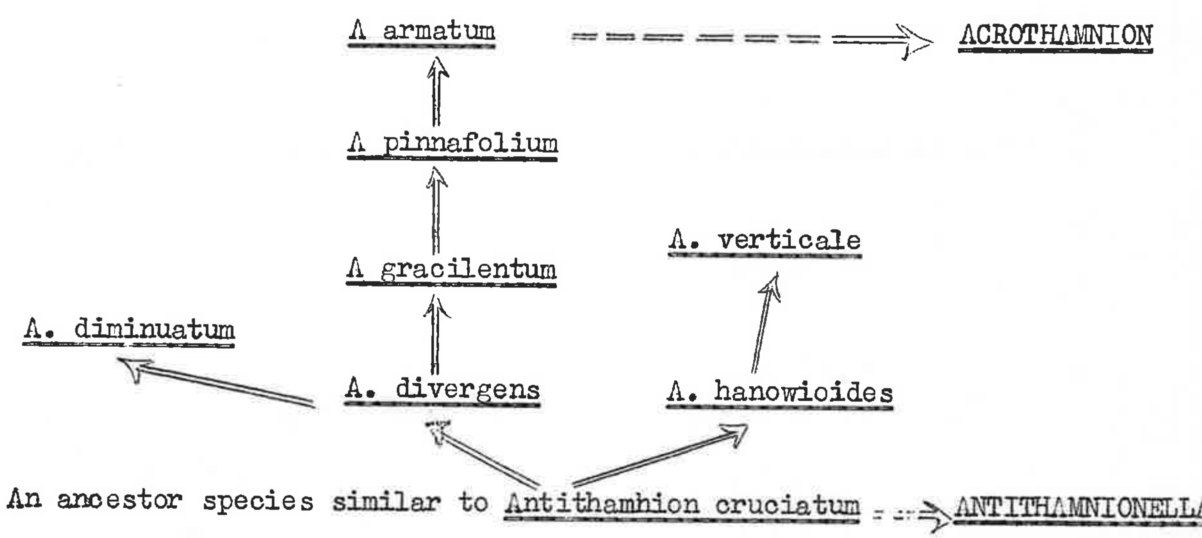
These trends are seen in: —

(1) Decussate to distichous arrangement of pinnae (the significance of this is discussed in relation to the phylogeny of the Crouanieae group in general.

(2) Increased regularity in arrangement of pinnules on pinnae, and a tendency from alternate to opposite arrangement.

(3) Decrease in number of procarps formed at a branch apex.

A suggested phylogenetic scheme for southern Australian species may, on the basis of these characters, be represented as follows: —



The ancestral form is likely to have shown characters indicative of instability of form. Such features are represented, for example, in *A. cruciatum* and *A. plumula* in the northern hemisphere, which occur in diverse forms. These species have decussately arranged pinnae and occur in several forms which vary in both number and position of pinnules on the pinnae. In these variable species each cell of the rachis usually bears only one pinnule and it is hence probable that stabilization of form first involved an alternate arrangement of pinnules on the rachis and that opposite pinnule arrangement followed. Along this line of development *A. divergens* and A. hanowioides (a rather more robust plant form) could have developed from the A. cruciatum type of thallus. In both species pinnae are decussately arranged and alternately branched. A divergens, which occurs in a variety of forms, is less stable than A. hanowioides. This polymorphism has caused some confusion in records of southern Australian species as, for example, in Harvey's records of A. cruciatum. It is now clear that Harvey's specimens are a form of A. divergens. Occasionally A. divergens shows at least one pair of opposite pinnules at the base of pinnae and this development is probably the forerunner of the pinna structure found in A. gracilentum where 3 or more pairs of opposite pinnules are consistently developed from the lower part of each pinna. A. gracilentum is also distinct and probably more advanced in having distichously arranged pinnae. This distichous arrangement is maintained in A. pinnafolium and A. armatum which are probably developed along the same line as A. gracilentum. Pinnae in A. pinnafolium all occur in opposite pairs from the rachis and thus an increasing number of opposite pairs of pinnae occur along the line from A. divergens ⟶ A. gracilentum ⟶ A. pinnafolium. Gland-cells of A. pinnafolium sometimes occur on special branches on the lower side of fully-formed pinnules as they do in A. gracilentum. Usually, however, they occur on shortened pinnules which could have developed by loss of the outer part of the pinnule (see under A. pinnafolium). This development may therefore follow from the form found in A. gracilentum.

A. armatum has a highly organized and stable form of thallus. Very little variation is seen in plant form and the pinnae are regularly, unilaterally branched (possibly derived from a pinnately branched form like A. pinnafolium). Lateral branches occur in place of pinnae and are characteristically developed so as to appear dichotomous with the main axis. The rather rigid thallus accentuates the regular organization of thallus structure.

A possible second line from A. divergens leads to A. diminuatum which differs from A. divergens in always having 1-3 pairs of opposite pinnules at the base of each pinna and particularly, in having a reduction in length and form of all pinnae on lower parts of the thallus and a reduced number of procarps formed on each branch apex. These latter two characters especially probably represent a more highly differentiated thallus than found in A. divergens.

A verticale differs from A. hanowioides chiefly in having distichous rather than decussate arrangement of pinnae. This is presumed to be a more highly organized form of thallus structure and hence A. verticale has been placed on the same developmental line, but ahead of A. hanowioides.

The possible phylogenetic position of the genus Antithamnion is discussed fully in relation to other genera of the group (Section X).

TYPE species: — Antithamnion cruciatum (Ag.) Näg. (European).

KEY TO THE SOUTHERN AUSTRALIAN SPECIES OF ANTITHAMNION

1. Pinnae decussate on axis... 2

1. Pinnae distichous on axis or rotated only slightly to accommodate overlap of pinnules. 4

   2. Pinnae less than 600µ long, upwardly curved and shorter on prostrate axes and lower parts of erect branches. Lower 1-3 pairs of pinnules opposite, upper ones alternate. Most pinnules branched with 1-several simple branches in same plane as pinnules ... . *A. diminuatum*

   2. Pinnae usually over 600µ long, curved upward of flexuous, not distinctly shorter in lower parts of thallus. Pinnules alternate (occasionally with lowest pairs opposite in *A. divergens*) usually simple or with short simple branches often not in plane of pinnules.. 3

3. Plant slender and flexuous. Pinnae to about 1500µ long; pinnules all alternate on a comparatively straight rachis or sometimes with lowest 1(-3) pairs opposite. Pinnules usually simple or with 1-several short branches from the lowest pinnules... *A. divergens.*

3. Plant not markedly flexuous. Pinnae usually 600-900µ long. Pinnules all alternate on a zig-zag rachis and bearing 1 (-several) short branches set at about 90° to the pinnules and not always in the same plane... ... ...*A. hanowioides*

   4. Lateral branches borne regularly on every 3rd-4th cell of axis in place of a pinna. Pinnae with 3-8 pairs of opposite pinnules in the lower part and alternate pinnules above. *A. gracilentum*

   4. Lateral branches borne on the basal cells of pinnae at irregular intervals along axis or in place of a pinna and appearing dichotomous with the main axis. All pinnules of each pinna opposite <u>or</u> alternate <u>or</u> unilateral. 5

5. Pinnules unilateral on upper side of rachides of pinnae. Lateral branches borne in place of a pinna and appearing dichotomous with the main axis... ... ... *A. armatum*.

5. Pinnules alternate or opposite. Lateral branches borne on basal cells of pinnae at irregular intervals along axis... 6

6. Pinnules alternate from zig-zag rachides of pinnae. Gland-cells borne on short branches on pinnules. *A. verticale*

6. Pinnules opposite from straight rachides of pinnae. Gland-cells borne on short branches which replace pinnules or, occasionally, on the 2nd-3rd cell of a fully - developed pinnule... ... ... *A. pinnafolium*

ANTITHAMNION DIVERGENS (J. Agardh) J. Agardh

J. Agardh 1892: 21. De Toni 1897: 1410. Lucas 1929a: 25.

Callithamnion divergens J. Agardh 1876: 19. Harvey Alg. Aust. ex. No. 545. Wilson 1892: 186.

Callithamnion cruciatum ~~C. Agardh~~, sensu Harvey 1849: pl. 164 (non C. Ag); 1860: 333; 1863, synop: ~~No.~~ 689; Alg. Aust. ex No. 545. Kützing 1849: 649; 1861: pl. 87.

? Callithamnion delicatulum Harvey 1854: 560; 1863, synop. ~~No.~~ 702. Agardh, J. 1876: 21.

? Antithamnion delicatulum (Harv.) De Toni 1897: 1415; Lucas 1909: 51. Lucas and Perrin 1947: 355.

TYPE Locality: — Georgetown, Tasmania (Gunn).

HOLOTYPE: — LD, Herbarium J. Agardh, No. 18804. Probable isotype in Harvey's herbarium, TCD, labelled as "Callithamnion cruciatum?" and placed under Antithamnion divergens.

DISTRIBUTION: — Widespread in southern Australia from King George's Sound, Western Australia, to Port Phillip Heads, Victoria, and Georgetown, Tasmania.

(Fig. 15).

General Features: — The plant is small with prostrate creeping axes which have erect unattached apices and bear pairs of pinnae which stand erect from each axial cell. It grows epiphytically on various algae, and the erect parts of the thallus are usually $<$ 0.5 cm. in height and have densely tufted axial apices marked by a small dense "clump" of young whorl-branchlets (pinnae). The axes are attached by simple rhizoids which develop a flattened digitate holdfast on contact with the host.

The thallus is delicate, soft and polymorphic due to variation in length of cells, particularly of the axis, and arrangement of pinnules on the pinnae.

Chromoplasts are small and rounded in the majority of cells, but may be irregularly narrow and elongate in large cells and particularly in those of the prostrate axes.

Structure of the thallus: —

(1) Form and Development of Main Branches: — Axes consist of cylindrical cells which when mature may be from 3 to 8 times as long as broad (average about 250 x 50µ).

Growth of the axis is monopodial and takes place by transverse divisions of a dome-shaped apical cell (Fig. 15B,C) which elongates before each division.

Lateral branches are borne on the basal cells of pinnae at irregular intervals along the axis (Fig. 15A, B,C). Occasionally the pinnae on the axial cell bearing the lateral branch develop a basal cell only.

(2) Development, Arrangement and Branching of Pinnae: — Pinnae are initiated on young axial cells two or three below the apex (Fig. 15C). A protrusion is first formed laterally from the cell and forms the initial cell of the rachis of the pinna. The pinnae are formed one after the other in opposite pairs on each cell and are decussately arranged on adjacent axial cells. This arrangement is more or less maintained even where the axis becomes attached, although with attachment to the host the axial cells are rotated so that divergence between pairs of pinnules is reduced.

The basal cell of each pinna is small (Fig. 15 A,D) and about as broad as it is long (12-20μ). These cells bear attachment organs and lateral branches. Other cells of the pinnae resemble axial cells but are not as large and become progressively smaller toward the tips of the rachides and pinnules (Fig. 15A). Each pinna bears alternate distichous pinnules, with occasionally one (-3) opposite pair of pinnules on the first cell above the basal cell. The pinnules are usually unbranched, but the lower ones occasionally bear one (to several) simple branches from the lower side. The rachis and pinnules of the pinnae are slender and taper gradually towards the tips.

Gland-Cells: — Gland-cells are borne on special short 2-3 celled branches, which arise from the upper end of a cell of the rachis of a pinna, in place of a pinnule (Fig. 15E,a) or on the under side of one of the lower cells (often the 2nd cell) of a pinnule (Fig. 15E,b). Gland-cells are scattered, rather sparsely over the thallus.

Organs of Attachment: — Attachment organs are produced from the basal cells of pinnae and develop as rhizoidal structures of several elongate cells. On contact with the host a branched process is formed which spreads and adheres to the host surface (Fig. 15A). The several main branches of the process are made up of 2-4 small cells each of which may bear an opposite pair of short branches. The whole process measures about 100μ in diameter.

Tetrasporangia: — Tetrasporangia are borne on the lower cells of the pinnae and may occasionally occur directly on the apex of a cell of the rachis in place of a pinnule. Usually, however, they are borne on the upper side of the lower cells of the pinnules or on the basal cells of the special short branches which bear the gland-cells (Fig. 15D). Only one tetrasporangium is borne on each cell at a time.

The tetrasporangia are sessile, ovoid, ~~about~~ 60-75 x 45-50µ and divide cruciately.

Spermatangia: — Spermatangial mother-cells are borne on special short branches from the outer end of the lower cells of the pinnules and occur most abundantly towards the lower part of the pinnae.

Each cluster is made up of a central axis of about 5-10 cells each of which bears a whorl of 4-6 cells (Fig. 15J) which each bear a further whorl of 4 small (6µ in length) spermatangial mother cells (Fig. 15K).

Development of Procarp and Carposporophyte: — Carpogonial branches are borne on the basal cells of pinnae (supporting cells) near branch apices. After successive initiation of a series of carpogonial branches, branch apices cease further growth, so that carposporophytes always mature near branch ends. Usually only one carpogonial branch occurs on each pinna (Fig. 15F). The carpogonial branch is 4-celled, curved around the supporting cell from the underside and develops a long trichogyne. The cells of the carpogonial branch are characteristic in shape, particularly the truncate-conical third cell (Fig. 15F).

After fertilization an auxiliary cell is cut off from the upper side of the supporting cell (Fig. 15G). The carpogonium develops a protrusion, which forms a connecting cell, in the direction of the newly-formed auxiliary cell (Fig. 15G). Presumably fusion between the carpogonium and the auxiliary cell occurs via this connecting cell, but actual stages showing this have not been seen. The auxiliary cell divides to form a lower foot-cell and an upper central cell which produces the first gonimolobe in a terminal position (Fig. 15H). At this stage there is distinct widening of the connection between the axial cell and the supporting cell with break-down of the pit-connection and fusion of the two cells. Further fusions occur between axial cell, supporting cell and foot cell so that individual cells become indistinguishable. Further groups of carposporangia are formed laterally (Fig. 15I). Cells of the thallus adjacent to the developing carposporophyte stain densely and possibly serve a nutritive function. The cell of the pinna adjacent to the supporting cell always enlarges a little (Fig. 15H).

The pinnae of the axial cells below the carposporophyte grow upward and surround and protect the carposporophyte. There does not appear to be any development of special protective pinnae (e.g. as found in *A. gracilentum*).

Discussion: —

Antithamnion divergens is an Australian species superficially similar to *A. cruciatum* which occurs in various forms in the northern hemisphere. Harvey (1860) described differences between the Tasmanian and European plant, fully realizing the polymorphism of the European species. He did not therefore propose a new species for the Australian plant, although he suggested that it would "possibly be better to regard it as a distinct but representative species."

Antithamnion divergens differs from the European A. cruciatum in having:

(1) Pinnules alternately arranged with, only occasionally, the lowest pair opposite. In A. cruciatum although varying in form, they are basically opposite or unilateral.

(2) Tetrasporangia sessile. A. cruciatum has tetrasporangia borne on a stalk of one (or sometimes two) cells.

(3) Attachment organs with comparatively larger terminal digitate adhesive organs on shorter, stouter rhizoids than in A. cruciatum, in which elongate rhizoids develop before any attachment structure is formed.

A. delicatulum (Harv.) De Toni may be synonymous with A. divergens, and if so would be the earlier name. However the type specimen (No. 339 of Harvey) is missing from TCD, and until its identity can be better established it seems best to use the name A. divergens.

ANTITHAMNION GRACILENTUM (Harv.) J. Ag.

J. Agardh 1892: 21. De Toni 1897: 1406; 1924: 494. Lucas 1909: 51. Yendo 1914: 278 (see note later).

Callithamnion gracilentum Harvey 1854: 560; 1863, synop: No. 701. J. Agardh 1876: 21. Wilson 1892: 187.

TYPE Locality: — Rottnest Island, Western Australia.

HOLOTYPE: — TCD, Herbarium of Harvey, No. 327.

DISTRIBUTION : — Throughout southern Australia from Rottnest Island, Western Australia to Port Phillip Heads, Victoria and at Reminie, Trial Harbour, west coast of Tasmania. Epiphytic on species of Cystophora (C. retorta (Mertens) J. Ag., C. intermedia J.Ag. and others).

(Figs. 16, 17 A-G).

General Features: — The thallus consists of prostrate, creeping main axes attached by branched rhizoids and erect parts (to 0.5 cms. high) is formed of the opposite distichously arranged pinnae and the unattached branch apices (Fig. 16A). As further attachment organs develop from the basal cells of the pinnae, axes of the younger branches become affixed to the host surface. Pinnae are distichous and consist of a central rachis which bears opposite pinnules in the lower part and alternate ones above. Cells are usually of the dimensions described below, but, very occasionally, the plant may be more delicate in form with cells of the axis and pinnae up to 6 times as long as broad. Chromoplasts vary from small and rounded in younger cells to irregularly elongate in the older cells (Fig. 16E).

Structure of thallus: —

(1) Development of Main Indeterminate Axes: — Growth is monopodial and occurs by transverse divisions of a dome-shaped apical cell which elongates before dividing (Fig. 16B). Pinnae are cut off from axial cells only 2-3 cells from the apex. Axial cells are usually rounded when young (Fig. 16B) but become cylindrical and about 220 x 100μ when mature. Pit-connections between cells are prominent.

Indeterminate lateral branches of the axis arise regularly and alternately at intervals of 3 (occasionally 4 (-6)) axial cells. (Fig. 16B, a,b,c). The axial cell bearing the lateral branch is smaller than other axial cells and develops neither pinnae nor attachment organs. The lateral branch arises as a protrusion from the axial cell which divides transversely (Fig. 16B, c,b) to form a chain several cells in length before the development of lateral pinnae. Subsequent development is similar to that of all branch apices (Fig. 16C).

Development, Arrangement and Form of Pinnae: — Pinnae are initiated opposite one another near apices of axes, and, as with lateral branches, are cut off from a lateral protrusion from the axial cell which divides transversely to form a chain of cells before the pinnules are initiated. The apical cell of the chain elongates before division as in the apical growth of an indeterminate branch.

Mature pinnae vary considerably in length, but are often about 1300μ long, with a small basal cell which usually stains more densely than other cells of the pinna. Cells of the rachis are about 3 times as long as broad, with the larger cells about 150 x 40μ. The pinnae are distichous with 3-8 pairs of opposite pinnules from the lower cells of the rachis and alternate ones above (Fig. 16D). Pinnules may occasionally bear simple branches of varying lengths from the lower side (Fig. 16D). Most pinnae make an angle of about 70-90° with the axis often forming the erect portion of the prostrate thallus. At apices, however, they are curved inward and upward and surround the growing point.

Pinnae behind the branch apex may appear decussate but this must be due to rotation of axial cells, as all pinnae are initiated opposite one another and in the same plane.

Gland-cells: -- Gland-cells occur on special short 2-4 celled branches from the lower side of the second, third or fourth cell (from the base) of a pinnule (Fig. 16 D, F, G).

Attachment Organs: — Attachment organs are produced from the lower side of the small basal cells of the pinnae. They are composed of elongate cells and are branched di- or trichotomously several times (Fig. 16 H-K). The ultimate cells are small, stain densely and form the actual attachment to the host.

Tetrasporangia: — Tetrasporangia are borne on the upper side of the basal (occasionally 2nd and 3rd) cells of pinnules. Only one tetrasporangium occurs on one cell at a time and the first tetrasporangia developed are on the lower pinnules of the pinna. Tetrasporangia are sessile on a short lateral protrusion from the cell of the pinnule (Fig. 17A). They are ovoid about 60 x 70-80μ within the thick gelatinous sheath, and divide cruciately.

Spermatangia: — Spermatangial clusters are borne on the upper side of the lower cells of the pinnules (Fig. 17B) and are concentrated toward the lower part of the pinna on the opposite pairs of pinnules.

Each cluster consists of a central rachis of 5-8 cells each cell of which bears a whorl of 4 cells. Each of these cells bears a further whorl of 4 cells from its outer end and the spermatangial mother cells are borne terminally in groups of 4 from these cells (Fig. 17C).

The protoplast of these cells stains densely and when mature is concentrated at the apex of the cell. The wall of the spermatangial cell remains after the spermatium is liberated.

Occasionally a second central rachis develops from the basal cell of the main rachis and a second cluster, usually smaller than the main cluster, is developed from it.

Development of Procarp and Carposporophyte: — Carpogonial branches are borne near the apices of axes and are produced on the basal cells of young developing pinnae (Fig. 17D). Two carpogonial branches very occasionally occur on the one basal cell. The initial of the carpogonial branch is ovoid (Fig. 17D(1)) and divides by irregular transverse divisions to give a 4-celled carpogonial branch with a total length (excluding trichogyne) of about 30µ (Fig. 17D(1-4)). The trichogyne develops terminally on the carpogonium and may reach 80-90µ in length (Fig. 17E).

Stages immediately following fertilization and early stages of carposporophyte development have not been seen. Only one carposporophyte develops at each branch apex.

In the mature carposporophyte complete fusions between cells occur and individual cells cannot be recognized (Fig. 17F). Cells of the main axis above the carposporophyte are displaced and pinnae borne on these upper axial cells remain small and undeveloped; other carpogonial branches are usually present. The cells of the pinna borne on the axial cell which bears the carposporophyte also remain small and immature. The axial cell, old supporting cell (basal cell of pinna) and derivative cells of the auxiliary cell (foot-cell and central-cell) fuse completely, become rigid and stain densely. The first terminally-developed gonimolobe bears several sterile cells which in turn give rise to groups of carposporangia (Fig. 17 F,G).

Pinnae and pinnules on axial cells below the carposporophyte curve upward and inward to envelop and protect the carposporophyte. Further special protective pinnules may develop from the basal cells of the pinnae and add to the protective sheath around the carposporangial groups.

Discussion: —

Antithamnion gracilentum has been found in southern Australia only as an epiphyte on species of *Cystophora* on rough coasts. It was recorded by Harvey (1854) as a "parasite on Fucoids". Yendo (1914) reports *Antithamnion gracilentum* from Japan as epiphytic upon *Galaxaura apiculata* Kjellm. He describes his plant, however, as having pinnules which are "unexceptionally alternate", and, as opposite pinnules at the base of the pinnae are characteristic of the species, it is doubtful whether his description applies to the same plant. *A. gracilentum* most closely resembles *A. divergens* (J. Ag.) J. Ag., but differs chiefly in arrangement of pinnules on pinnae, form of attachment organs and lateral branches initiated at regular intervals.

ANTITHAMNION PINNAFOLIUM n. sp.

Thallus prostratus ramis erectis usque ad 1½ cm altis. Vortico-ramuli oppositi, distichi, 760-1000μ longi, cellula basale parva instructi; rami oppositi, distichi, simplices (interdum basales ramosi). Cellulae glandulosae in ramis brevibus specialibus positae. Tetrasporangia, spermatangia et carposporophyti ignoti.

TYPE Locality: — Stanley Beach, Kangaroo Is., South Aust.

HOLOTYPE: — AD, A29,504, epiphytic on *Sargassum*.

DISTRIBUTION: — Known only from Elliston, Eyre Peninsula, South Australia and the type locality, epiphytic on *Rhodophyllis membranacea* Harvey and on *Dilophus* sp.

(Fig. 17 H-N)

General Features: — The plant consists of a creeping prostrate axis with erect parts formed from apices of lateral branches to 1.5 cm. high. Each axial cell bears a pair of opposite, distichously arranged, pinnae bearing opposite distichous pairs of pinnules. The plant attaches by rhizoids which arise on the underside of the prostrate axis from the small basal cells of the pinnae.

Structure of Thallus: —

Form and Development of Main Branches: — Axes elongate by transverse divisions of a dome-shaped apical cell, and a chain of 15-20 small rounded cells terminates each axis. Mature axial cells are cylindrical and about three times as long as broad (e.g. 64 x 190µ). Lateral branches arise at irregular intervals (2-7 cells apart) from the basal cells of pinnae, and develop similarly to apices of the prostrate axes.

Development, Arrangement and Branching of Pinnae: — Pinnae are initiated as protrusions from about the second cell below the branch apex and a rachis of 10-13 cells is formed before the first pinnules are initiated, on the outer side of the central rachis cells (Fig. 17H). The upper several cells and the basal cell, which always remain small, do not bear pinnules. Mature pinnae are 18-22 cells (760-1000µ) long with rachis cells about $1\frac{1}{2}$-$2\frac{1}{2}$ times as long as broad (25 x 50-60µ). Pinnules occur in opposite pairs and are simple or occasionally bear 1-4 simple branches, particularly from the basal pinnules. Average pinnules are 9-11 cells (315-380µ) long (Fig. 17I).

Gland-Cells: — Gland-cells usually occur on shortened pinnules 4-6 cells long (Fig. 17J), but occasionally the full pinnule is developed (Fig. 17K). The reduced condition is probably derived from a full pinnule in which the outer axial cells are lacking, and hence is analogous to the lower 2-3 cells of the pinnule together with the short gland-bearing branch.

Mature gland-cells are about 24µ long, rounded on the upper surface and usually occur in the central and lower parts of pinnae.

Attachment Rhizoids: — The prostrate axis is attached by digitate processes developed terminally on rhizoids arising from the basal cells of mature pinnae. Each rhizoidal initial (Fig. 17L) develops a whorl of 2-3 cells from the outer end (Fig. 17M) and each cell of this whorl may form a rhizoid of several elongate cells (Fig. 17N). The branched attachment process develops on contact with host tissue.

Tetrasporangia, Carposporangia and Spermatangia: — Unrecorded.

Discussion: —

The species is tentatively placed in the genus *Antithamnion* awaiting collection of fertile material. It agrees with this genus in habit and in position of gland-cells developed on a special short 2-4 celled branch. It may be closely related to *Antithamnion gracilentum*.

ANTITHAMNION ARMATUM (J. Ag.) De Toni 1897: 1398. Lucas 1909: 51.

Callithamnion armatum Agardh J. 1884: 3.

TYPE Locality: — "Novae Hollandiae".

TYPE: — LD, Herbarium of J. Agardh. No. 18041.

DISTRIBUTION: — Flinders Bay, Western Australia to Robe and Stanley Beach, Kangaroo Island, South Aust.

(Fig. 18 A-J).

General Features: -- The plant is small with prostrate axes terminating in an unattached part of the thallus usually less than 2 cm in length. Branching is irregular with branches diverging by almost 90° (Fig. 18A), and lateral branches initiated at the apex of the axis in place of a pinna. Pinnae are opposite in pairs on each axial cell and are distichously arranged. Pinnules occur unilaterally on the upper side of the pinnae and may bear short branches from the outer side of each cell. The pinnae are approximately horizontally inserted and curve upward in the centre. The upper ends of the pinnules of one pinna usually overlap the pinna above so that adjacent pinnae are deflected slightly to one side or the other to accommodate the overlapping of the pinnules (Fig. 18B). The deflection occurs regularly so that alternate pinnae are rotated in the same direction.

The thallus is firm in structure with pinnae and pinnules held more or less consistently in place.

Structure of Thallus: —

(1) Form and Development of Main Branches (Indeterminate Branches): —

Axes are developed by transverse divisions of an elongate dome-shaped apical cell with pinnae initiated only one or two cells below the apex (Fig. 18E). Several axial cells below the apex are small, immature and rounded to pear-shaped in form (Fig. 18D,E). Mature axial cells are cylindrical and one or two times as long as broad (about 125 x 215μ) with prominent pit connections between cells.

Branching of the axis is irregular and lateral branches arise near the branch apex in place of a pinna and appear to form a dichotomy with the original axial apex (Fig. 18D). The lateral branch initial is similar in form to the main axis. An angle of about 90° usually occurs between lateral branch and axis.

(2) Development, Arrangement and Branching of Pinnae: — Pinnae occur in pairs from the upper part of each axial cell and are opposite one another and distichously arranged upon the axis. They develop initially as lateral protrusions from the axial cells immediately below the axial apex (Figs. 18D,E), with each pair forming one initial after the other. Pinnae develop quickly and those on axial cells only several below the apex are almost mature in structure with well-developed pinnules (Fig. 18E).

The first development of pinnules occurs on the central cells of the rachis of the pinna (Fig. 18E, a and b). The mature pinna is usually 8-12 cells in length totalling about 500-650μ, but is often shorter on the attached parts of the thallus. The cells of the rachis are progressively larger from the base of the pinna towards the centre and taper again to an abrupt acute apex. When mature the rachis of the pinna is set at right angles to the axis with an upward curvature in the central region. A pinnule of 2-10 cells is borne on the upper side of each cell of the rachis (except the basal cell and the one or two small terminal cells) with the longest ones developed from the central cells of the pinna.

A simple short outwardly directed branch occurs on each of the lower and central cells of the pinnule. The lowest branches of the pinnules are often reduced in length and bear gland-cells (Fig. 18B). Pinnules diverge slightly from a vertical position (parallel to the central axis) towards the outside (Fig. 18B).

Gland-cells: — Gland-cells are prominent and are borne on special short branches of 1-3 (usually 2) cells in length on the lower cells of the pinnules. One to four may occur from adjacent cells of the one pinnule, and are formed in place of the simple outwardly-directed branches as occur on other cells of the pinnule (Fig. 18C).

Each gland-cell is about 20µ in diameter and is attached by a fine connection to the basal cell of the special short branch which bears it.

Attachment Organs: — Rhizoidal attachment filaments are produced from the lower side of the basal and second cells of the pinnae. One to three may form on a cell (Fig. 18F). Before attachment the filament is composed of elongate cells (Fig. 18H) and may branch once or twice (Fig. 18G). On contact with the host a digitate attachment process develops terminally and the cells of the filament become comparatively shorter and broader (Fig. 18I).

Tetrasporangia: — Tetrasporangia have been found on only one plant (AD, A 3481, from West Bay, Kangaroo Island, South Aust). They are borne on the lower side of the basal cells of the special short branches which bear the gland-cells. Each tetrasporangium is sessile, ovoid, about 45 x 75μ within the thick gelatinous sheath and cruciately divided (Fig. 18J). Only one tetrasporangium occurs from a cell at one time.

Spermatangia: — Not recorded.

Procarp and Carposporophyte: — Only one female plant has been available bearing only mature carposporophytes. Detail of procarp development has not, therefore, been studied. The carposporophyte is, however, similar to that described for other species of *Antithamnion* and is formed from one of a series of 4-8 procarps borne at each fertile branch apex. The number of procarps developed is thus less than in some species of *Antithamnion* and may represent an advanced form closely related to *Platythamnion* or *Acrothamnion*.

Discussion: —

In vegetative features the plant is similar to *Antithamnion* especially in the form and position of gland cells and the cruciately divided tetrasporangia. Its taxonomic position must, however, remain uncertain until the position and development of the carposporophyte can be investigated in detail.

<u>ANTITHAMNION DIMINUATUM</u> n.sp.

Thallus prostratus ramis erectis usque ad 0.4 cm altis. Vortico-ramuli curvato-adscendentes, decussati, usque ad 580μ longi, cellula basale parva instructi; ramis distichis, inferne 1-3 paribus oppositis, superne ramis 1-3 alternatis plerumque ab latere inferiore instructi. Cellulae glandulosae in ramis brevibus specialibusque ab latere inferiore instructi. Cellulae glandulosae in ramis brevibus specialibusque ab latere inferiore vortico-ramulorum positis. Tetrasporangia et spermatangia ignota. Quisque ramus uno carposporophyto instructus, et procarpi (4-8) in cellulis basalibus pinnarum in cacuminibus ramorum positi.

<u>TYPE Locality</u>: — Middle River, Kangaroo Island, South Australia.

<u>HOLOTYPE:</u> — ADU A 13,031

<u>DISTRIBUTION</u>: — Known only from the type locality, epiphytic on coralline algae.

(Fig. 18 K - N).

<u>General Features</u>: — The thallus consists of prostrate axes with densely arranged lateral branches which form erect portions of the thallus up to 0.4 cm. long. Pinnae are in opposite pairs from each axial cell and curve upward towards the branch apex (Fig. 18K). They are reduced in length in the prostrate axes and lower parts of the upright branches. Each pinna bears 1-3 opposite pairs of pinnules from the lower rachis and alternate pinnules above. Most pinnules bear 1-several simple branches (Fig. 18L).

Form and Development of Main Branches: — Growth occurs from the transverse divisions of a dome-shaped apical cell to form axes of cylindrical cells. Mature axial cells vary considerably in proportion and may be from $1\frac{1}{2}$ to 4 times as long as broad, averaging about 100 x 30μ.

Lateral branches are borne at irregular intervals along the axes from the basal cells of pinnae.

Development, Arrangement and Branching of Pinnae; — Pinnae are initiated from axial cells 1-several cells below the apex of branches. They form in opposite pairs, decussately arranged always with one pinna of each pair initiated before the other. The rachis elongates before pinnules are developed.

Each mature pinna curves upward particularly in the upper part of branches and bears opposite pinnules at the base (1-3, but usually 2, pairs) and alternate ones above (Fig. 18L). The cells of the rachis are often somewhat zig-zag where pinnules are borne alternately. The longer pinnae may grow to 580μ in length. The basal cell of the rachis always remains smaller than the cells immediately above it and it does not bear pinnules.

Pinnules are usually branched (often on the lower side) with 1-3 simple branches developed in the same plane as the pinnules.

Gland-Cells: — Gland-cells occur on special short 2-3 celled branches on the lower side of pinnules and most commonly in the central region ofthe pinna. Occasionally a pinnule may be reduced to form a short gland-bearing branch. Each gland-cell is rounded and about 12μ long.

Attachment organs: — Rhizoidal attachment organs are borne on the lower side of the basal cells of pinnae. Several simple rhizoids may arise from each basal pinna cell and on contact with the host these rhizoids contract and form a digitate attachment process.

Tetrasporangia and Spermatangia: — Not recorded.

Development of Procarp and Carposporophyte: — Carpogonial branches are initiated successively at branch apices on the basal cells (supporting cells) of young pinnae. There are usually fewer (4-8) procarps formed than in other species of *Antithamnion* where between 8 and 20 are commonly developed. Each 4-celled carpogonial branch is about 24μ long and curves upward from its point of attachment on the lower side of the supporting cell (Fig. 18M). A trichogyne, about 120μ long, develops from the carpogonium (Fig. 18N). Elongation of the branch axis ceases and only one carposporophyte matures on each branch.

Carposporophyte development is similar to that found in other species of *Antithamnion* with the terminal rounded group of carposporangia matured before the lateral groups (Fig. 18N).

Discussion: --

The branching of this species shows a tendency towards the development of distinct prostrate and erect portions of the thallus in having the pinnae reduced in form on the prostrate and lower parts of the branch system. The erect branches still retain, however, the characteristics of the genus *Antithamnion* in developing rhizoids in the lower part as they continue to elongate from the apex. In other features of habit the plant is typically an Antithamnion. The number of procarps formed at a branch apex is usually less than the 8-20 found in other species.

The plant is close to A. divergens but differs from this species in being a smaller plant usually with branches on the pinnules.

ANTITHAMNION HANOWIOIDES (Sonder) De Toni 1897: 1398. Lucas 1909: 51. Lucas and Perrin 1947: 352.

Callithamnion hanowioides Sonder 1853: 674; 1855: 512. Agardh, J. 1876: 26. Harvey 1863, synop. No. 697. Wilson 1892: 187.

Callithamnion spinescens sensu Harvey 1854: 560 (not Kützing) (see later note).

TYPE Locality: — St. Vincent's Gulf (probably near Adelaide), South Aust., Lectotype from Wilson's Promontory, Victoria.

LECTOTYPE: — MEL. No. 10283 (Sonder's original specimen is apparently lost, although his drawings, possibly of the holotype, are in MEL).

DISTRIBUTION: — Common throughout southern Australia, from Western Aus. to Wilson's Promontory, Vic., including Tasmania, Epiphytic on a wide variety of algae (Chlorophyta, Phaeophyta and Rhodophyta) and on marine angiosperms, especially species of Posidonia.

(Fig. 19).

General Features: — The plant is small and consists of branched creeping axes, the unattached ends of which may be 2(-3) cm long, and can be easily recognized by their terete, spongy appearance and curved, densely pigmented branch tips. Attachment is by groups of rhizoidal organs developed from the basal cells of the pinnae.

Two opposite pinnae occur on each axial cell and are more or less decussately arranged usually with a divergence of less than 90° between pairs on adjacent axial cells. The pinnae in unattached parts of the plant curve upward and inward, while on attached parts they may be shorter and almost erect from the creeping axis (Fig. 19A). Each pinna bears alternate pinnules which branch one to several times. Apices of both pinnae and pinnules are stiff and abruptly pointed giving the thallus a regularly spiny appearance (Fig. 19C).

Structure of Thallus: —

(1) Form and Development of Main Branches: — Axial growth takes place by transverse divisions of a dome-shaped apical cell with the initiation of pinnae occurring 2 or 3 cells below the apex.

Lateral branches are produced at irregular intervals along the axis and are borne on the small basal cells of the pinnae (Fig. 19B).

Mature axial cells are cylindrical, with prominent pit-connections (Fig. 19B), and are once to twice as long as broad, (100 -150) x (150-220) μ. Plants having more elongate thallus cells tend also to have slightly more elongate acute apices to their pinnules.

(2) Development, Arrangement and Branching of Pinnae: — Pinnae occur in pairs, attached just above the centre of each axial cell. They are more or less decussately arranged, but usually are rotated by about 45° (rather than 90°) from the pair on the adjacent axial cell. Pairs on alternate axial cells are superimposed.

Each pinna is about 600-900µ long and is curved upward and inward on the unattached parts of the thallus. Pinnae arising from axial cells of the prostrate thallus may be more or less erect or, at times, curved away from the branch apex.

Pinnae are branched alternately and distichously with one pinnule of about 7-10 cells borne almost horizontally from each cell of the zig-zag rachis (Fig. 19C). Each pinnule bears one to several short stiff branches which may not be distichously arranged and which always diverges from the axis of the pinnule by 45° to 90°. All apices are acute and the thallus is thus spiny in appearance. The lowest 1 or 2 pinnules on each pinna may be more branched than those above.

The basal cell of each pinna is small, often shortly conical in shape with the face flattened against the cell of the main axis and bearing the rachis of the pinna from its summit (Fig. 19B).

In plants having comparatively short axial cells, the pinnae are densely arranged and it is often these plants which also bear more than one branch on each pinnule.

Gland-cells: — Gland-cells are prominent, particularly at branch apices and on densely branched plants in which more than one may be borne on a pinnule. Each gland-cell (24-30µ diameter) occurs on a special short branch of 3-5 cells in length (Fig. 19C,D) which is usually borne from the lower, outer end of the second (or third) cell of the pinnule.

Attachment organs: — Attachment organs develop from the lower side of the basal cells of the pinnae and occur in dense clusters in the lower parts of the unattached portions of the plant. One basal cell of a pinna bears three (often 4-6) rhizoidal initials. Each of these cells produces from its outer end a further 3-6 cells each of which develops a cluster of about 5-8 cells which in turn bear two elongate rhizoidal filaments composed of very elongate cells varying considerably in length (Fig. 19E). These filaments may each branch several times. The filaments of each dense cluster often grow to 600μ or more in length and form dense masses on the underside of the unattached branches. Terminal cells of the rhizoids usually stain densely. On contact with the host surface a digitate attachment process is formed. (Fig. 19F, G). Mature functional attachment organs are usually arranged in much smaller groups, often of only several filaments, and are frequently made up of cells which are comparatively shorter and broader. Many filaments of the clusters apparently do not adhere to the host and are soon lost. Berthold (1882: 607) describes a shortening with thickening of the walls of the cells of the rhizoids in A. cruciatum after making contact with the host. It is possible that this also occurs in this species and accounts for the differences in form of the attached and unattached organs. Rosenvinge (1923-24: 361), also in reference to A. cruciatum, describes the loss of the outer filaments of a cluster when the central ones become attached.

Tetrasporangia: — Most tetrasporangia are borne on the lower cells of the lower pinnules of each pinna (Fig. 19H) but a few may be scattered closer to the ends of the pinnules, and towards the outer part of the pinna. Only one tetrasporangium develops from each cell of a pinnule at one time, although a double gelatinous wall is sometimes evident, suggesting that a second tetrasporangium occurs in the position of a previous one which has been shed (Fig. 19H,a). Each mature tetrasporangium is sessile, ovoid, approx. 55-65 x 45-50μ within the gelatinous sheath, and is cruciately divided.

Spermatangia: — Spermatangial mother-cells are borne terminally on the cells of special short branches produced on the upper side of cells of the pinnules. As with tetrasporangia they are developed first from the basal and lower cells of the pinnules.

Each special branch consists of a rachis about 50μ long, consisting of 4-7 cells. The basal cell may bear a lateral branch with a rachis several cells in length (Fig. 19 Ia). The lower cells of the rachis each bear a whorl of 2-4 (often 3)vegetative cells which usually bear in turn a further whorl of 2-3 sterile cells, before producing the spermatangial mother cells terminally from the outer end of these cells. The upper cells of the central rachis usually support one whorl of sterile cells upon which the spermatangial cells are borne terminally, and at the apex of the rachis the spermatangial mother cells are borne directly upon the apical cell (Fig. 19I).

Development of Procarp and Carposporophyte: — Carpogonial branches are borne on the basal cells of young pinnae at branch apices. Each carpogonial branch initial is produced on a pinna only 2-3 cells below the apical cell of the branch (Fig. 19M). With further axial growth, a series of 10–16 carpogonial branches may be produced on the one branch apex. Axial elongation does not continue and with the development of a carposporophyte the branch apex is deflected laterally. Only one carposporophyte develops on one branch apex.

The carpogonial branch initial is attached to the lower side of the basal cell of the pinna (supporting cell) (Fig. 19J) and enlarges and divides to form a 4-celled carpogonial branch about 30µ long, which is curved upward around the supporting cell (Fig. 19K).

The first two successive divisions in the formation of the carpogonial branch are transverse and the third division is oblique giving cells of consistent characteristic shape (Fig. 19K,L). A long trichogyne, 80–100µ long, with a basal swelling develops from the carpogonium (Fig. 19L). The rachis of the pinna continues to grow after initiation of the carpogonial branch, but pinnules are seldom developed.

After fertilization the carposporophyte probably develops rapidly, as few stages of its growth have been seen. The trichogyne is lost and the supporting cell enlarges upwardly (Fig. 19M,N) and cuts off an auxiliary cell on the upper side. This cell stains densely while the old supporting cell often appears to lose its protoplast completely. Fusion occurs between this auxiliary cell and a connecting cell from the carpogonium (Fig. 19 O) and presumably the diploid nucleus is transferred to the auxiliary cell. Following this fusion there is rapid development of the foot-cell and central cell and a large terminal gonimolobe is formed. Widening of connections between axial cell and cells of the carposporophyte also occurs (Fig. 19 P,Q). The pit-connection between the axial cell and the residual supporting cell is broken down and the foot-cell fuses with the supporting cell. The second cell of the pinna (adjoining the basal supporting cell) becomes enlarged and stains densely (Fig. 19Q). The first gonimolobe forms a large vegetative cell from which two further vegetative cells develop on the upper side (Fig. 19 P-R). Each of these bears several cells which expand and divide to give basal vegetative cells and groups of carposporangia (Fig. 19 P-R).

A second and third gonimolobe are later cut off laterally from the central cell (Fig. 19R).

The pinnae borne on the axial cells below the carposporophyte curve upward to surround and protect the carposporangia. The cells of the rachis and pinnules at the base of these pinnae remain small (Fig. 19S). Gland-cells at the fertile branch apices are prominently developed on the young and immature pinnae.

Discussion: —

A. hanowioides is perhaps the most abundant species of Antithamnion on southern Australian coasts. This led Harvey (1854: 560), following Sonder's (1846: 166) account of Preiss' Western Australian collections, to distribute it as Callithamnion spinescens Kütz? (Harvey No. 540), although he was aware of dissimilarities between the two species. C. spinescens Kütz. (1843: 373) refers, however, to a completely different species having widely separated, comparatively short pinnae arranged in whorls of 4.

ANTITHAMNION VERTICALE (Harvey) J. Agardh 1892: 20. De Toni 1897: 1397. Lucas 1909: 51. Lucas & Perrin 1947: 352.

Callithamnion verticale Harvey 1854: 561. J. Agardh 1876: 25. Wilson 1892: 187.

Callithamnion horizontale Harvey 1854: 560. J. Agardh 1876: 26.

Antithamnion horizontale J. Agardh 1892: 20. De Toni 1897: 1397. Lucas 1909: 51; 1929: 52. Lucas & Perrin 1947: 352. Reinbold 1898: 53.

Callithamnion dimorphum Harvey 1863, synop. ~~No.~~ 695.

TYPE Locality: — Garden Island, Western Aus.

TYPE: — TCD, Herbarium Harvey, No. 267.

DISTRIBUTION : — Rottnest Is., Western Aust., to Robe, South Aust.

General Features: — In vegetative structure the plant is similar to Antithamnion hanowioides but differs in the degree of rotation of the pairs of pinnae on adjacent axial cells and in the curvature of the pinnae.

The thallus consists of prostrate and erect parts having, as in A. hanowioides: —

(1) Axial growth by divisions of a dome-shaped apical cell to form an axis of cylindrical cells which, when mature, are about twice as long as broad (130 x 250µ).

(2) Lateral branches borne at irregular intervals from the basal cells of the pinnae.

(3) Pinnae arranged in opposite pairs, each pinna up to 900µ in length with a zig-zag rachis and small hat-shaped basal cell.

(4) Pinnules simple, or with one to several simple branches on the lower side, and alternately arranged from cells of the rachis

of the pinna. Lowest pinnule(-s) often more branched than upper ones. Relative arrangement and divergence of pinnules and pinnae as in _A. hanowioides_.

(5) Gland-cells borne on special short branches 3-5 cells in length on the underside of the pinnules and usuallyfrom the 2nd (or 3rd) cell.

(6) Attachment by rhizoidal filaments which develop in clusters from the basal cell of each pinna. Only a few from each cluster attach to the host by means of a digitate holdfast. These contract by shortening and broadening of their cells while non-functional ones are lost.

Reproductive Organs — Not recorded.

Antithamnion verticale differs from _A. hanowioides_: —

(1) In having an apparently distichous arrangement of the pairs of pinnae, and

(2) The rachis of each pinna set at almost 90° with the main axis.

In _A. hanowioides_ the decussate arrangement of the pinnae is often modified to a rotation of about 45° rather than 90° between pairs of pinnae on adjacent axial cells. The degree of rotation is however not consistent, and as the pinnae are stiff and curved upward in unattached parts of the thallus (Fig. 19A (_A. hanowioides_)) this rotation may be necessary to accommodate the overlapping pinnae. This is also suggested by the fact that axial cells of the attached parts of the axis which bear almost erect pinnae, are often not rotated.

Plants of A. verticale occasionally show some rotation between adjacent axial cells, as, for example, where attachment rhizoids, formed alternately from basal cells of pinnae, pull downward to right and left respectively and cause rotations of up to 45° in adjacent axial cells. In A. ~~dimorphum~~ verticale and A. hanowioides the initiation of pinnae usually shows a small degree of rotation of pairs on adjacent axial cells.

Discussion: —

Antithamnion verticale and A. horizontale were originally described as separate species (Harvey 1854) on the basis of having the flattened surface of the distichously branched pinnae either vertically or horizontally orientated on the axis.

Individual plants show variation between the vertical and horizontal position of pinnae and there is often marked variation even on the one plant. For example the pinnae may appear vertically arranged where the attached portion of the plant is epiphytic upon a flattened host, but may tend towards the horizontal in unattached parts of the thallus. This suggests that the position of the pinnae probably varies with external factors. This was recognized by Harvey (1863; synop: 695) when he united and redescribed the two species as Callithamnion dimorphum. On a priority basis the name must revert to one of the earlier epithets and A. horizontale is here included as a synonym of A. verticale. J. Agardh (1876) quotes differences in dimensions of axial cells and pinnules between A. verticale and A. horizontale. Variations greater than those indicated by Agardh, occur between plants and even between parts of the same plant, and variations of this degree cannot be used to separate the species.

Although A. verticale is similar to A. hanowioides, the differences (in curvature and position of insertion of pinnae on adjacent axial cells) are sufficiently consistent to distinguish the two species.

DOUBTFUL SPECIES OF ANTITHAMNION

1. ANTITHAMNION AUSTRALE (J. Ag.) De Toni 1897: 1407. Lucas 1909: 51.

Callithamnion australe J. Agardh 1841: 42; 1851: 26; 1876: 21; 1885: 2. Kutzing 1849: 649.

TYPE Locality: — Pt. Phillip, Vic.

TYPE: — LD, Herbarium J. Agardh, No. 17960 (on Pterocladia lucida (R. Br.) J. Agardh). Probable isotype in MEL, No. 10269.

DISTRIBUTION: — Known only from the type locality.

The species does not belong to Antithamnion, nor to Antithamnieae. It is distinct in having:

(1) Rounded branch apices and large thallus cells.

(2) Opposite, distichous whorl-branchlets, with several cells borne from each basal cell; each of these cells may develop into a branch of the whorl-branchlet.

(3) Attachment organs borne in opposite pairs from the lower end of each axial cell (i.e. from opposite end of cell to that bearing whorl-branchlets).

(4) Terminal digitate attachment organ in the form of a whorl of fine apparently dichotomously branched branches on each rhizoid.

Investigation of fresh material is necessary to determine the identity of the species.

2. ANTITHAMNION FLACCIDUM (H. & H.) De Toni 1897: 1414.

Callithamnion flaccidum Hooker and Harvey 1845: 273; Harvey 1860: 334.

TYPE Locality: — Cape Horn.

TYPE: — Kew.

DISTRIBUTION: — One record from Tasmania (Gunn). Sub-antarctic, New Zealand.

Harvey (1860) reports the species from Tasmania (Gunn) but mentions that the specimens are not in good order. It is doubtful whether Gunn's specimen agrees with the type of Callithamnion flaccidum from Cape Horn, and careful checking of the Australian plant is necessary. Three specimens labelled Antithamnion flaccidum in MEL are not of this species. No other material is at present available.

3. ANTITHAMNION NIGRESCENS J. Agardh 1894: 116. De Toni 1897: 1404. Lucas 1909: 51. Lucas & Perrin 1947: 353.

TYPE Locality: — Port Phillip Heads, Victoria.

TYPE: — LD, No. 18128, Herb J. Agardh.

DISTRIBUTION: — Known only from the type collection.

The type specimen was collected by J. Bracebridge Wilson (2-II-1892) and there has been no further record of the species. It appears, however, to be distinct from other known species of Antithamnion or related genera and is closest in form to Platythamnion nodiferum in which the rachis of each whorl-branchlet (pinna) is extended further than usual beyond the unilaterally arranged pinnules.

4. ANTITHAMNION PLUMULA (Ellis) Thur. 1863: 112.

De Toni 1897: 1400; 1924: 493. De Toni & Forti 1922: 55. Lucas 1909: 51; 1929a: 25. Lucas & Perrin 1947: 352. May 1946: 123.

Callithamnion plumula Lyngb. 1819: 127.

J. Agardh 1851: 29. Harvey 1847: 412; 1860: 333; 1863, syn: 690. Wilson 1892: 187.

Callithamnion plumula var. investiens J. Ag. 1876: 24.

(Other synonomy is not applicable to the southern Australian plant, e.g. Conferva plumula Ellis 1768).

Antithamnion plumula is a northern hemisphere species and records from southern Australia are rare. The only specimens available are from Port Phillip Heads (J. Bracebridge Wilson, 6-II-1893, MEL 10258), although there are records of collections from Georgetown, Tasmania (Gunn, Harvey, Archer) in Harvey (1860) and more recently (May 1946) from 5 fathoms in D'Entrecasteaux Channel, Tasmania (Tubb). According to May the species is abundant along the coast of New South Wales from Bateman's Bay to Jervis Bay.

The southern Australian plant agrees well with specimens of Antithamnion plumula in Harvey's herbarium, TCD, and with recently collected plants from Trevone, Cornwall, U.K. (Womersley, 13-VIII-1964, AD, A28,324).

Kylin (1925) has included Antithamnion-like plants having unequal pinnae in whorls of 4 (2 opposite long pinnae and 2 opposite short pinnae) in the genus Platythamnion J. Ag. and has described several species from the west coast of America, e.g. Antithamnion plumula var. crispum = Platythamnion pectinatum Kylin½. The southern Australian plant has pinnae arranged in this manner and also differs from other species of Antithamnion in southern Australia in developing a much larger, branched, erect thallus (2-8 cms), with probably sessile gland-cells and a comparatively reduced number of procarps per branch apex each developed on the basal cell of a reduced pinna. The latter two features cannot be distinguished with certainty from the dried material available. Kylin (1956) believes that this reduction in length of fertile pinnae found in Platythamnion, and in which the genus simulates Antithamnion pacificum, is of phylogenetic significance and indicates a more advanced development than occurs in those species in which the procarp is developed on a pinna of normal length.

The genus Antithamnion is limited to include only small creeping plants in which the unattached part of the prostrate thallus forms the erect portions, in which gland-cells are borne on special short (2-4 celled) branches and which successively produces 8-20 procarps at each branch apex.

Following these distinctions it is probable that the form of Antithamnion plumula which occurs in Australia should be included in the genus Platythamnion. ~~probably as Platythamnion plumula nov. comb.~~ Examination of fresh material is, however, necessary for specific determination. The identity of Callithamnion plumula var. investiens J. Ag. is discussed with Platythamnion nodiferum (J.Ag.) nov. comb.

PLATYTHAMNION J. Agardh 1892

The genus Platythamnion J. Agardh was based upon Callithamnion heteromorphum J. Ag. from California as the type species. J. Agardh (1892) separated it from Callithamnion mainly on the basis of cruciately divided tetrasporangia, and the initial development of carposporangia. Until the present time records have confined the genus to the west coast of north and south America.

In reproductive features it resembles Antithamnion and, according to Kylin (1925), is therefore closely related to the latter genus. It is, however, distinct and differs from Antithamnion in having: —

(1) Whorls of 4 whorl-branchlets (pinnae) (two lateral larger ones and 2 transverse smaller ones) from each axial cell. In Antithamnion there are pairs of equal pinnae from each cell.

(2) Lateral branches developed alternately and rapidly so that the growing apex is deflected away from the newly-formed branch. The branch apex is consequently characteristic in form and differs from Antithamnion in which there is no deflection of the main axis with production of lateral branches.

(3) Gland-cells, sessile on the central cells of the pinnae or on the pinnules. They are not produced on a short special 2-4-celled branch as occurs in Antithamnion.

Species of Platythamnion are larger than those of Antithamnion and usually attach by a discreet holdfast without a creeping portion at the base of the thallus as found in Antithamnion. Previously recorded species

→ of *Platythamnion* grow to at least 8 cm. in height which is considerably larger than most species of *Antithamnion* (*A. hanowioides* grows to 3 cm. and has the largest unattached portion of thallus for southern Australian species).

Similarities in reproduction in particular suggest that the genus has developed from an *Antithamnion*-like ancestor and has evolved mainly in vegetative features. Kylin (1925) describes northern American species of *Platythamnion* and comparison with his figures confirms the identity of the Australian plant.

Harvey (1847: 489) described *Callithamnion simile* from Christmas Harbour, Kerguelen's Land, and later (1854: 561) included plants from Western Australia (King George's Sound and Rottnest Is. Alg. Aust. exs. No. 543) as the same species. J. Agardh (1876: 25) considered three species to be included in *Callithamnion simile* Harvey and separated two Australian species from the Kerguelen plant. He named one Australian species (Port Fairy, Victoria) *C. nodiferum* and referred the other to *C. plumula*, as var. *investiens*.

No plant of *Callithamnion simile* Harvey from Kerguelen has been examined, but *C. plumula* is decidedly distinct from the Australian *C. nodiferum*. From Harvey's description (1847: 489) *C. simile* is a smaller plant ($2\frac{1}{2}$-12 cm) than *C. nodiferum* with less consistently regular lateral branching and shorter pinnae (560μ) bearing pinnules often more compoundly branched than those of the southern Australian species.

Thus C. nodiferum must remain as a distinct species at least until the Kerguelen's Land plant is known in more detail.

Detailed investigation of ~~Anti~~ Calli thamnion nodiferum has shown that the species belongs to the genus Platythamnion. It agrees with the type species in arrangement of pinnae, development of lateral branches and in reproductive features, and differs mainly in being a much larger plant (to 20 cm) with axes which are strongly corticated with rhizoids in the lower parts of the thallus. Rhizoidal cortication has probably developed with the increase in thallus size and is not a feature sufficient to exclude it from the genus. One plant (AD, A29,286) shows strong development of both tetrasporangia and carposporangia on the same plant. The species most closely resembles Platythamnion pectinatum Kylin (~~Kylin~~ 1925: 53 fig. 34a-c) but differs in structure of pinnae, size of plant and in having a corticated axis. It is probable that ~~C.~~ Callithamnion plumula var. investiens (see above) also belongs to this genus.

TYPE species: — Platythamnion heteromorphum (J.Ag.) Kylin.

PLATYTHAMNION NODIFERUM (J. Ag.) nov. comb.

Antithamnion nodiferum (J. Agardh) J. Agardh 1892: 20. De Toni 1897: 1404; 1924: 494. Lucas 1909: 51; 1929: 52; 1929a: 25. Lucas & Perrin 1947: 353. Reinbold 1898: 53.

Callithamnion nodiferum J. Agardh 1876: 25.

Callithamnion simile sensu Harvey 1854: 561; 1862: pl. 207: 1863; synop: ~~No.~~ 691 (See note under generic description).

TYPE Locality: — Pt. Fairy, Victoria.

TYPE: — LD, Herb. Agardh, No. 18139 (Harvey No. 543).

DISTRIBUTION: — From Rottnest Island, Western Aust. (Harvey) to Sealer's Cove, Victoria.

(Fig. 20).

General Features: — The plant grows to about 20 cm in height and is attached by a fibrous discoid holdfast. Several branches arise from the base and these become twisted and densely matted with the lateral branches in the lower part of the plant. Axial cortication of somewhat curly filaments occurs in the older parts of the thallus and adds to the density of the tangled mat of twisted branches.

Distinctive features of the thallus organization are:

(1) Arrangement of lateral branches, which occur alternately at equal intervals along the axis making a constant angle of about 60° with the axis;

(2) Form of the opposite pairs of major pinnae which are almost horizontal to the axis, often with recurved apices, and which usually bear unilaterally arranged pinnules on the upper side (Note — a pair of minor pinnae also occur from the upper part of each axial cell. See later description on arrangement of pinnae). (Fig. 20A).

Structure of the Thallus: —

(1) Form and Development of Main Branches: — Growth takes place by transverse divisions of a dome-shaped apical cell and pinnae initials develop on cells only one or two below the apex. A long series of immature axial cells remains at actively-growing axial apices (Fig. 20B). Cells of

the mature axis are from 1 to $2\frac{1}{2}$ times as long as broad and measure 250-300µ x 100-150µ.

Lateral branches are borne alternately to right and left on the basal cell of a major pinna on every 4th-6th axial cell. At the base of a new axis 9-15 cells may occur before lateral branching commences. A new lateral branch quickly just overtops the main branch apex (Fig. 20B - A_1 represents the main axis and B_1, B_2 and B_3 are three lateral branches each initiated opposite a major pinna). Branching is thus monopodial and the curvature of the axis away from each new lateral branch is due to the rapid growth of the branch causing an oblique deflection of the axial apex (Fig. 20B - the apex A_1 is deflected to the left due to the enlargement of the axial cell on the face bearing the lateral branch B_3).

(2) Development, Arrangement and Branching of Pinnae: — Each mature axial cell bears a whorl of four pinnae from its upper part. The pinnae are arranged in opposite pairs with each pair set at 90° to the other. The pair of pinnae which lie in the plane of lateral branching of the thallus (referred to as the major pinnae) are larger and more branched than the second pair which lie between them (the minor pinnae). Pinnae are initiated as protrusions from axial cells immediately below the branch apex and develop rapidly to form a simple tapering chain of cells which constitutes an unbranched pinna. The development of pinnules is not consistent and uppermost pinnae may bear none or, at most, one or two pinnules, while pinnae about the centre of the thallus may bear several, simple or occasionally branched, pinnules arranged unilaterally along the upper side of the rachis of the pinna (Fig. 20E). The pinnules toward the base of the pinna may be branched with simple horizontal branches on the outer side, while the 2nd to 5th cells of the pinna usually bear the most robust pinnules,

The major pinnae are from 9-18 cells (600-900µ) in length with cells of the rachis about 1 to 2 times as long as broad (average 60x30µ). The cells are somewhat smaller towards the base of the pinna which also tapers to an acute tip. Pinnae from the centre to lower parts of the thallus may be a few cells longer than those above, bear several more pinnules, and have branches on the pinnules towards the base of the pinna. The rachis of mature pinnae is usually curved upward in the central part with a downward curve, or occasionally a distinct hook, at the tip. Thorn-like processes of one or two small cells with abrupt acute points and set in thick gelatinous sheaths may occur on the small cells at the outer ends of pinnae in the upper parts of the plant (Fig. 20C). These are lost later and are not found in older pinnae.

The minor pinnae of the central and upper parts of the thallus are smaller than the major pinnae. In upper parts of the plant they are simple and unbranched and usually curved more or less upwardly (Fig. 20E) while in the central thallus they usually bear several simple pinnules.

Towards the base of the thallus all four pinnae of each whorl are equivalent in form, are stiff and densely branched and lack regularity in planes of branching which is characteristic of the central and upper parts of the thallus.

Gland-Cells: — Gland-cells are prominent, particularly in the younger parts of the thallus, and are borne on the upper side of the 3rd or 4th (-5th) cell of the rachis of a pinna. Occasionally they also occur on the outer side of the third or fourth cell of the first or second pinnule on a pinna. Gland-cells are sessile, almost spherical, about 40-45µ in diameter within the gelatinous sheath and have a pitted surface appearance (Fig. 20D,E).

Axial Cortication: — The lower parts of the thallus are covered by a dense rhizoidal cortication of the axis. Rhizoids are developed on the lower side of the basal cells of the pinnae (Fig. 20F) and finer ones may occur from the lower cells of special branches such as those bearing the tetrasporangia (Fig. 20F,b). The rhizoids extend downward, branch occasionally and intertwine with the pinnae which, in this part of the thallus, curve downward (Fig. 20F). Where the tips of the rhizoids come in contact with the substratum a branched attachment organ may be formed (Fig. 20G).

Tetrasporangia: — Tetrasporangia are borne on special branched branches developed on the outer side of the lowest one or two cells of the first and second pinnules of any of the 4 pinnae of a whorl (Fig. 20B).

Tetrasporangia are borne laterally on the branches of the special branch and are sessile, ovoid when young but almost spherical when mature (33-40µ diam. within the gelatinous sheath) and divide cruciately (Fig. 20R-V). A second tetrasporangium may develop within the gelatinous sheath of a previous tetrad as a double sheath often occurs around a tetrasporangium (Fig. 20H,W).

Spermatangia: -- Spermatangial clusters are borne on the lower cells of the pinnae and basal pinnules. Each cluster consists of a special branch which branches several times and bears terminally from each cell of the final order of vegetative branching a growth of three or four spermatangial mother-cells (Fig. 20P). Some clusters may be very densely branched. The spermatangial mother-cells are cut off from elongate protrusions of the terminal vegetative cell (Fig. 20Q) and become rounded and 3-5µ diam, with densely staining protoplasts. The complete structure is surrounded by a thick gelatinous sheath.

Development of Procarp and Carposporophyte: — Carpogonial branches are borne on the basal cells of the pinnae and are usually initiated from the lower part of the cell and curve upward around it. As many as four carpogonial branches may be borne on one whorl of pinnae (one on each pinna), but more often they occur only on the major pinnae. Initiation of carpogonial branches commences near the branch apex (Fig. 20I). Elongation of the axis and further initiation of carpogonial branches continues until about 8-20 carpogonial branches are formed (Fig. 20N) before axial elongation ceases. Carpogonial branches on adjacent pinnae are directed alternately to either side of the basal (supporting) cell of the pinna above so that they do not overlap one another. Pinnae bearing carpogonial branches continue to grow until fully developed.

Each carpogonial branch is formed by three successive transverse divisions of the initial to give a 4-celled carpogonial branch with elongate trichogyne (Fig. 20J-M).

Stages in development of the carposporophyte have not been observed. Only one carposporophyte matures at each branch apex. Carposporangia are produced in rounded groups developed successively from a rounded central cell (Fig. 20 O) with the terminal group produced first. The carposporangia are formed by divisions of cells cut off from the outer end of large initial cells which remain vegetative.

The carposporophyte is protected during development by the upcurving of the surrounding pinnae.

Discussion: —

Included in notes on genus.

BALLIA Harvey 1840 .

The genus was described by Harvey with Ballia brunonia as the type species and he considered it very probably the same plant as C. Agardh's Sphacelaria callitricha. C. Agardh described Sphacelaria callitricha from a faded specimen and although Harvey recognised similarities to the genus Sphacelaria in his new plant he described it as "abundantly distinct" primarily on the basis of colour, but also on features such as substance and joint structure.

The genus is widespread in cooler seas of the southern hemisphere with Ballia callitricha occurring abundantly in the cool temperate and sub-antarctic regions. Its ability to reinitiate growth of whorl-branchlets is distinctive and has been responsible for the confusion and synonomy which has been associated with the species. Many specimens from southern Australia have been examined, but for a complete understanding of the species, further detailed comparisons with collections from other localities is essential.

Other species, e.g. Ballia mariana and Ballia ballioides, are less widely distributed, occur less frequently and are comparatively well-defined species.

In growth pattern and thallus structure the genus is highly specialised in comparison to other genera of the Antithamnieae. Unfortunately sexual reproduction is not known (except for one spermatangial plant of B. mariana), for southern Australian species and hence the tribal affinities of the genus cannot be surely determined. Schmitz and Hauptfleisch (1897) describe 4-celled slightly curved carpogonial branches developed in the axils of whorl-branchlets and which developed cystocarps surrounded by an involucre of short branches. Laing (1905 p.400), and probably following Schmitz and Haptfleisch, has recorded some details of procarp and gonimoblast formation for the genus, but gives neither figures nor reference to the species described. Hommersand (1963, p. 332) states that procarps are "produced on small fertile side branches", but again does not give species nor origin of the information. Characteristic features of the genus are: —

1. Thallus usually over 15 cm in height, distichously (or tristichously) branched with opposite arrangement of 2 or 3 whorl-branchlets from each axial cell. B. scoparia and B. hirsuta are sometimes less than 15 cm high and are not distichously branched. (Ballia sertularioides (Suhr) Papenfuss is apparently a much smaller plant, and is not recorded from southern Australia (Papenfuss 1940; Baardseth 1941). According to Suhr (1840) the type specimen of Callithamnion sertularioides is " 6 lines" (≡ 1.15 cm) high).

2. Whorl-branchlets (except in Ballia hirsuta and B. scoparia) are borne laterally on the axis and bear regularly arranged branches which may themselves be simple or branched (usually the whorl-branchlets are of pinna-form with opposite distichous pinnules).

3. Growth occurs from a large apical cell and the axes are somewhat cartilaginous in texture and densely corticated in the upper-central to lower parts of the thallus. Cortication is by means of (a) short branches borne on the basal cells of whorl-branchlets, and (b) descending rhizoidal filaments which bear short outwardly-directed branches (B. scoparia and B. hirsuta differ in the origin

of cortical filaments as described below). Attachment is by means of a holdfast formed from densely matted and interwoven rhizoidal filaments.

4. Axial cells are cylindrical and fit closely against adjacent cells. In B. callitricha and B. pennoides the cell junctions are particularly specialized and overlap one another. In all species (except B. mariana and B. ballioides) the pit-connections are capped on either side by dome-shaped structures not known in other genera.

5. Gland-cells, as occur in all other genera of Antithamnieae, are entirely lacking.

Ballia scoparia differs from other species in a number of features. Its inclusion in the genus is discussed below, and, although probably better placed in a separate genus, it is tentatively left with Ballia at least until its sexual reproduction is known. B. hirsuta is similar to B. scoparia in growth of thallus and branching, but is comparable with other species in developing outward branches from the rhizoidal filaments.

In its consistent and specialized thallus structure the genus is phylogenetically advanced. Several trends are apparent within the genus, particularly in respect to growth pattern and simplification of whorl-branchlet structure.

Growth is basically monopodial and in B. mariana and B. ballioides whorl-branchlets and their branches are determinate in length. B. callitricha is, however, distinct in its ability to reinitiate growth of the rachides of whorl-branchlets. This could represent a step toward the growth pattern seen in *B. scoparia* and in *B. hirsuta* where most young whorl-branchlets continue to grow and branch indefinitely thus obscuring the dominance of a single central axis at branch apices. *B. scoparia* and *B. hirsuta* also produce branchlets, equivalent to whorl-branchlets, of determinate growth and thus retain a link with the growth pattern of other species. *B. hirsuta* and *B. scoparia* are probably the most highly evolved of any species of the Antithamnieae in superceding the thallus habit of a central axis bearing whorls of determinate whorl-branchlets from each cell.

A change in form of branchlet accompanies the change in growth pattern in *B. scoparia* and *B. hirsuta* and produces a thallus which is very different in form from that of other species. The commencement of the formation of an unbranched whorl-branchlet probably occurs in *B. callitricha* where elongation of the rachis and shedding of the pinnules can result in an elongate, simple branchlet comparable with the form found in *B. hirsuta* and in *B. scoparia*. A further difference in *B. scoparia* is the complete absence of whorls of branchlets; instead branchlets are produced at regular intervals along the axes.

Filaments which corticate the axis of *B. scoparia* arise from small cells produced on the axial cells of the thallus and these probably represent residual basal cells from which branchlets could once have arisen. Upwardly directed rhizoids sometimes develop from these cells, and very likely represent modified branchlets. The axial cortication of *B. hirsuta* is probably intermediate between *B. scoparia* and other species of *Ballia*. Outwardly directed short branches, similar in form to normal branchlets are produced from cells of the corticating rhizoids. These are comparable in position of origin to the comparatively shorter branches which arise from the rhizoids in other species of Ballia or to the condition in B.scoparia where all branches of rhizoids are modified to a rhizoidal form.

The structure of whorl-branchlets has probably evolved, as has probably also occurred in Antithamnion, from alternately-branched pinnules (B. mariana) to oppositely-branched pinnules (B. ballioides, B. callitricha), and finally to unbranched pinnules (B. pennoides) or complete absence of pinnules (B. scoparia and B. hirsuta).

Ballia pennoides is similar to B. callitricha, while B. mariana and B. ballioides are probably more primitive in features of growth, pinna form and axial cell structure than the other species.

TYPE species: — Ballia callitricha (Ag.) Mont.

Key to the southern Australian species of Ballia

1. Thallus elongation chiefly from the apices of distinct main axes. Each axial cell bears a whorl of 2-3 whorl-branchlets which are distichously (or tristichously) arranged... 2

1. Thallus elongation from a number of equivalent branches. Branchlets borne singly on non-adjacent axial cells. Branching not distichous (nor tristichous)... 5

   2. Whorl-branchlets in whorls of 3 from each axial cell. Each whorl composed of one long branchlet opposite a pair of short branchlets... 3

   2. Whorl-branchlets in opposite pairs (in 3's in the tristichous form of B. callitricha) from each axial cell and usually about equal in length 4

3. Pinnules of pinna-like branchlets in whorls of 3 from each cell of the rachides of the pinnae and arranged in longitudinal rows (2 above and 1 below) along each rachis. Pinnules usually alternately branched... ... ... B. mariana

3. Pinnules of pinna-like branchlets distichous in opposite pairs from each cell of the rachides of the pinnae; each pinnule bearing pairs of simple opposite branches... ... ... B. ballioides

   4. Pinnules of the pinna-like branchlets and the short branches, which arise from basal cells of pinnae, always simple and unbranched... ... ... B. pennoides

   4. Pinnules of the pinna-like branchlets branched with opposite pairs of simple branches. Short branches, which arise from basal cells of pinnae, always branched ... . B. callitricha

5. Thallus with dense development of simple branchlets. Axes densely corticated with much-branched, interwoven, rhizoidal filaments but without outwardly-projecting branchlets produced from the cells of the filaments... ... ... B. scoparia.

5. Thallus of a number of discrete axes each densely corticated with branched, interwoven, rhizoidal filaments and shaggy with a dense development of outwardly-projected short branchlets (to 3000μ long) produced from the cells of the filaments... ... B. hirsuta.

BALLIA MARIANA Harvey 1855.

Harvey 1855: 335; Alg. Aus. exs. No. 499; 1862: pl. 212. J. Agardh 1876: 58. De Toni 1897: 1394. Lucas 1909: 51; 1929: 52. Lucas and Perrin 1947: 350. Reinbold 1898: 51. Wilson 1892: 186.

TYPE Locality: — Port Fairy, Victoria.

TYPE: — TCD, Herbarium Harvey, No. 499.

DISTRIBUTION : — From Elliston, South Australia to Port Phillip, Victoria.

(Fig. 21 A - E).

General Features: — The thallus is to 20 cm high with axes densely corticated by rhizoidal filaments in the central and lower parts. Attachment is by means of a holdfast formed from an interwoven mat of similar filaments. Growth is distinctly monopodial and axial elongation occurs by transverse divisions of a dome-shaped apical cell. The general pattern of development is similar to that described for Ballia ballioides. Mature axial cells are about $1\frac{1}{2}$-2 times as long as broad (about 250 x 130µ) in the uncorticated parts of the axes. Each axial cell bears a whorl of three whorl-branchlets (pinnae) from its upper part. The whorl consists of one long major pinna (to 1700 µ long) and an opposite pair of shorter minor pinnae (to 700µ long) which are directed more or less upward. The major pinnae are alternate and distichous on the axis and the base of each is overlapped by and lies between the pair of minor pinnae formed on the axial cell below (Fig. 21A). The basal cell of the rachis of each long pinna remains slightly smaller than the rachis cells immediately above it, which are 2-3 times as long as broad. The rachis tapers outwardly and terminates in a curved chain made up of smaller cells which are approximately as long as broad.

Each long pinna usually bears three longitudinal rows of pinnules made up of whorls of three from each cell of the rachis. The pinnules are arranged with an upper pair and a single pinnule on the lower side of each cell. The upper pair form two longitudinal rows which may envelop the single row on the lower side of the next long pinna above.

Each pinnule is branched with opposite or, more often, alternately arranged simple branches and terminates in a comparatively long, unbranched tip. Pinnules of the single row on the lower side of the rachis sometimes bear three rows of branches. The ends of the pinnules of the upper row curve inward toward one another. Minor pinnae are branched similarly to the pinnules of the major pinnae but often with longer branches. They may bear either 3 or 2 rows of branches on the rachis (Fig. 21B). Density of branching and length of branches varies from plant to plant and between older and younger parts of the same plant. Lateral branches of indeterminate growth develop in place of major pinnae, and usually occur as alternate pairs borne on adjacent axial cells at intervals of 9-12 axial cells.

Cortication of the axes commences in the upper to central part of the thallus and forms a dense cover over the older axes. Small branches, similar in form to reduced pinnules occur from the basal cells of pinnae and these intertwine with curved lateral branches which are produced outwardly from descending rhizoids which also arise from the basal cells of pinnae (Fig. 21C). This form of axial cortication is identical with that of <u>B. ballioides</u>.

Tetrasporangia: — These are borne terminally on branches of short special branches produced on the lower cells of pinnae and pinnules. These branches may develop on the basal cell of the rachis or may replace normal branches of the lower to central pinnules (Fig. 21D). Tetrasporangia are cruciately divided and about 30μ diameter when mature.

Spermatangia: — Spermatangia are borne terminally on cells of pinnule branches especially in the upper parts of the plant (Fig. 21E). All pinnules on the pinnae may be fertile.

Carposporophytes: — unknown. Groups of fungal spores simulating rounded groups of carposporangia often occur on the young parts of the plant near branch apices. Pinnules with curved elongated branches appear to form an involucre surrounding the groups.

Discussion: —

Ballia mariana is structurally very similar to B. ballioides and differs chiefly in the branching pattern of the pinnules. The thallus in both species is of similar size and has identical patterns of lateral branching, cortication and tetrasporangium development. Dried fresh plants of B. mariana are usually paler in colour than those of B. ballioides. One male plant of B. mariana is the only known certain record of a sexual plant of any species of Ballia in southern Australia.

BALLIA BALLIOIDES (Sonder) nov. comb.

Ballia robertiana Harvey 1855: 335; alg. Aust. exs. No. 500; 1858: pl. 36; 1860: 332. J. Agardh 1876: 58. De Toni 1897: 1394; 1924: 491 (under B. beckeri). Dickinson 1949: 29. Lucas 1909: 51; 1929: 52; 1929a: 25. Lucas & Perrin 1947: 349. Reinbold 1897: 60. Wilson 1892: 186.

Callithamnion ballioides Sonder 1852: 674.

TYPE Locality: — Guichen Bay, South Aust. (F.v.Mueller).

TYPE: — MEL, 8545.

DISTRIBUTION: — From Port Elliot, South Australia, to Port Phillip, Victoria, and in Tasmania (Southport, Stuart).

(Fig. 21, F-I)

General Features: — Thallus 10-12 (-18) cm. high with axes densely corticated with twisted rhizoidal filaments in the central to lower parts. Attachment is by a fibrous holdfast formed from densely interwoven rhizoids. Dried plants are dark in colour, with only new growth being sometimes paler.

Growth is monopodial (Fig. 21H) with a distinct central axis which bears a whorl of whorl-branchlets (pinnae) from each cell. Lateral branches occur in place of pinnae and often form in alternate pairs from two adjacent axial cells with intervals of 8-12 axial cells between pairs. Mature axial cells are about $1\frac{1}{2}$-2 times as long as broad (e.g. about 320x190μ in the uncorticated parts of the thallus).

Each whorl of pinnae is borne on the upper part of each axial cell and consists of one long (major) pinna with a pair of short (minor) pinnae opposite to it (Fig. 21, F, G).

Major pinnae are distichous and alternately placed on the main axes. Each major pinna (Fig. 21H, No. 1) usually bears 10-13 (-16) pairs of pinnules and is about 1500(-2000)μ long. Each pinnule bears pairs of opposite, distichous simple branches which are close together and normally touching one another. The complete pinnule has the pinna form of Acrothamnion preissii, but lacks a terminal gland cell. The final cells of the rachis of the pinna bear opposite, simple, pinnules which together form a structure similar to a normal single pinnule. The basal cell of each pinnule usually bears only one branch which is on the lower side and is shorter than the adjacent pairs of branches. The mature pinnules are characteristic in shape and are larger at the base of the pinna than at the outer end. The lower and outer pinnules are about 380μ and 130μ long respectively. The cells of the rachis of the pinna also taper towards the outer part; central cells are about 170 x 90μ. The basal cell of the rachis is smaller than the cells above. Initial stages in the formation of pinnae and pinnules occur as in Fig. 21H, a & b. The minor pinnae which occur in pairs opposite each major pinna are variable in form. Frequently they consist of an inwardly curved rachis, 600-800(-1000) μ long, which bears pairs of simple pinnules (Fig. 21F, Nos. 2 and 3), which may in turn bear simple branches. There may be one to several branches on the lower pinnules, or branches may occur unilaterally along the lower (or upper) side of a pinnule, or, as occurs frequently in the type fragment, each pinnule may be similar in form to a pinnule of the major pinna.

The axis in the central and lower parts of the thallus becomes densely corticated with rhizoidal filaments which arise from the basal cells of the pinnae and which become densely intertwined. In the lower parts of the plant they are mixed with the shorter pinnae. An inner layer of filaments grows downward and outwardly-projecting branches arise from them. These branches are curved and branched and become densely interwoven to form a tangled mat over the axes. Similar curved filaments arise directly from the basal cells of the pinnae (Fig. 21F). These are the earliest form of cortication and loosely cover the axis before the vertical filaments are initiated.

Tetrasporangia: -- Tetrasporangia occur terminally on special branched pinnae which occur on the basal cells of the normal pinnae or which may replace the lower pinnules usually on the upper side of the rachis. Each tetrasporangium is cruciately divided and 35-40µ diam. when mature (Fig. 21 I).

Spermatangia and Carposporangia: — Spermatangia are not recorded. "Favellae" were reported by Harvey (1858) for Ballia robertiana but there is no other record of carposporophyte development and it is likely that Harvey's favellae were groups of fungal spores such as are commonly associated with the species.

Discussion: —

Ballia robertiana Harvey is synonomous with Sonder's earlier Callithamnion ballioides which epiphet, on the basis of priority, must be retained. The type of Harvey's Ballia robertiana (Port Fairy) is in TCD, No. 500. Ballia ballioides is variable particularly in the form of the two shorter pinnae which occur in each axial whorl. Gradations in branching form of these pinnae occur even on the same plant. The species is, however, clearly distinct in habit, axial cortication and especially in the form and arrangement of the pinnae. Ballia beckeri Schmitz ex Mazza, from the Kowie, South Africa, closely resembles B. ballioides in many respects. De Toni (1924) considers the two species to be hardly distinguishable but Dickinson (1949) states that "microscopically the two are widely different" and bases her conclusion on:

1. Difference in width of frond just below tip (1-1.75 mm in B. beckeri and 0.75 - 1 mm in B. robertiana).
2. Laxity in habit of B. beckeri compared with that of B. robertiana.
3. Length of plant to 20 cm. in B. beckeri and about 10-15 cm. in B. robertiana.
4. Absence of pinnules on the first 3-5 distal joints of the larger pinnae.

In consideration of the variation in form which may occur within a plant, the first three of Dickinson's points of comparison are insignificant in separating the species. Only one South African plant has been available for comparison but it shows a distinct reduction and modification in form of the lower pinnules on the upper side of the major pinnae, and, on this basis, it is suggested that B. beckeri be retained as a distinct species until detailed comparison can be made with the type specimen and with fresh collections of B. beckeri.

BALLIA CALLITRICHA (Ag.) ~~Montagne~~ Kützing 1843: 293.

Montagne 1845: 94. J. Agardh 1851: 75; 1876: 57; 1879; ~~taf.~~ pl. III, fig. 1-11. Cotton 1915: 190. De Toni 1897: 1393; 1924: 491. Gain 1912: 75. Harvey 1860: 332; 1863; synop: ~~No.~~ 656. Kylin & Skottsberg 1919: 70. Laing 1905: 400; 1927: 174. Lucas 1909: 51; 1929: 52; 1929a: 25. Lucas & Perrin 1947: 350. Reinbold 1897: 60; 1899: 50; 1907: 575. Wilson 1892: 186.

Ballia brunonia Harvey 1840: 191, ~~taf.~~ pl. 9. Sonder 1852: 674; 1855: 513.

Ballia brunonis Harvey 1847: 410.

Sphacelaria callitricha Agardh 1824: 166; 1823-28; 23.

Other synonyms referable to Ballia callitricha, but which have not been recorded for the southern Australian plant are; (type material of these plants has not been checked):

Ballia hombroniana Montagne 1842: 9; 1845: 94.

Ballia brunonis var. hombroniana (Mont.) Harvey, 1847: 190. J.D. Hooker 1845: 190

Ballia hombronii Kützing 1862: ~~taf.~~ pl. 38.

Ballia crassa (C.Ag) Kützing 1849: 664.

Sphacelaria crassa Agardh 1824: 167; 1823-28: 23.

TYPE Locality: — ~~Maluinas Island,~~ Falkland Islands.

TYPE: — LD. Herbarium C. Agardh, No. 19357.

DISTRIBUTION: — Widely distributed throughout cooler seas of the southern hemisphere, particularly in the sub-antarctic. In southern Australia Harvey (1863) records it as rare in Western Australia and there are no recent records of it in this locality (one specimen from Geographe Bay, W.A., 1881, (MEL 8515)). It occurs abundantly from Elliston, South Australia, to Port Phillip Bay, Victoria, and on the north and east coasts of Tasmania.

(Fig. 22 A-I).

General Features: — Thallus to 36 cm. in height although commonly about 20 cm. Axes of the central and lower thallus are densely corticated with rhizoidal filaments and attachment is by means of a holdfast of closely interwoven rhizoids. Growth occurs by transverse division of a large dome-shaped apical cell (Fig. 22B). Main axes consist of cells 2-4 times as long as broad (about 320x130µ, in the uncorticated parts of the thallus). Mature axial cells are characteristic in form, being convex at the upper end, when viewed laterally (Fig. 22H) and concave at the lower end to fit over the upper convex part of the cell below. In face view each cell appears flattened across both upper and lower ends and the "flaps" formed from the downward extensions of the lateral concavity of the lower end of each cell overlap the upper end of the cell below (Fig. 22C). The flaps are formed soon after the new axial cell is cut off at the growing apex (Fig. 22 F,G). The basal cells of whorl-branchlets (pinnae) which occur in opposite pairs from the upper part of each axial cell, are cut off early from the upper part of each axial cell (Fig. 22B). Pit-connections between axial cells are capped both above and below by small rounded structures which stain densely. In corticated axial cells these are almost spherical, but somewhat compressed transversely, and have a central, longitudinal hole allowing connection between cells via the pit-connection (Fig. 22 I). The structures are very easily, if not naturally, displaced within the cell. Similar structures occur in axial cells of the longer pinnae. These pinnae bear opposite pairs of distichously-arranged branched pinnules (Fig. 22A) which consist of a central axis bearing opposite pairs of simple branches and may be distinguished from pinnae by the simpler cell structure of their axes. Archer (1876) has described and figured in detail the form and development of the highly specialized axial cells and their connections.

B. callitricha is distinctive in growth habit. When first formed pinnae and pinnules appear to be determinate in length and are usually regularly arranged. Periodically, however, axial growth of pinnae (and less frequently of pinnules) is reinitiated and the rachides elongate considerably (often up to 7 mm) in length (Fig. 22D). No further pinnules are formed so that the newly formed long rachides are unbranched and consist of cylindrical cells which fit together without or with only small convexities and concavities at cell junctions. Pit-connections also lack, or have only very small accessory caplike structures. The change in cell form marks the point of origin of the new growth phase in a rachis. Pinnules are often finally lost from these elongate rachides. In cases where the axes of pinnules continue growth the elongation is similar to that which occurs in the rachides of pinnae and no further pinnule branches are initiated. This ability to reinitiate apical growth is seen also in the regeneration which can occur terminally from any axis which is broken or injured. New growth is frequent from rachides of pinnae, and also from pinnules, as well as from main axes.

Many denuded plants, still apparently fresh, are found in drift material and it is possible that after shedding of pinnules the elongated rachides of pinnae are finally shed and regrowth occurs from the basal cells. Harvey (1840) recorded the frequent occurrence of denuded plants during winter and quoted the supposition of Robert Brown that this annual shedding may form a means of vegetative propagation. Plants have been collected at all times of the year on South Australian coasts, but no evidence has been found to suggest that denudation occurs naturally nor at any one season of the year. Harvey's observations could be the result of rough winter seas and hence comparatively greater battering of the drift plants.

The various stages which occur in this unusual growth pattern are no doubt responsible for much of the confusion and synonomy which has occurred within this species. Only with observation of a large number of plants can the pattern of development be followed.

Lateral branches occur, often in pairs, in the position of pinnae. Pairs are formed at irregular intervals along the axes and may be up to 9 (occasionally more) axial cells apart. Axial cortication consists of (a) branched short, curved branches arising from the basal cells of pinnae. (b) descending rhizoids similar to those described for B. ballioides and B. mariana. These arise also from basal cells of pinnules, (c) curved outwardly projecting short branches from the cells of these rhizoids. These again are similar to those seen in B. ballioides and B. mariana.

Tetrasporangia: — Tetrasporangia are borne on special branches which develop on the basal cells of pinnae (Fig. 22E). Each tetrasporangium is terminal on a branch or lateral on a single stalk-cell and when mature, is about 48µ diam. and cruciately divided.

Spermatangia: — Not recorded.

Carposporangia — Not known from southern Australia (see generic description).

Discussion: —

B. callitricha is very common in southern Australia, including Tasmania. Many hundreds of plants have been examined from diverse localities and at all seasons of the year. No sexual plants have been found and tetrasporangial plants occur only rarely. Australian specimens were first found by Robert Brown in Bass Strait and at Port Dalrymple, VDL (Tas), in 1803. Harvey (1840) recognised that Agardh's description of *Sphacelaria callitricha* from Falkland Is. probably referred to a battered specimen of the same plant. He erected the genus *Ballia* ~~to~~ and included Agardh's plant as ~~it with~~ the type species, *B. brunonia*, named in honour of Robert Brown and described from specimens from Port Arthur and Circular Head, Tasmania. ~~as the type species.~~ Montagne (1845) recognised this synonomy, but at the same time separated *B. hombroniana* as a distinct species based obviously on a plant of *B. callitricha* at a different stage of growth.

Thallus structure is highly specialised, especially in cell form and growth habit, and probably represents a stage well in advance of other genera of the Antithamnieae. Although occurring in a variety of forms due to various growth stages, *B. callitricha* is easily recognised by the form of the pinnules. ~~which~~ These consist of an axis, which varies considerably in length from 4 to about 16 cells, but always bears opposite distichous pairs of simple branches which are orientated obliquely to the pinnule axis and which are close together and nearly always touch one another. Even in plants where axes and rachides have elongated and most pinnules have been shed, some few pinnules have always been found in some part of the plant, often towards the base, which are sufficient for identification. *B. callitricha* is easily recognisable by the loosely branched short corticating pinnae which arise from the basal cells of the normal pinnae. These do not occur in other southern Australian species of *Ballia*.

Plants with tristichous branching, in place of the more usual distichous form, are not uncommonly found. In other ways these plants are identical with distichously-branched plants and a change from distichous to tristichous habit may occasionally occur on the one plant.

BALLIA PENNOIDES n. sp.

Thallus usque ad 25 cm altus. Axes filamentis rhizoideis inferne dense corticati, quoque cellula superne concava, inferne convexa; foveo-colligationes structuris in forma tholi factis tecti. Vortico-ramuli oppositi, distichi, usque ad 5000μ longi; e cellulis infimis ramis simplices et curvati usque ad 900μ producti. Rami oppositi, distichi, non ramosi. Tetrasporangia, spermatangia et carposporophyti ignoti.

TYPE Locality: — Robe, South Australia.

HOLOTYPE: — AD, A 19,999.

DISTRIBUTION: — Known only from the type locality and from one specimen in Harvey's Herbarium, TCD, labelled VDL. One sheet of 4 specimens from Guichen Bay (MEL 8487) is labelled Sphacelaria ? sonderiana and is identical with the type material.

(Fig. 22 J - M; Plate 5).

General Features: — The plant grows to 25 cm in height, is densely corticated in the central and lower parts of the axes and attached by a rounded holdfast composed of a dense mass of firmly interwoven filaments.

Growth occurs, as in other species of Ballia, by transverse divisions of a large dome-shaped apical cell (Fig. 22K). Axial cells in lateral view are slightly concave at the lower end to fit over the convex upper end of the cell below. In face view the lower end is convex and the upper end concave. The flaps are less conspicuous than in B. callitricha, but caplike dome-shaped structures which cover the pit-connections at cell junctions are more prominent. They enlarge rapidly and are easily detached even in comparatively young cells. Comparisons have not been made in fresh material.

Each axial cell bears a pair of opposite whorl-branchlets (pinnae) which are initiated laterally, but, when mature, are often directed upwardly, overlap and lose the appearance of regularity in arrangement. They are attached by a group of basal cells rather more pronounced than in B. callitricha and which may extend at least two-thirds of the length of the axial cell. Pinnae vary considerably in length (generally up to 5000μ long) and consist of a rachis of cells similar to those of the main axis each of which bears a pair of opposite unbranched, pinnules. The pinnules are 5-8 cells long and are composed of simple cells without the elaboration which develops at the junctions between cells of the main axes. The tips of pinnules are acute and tend to be recurved. Several cells without pinnules occur at the tip and at the base of each pinna (Fig. 22L). Several short unbranched, inwardly-curved branches (up to 900μ long) arise from the group of cells at the base of each pinna. These branches are of simple cells and taper gradually towards the base and usually acutely at the tips (Fig. 22J, L). Initials of these branches also have a characteristic large apical cell (Fig. 22M).

Cortication of the axis consists at first of these branches. Descending rhizoidal filaments are also produced from the basal cells of pinnae (Fig. 22J). These rhizoids bear outwardly-projected simple branches similar in form to the curved branches borne directly from the basal cells of the pinnae, and axes in the upper-central and lower parts of the thallus are densely covered by a thick interwoven mat of rhizoids and short branches.

Lateral branches usually occur singly rather than in opposite pairs as in Ballia callitricha. They are produced at unequal intervals along the axes and are alternate or, sometimes with 2 or more adjacent ones on the same side of the axis.

Tetrasporangia, Spermatangia and Carposporangia: — Not recorded.

Discussion: —

Although comparatively rare the plant is quite distinct from Ballia callitricha, which it most closely resembles in southern Australia. It differs specifically in having (1) pinnules which are never branched, (2) short branches at the base of pinnae which are simple, curved and tapered towards the base, (3) lateral branches singly produced and seldom in opposite pairs.

The greatest difference is in the form of the pinnae. Regrowth of pinnae rachides, as occurs commonly in B. callitricha, has not been seen in the limited number of plants examined. The specimen in Harvey's Herbarium, TCD, (labelled VDL) which is probably this species shows some growth of rachides and consequent loss of pinnules.

Elongation of rachides would produce a pinna structure close to that shown by Papenfuss (1940a: 222) for Ballia sertularioides (Suhr) Papenfuss which is known from localities near Cape Town and from Tristan da Cunha (Baardseth 1941b.p96). Comparison of figures given by both Papenfuss and Baardseth suggests that rachis elongation occurs as it does in B. callitricha. B. pennoides differs from B. sertularioides in having a much larger and strongly corticated thallus while B. sertularioides is only 6 lines (≡ 1.15 cms) high (Suhr 1840) and completely lacks axial cortication.

<u>BALLIA HIRSUTA</u> n. sp.

Thallus usque ad 14 cm, hirsutus, axibus compluribus e basi crescentibus instructus. Axes teretes, filamentis rhizoideis corticati, foveo-colligationes structuris in forma tholi factis tecti. Ramuli determinati usque ad 3000μ longi, non verticillati, in filamentis rhizoideis crescentes, in cellulis superioribus hamis spinosis praediti. Cellulae ad apicem magnae, ad apicem quaeque axis ramis pluribus crescentibus. Tetrasporangia, spermatangia et carposporophyti ignoti.

<u>TYPE Locality</u>: — Catamaran, Recherche Bay, Tasmania.

<u>HOLOTYPE</u>: — AD, A 27,746.

<u>DISTRIBUTION</u> : — Known from Green Pt. on the west coast and from Bicheno, Cape Forestier and Catamaran on the east coast of Tasmania. Known also from Kaikoura (AD, A 4707), Goose Bay (south of Kaikoura) (AD, A 11,499), New Zealand, and from Stewart Is. (AD, A 9175).

(Fig. 21 J-L: Plate 6)

<u>General Features</u>: — Thallus to 14 cm in height and characteristic in form with numerous shaggy axes arising from the base. Each axis is densely clad with short erect branches. The thallus is attached by a holdfast of matted and interwoven rhizoids, and erect corticating branches are initiated as lateral branches from these filaments (Fig. 21J).

Growth occurs from large dome-shaped apical cells and, as in <u>B. scoparia</u> is not restricted to the main axis alone. Lateral thallus branches in the upper part of the plant also grow indefinitely and themselves produce new branches. Only one branch occurs from a single axial cell and these may be irregularly distributed along the axis from 1 to several cells apart. The cells of the axes are of the same form as in B. scoparia and are usually 3 to 4 times as long as broad (about 190 x 100μ) in the uncorticated parts of the axis. Adjacent cells fit closely together and pit connections are capped on either side by dome-shaped structures.

Axes are densely corticated with a mat of interwoven branched rhizoidal filaments (Fig. 21K) which arise from cells similar to basal cells of undeveloped branches, produced on axial cells between those bearing fully formed branches. Cells of the rhizoids bear corticating branches (to 3000μ long) which are upwardly directed, branch several times, are determinate in length and usually terminate acutely with several small spine-like hooks on the cells near the tip (Fig. 21L). They are thus comparable in form with branchlets produced from axial cells in B. scoparia.

These branches form a dense covering over the axes and are responsible for the shaggy appearance of the thallus. They are initiated soon after each rhizoid commences to elongate and usually a group of several branches occurs from cells near the base of the rhizoid. They are produced at wider intervals lower down on the rhizoids.

Tetrasporangia, Spermatangia and Carposporangia: — Not known.

Discussion: —

This species is known only from the colder regions of southern Australia, New Zealand and Stewart Is. It differs from Ballia scoparia in having a number of axes, each densely clothed with short corticating branches, arising from the holdfast. The short branches which arise from cells of the corticating rhizoids which cover the axes, are comparable with the horizontal outwardly-projecting, short, corticating branches of other species of Ballia (not B. scoparia) or to the branchlets of B. scoparia. In other species, however, short branches from the rhizoids always remain comparatively short and do not extend far beyond the tangle of corticating filaments.

BALLIA SCOPARIA (H. et H.) Harvey 1860.

Harvey 1860: 333; 1858-63 (1860): pl. 168. J. Agardh 1876: 59. Archer 1876: 228: pl. 29, Figs. 1-11. Cotton 1915: 190. De Toni 1897: 1395; 1924: 491; 1896: 228. Laing 1905: 401; 1927: 174. Levring 1960b: 61. Lucas 1909: 51; 1929a: 25. Lucas & Perrin 1947: 351. Skottsberg 1923: 61. Wilson 1892: 186.

Callithamnion scoparium Hooker and Harvey 1845a: 273; J.D. Hooker 1847: 490: pl. 189, fig. 3; 1855: 259. J. Agardh 1851: 35. Sonder 1852: 675; 1853:512
Phlebothamnion scoparium Kützing 1849: 656; 1862: pl. 6, figs. c-f.

TYPE Locality: — Berkeley Sound, Falkland Is.

TYPE: — TCD, Herbarium Harvey, Alg. Aust. Exsicc. No. 502.

DISTRIBUTION: — The species is widely distributed in the southern hemisphere occurring mainly in colder waters. In southern Australia it occurs from Brown's Beach, Yorke Peninsula, S.A. to Mallacoota, Victoria and around the coast of Tasmania including Cape Sorrell and Remine on the west coast to Bicheno on the east coast.

(Fig. 23 A - L).

General Features: — Thallus to 20 cm. high densely corticated below with curly rhizoidal filaments and increasing in length from the apices of numerous branches (Fig. 23 A,F). The apical cell is dome-shaped, elongates and cuts off axial cells by transverse divisions. Branches are initiated as lateral protrusions from the second cell (Fig. 23 B-E). Each lateral branch usually produces an axis of 6(5-7) cells before commencing to branch and thereafter new branches are initiated usually at intervals of 3 (2-4) cells. Occasionally branches are formed which do not elongate and these are characterised by an acute tip and a series of short spine-like cells near the branch tip (Fig. 23 F,G), and are probably equivalent to the branchlets of other species of Ballia. These branches sometimes produce further spined lateral branches. At periods of rapid growth the majority of upper axes are terminated by actively-dividing dome-shaped densely-protoplasmic apical cells. At other periods, and in lower parts of the thallus, branches of limited growth are more common. Axial cells fit closely against one another so that the small pit-connection between the cells is obscured. As in B. callitricha, it is usual for the pit-connections to be flanked on either side by small dome-like structures. In young cells strands of cytoplasm are seen to pass through the centres of these structures. It is usual for the upper end of each cell to be slightly convex and fit closely into the concave lower end of the cell above. Cells of the uncorticated branches are about three times as long as broad (190 x 64u). In corticated axes the cells may be considerably larger.

The central and lower parts of the thallus are covered by a mat of corticating rhizoids. These arise from small basal cells which develop on the axial cells (Fig. 23 J,K). The rhizoids grow downward, branch profusely (Fig. 23L), twine around the axis and interweave with one another.

Corticating filaments may also grow upward from the basal cell and curl around the axis. Occasionally a normal branch is produced upwardly from the same cell. This suggests that upwardly growing cortical rhizoids are modifications of normal branches (or branchlets). The plant attaches by a holdfast formed of a fibrous, entangled rhizoidal mat of filaments.

Tetrasporangia: — Tetrasporangia are cruciately divided although they appear tetrahedral, and are 24-28µ diam. when mature. They occur terminally on the branches of special short, much-branched branches borne on the lower cells of thallus branches in the upper part of the plant. Four or more tetrasporangia may occur on one cell (Fig. 23 H,I).

Carposporangia: — In his early descriptions Harvey noted and figured structures which he believed to be groups of carposporangia and described these (1860) as involucres composed of very numerous, incurved whorled ramuli. He did not find "favellae" in them.

In the many collections made around the coasts of southern Australia no carposporophytes have been found and it seems certain that the structures referred to by Harvey were epiphytes which are often associated with the plant and which agree quite well with Harvey's figures.

Discussion: —

Hooker and Harvey (1845) described the species as Callithamnion scoparium because of its resemblance in habit to Sphacelaria scoparia Agardh. The species is distinguished by:

1. Closely adjacent axial cells, with small inconspicuous pit-connections flanked by dome-like structures.

2. Growth pattern with growth occurring from the apices of numerous branches rather than from a single central axis.
3. Single branches (or branchlets) occurring from about every 3rd axial cell (often commencing from about the 6th cell at the base of the branch). Whorls are never formed on axial cells.
4. Axial cortication by rhizoids borne on short basal dells which do not support normal branches (very rarely they may occur on the basal cell of a branch).
5. Tetrasporangia which are terminal (up to 4 or more on each cell) on the branches of special short branches borne on the upper side of the lower cells of thallus branches.

These characteristics suggest that the species should probably be excluded from the genus _Ballia_ which has unlimited growth from a single main axis and whorls of determinate branchlets from each axial cell. It resembles other species of _Ballia_ in the rather cartilaginous texture of the axial cells, the form of apical cells and the presence of dome-shaped structures associated with pit-connections as occur in _B. callitricha_ and _B. pennoides_. Until details of sexual reproduction can be compared the species is left in its present position.

R.M. Laing (1905) considers _Rhodochorton parkeri_ Harvey-Gibson to be synonomous with _Ballia scoparia_. The original description of this plant (Harvey-Gibson, 1893) based on a New Zealand collection, is insufficient to establish synonomy with _Ballia scoparia_ as known for southern Australia and careful checking of the type material is necessary.

ACROTHAMNION J. Agardh 1892.

J. Agardh separated Acrothamnion from Callithamnion mainly on the basis of tetrasporangial features. While in Callithamnion the tetrasporangia are triangularly divided and are borne on branches of the whorl-branchlets the type species of Acrothamnion has cruciately divided tetrasporangia which occur on special protrusions at the base of the whorl-branchlets.

Whorl-branchlets, in the form of pinnae, occur in Acrothamnion either opposite or in whorls of 3-4 and this feature was also used by J. Agardh in his classification of Callithamnion-like genera. De Toni (1924) placed the genus Acrothamnion in the sub-family Spermothamnieae of the Ceramiaceae. Kylin (1956) included it in the Crouanieae and Hommersand (1963) transferred it to his newly-formed tribe Antithamnieae of the sub-family Ceramioideae. It must undoubtedly remain close to Antithamnion and its taxonomic position will be discussed more fully in relation to its phylogenetic relationships.

Characteristics of the genus, beyond those given originally by J. Agardh, are: —

1. A thallus consisting of a prostrate axis from which arise distinct erect branches. These are distinct from the unattached branch apices which form the erect portions of the plant in Antithamnion.

2. Decrease in length and branching of pinnae towards the base of erect axes.

3. Whorls of 2 or 4 pinnae which may be equal or unequal in form and arranged regularly or dorsiventrally on the axis. The basal cell of the rachis is always small as in Antithamnion.

4. Gland-cells terminal on rachides of the pinnae, and hence developed after the rachis of the pinna has fully elongated. In other genera, lateral development of gland-cells often occurs early in the formation of a pinna.

5. Procarps developed on the basal cells of successively formed pinnae at branch apices (as in *Antithamnion* but only 4-8 occur on a branch apex instead of 8-20). Known only for *Acrothamnion preissii*.

6. As described by J. Agardh, cruciately divided tetrasporangia occur at the base of pinnae.

Detail of the genus is based chiefly on *Acrothamnion preissii*, the type species, and the only species of which adequate material is available. The distinctive characteristic of all species is the terminal gland-cell. In all other genera of the Antithamnieae gland-cells are laterally developed even when borne on the terminal cell of the apex of a pinna or pinnule. Besides *Acrothamnion preissii* the genus includes *A. arcuatum* n.sp. which is only poorly known from dried material, and *A. butleriae* (Collins) Kylin from Jamaica and Barbados. This latter species is of particular interest in that it develops only 2 pinnae, as an opposite pair, from each axial cell (Borgesen 1920: 465, as *Antithamnion butleriae*) and thus extends the variation of pinna form and arrangement known for the genus.

All pinnae characteristically have distichous pinnately arranged pinnules, but these may be arranged:

(a) As an opposite pair (*A. butleriae*) or in a whorl of 4 (*A. preissii*, *A. arcuatum*),

(b) evenly spaced in a whorl (*A. arcuatum*, *A. butleriae*) or dorsiventrally arranged (*A. preissii*),

(c) equal in length(*A. arcuatum*, *A. butleriae*) or unequal (*A. preissii* (2 long + 2 short)),

(d) with variation in form and reduction in number of pinnules on the one plant (*A. butleriae*, *A. preissii*) or apparently equal throughout the plant (*A. arcuatum*).

This variation in pinna structure suggests that the genus has not reached a stable vegetative condition. This is also indicated in *A. butleriae* for which Boergesen (1920) describes and figures the occasional production of gland-cells terminally on pinnules. It is likely that these represent relics, while the single terminal gland-cell on the pinna rachis is the normal condition.

Reproduction is known only in *A. preissii* and can only be discussed with reference to phylogenetic trends as shown by a single species.

Acrothamnion shows closer relationships with *Antithamnion* than with other genera of the Antithamnioneae in having:

(1) Distichous, pinnate form of pinnules (compare particularly with *Antithamnion pinnafolium* which also develops gland-cells near the ends of pinnules and, although laterally developed may lead to terminally developed gland-cells in *Acrothamnion*).

(2) Small basal cell to pinnules (not found in other genera of Antithamnieae).

(3) Whorls of 2 pinnae in *Acrothamnion butleriae*.

(4) Tetrasporangia which are divided cruciately although appearing tetrahedral

(5) Procarps of the form found in *Antithamnion* but reduced to 4-8 per branch apex (*Antithamnion* usually develops 8-20 per branch).

On the basis of these features it is suggested that Acrothamnion is developed from an Antithamnion-like ancestor, and because Antithamnion characteristically has pinnae in opposite pairs, Acrothamnion butleriae with 2 pinnae per whorl is possibly the most primitive species. The occasional development of relic gland-cells also suggests its primitive nature. Instability of pinna form occurs also in Acrothamnion preissii in which 4 pinnae are formed (sometimes reduced to 3 in the lower parts of the plant by loss of one of the minor pinnae). Acrothamnion arcuatum with evenly-spaced whorls each of 4 pinnae is the most stable form, and hence is probably the most advanced. Details of its structure, however, need confirmation from investigation of fresh material.

TYPE species: -- Acrothamnion preissii (Sond.) nov. comb.

Key to the Southern Australian species of Acrothamnion.

1. Whorl-branchlets (pinnae) arranged dorsiventrally in each whorl consisting of 2 opposite major pinnae between which 2 (or one) minor pinnae occur... ... ... A. preissii

1. Whorl-branchlets (pinnae) arranged in evenly-spaced whorls each of 4 equal pinnae... ... ... A. arcuatum

Note: Acrothamnion butleriae, although referred to in the above discussion, does not occur in southern Australia.

ACROTHAMNION PREISSII (Sond). nov. comb.

Callithamnion preissii Sonder 1845: 19; 1847: 166. Agardh, J. 1851: 33; 1876: 25. Kuetzing 1849: 651.

Antithamnion preissii De Toni 1897: 1414.

Callithamnion pulchellum Harvey 1854: 561; 1863, synop: ~~No.~~ 692. J. Agardh 1876: 20. De Toni 1897: 1338. Lucas 1909: 49. Lucas and Perrin 1947: 333.

Acrothamnion pulchellum (Harv.) J. Agardh 1892: 25, figs. 6–10. De Toni 1924: 451. Reinbold 1898: 53; 1899: 50. Tokida and Inaba 1950: 124.

TYPE Locality: — Rottnest Island, Western Aust.

HOLOTYPE : — MEL, 10260, Preiss No. 2536.

DISTRIBUTION: — From Champion Bay , Western Australia to Port Campbell, Victoria, occurring epiphytically on a variety of algae (e.g. Ballia callitricha, B. mariana, Wrangelia crassa, Acrocarpia paniculata and Codium mamillosum).

(Fig. 24).

General Features: — The plant consists of a creeping prostrate portion attached to the host by digitate rhizoids and bearing free, erect branches up to 1.5 cm long (Fig. 24A).

Each axial cell bears two opposite major whorl-branchlets (pinnae), each with distichous, pinnately arranged, opposite pinnules and usually terminated by a conspicuous gland-cell (Fig. 24 B,K). Two minor pinnae, reduced to one in the central and lower parts of the thallus, occur side by side between the pairs of major pinnae. These are unilaterally placed on the axes, all minor pinnae on the one branch being on the same side so that the branch is distinctly dorsiventral (Fig. 24B).

Structure of the Thallus: —

(1) Form and Development of Main Axes: — Elongation of the prostrate axis occurs by transverse divisions of the dome-shaped terminal cell (Fig. 24D). Often only two pinnae, reduced in form, are developed on each cell of this axis; the basal cell of one pinna of the pair bears an erect branch while the other produces rhizoidal attachment organs (Fig. 24D a & b). Erect branches occur at irregular intervals, usually close together, along the axis and soon become dominant over the pinna developed on the same cell (Fig. 24Dc). Each erect branch may bear several lateral branches which also arise from the basal cell of a pinna (Figs. 24A,Ba).

Mature axial cells in the erect branches are about $1\frac{1}{2}$-3 (-5) times as long as broad ((40)-50-60 x 120-160 (-190)µ). The lower cells of lateral branches may be smaller than those above so that the branch tapers towards the base. Variation in proportions of axial cells results in variation in overlap of the pinnae and proximity of the pinnules.

(2) Development, Arrangement and Branching of Pinnae: — Pinnae are initiated one to three cells below the apex of branches and form initially a chain of rachis cells, the basal cell of which always remains smaller than those next above it. Cells of the rachis are about as long as broad (to 65µ). The two major pinnae develop simple, distichous, opposite

pinnules and, when mature, are up to 380 (-580)µ long with a rachis of 10-12 (-14) cells. The longest pinnules are toward the base of the pinnae and are about 9 cells 125 (-190)µ long, (Fig. 24B). Two (sometimes only one) minor pinnae are initiated on one side of the axis between the two major pinnae; one is nearly always lost before long so that on most of the thallus only one occurs. The minor pinnae vary in form (Fig. 24 E-I), becoming more reduced from the upper to the lower parts of the plant. The longer ones have a rachis of about 9 cells (150(-300)µ). The major pinnae may also be reduced towards the base of the plant so that a general reduction in size of all pinnae occurs. Those on the prostrate axis are always reduced in both size and form and often bear unilaterally arranged pinnules only.

Gland-cells: — Gland-cells occur terminally on the rachides of both major and minor pinnae and hence do not form until the apical cell of the rachis has ceased to divide transversely. The final pair of pinnules curve upward and clasp the somewhat elongate and often angular gland-cell which is about 25 x 18µ (Fig. 24L). When a gland-cell does not develop several small cells occur at the apex of the pinna (Fig. 24K).

Rhizoids and Attachment Organs: — No axial cortication occurs, but on the prostrate axes rhizoidal attachment organs are borne on the basal cells of the pinnae. Several multicellular rhizoids, sometimes sparingly branched, may arise from one basal cell. When young the rhizoids are narrow and elongate, but on attachment to the host, the cells contract somewhat and a digitate holdfast develops terminally (Fig. 24D, b & d).

Tetrasporangia: — Tetrasporangia are borne terminally on elongate protrusions from the upper side of the basal cells of the pinnae. They are usually single on the major pinnae in the upper parts of the thallus (Fig. 24J), but occasionally more than one may develop on a cell; they may also occur on minor pinnae.

Each tetrasporangium is spherical when mature, about 40μ diam. within the gelatinous sheath and division is cruciate although sometimes forming sporangia apparently tetrahedral in form.

Spermatangia: — Spermatangial mother cells (2.5 - 4.5 μ diameter) are borne in terminal clusters of 2-4 cells on branches of modified pinnules usually toward the basal part of the pinnae. The axis of the fertile pinnule is usually only 3-5 cells long and with branches from each cell; occasionally, however, branching with development of spermatangial mother-cells takes place from the several uppermost cells of an elongate pinnule.

The branches which bear the spermatangial mother-cells consist of 1-4 successive whorls each of 2-4 cells (fig. 24C).

Development of Carpogonial Branch and Carposporophyte: — Carpogonial branches, of the form found in *Antithamnion*, develop on the basal cells (supporting cells) of young pinnae near branch apices (Fig. 24 P,M). Four to eight may develop successively on one branch apex, and two of these may initiate early stages in development of the carposporophyte. After fertilization an elongation from the base of the carpogonium develops towards the rounded auxiliary cell cut off from the upper side of the supporting cell (Fig. 24N). Presumably fusion occurs between this protrusion of the carpogonium and the auxiliary cell. The auxiliary cell then divides transversely to form a lower foot cell and an upper rounded central cell (Fig. 24 O). The first gonimolobe develops terminally from the central cell and cuts off several sterile cells which in turn give rise to the carposporangia (Fig. 24 P,Q,R). The second gonimolobe is lateral and develops carposporangia by a similar series of cell divisions (Fig. 24 P,Q,R.).

After initiation of carpogonial branches the branch apex ceases further elongation, and the carposporophyte is protected by the upwardly directed surrounding pinnae. Pinnae on the upper cells of the branch apex remain immature often with several smaller cells at the base (Fig.24 P).

Discussion: —

Individual plants vary in form due to variation in cell size and proportion. The type material, for example, has comparatively short cells and, hence, close proximity of adjacent pinnae and pinnules. One collection from Flinders Bay, W.A. (AD, A 29,287) represents another extreme in form, and approximate limits for dimensions of plants from this collection have been indicated in brackets in appropriate places. Many intermediate forms are recorded, and cell size is not a satisfactory feature for the separation of species. A Japanese species has also been described (Yendo 1916: 262; Yamada 1928: 528; Yamada and Inagaki 1935: 37) as Acrothamnion pulchellum sensu? Yamada (not J. Agardh) but it is probably more closely related to the New Zealand Antithamnion applicitum J. Ag. The species Acrothamnion pulchellum J. Ag. is described by Tokida and Inaba (1950) as having sessile tetrasporangia on the basal cells of pinnae but without the elongate protrusion which occurs in the Australian species. This Japanese plant may therefore also represent a different species. Acrothamnion pulchellum (Harv.) J. Ag. is identical with the earlier described species Callithamnion preissii Sonder. On the basis of priority, the latter epiphet must be retained. The type of Harvey's C. pulchellum is in TCD, Herbarium Harvey, No. 230.

ACROTHAMNION ARCUATUM n. sp.

Thallus prostratus ramis erectis 1 aut non nullis cm altis. Vortico-ramuli 4 e quoque cellula, usque ad 200μ longi, cellula infima parva praediti, curvato-adscentententes. Vortico-ramuli ramis 1-jugatis, 2-6 cellulae longis, exteriore obliquis, saepe ab latere superiore 1-pluribus ramis brevibus instructis. Cellulae glandulosae in rachidibus vortico-ramulorum terminales. Tetrasporangia, spermatangia et carposporophyti ignoti.

TYPE Locality: — Middle River, Kangaroo Is., South Aus.

HOLOTYPE: — AD, A 3426.

DISTRIBUTION : — Known only from the type locality. Growing on coralline algae.

(Fig. 23 M - O).

General Features: — The plant consists of long unattached axes, one to several cm. high, arising from prostrate axes which adhere to the host by means of branched rhizoidal filaments bearing digitate terminal attachment organs.

~~Cells of the main axes are about 190 x 50μ. Each cell bears from its~~ upper end a whorl of 4 evenly-spaced whorl-branchlets (pinnae) up to 200μ long, which curve upward and finally inward, usually to about the base of the whorl above (Fig. 23M). The rachis of eadh pinna is 5-8 cells in length, the basal one of which is much smaller than those directly above it. Each cell of the rachis bears a pair of two short pinnules (2-6 cells long) from its upper end. The pinnules are usually directed obliquely outward, and each, particularly the lower ones, may bear 1-several short, simple branches usually on the upper side (Fig. 23N). Gland-cells occur terminally on the rachis of the pinnae and are most abundant in the young parts of the thallus (Fig. 23 O). The species agrees with Acrothamnion in having: —

1) prostrate and erect axes,

2) pinnately branched pinnae with small basal cell to rachis. Pinnae of Acrothamnion preissii have simple unbranched pinnules, while in this species the pinnules may be simply branched. Pinnae of each whorl are of equal length in this species, while Acrothamnion preissii bears two long and two short dorsiventrally arranged pinnae per whorl.

3) Terminal position of gland-cells.

Acrothamnion arcuatum is tentatively included as a second Australian species of the genus. The plant shows similarity with Trithamnion particularly in form of pinnae which in both species are curved upward and have similar pinnule form. The presence of 4 long, equal pinnae surrounding the carposporophyte in Trithamnion may indicate a phylogenetic link with species which normally bear 4 pinnae in each whorl. Unfortunately the available material of Acrothamnion arcuatum is not fertile and its taxonomic position must remain uncertain until fresh material is collected.

MACROTHAMNION n. gen.

Thallus plerumque grandis (usque ad 30 cm) irregulariter ramosus. Axes inferne filamentis rhizoideis corticati. E quoque cellula vortico-ramuli 3 (2), simplices ver ramosi, saepe in cellulis superioribus processis spinosis instructi. Cellulae glandulosae in ramis specialibus brevibusque. Tetrasporangia et spermatangia in ramis glanduliferis posita. Tetrasporangia cruciata. Procarpi ((4-) 8-20) in cellulis basalibus vortico-ramulorum e cacuminibus ramorum natorum. Carposporophyti globis rotundatis carposporangiorum, globo terminale primum crescente, instructi.

Macrothamnion, as the name suggests, includes some of the larger species of Antithamnieae.

Macrothamnion mucronatum, growing to 30 cm, is comparable with species of Ballia which are the largest in the group. Macrothamnion secundum and M. pectenellum (to 8 cm and 4 cm respectively) are also much larger than species of Antithamnion and Acrothamnion.

Characteristic features of the genus are: —

1) Large thallus usually attached by a distinct holdfast and axially corticated with rhizoids in the lower part.
2) Whorl-branchlets in whorls of 3 (sometimes 2 in M. pectenellum) from the upper part of each axial cell.
3) Gland-cells on special short 2-4 celled branch which may, particularly in M. mucronatum, branch further and support 2-14 gland cells.
4) Tetrasporangia borne on the short branch which bears the gland-cells.
5) Development of procarp and carposporophyte as in Antithamnion.

Although carposporophyte development is similar to that of *Antithamnion* the genus is distinct in plant size and form, number of branchlets per whorl and position of tetrasporangia. Several features within the genus show a marked phylogenetic gradation,

1) Thallus organization with whorls of 2-3 unequally branched branchlets (*M. pectenellum*) to consistent whorls of 3 unequally-branched branchlets (*M. secundum*) and finally to constant whorls of 3 unbranched branchlets (*M. mucronatum*). Possible relationships of *M. pectenellum* to both *Antithamnion* and Antithamnionella are discussed with the phylogeny of the group.
2) Single gland-cells borne on short 2-celled branches (*Macrothamnion pectenellum*) as in *Antithamnion* to a special branch which may elongate and produce 2 or 3 gland-cells (*Macrothamnion secundum*) or which may be further branched and develop up to 14 gland-cells (*M. mucronatum*). This is the only genus of Antithamnieae which shows any gradation in gland-cell development, and in this instance, the development may be interpreted as an extension of the special branch system rather than as a change in gland-cell position.
3) Axial cortication is sparse and holdfast development uncertain in *M. pectenellum*, but in *M. mucronatum* is strongly developed and a distinct holdfast is always produced.
4) Tetrasporangia are borne on the special branches which bear gland-cells. Consequently more tetrasporangia are produced on the much-branched branches of *M. mucronatum* than in the other species.

These features, as well as plant size, suggest that *M. pectenellum* is the most primitive of the species of *Macrothamnion* while *M. mucronatum* has a comparatively highly organized thallus structure.

TYPE Species: — *Macrothamnion mucronatum* (J. Ag.) nov. comb.

Key to the Southern Australian Species of Macrothamnion

1. Thallus up to 30 cm. high bearing whorls of 3 unbranched whorl-branchlets from each axial cell. Gland cells 1-14 on short, often much branched special branches... ... ... *M. mucronatum*

1. Thallus not more than 8 cm. high. Axial cells bearing whorls of 3 (sometimes 2 in *M. pectenellum*) whorl-branchlets, some of which are always secundly branched with 1-5 simple branches. Gland-cells 1(-3) on simple 2-4 celled short special branches.. 2

   2. Thallus slender, sparsely-branched and up to 4 cm. high. Whorl-branchlets in whorls of 2 or 3. Gland-cells single on a short 2-celled branch... ... ... *M. pectenellum*

   2. Thallus more or less robust, much branched and up to 8 cm. high. Whorl-branchlets consistently in whorls of 3. Gland-cells on special short branches which are sometimes extended and bear 2-3 gland-cells... ... ... *M. secundum*.

MACROTHAMNION MUCRONATUM. (J. Ag). nov. comb.

Antithamnion mucronatum (J. Ag.) Naegeli 1861: 146. De Toni 1897: 1410; 1924: 497. De Toni and Forti 1922: 55. Laing 1905: 404; 1927: 175. Lucas 1909: 51; 1929: 52; 1929a: 25. Lucas & Perrin 1947: 355. Reinbold 1899: 50.

Callithamnion mucronatum J. Agardh 1851: 29; 1876: 19. Harvey 1860: 334; 1863, synop. ~~No.~~ 688; Wilson 1892: 187.

Callithamnion acanthophorum Kutzing 1849: 647; 1861: taf. 80a-c. (mis-spelled "acanthocarpum" by Sonder 1852: 673 and Harvey 1863, synop. No. 688).

Callithamnion pellucidum Harvey 1847: 412.

Spyridia pellucida Harvey 1844c: 449.

Ballia hamulosa J. Agardh 1894: 120; 1897: 27; De Toni 1897: 1395; Dickinson 1949: 2. Lucas 1909: 51; 1929: 52. Lucas & Perrin 1947: 352 Reinbold 1897: 60; 1898: 51.

Callithamnion cruciatum Harvey 1844c: 453; 1847: 412 has been given as a synonym for Antithamnion mucronatum. There is no evidence that Harvey intended the latter to be included in his reference to Callithamnion cruciatum in either of the above accounts. In fact in both cases he refers also to Spyridia pellucida (1844c: 449) and (1847: 412 (as Callithamnion pellucidum)). Later (1860: 333-334) he quotes Spyridia pellucida as a synonym for Callithamnion mucronatum used earlier by himself and it is unlikely that he would include reference to the one plant under two names in both papers. Harvey 1860: 333-334 explains having mistakenly sent a specimen of Antithamnion mucronatum to J. Agardh labelled as Callithamnion cruciatum.

It is probable that the acceptance of C. cruciatum as a synonym for C. mucronatum from that time onwards has been the result of this mistake.

TYPE Locality: — "Van Dieman's Land" (Tasmania).

TYPE: — LD, Herbarium Agardh, No. 18832.

DISTRIBUTION : — From Pt. Peron, Western Australia, to Sorrento, Victoria, and northern coast of Tasmania.

(Fig. 25).

General Features: — The plant grows to about 30 cm in height, is lax in form and attached by a fibrous discoid holdfast. Several main branches arise from the base and these, together with lateral branches produced in the lower parts of the plant, twine together to give a matted, felt-like axis which is particularly well developed in larger and older plants, and which is more or less consolidated by the intertwining of numerous rhizoidal ~~plants~~ filaments corticating the axes. Lateral branches occur at short irregular intervals (less than 12 axial cells apart and usually separated by about 3-6 cells) and are directed upwardly (Fig. 25A). In large plants and rapidly growing parts the simple whorl-branchlets (probably equivalent to reduced pinnae) occur in whorls of three and are also orientated upward, but may become almost horizontal to the axis in lower parts of the plant and in small forms. In all plants the gland-cells are conspicuous. The young whorl-branchlets are concentrated at the tips of the branches which appear ocellate as described by J. Agardh (1876: 19). Variation in form will be discussed in relation to thallus structure.

Structure of the Thallus: —

(1) Form and Development of Main Branches: — Growth occurs by means of transverse divisions of a dome-shaped apical cell (Fig. 25C) and the branch apices are protected by the upwardly-directed whorl-branchlets borne on the axial cells immediately below. Growth is monopodial. Average mature axial cells vary in size in individual plants between about 500 x 300μ and 300 x 200μ, while near the base of the plant they may be up to 900 x 300μ.

Lateral branches are produced on the upper side of the basal cells of pinnae at irregular intervals along the axes.

(2) Development and Arrangement of Whorl-branchlets: — Whorl-branchlets are simple and consist, when mature, of 10-20 cells tapering acutely to a mucronate tip. The basal cell is smaller than other cells near the base of the chain and the mature whorl-branchlets are from 1200μ to 1800μ in length (Fig. 25D).

The whorl-branchlets are evenly-spaced in whorls of three from the upper part of each axial cell and are initiated 2 or 3 cells below the apical cell of a branch. There is rotation of whorls on adjacent axial cells so that pinnae on alternate cells are superimposed. Rotation in the order of initiation of whorl-branchlets is not consistent, although rotation of 60° in position of initiation of the first formed branchlet is of most frequent occurrence (Fig. 25B).

Apices of young whorl-branchlets are characterised by the mucronate form of the gelatinous sheath of the apical cell and by the presence of small cells covered by a thorn-or hook-shaped sheath which occur, often in pairs, on the upper part of cells at the apex of the whorl-branchlet (Fig. 25H). These structures are never found on the older whorl-branchlets and presumably fall off later. Gland cells are prominent on the lower cells of the whorl-branchlets.

Variation in length of whorl-branchlets and length of axial cells results in wide variation in comparative lengths, so that whorl-branchlets may cover 1 to 6 axial cells. This results in great variations in the density of coverage by whorl-branchlets over the axes of the thallus.

Gland-Cells: — Gland-cells are produced on the second (terminal) cell of special short branches borne on the upper part of the lower cells of the whorl-branchlets (Fig. 25D,F). The cell bearing the gland-cell may later divide so that the special short branch may become 2-4 cells in length, while the basal cell produces branches (Fig. 25F) which bear additional gland-cells (Fig. 25G). Up to 14 gland-cells have been found on one special branch. The special branches bearing gland-cells may be borne singly on a cell or occasionally in opposite pairs.

Gland-cells are about 30µ in diameter and often have a densely refringent thickened band on the outer side (Fig. 25 F,G). Initials (Fig. 25E) are developed on the young, immature whorl-branchlets and are concentrated near branch apices.

Axial Cortication: — Rhizoids develop from the lower side of the basal cells of the whorl-branchlets in the lower parts of the thallus and clothe the axis, particularly at the base of the plant, with a dense felt-like mat similar in structure to the spongy holdfast. (Fig. 25 F, K, L). Several, often 3, rhizoids are borne on each basal cell. Each is composed of elongate cells, is occasionally branched and grows downward, although initially they may protrude in various directions. Branched attachment processes may form terminally on a rhizoid on contact with the host surface.

Tetrasporangia: — Tetrasporangia are borne on the branches of the special short branches bearing the gland-cells (Fig. 25I). Each tetrasporangium is sessile, 50-60μ diam. when mature and divides cruciately although the resulting tetrad sometimes has a tetrahedral appearance.

Spermatangia: — In spermatangial plants the special short branches bearing gland-cells produce further branches which divide dichotomously several times and bear terminal groups of 2-4 spermatangial mother cells each having an apically staining protoplast (Fig. 25J).

Development of Carpogonial Branch and Carposporophyte: — Carpogonial branches are initiated close to the branch apex on the basal cells of the whorl-branchlets and 8-20 carpogonial branches are formed successively before elongation of the branch apex ceases. Only one carposporophyte develops at an apex. Each carpogonial branch develops from the lower part of the basal cell of the whorl-branchlet (the supporting cell) and divides by successive divisions (2 transverse, followed by 1 oblique division) to form a 4-celled carpogonial branch which curves upward around the supporting cell (Fig. 25 M-P). The terminal trichogyne developed from the carpogonium may be up to 150 μ in length.

Development of the carposporophyte follows the same pattern as described for Platythamnion nodiferum. Complete fusions occur between the axial cell, the residual supporting cell and the fusion cell. The central cell is large and cuts off a terminal gonimolobe followed by two lateral gonimolobes. The gonimolobe forms a comparatively large vegetative cell which cuts off several further sterile cells each of which gives rise to a group of carposporangia. The groups when mature together measure about 600µ across (Fig. 25 Q). Individual carposporangia are about 25 x 40µ.

Discussion: —

Macrothamnion mucronatum shows gradation in size and form within its wide distribution and common occurrence. One extreme is represented by the form of the type specimen. It has axial cells averaging 500 x 300µ and whorl-branchlets set at a wide angle (almost horizontal) to the axes and which are 1-1½ mm long (≡ to 2-2½ axial cells in length or, at the base of the plant, to 1 or >1 axial cell). The plant is usually smaller (up to 15 cm. high) and less heavily corticated than the other form. The other extreme of thallus form has axial cells about 300 x 200µ (up to 900 x 300µ at the base of the plant) and whorl-branchlets 1½-2 mm long which are set almost vertically, parallel to the axis, and~~, with~~ which cover 6-7 of the shorter axial cells ~~cover 6-7 axial cells over~~ in most parts of the thallus and 2-3 at the base of the plant. These plants are usually larger (up to 30 cm. in height) and in some the lower parts of the plant nearly always have a form similar to that found in the type specimen. In all plants the whorl-branchlets are vertical wherever new growth occurs, and it seems probable that the larger plant forms are due to rapid growth and possibly occur in deeper water. All plants are similar in reproductive features and vegetative structure, with variations occurring only in size of cells and in angle of insertion of whorl-branchlets.

Callithamnion acanthophorum (Kuetzing 1861, pl. 80 a-c) is unlike Macrothamnion mucronatum in having simple whorl-branchlets distichously arranged in opposite pairs. In all southern Australian plants the whorl-branchlets are consistently arranged in whorls of three and the gland-cells, not shown in Kuetzing's figures, are very prominent. It seems likely that Kuetzing's plant should be regarded as a distinct species. Its generic identity cannot be clarified without detailed examination.

One plant in AD from Harvey's Alg. Aust. Exsicc. No. 546-I(the number given by him to Callithamnion mucronatum) agrees with Kuetzing's figures and from the more delicate plant form, the arrangement of whorl-branchlets and tetrasporangia borne secundly on the whorl-branchlets is definitely not Macrothamnion mucronatum. This suggests that Harvey's collection contains more than one species. A specimen of Harvey's 546-H agrees with M. mucronatum.

The description given by Laing (1905: 404) for a New Zealand species referred to Antithamnion mucronatum, more closely agrees with the southern Australian species, Macrothamnion secundum n. sp.

Note: — Callithamnion griffithsioides Sonder 1855: 512 is a further synonym of Macrothamnion mucronatum. Sonder's type of this species from Wilson's Promontory 1853 is in MEL, No. 641, with also a probable isotype No. 646. Both are poor fragments of Macrothamnion mucronatum. The plant later referred to by Harvey (1860, Phyc. Aus., Pl. 167 and Fl. Tas. II, p. 332) as Callithamnion griffithsoides is a different species.

include in syny. on p. 214

MACROTHAMNION SECUNDUM n. sp.

Thallus fruticosus, usque ad 8 cm altus; axis filamentis rhizoideis corticatus. E quoque cellula 3 vortico-ramuli 1200-1600μ longi, interdum non ramosus, sed plerumque ab latere superiore 1-5 rami simplices producti; in statu juventus acuti, sape processis spinosis prope apices instructi. Cellulae glandulosae in ramis specialibus 2 (-3) - cellulatis positae. Tetrasporangia et spermatangia in ramis specialibus glanduliferis. Tetrasporangia cruciata. Quisque ramus uno carposporophyto ad cacumen procarpos (usque ad 18) pariente, instructus.

~~HOLO~~TYPE Locality: — Vivonne Bay, Kangaroo Is., South Aust.

HOLOTYPE: — AD, A 20,161.

DISTRIBUTION : — South Australia - Tunkalilla, Robe and Nora Creina on the mainland coast and Pennington Bay, Vivonne Bay and Stanley Beach on Kangaroo Island. Occurs on reefs and in rock pools of upper sub-littoral to lower-littoral zones.

(Figs. 26, 27A-N; Plate 7).

General Features: —

The plant grows up to 8 cm in height and forms a branched, bushy thallus with a dense coverage of whorl-branchlets over the axes (Fig. 26A). Attachment is by a small matted holdfast of rhizoidal filaments and the bases of the main branches, which are also axially corticated with rhizoids, often twist together as they do in Macrothamnion mucronatum. The whorl-branchlets are simple or have one to several unilaterally arranged branches, usually on the upper side. Both the rachis of the branchlet and its branches curve, often obliquely, upward (Fig. 26C).

Structure of Thallus: —

(1) Form and Development of Main Branches: — Axial elongation is by means of transverse divisions of a dome-shaped apical cell with the initiation of whorl-branchlets from the second or third cell below the apex (Fig. 26B). Mature axial cells are 2-4 times as long as broad and average about 300 x 140µ.

Lateral branches occur on the upper side of the basal cells of whorl-branchlets and develop at intervals of 4-8 cells, irregularly placed along the axes.

(2) Development and Branching of the Whorl-Branchlets: — Whorl-branchlets occur in evenly-spaced whorls of three from the upper part of each axial cell, (Fig. 26C). Each whorl is rotated from the whorl on the adjacent axial cell by 60°, so that whorls are superimposed on alternate axial cells. Whorl-branchlets may be unbranched but usually bear from one to five simple branches (Fig. 25 C,E), each of which when young has a mucronate tip (as in *M. mucronatum* (Fig. 26D)). These tips are usually lost as the whorl-branchlet becomes older leaving a rounded apex. Hook-like structures, as seen in *M. mucronatum*, occasionally occur on the upper cells of young whorl-branchlets but are comparatively rare. Average whorl-branchlets range from 1200µ to 1600µ in length. The basal cell of the rachis is smaller and more rounded than the next following cells, while, towards the apex the cells are smaller and form a tapering tip to the whorl-branchlet.

Gland-cells: — Gland-cells are small (up to about 25μ diameter, often 16-20μ), and are borne on a special 2 (-3)- celled short branch borne on the upper part of cells towards the base of the whorl-branchlets (Fig. 26 C,E). They are often more numerous on the younger parts of the thallus. Occasionally the second cell of the special short branch enlarges and cuts off a second gland-cell together with a further small sterile cell; the original gland-cell degenerates (Fig. 27 A-D). Very occasionally a third gland-cell can develop by a further similar elongation of the short branch. A thickened band can often be distinguished on the outer side of gland-cells.

Rhizoids and Attachment Organs: — The lower part of the thallus is axially corticated with sparingly-branched rhizoidal filaments. These rhizoids develop from the lower side of the basal cells of the whorl-branchlets and grow downwards forming a loose tangled sheath to the axis. Towards the base of the plant the rhizoids are robust and, on contact with a solid object, form digitate attachment organs (Fig. 26G). In the upper parts of the plant the young filaments are much finer (Fig. 26F) and may protrude in any direction from the axis.

Tetrasporangia: — Tetrasporangia are produced on the special short branches which bear the gland-cells. Several tetrasporangia may be produced successively from the first cell of the branch which enlarges, usually on the lower side, so that the gland-cell becomes displaced upwardly (Fig. 27 E,F,G). Usually not more than three develop from one cell at a time. Occasionally, as when a second gland-cell develops, the short branch may elongate and additional tetrasporangia develop from the cells of the elongated branch. (Fig. 26H - tetrasporangia developed on the first cell are omitted). The tetrasporangia are sessile, ovoid, 70-85μ in length within the gelatinous sheath, and divide cruciately. Occasionally a double gelatinous sheath surrounds a tetrasporangium, suggesting that a second one may develop within the sheath of the original tetrasporangium (Fig. 27I).

Spermatangia: — Spermatangial cells are borne terminally on extensions of the special short branches which bear the gland-cells. The basal cell of the special short branch produces a sterile cell outwardly which bears a whorl of four cells from its outer end. Each of these cells bears a further whorl of sterile cells each of which produces terminally a group of 2-4 spermatangial mother cells with apical protoplast (Fig. 27J).

Development of Carpogonial Branch and Carposporophyte: — Carpogonial branches develop close to the branch apices on the basal cells of young whorl-branchlets (Fig. 27K). One may occur on each branchlet of a whorl. They are produced successively so that up to 18 may be developed at a branch apex before axial elongation ceases. The carpogonial branch is initiated from the lower part of the basal cell of the whorl-branchlet (supporting cell) and divides by successive divisions (2 transverse, followed by 1 oblique) to give a 4-celled carpogonial branch which curves upward around the supporting cell. An elongate trichogyne (to 450μ) develops from the carpogonium (Fig. 27K).

Development of the carposporophyte, after fertilization, is similar to that in M. mucronatum. Only one develops at each branch apex. A connecting cell is cut off from the base of the carpogonium (Fig. 27L) and this cell fuses with a protrusion from the upper side of the supporting cell, which separates as the auxiliary cell (Fig. 27 L,M). The central cell is formed from the upper part of this cell and develops several successively formed gonimolobes. Each gonimolobe forms a rounded group of carposporangia in which the first 2 orders of cell divisions produce cells which remain vegetative (Fig. 27N).

The carposporophyte is protected by the surrounding upcurved whorl-branchlets.

Discussion: —

The species has been recorded only from a small area of South Australia, the most northerly collection being from rocks at Tunkalilla Beach. Plants of this collection are not as robust as those from further south, suggesting that the plant may thrive better in cooler temperatures. The species is quite distinct from M. mucronatum in size and form of plant, branching of whorl-branchlets and in form of special short branches which bear gland-cells, tetrasporangia and spermatangia.

MACROTHAMNION PECTENELLUM n. sp.

Thallus ca. 3 cm altus, interdum filamentis rhizoideis inferne sparse corticatus. Vortico-ramuli 2-3 e quoque cellula, curvato-adscendentes, in juventu acuti, ramis simplicibus vel nullis instructi. Cellulae glandulosae 1 aut plures, in ramis specialibus 2-cellulatis plerumque ab latere superiore vortico-ramulorum productis. Tetrasporangia cruciata, ca 80µ diametro, in ramis specialibus glanduliferis posita. Spermatangia ignota. Quisque ramus uno carposporophyto, ad cacumen ca. 12 procarpos pariente, instructus.

TYPE Locality: — South Arm, on South-west coast of Tasmania.

HOLOTYPE: — AD, A 28,033.

DISTRIBUTION : — Known only from the type locality growing on cockles and from Sorrento, Victoria (AD, A 22,771) collected from a depth of 35 ft. in the channel.

(Fig. 27 O - S).

General Features: — The plant grows to about 3 cm in height and is only sometimes lightly axially corticated near the base. It attaches by a primitive form of holdfast composed of loosely intertwined rhizoidal filaments most of which individually produce a branched, digitate attachment organ.

Each axial cell bears a whorl of two or three whorl-branchlets which may be secundly branched with 1-3 simple branches or may be completely unbranched. The whorl-branchlets curve upward and each bears several gland-cells.

Form and Development of Main Branches: — Growth occurs by transverse divisions of a dome-shaped apical cell and a short chain of immature round axial cells is formed at the branch apex. The growing tip is protected by the upward curvature of the whorl-branchlets below.

Mature axial cells are cylindrical and usually 3-4 times as long as broad (about 220 x 80μ). Lateral branches are borne on the upper side of the basal cells of whorl-branchlets and are produced at unequal intervals along the axes.

Development and Branching of Whorl-Branchlets: — Whorl-branchlets are initiated on the second or third cell of the branch apex. When young they have an extremely acute tip, but, later, as in *Macrothamnion mucronatum* and *M. secundum*, this is lost and the tip is comparatively rounded (Fig. 27 Q,R). The basal cell of each mature whorl-branchlet remains smaller than the cells adjacent to it. Whorl-branchlets occur in whorls of 2 or 3 from the upper part of each axial cell (Fig. 27 O,P), and are up to 1 mm. long. When 2 occur the whorl-branchlets may be opposite and almost decussately arranged or they may appear as 2 adjacent branchlets of a whorl of three from which the third one is missing. Whorls of 3 whorl-branchlets are equally spaced around the axial cell.

Gland-Cells: — Gland-cells, about 25µ diam., are borne on short 2-celled special branches near the outer ends of cells of the whorl branchlets (Fig. 27S). Often several occur on adjacent cells at about the centre of a whorl-branchlet (Fig. 27 O,P).

Attachment Organs: — The plant is attached by rhizoidal filaments which are borne on the lower side of the basal cells of whorl-branchlets in the lower part of the plant, and form a sparse rhizoidal cortication around the lower axes. The filaments become intertwined at the base of the thallus and individual rhizoids attach by means of a small terminal digitate process. The number of rhizoids formed varies considerably in different plants so that some develop a discrete holdfast as an attachment organ and others attach more or less by individual rhizoids.

Tetrasporangia: — Tetrasporangia are borne on the special short branches which support the gland-cells and develop as already described for M. secundum. Several tetrasporangia develop successively from the short branch and when mature are ovoid in form, about 80µ long, and cruciately divided.

Spermatangia: — Not recorded.

Development of Procarp and Carposporophyte: — Procarps are initiated on the basal cells (supporting cells) of whorl-branchlets at branch apices and about a dozen procarps usually develop at each apex. The 4-celled carpogonial branch is initiated from the lower side of the supporting cell and curves upward. It is formed by successive divisions (2 transverse, and 1 oblique) of the initial cell and an elongate trichogyne terminates the carpogonium. The carposporophyte develops as has been described for Macrothamnion secundum to produce rounded groups of carposporangia. Only one carposporophyte develops at a branch apex.

Discussion: —

The thallus of Macrothamnion pectenellum is much smaller and more slender than that of M. secundum but in features of reproduction the two species are identical. The whorl-branchlets arranged in whorls of two or three and unequally branched, suggest relationship with the genus Antithamnionella. The plant however, is placed in Macrothamnion due to the position of gland-cells and features of reproduction. It is probably a comparatively primitive species and may represent an early phase toward the highly evolved plant form found in M. mucronatum.

ANTITHAMNIONELLA Lyle 1922

The species of *Antithamnionella* described here constitute the first record of this genus from Australia, although it has been recorded from other widely separated areas — Europe, South Africa, Cape Horn and Tristan da Cunha and a total of 5 species are already known. Lyle (1922) separated the genus from *Antithamnion* chiefly on the tetrahedral (instead of cruciate) division of tetrasporangia and on the presence of verticils of 3 whorl-branchlets. Feldmann-Mazoyer (1940) considered this to be insufficient evidence to separate the genus from *Antithamnion* but Kylin (1956) maintained Lyle's genus with the additional species added by de Valéra (1939) and Baardseth (1941b).

There are other features, both vegetative and reproductive, besides Lyle's characters, which justify the maintenance of the genus and separate it from *Antithamnion*:-

1. The development of erect lateral branches from the prostrate axes as also found in *Acrothamnion*. In *Antithamnion* the erect parts of the thallus are formed from the unattached ends of a prostrate thallus, or from upwardly directed whorl-branchlets.
2. Lateral branches usually produced in place of a whorl-branchlet. In *Antithamnion* they occur on the basal cells of whorl-branchlets (except in *A. gracilentum* in which they replace a whorl-branchlet).
3. Inconsistency in both number of branchlets per whorl and in branching of whorl-branchlets. In southern Australian species of *Antithamnion* both form and number of whorl-branchlets remain comparatively constant.

4. Gland-cells sessile on 2nd - 5th cell of whorl-branchlets (except in Antithamnionella glandifera which may bear up to 20 gland-cells on a single whorl-branchlet). The gland-cells of Antithamnion are borne on a short 2-4 celled special branch.

5. Tetrahedral division of tetrasporangia (used by Lyle in original description of genus). Division is cruciate in Antithamnion.

6. Carposporophyte development showing: —

   (i) Reduction in number of procarps to 1-3 per branch apex. Usually (4-) 8-20 occur at each branch tip in Antithamnion.

   (ii) Reduction in length of whorl-branchlet bearing the procarp to only one poorly developed cell besides the basal (supporting) cell and having no other whorl-branchlets borne on the fertile axial cell. In Antithamnion each procarp is developed on the basal cell of a young whorl-branchlet several cells long and with the normal number of whorl-branchlets produced on each axial cell.

TYPE species: — Antithamnionella sarniensis Lyle (European).

Notes on the Phylogeny of Antithamnionella with especial reference to Antithamnion.

Species of Antithamnionella occurring in southern Australia may represent two separate lines of development (1) a northern hemisphere (European) line represented by A. spirographidis which has probably been introduced to Australia and (2) a southern Australian line represented by A. tasmanica and A. glandifera.

It seems likely that Antithamnionella is primitive in thallus form when compared with Antithamnion. This is indicated by instability in number, form and order of initiation of whorl-branchlets even within individual plants. Within the genus the number of branchlets per whorl ranges from 3-4 (as in Antithamnionella tasmanica) to 1-2 (-3) (as in A. glandifera) and actually varies even on individual plants. Reduction in number and stabilization of form and number is usually indicative of greater structural efficiency and, hence, of a more advanced condition.

Thus within the southern Australian species of Antithamnionella, A. tasmanica with 3-4 branchlets per whorl possibly represents the most primitive vegetative form.

In carposporophyte development also A. tasmanica is probably the most primitive of the three species known from southern Australia.

(a) Although 1 (-2-3) procarps may develop at each branch apex in all three species, the higher numbers occur more frequently in A. tasmanica.

(b) The outer sterile cell of the 2-celled whorl-branchlet which bears the procarp shows least modification in A. tasmanica where it appears similar to a normal cell of a whorl-branchlet (see figs. showing carposporophyte structure for individual species).

(c) Up to 6 groups of carposporangia develop from each carposporophyte in A. tasmanica, while it is usual for only 3 to form in both A. spirographidis and A. glandifera.

Carposporophyte development, as distinct from thallus organization, is probably more advanced in Antithamnionella than in Antithamnion. This is indicated by greater specialization in:

(i) the comparatively reduced number of procarps developed at each branch apex (1-3 in Antithamnionella and (4-) 8-20 in Antithamnion).

(ii) Greater reduction and specialization of the short whorl-branchlet which bears each procarp. In Antithamnion this whorl-branchlet consists of several cells beyond the basal (supporting) cell, while in Antithamnionella it is reduced to only one cell (small and modified in form in A. spirographidis and A. glandifera) besides the basal (supporting) cell.

(iii) Complete lack of development of other whorl-branchlets on the axial cell bearing a procarp.

A second whorl-branchlet develops in Antithamnion. The genus Antithamnionella shows some similarities to Antithamnion cruciatum. Probably the most significant of these are:

(i) variety in form. Although A. cruciatum constantly bears opposite pairs of whorl-branchlets, these branchlets are inconsistent in branching and a variety of forms occurs.

(ii) Tendency toward the production of simple branches (often unilateral) on whorl-branchlets in both Antithamnion cruciatum and in Antithamnionella. Schiffner (1916) noted that Antithamnion spirographidis showed a tendency to produce secund pinnules on the lower side of the rachis of the whorl-branchlet rather than on the upper side as found in Antithamnion cruciatum.

(iii) Tetrasporangia in Antithamnionella are tetrahedrally divided but may occasionally appear from the form of the spores to have divided cruciately. This suggests that timing rather than position of the divisions differs in the two genera.

These features suggest that, although generically distinct, *Antithamnionella* is probably not far removed from a primitive form of *Antithamnion*, such as *A. cruciatum* and probably has developed parallel to the line of development seen within *Antithamnion*. Unfortunately detail of carposporophyte development for *Antithamnion cruciatum* is not known, but it seems probable that *Antithamnion* has advanced vegetatively within the genus while ~~the present species of~~ *Antithamnionella* represents specialization and advance in carposporophyte development.

Key to southern Australian species of *Antithamnionella*.

1\. Lateral branches developed at irregular intervals along axes. Whorl-branchlets in whorls of 3-4. Carposporophyte producing up to 6 somewhat elongate groups of carposporangia. ... ... *A. tasmanica*.

1\. Lateral branches borne at regular intervals along axes usually on every 3rd or 4th cell. Whorl-branchlets in whorls of 1-2 (-3). Carposporophyte usually producing 3 rounded groups of carposporangia (Only occasionally more than 3 groups)... ... 2.

2\. Whorl-branchlets usually simple, about 250μ (occasionally to 380μ) long. Gland-cells sessile on upper side of 2nd-3rd cell of whorl-branchlet; more abundant in upper parts of plant... ... ... *A. spirographidis*

2\. Whorl-branchlets simple (50-60μ long) in upper part, branched (-250μ long) in lower part of thallus. Gland-cells numerous (up to 20) on whorl-branchlets. Most abundant in lower parts of plant. ... *A. glandifera*.

ANTITHAMNIONELLA TASMANICA n. sp.

Thallus prostratus ramis erectis usque ad 0.8 cm altis. E quoque cellula 3-4 vortico-ramuli 200-250μ longi, sine ramificatione aut ab latere superiore unilateraliter ramosi, producti. Cellulae glandulosae sessiles in cellula tertia ad quinta vortico-ramulorum. Tetrasporangia tetrahedralia, sessilia in cellula infima aut subinfima vortico-ramulorum in thallo superiore. Spermatangia in ramis specialibus brevibusque (e 1-5 cellulis compositis) in rachidibus vortico-ramulorum. Procarpi 1 (-3) in ramulis 2-cellulatis prope apices ramorum positi.

TYPE Locality: — Bicheno, Tasmania.

HOLOTYPE: — AD, A 28,007.

DISTRIBUTION: — Growing on corallines in surge channels on granite at Rice Beach, Blowhole and Peggy's Point, Bicheno, Tasmania. Also in Victoria from Lawrence Rock, Portland, and from Bridgewater Bay, growing on Pyura stolonifera, and from Fairhaven, east of Lorne, growing on Dictyota sp.

(Fig. 28).

General Features: —

The plant is small with a creeping prostrate portion from which arise erect branches to about 0.8 cm. high. The branches bear whorls of 3-4 simple or unilaterally branched whorl-branchlets from the upper part of each axial cell. Axial cells are about six times as long as broad, but near branch apices they are comparatively short which results in dense overlapping of the whorl-branchlets giving ocellate branch tips. The prostrate part of the thallus is attached by multicellular rhizoids which bear terminal digitate holdfasts (Fig. 28A).

Structure of Thallus: —

(1) Form and Development of Main Branches: — Growth occurs by transverse divisions of an elongate dome-shaped apical cell with whorl-branchlets initiated (in actively growing apices) 3-7 cells below the apex (Fig. 28B). A chain of up to 20 transversely elongate immature axial cells is sometimes conspicuous at branch apices.

Mature axial cells are (100-200) x (30-60)μ or occasionally longer in older axes. Lateral branches arise irregularly and apparently in place of whorl-branchlets in the erect parts of the thallus, although on the prostrate axis they arise from a basal or second cell of a whorl-branchlet (Fig. 28G).

(2) Development, Arrangement and Branching of Whorl-branchlets: — Whorl-branchlets are initiated as chains of cells from axial cells several below branch apices. The terminal cell of a developing whorl-branchlet may be 25μ long before it divides. Branchlets of each whorl are initiated successively on the axial cell, as described and figured for *Antithamnionella sarniensis* Lyle (de Valéra, 1939). Each whorl usually consists of four, occasionally three, evenly-spaced whorl-branchlets which are erect or oblique to the axis. Each mature whorl-branchlet consists of about 10-12 cells and is 200-250μ long. Whorl-branchlets may be simple, especially in older parts of the thallus, or may bear one to several simple branches which are often, but not always, unilaterally arranged on the rachis (Fig. 28 C,D). Branching of whorl-branchlets is more common in sexual plants than in those bearing tetrasporangia.

Gland-cells: — Gland-cells are sessile, about 12–18µ long, on the 3rd-5th (commonly 4th) cells of the rachides of the whorl-branchlets (Fig. 28 C,D,E). They are usually single on a whorl-branchlet but very occasionally 2 occur on adjacent cells.

Rhizoidal Attachment Organs: — The prostrate axis attaches by means of rhizoids from the basal cells of whorl-branchlets (Fig. 28 F,G). When young these consist of several elongate cells (Fig. 28F), which, on contact with the host, contract to form a comparatively shorter, broader structure which develops a terminal digitate holdfast (Fig. 28 G). The cells of the rhizoids are close together and the junctions are sometimes visible only in the gelatinous sheath which surrounds them. Although usually single, up to three may develop on one basal cell.

Tetrasporangia: — Tetrasporangia are borne successively on the upper side of the basal cells, and rarely the second cell, of whorl-branchlets in the upper parts of the thallus.

Each tetrasporangium is sessile, elongate when young, but spherical, about 40µ diam. and tetrahedrally divided when mature (Fig. 28E). Two tetrasporangia may occur on a cell at one time and the occasionally-double gelatinous sheath surrounding the tetrasporangium suggests that a second one may develop after the original one is shed.

Spermatangia: — Spermatangial mother-cells (2.5µ diam~~eter~~) are cut off laterally from cells of short chains, 1-5 cells long, (Fig. 28I), borne on the upper side of the cells of the rachides of the whorl-branches in upper parts of the thallus (Fig. 28H). Spermatangial mother-cells may also develop directly on cells of branches of the whorl-branchlets or from short chains borne on the branches.

Development of Procarp and Carposporophyte: — Carpogonial branches are borne on the basal cells of young two-celled whorl-branchlets several cells below branch apices. The basal cell of the whorl-branchlet is rounded and forms the supporting cell, while the second (terminal) cell remains small and insignificant and is usually completely lost during development of the carposporophyte. No further whorl-branchlets are initiated on the axial cell which bears the procarp, and the branch apex, which ceases further growth, is deflected away from the carpogonial branch (Fig. 28J). Usually only one procarp develops at a branch apex, but 2 or 3 may be initiated, although only one carposporophyte develops.

As in Antithamnion the 4-celled carpogonial branch is formed by 2 successive transverse and one oblique division, but a comparatively shorter trichogyne, 40-50µ long, develops from the carpogonium, (Fig. 28J). After fertilization a protrusion develops from the carpogonium toward the supporting cell. The auxiliary cell develops from the upper side of the supporting cell (Fig. 28K,L) and probably fusion by means of a connecting cell between the carpogonium and auxiliary cell occurs almost simultaneously with the separation of the auxiliary cell from the supporting cell.

The auxiliary cell divides to form a lower foot-cell and an upper central cell from which the first gonimolobe develops terminally (Fig. 28M). As the carposporangial groups develop, complete fusion occurs between the axial cell, residual supporting cell and foot-cell of the carposporophyte (Fig. 28N) and there is a widening of the connection between the foot-cell and the central cell. At least six successively developed carposporangial groups may occur on the central cell at one time. Each gonimolobe is initiated as a protrusion from the central cell and cuts off 2 lateral cells from the outer end (Fig. 28P a and b). The initial cell remains sterile while the two secondary cells divide repeatedly to form elongate groups of carposporangia.

There is no involucral development around the carposporophytes and elongation of the axes is carried on by lateral branches developed below the carposporophyte.

Discussion: —

The Tasmanian species differs from other species of Antithamnionella mainly in length and branching of whorl-branchlets. It resembles most closely A. seriata Baardseth (1941b) which also has secundly-branched whorl-branchlets. A. tasmanica is however, a much smaller plant (A. seriata is 2 cm. high with shorter whorl-branchlets bearing comparatively longer branches and tetrasporangia confined to the basal cells of the whorl-branchlets).

Further discussion on the relationships of Antithamnionella is included in Section X.

ANTITHAMNIONELLA SPIROGRAPHIDIS (Schiff.) nov. comb.

Antithamnion spirographidis Schiffner 1916: 137, figs. 19-27.

TYPE Locality: — Trieste (Schiffner 1916).

TYPE: — ? (Possibly W., BM. or B.)

DISTRIBUTION : — On barge, Pt. Adelaide, South Australia. (A second collection comes from Rozelle screens, White Bay Power Station, New South Wales and although not strictly southern Australia, is of interest in representing an area of harbour activities). Mainly a northern hemisphere species.

(Fig. 29).

General Features: — Small, delicate plant with creeping prostrate axis bearing flexuous, unattached branches (up to 1 cm. in length) from every 4th (occasionally 3rd) cell. Lateral branches also bear further similarly arranged lateral branches. Each cell of the axes bears a pair (occasionally 1 or 3) of opposite simple whorl-branchlets. On erect branches these may be either opposite or unilaterally arranged with one whorl-branchlet from each cell (Fig. 29 A,B). Whorl-branchlets produced on erect lateral branches are usually distichously arranged (Fig. 29 A,B).

Structure of Thallus: —

(1) Form and Development of Main Axes of prostrate and erect branches: —

Growth takes place by transverse divisions of an elongate dome-shaped apical cell and lateral branches and whorl-branchlets are initiated several cells below the apex (Fig. 29C).

Lateral branches, produced in place of whorl-branchlets, occur usually on each 4th cell of the axis. A young lateral branch is similar to a whorl-branchlet and develops an axial chain of about 10-15 cells before whorl-branchlets are initiated (Fig. 29C, branches 1,2,3).

Cells of the axis are about 3-6 times as long as broad, and in mature prostrate parts of the thallus are about 180-230 x 30-50µ.

(2) Development and Form of Whorl-Branchlets: — Whorl-branchlets occur in pairs or singly from axial cells several below the apex of axes and are initiated as elongate protrusions from the axial cells (Fig. 29C). Mature whorl-branchlets are simple consisting of a chain of cells each about 16-20µ long and measuring totally about 250µ in length. Occasional whorl-branchlets are upto 380µ long. Whorl-branchlets develop irregularly at the branch apex and do not necessarily mature successively on adjacent axial cells.

Gland-Cells: — Gland-cells occur mostly in the upper parts of the plant and are cut off from the upper side (Fig. 29D a,b,c) of the second or, occasionally the third, or second and third cells of the whorl-branchlets. Each gland-cell is about 10-12µ in diameter, is pitted and curves partly around the parent cell.

Attachment Organs: — Slender rhizoidal attachment filaments arise from the basal cells of the whorl-branchlets and occasionally also from the second cell (Fig. 29E). On contact with the host they develop a terminal digitate process which adheres to the host surface and the cells of the rhizoids contract and become proportionally shorter and broader. The basal cell of the whorl-branchlet enlarges and becomes comparable in form with the cells of the rhizoid (Fig. 29F). Occasionally a branch shoot arises from a cell of the digitate attachment process (Fig. 29G) and presumably develops into a normal shoot.

Tetrasporangia: — Tetrasporangia are borne on the upper, outer end of the basal, and occasionally the second cell of the whorl-branchlets in unattached parts of the thallus (Fig. 29P). Each mature tetrasporangium is sessile, ovoid, about 40-48 x 30-35µ within the gelatinous sheath and tetrahedrally divided. Only one tetrasporangium develops from a cell of the whorl-branchlet at one time and successive stages of development are scattered irregularly on each branch.

Spermatangia: — Spermatangial mother-cells are borne in whorls of 2-4 directly upon the axial cells of a special short branch (12-18µ long) developed on the upper side of the lower cells of the whorl-branchlets. Occasionally two spermatangial branches at different stages of development are borne on the same cell of the whorl-branchlet (Fig. 29R, a & b). Each special branch consists of an axis of 3-5 cells with the spermatangial mother-cells developed from protrusions towards the upper part of these cells (Fig. 29 S,T). The spermatangial mother-cells measure about 3-4µ in length.

Development of Procarp and Carposporophyte: — Carpogonial branches are produced on the basal cells of young whorl-branchlets (2 cells in length) near branch apices. Only one carpogonial branch occurs initially at each apex, although a further one, at least, may be produced later (Fig. 29L). Only one carposporophyte matures on one branch apex. The branch axis bends away from the cell bearing the fertile branchlet so that the apex, which is limited in growth after the initiation of the carpogonial branch is directed away from the carpogonial branch (Fig. 29 I,J). The whorl-branchlet bearing the carpogonial branch does not elongate beyond 2 cells in length. Further growth of the thallus occurs from a lateral branch below the fertile whorl-branchlet.

Prior to the initiation of the carpogonial branch the basal cell of the young whorl-branchlet enlarges, becomes rounded and stains densely (Fig. 29H). The carpogonial branch initial develops from this cell and divides by a series of three successive transverse divisions to give a 4-celled carpogonial branch (Figs. 29 I,J,K). An elongate trichogyne develops terminally from the carpogonium (Fig. 29K). The carpogonium is more or less conical in form. After fertilization fusion between the carpogonium and auxiliary cell, cut off from the upper part of the supporting cell, occurs by means of a connecting cell (Fig. 29L). This stage has only been observed a few times, but it appears that separation of the auxiliary cell from the supporting cell occurs rapidly and probably simultaneously with the fusion of the connecting cell (developed from the carpogonium) and the auxiliary cell. After this fusion has occurred the carpogonial branch degenerates and the auxiliary cell divides into a lower foot cell and an upper central cell. The first gonimolobe is terminal and develops from the upper side of the central cell (Fig. 29M,N). Further gonimolobes form laterally and successively with usually three reaching maturity. As the gonimolobes develop, fusions with widening of the connections take place between the cells of the carposporophyte and the axial cell (Fig. 29 O). Carposporangia are formed from successive divisions of the cells produced from the first gonimolobe initial.

Discussion: —

Antithamnionella spirographidis was first recorded from the Adriatic Sea (Schiffner 1916), and has since been found associated with dockyards and harbour activities on the south coast of Britain (Devonport Dockyard, Plymouth Sound) where sea temperatures range from 14°C to 24°C (Westbrook, 1934) and at Cherbourg, North France (Feldmann, 1937).

The present record is the first from Australian waters and it seems likely that it has been introduced from Europe to Port Adelaide by the movement of ships. The plant agrees with descriptions of *A. spirographidis* by Schiffner (1916), Westbrook (1934), Feldmann (1937) and Feldmann-Mazoyer (1940).

Tetrasporangia in the southern Australian plants are tetrahedrally divided even when arrangement of the sporangia suggests cruciate division. Westbrook (1934) described procarp and carposporangial features, but lacked early stages in the development of the carposporophyte. Several successive collections from Port Adelaide showed the beginning of tetrasporangial development in July (several plants only found fertile) with an increase in proportion of tetrasporangial plants until November when nearly all plants were fertile and a few sexual plants were also found. A similar seasonal sequence is recorded by Westbrook (1934) for Plymouth where she records tetrasporangial plants in June followed by sexual plants in August and December.

Portions of tetrasporangial plants were placed on slides in sea-water and left to germinate. The tetraspores were liberated from the parent plants overnight, but did not become attached to the slides until 48 hours later. Germination commenced almost immediately and early stages (Fig. 29 Qa-c) were observed between 24 and 48 hours later.

<u>ANTITHAMNIONELLA GLANDIFERA</u> n.sp.

Thallus usque ad 2.5 cm altus. Rami laterales regulariter e quoque cellula tertia axis producti. E quoque cellula 1-3 vortico-ramuli usque ad 250µ longi, illi plerumque simplices superne, inferne irregulariter ramosi, producti. Cellulae glandulosae sessilie, in ramis inferioribus 15-20, in superioribus pauciores. Tetrasporangia et spermatangis ignota. Procarpi 1 (-2), in ramulo 2-cellulato in cellula tertia axiale ad apicem rami positi.

<u>TYPE Locality</u>: — St. Vincents Gulf, 3-5 miles off Outer Harbour, South Aus.

<u>HOLOTYPE</u> : — AD, A 26,660.

<u>DISTRIBUTION</u> : — Known only from the type locality, probably growing on Posidonia, and from Beauty Point, River Tamar, Tasmania, (AD, A 28,019), growing on an old barge.

(Fig. 30).

General Features: — The plant is epiphytic, up to $2\frac{1}{2}$ cm. in height, attached at the base by rhizoids which develop a terminal digitate holdfast.

The erect thallus is laterally branched, from about every third axial cell, and each cell of the axis bears a whorl of one to three unequally-spaced whorl-branchlets of which the longest are up to about 250µ long (Fig. 30A). Whorl branchlets in upper parts of the plant are usually unbranched while those below are irregularly branched and bear prominent, sessile gland-cells. Branching and number of gland-cells both tend to increase towards the lower part of the thallus. Chromoplasts in mature cells are narrow and elongate, usually running the complete length of each cell.

Structure of Thallus: —

(1) Form and Development of Main Branches: — Growth occurs by transverse divisions of a dome-shaped apical cell and a chain of small immature cells is formed at branch apices (Fig. 30B). Mature axial cells are cylindrical, often with a tendency to broaden at the lower end. They are usually about 4 or 5 times as long as broad (about 400 x 96µ at the base of the thallus and 100 x 25µ in the central region).

Lateral branches occur in place of whorl-branchlets and usually on every 3rd axial cell (Fig. 30B, a-d). At the base of a new branch there is often an interval of 6 cells before the first lateral branch occurs (Fig. 30 A, a). The branches are irregularly placed around the axis. At the base of the thallus new lateral branches may arise from the basal cell of a whorl-branchlet (Fig. 30C).

(2) Development, Arrangement and Branching of Whorl-branchlets: — Whorl-branchlet initials are elongate (Fig. 30 B) and arise irregularly from immature axial cells near branch apices. Mature axial cells usually bear two whorl-branchlets but sometimes there is only one, or, occasionally, three develop. They arise without a regular pattern of initiation on either individual or successive axial cells. In upper parts of the plant they are commonly simple, 2-5 cells (50-60µ) long often with a terminal hair, especially when young. Branching increases progressively towards the base of the erect thallus where they may be up to 250µ in length (Fig. 30, E, F, G whorl-branchlets from the upper to central regions of the thallus). Whorl-branchlets are attached to the axis at an angle of 45° - 90°.

Gland-Cells: — Gland-cells are sessile on cells of the whorl-branchlets (including branches of the whorl-branchlets) and are very prolific in the lower parts of the thallus. They are sparse in the upper thallus only occurring on an occasional whorl-branchlet on either the basal or second cell; several gland-cells occur on the lower to central cells of whorl-branchlets in the central thallus, while, towards the base of the plant, 15-20 gland-cells may occur on one whorl-branchlet with often two produced on a single cell (Fig. 30 I).

Each gland-cell is cut off laterally from a cell of a whorl-branchlet and is up to 25 µ long and curves around the parent cell (Fig. 30H). Mature gland-cells are very dense and appear porous in structure (Fig. 30J).

Attachment Organs: — Attachment is by rhizoids which develop from the basal cells of the whorl-branchlets in the lower parts of the thallus (Fig. 30K). Each rhizoid is several cells in length and develops a terminal, often dichotomously branched, holdfast (Fig. 30L).

Occasionally branch apices of the erect thallus develop attachment rhizoids when in contact with host tissue, and possibly new plants can arise by this means.

Tetrasporangia and Spermatangia: — Not recorded.

Development of Procarp and Carposporophyte: — The procarp is developed usually on the third cell below the branch apex (Fig. 30 M, N) and no further elongation of the axis occurs. Occasionally two procarps are produced one below the other on separate axial cells (Fig. 30 O).

The carpogonial branch is attached to the lower part of the supporting cell which is the basal cell of a young 2-celled whorl-branchlet. The second (terminal cell) of the whorl-branchlet is reduced in size and forms a distinct small, sterile cell on the larger, denser supporting cell. When this sterile cell occurs, from the orientation of the procarp, on the upper face of the supporting cell (Fig. 30 O) it appears similar to sterile cells found in certain other groups of the Ceramiaceae. The phylogenetic implication of this is discussed later. The 4-celled carpogonial branch, as in Antithamnion, is formed by 2 transverse divisions followed by 1 oblique division. The auxiliary cell, cut off from the upper side of the supporting cell, has not been seen but its derivatives, the foot- and central-cell (Fig. 30P) are similar to those in related species.

The central cell develops a terminal gonimolobe followed successively by at least two lateral ones (Figs. 30 P,Q). Carposporangial groups are rounded when mature.

There is no protective involucre formed and further axial growth takes place by lateral branches from the axial cells below the carposporophyte.

Discussion: —

This species is distinct from other species of *Antithamnionella* in number and arrangement of whorl-branchlets, in the prolific production of gland-cells in the lower parts of the thallus and in the form of the terminal whorl-branchlet cell developed beyond the procarp. The position of the procarp is also closer to the branch apex than in other Australian species of *Antithamnionella* including *A. spirographidis*.

The specimen (AD, A 28,019) from Beauty Point, River Tamar, Tasmania, was growing on an old barge and probably belongs to this species. It agrees with *A. glandifera* in form of whorl-branchlets and in position and number of gland-cells per branchlet, but differs in having much denser branching and a tendency, due to shorter axial cells, for whorl-branchlets to overlap.

HETEROTHAMNION J. Agardh 1892.

The genus Heterothamnion is confined to the southern coast of Australia and, until the present time, has been poorly known with H. muelleri as the type and only species. J. Agardh separated it from Callithamnion on the verticillate arrangement of determinate branches and the position of tetrasporangia. The genus is maintained by Kylin (1956) although few other authors have recognized it as distinct. Three species are here described from southern Australia, each of which occurs on a single host plant (2 species on Cystophora platylobium and 1 species on Cystophora siliquosa).

The genus is distinguished by the following combination of features: —

1. All species form dense tufts usually on the receptacles of Cystophora spp.
2. The thallus consists of sparingly branched erect axes which taper towards the base and attach to the host by penetration of branched rhizoids between cells of the host tissues. Some penetration of rhizoids into host tissue may also occur in Perithamnion and in Tetrathamnion, but these genera are distinct in thallus structure.
3. Each whorl-branchlet consists of a distinct rachis (of 5-10 cells) which may or may not bear branches, in contrast to a whorl-branchlet composed of whorls of cells from the outer end of each successive cell (as in Tetrathamnion and Perithamnion).
4. Decrease in length, branching and number of whorl-branchlets towards the base of the thallus.
5. Groups of carposporangia borne on an elongate sterile cell. In most genera this sterile cell is more isodiametric in form.

There is no good evidence within the genus indicative of any phylogenetic line of development. In vegetative features the three species are very similar and vary only in size and distribution of branches of whorl-branchlets. There is no significant sequence in order of arrangement of these branches of the whorl-branchlets between species. Procarps occur either singly or in twos on the 2nd-3rd cell below the apex in H. muelleri and H. sessile. In H. episiliquosum 2-4 procarps are borne always on the 3rd axial cell below the apex. This increase in number of procarps per axial cell, and stabilization in the position of the procarps may indicate a trend towards more advanced reproductive organization.

TYPE species: — Heterothamnion muelleri (Sond). J. Ag.

Key to southern Australian species of Heterothamnion

1. Tufts occurring only on *Cystophora siliquosa*. Whorl-branchlet 5-6 cells (to 200µ) long, in central thallus, about 4 cells long in lower thallus.
Procarps in whorls of 2-4 on the 3rd axial cell below the branch apex... ... ... *H. episiliquosum*

1. Tufts occurring only on *Cystophora platylobium*. Whorl-branchlets 9-12 cells (to 380µ) long in central thallus, 6-8 cells long in lower thallus.
Procarps borne singly, or in twos, from 2nd or 3rd cell below branch apex.. 2

2. Whorl-branchlets usually unbranched, up to 9 cells (320µ) long, often curved upward. Tetrasporangia 30-40µ diam., borne successively on a distinct stalk cell ... ... *H. muelleri*

2. Whorl-branchlets usually branched, 9-12 cells (to 380µ) long, often with tips curved downward. Tetrasporangia 25-30µ diam., sessile.. ... ... *H. sessile*

<u>HETEROTHAMNION MUELLERI</u> (Sonder) J. Agardh 1892: 25. Kylin 1956: 373.

<u>Callithamnion muelleri</u> Sonder 1855: 513. J. Agardh 1876: 27. De Toni 1897: 1337. Harvey 1863, synop: ~~No.~~ 699; Alg. Aus. exs. No. 526. Lucas 1909: 49. Lucas and Perrin 1947: 333. Wilson 1892: 187.

<u>TYPE Locality</u>: — Wilson's Promontory, Victoria.

<u>HOLOTYPE</u>: — MEL, 10249.

<u>DISTRIBUTION</u> : — South coast of Kangaroo Island and Robe, South Australia, to Wilson's Promontory, Victoria. Epiphytic on <u>Cystophora platylobium</u> (Mertens) J. Ag.

(Fig. 31 A-O).

<u>General Features:</u> — The plants occur in tufts on the receptacles of <u>Cystophora platylobium</u>, attached by rhizoids which penetrate between the cells of the host tissue. The erect thallus is up to 0.5 cm. high and branched several times (Fig. 31A). The main axis tapers towards its base and each cell bears a whorl of 2-4 (usually 4) whorl-branchlets. The whorl-branchlets are inserted at right angles to the axis, are usually simple and curve upwards (Fig. 31A).

<u>Structure of the Thallus:</u> —

(1) <u>Form and Development of Main Axes:</u> — Growth of the erect axis occurs by transverse division of a dome-shaped apical cell (Figs. 31 B,C) and must be restricted as the axis approaches its mature height. The young plant develops rhizoids downwardly, which penetrate the host tissue, and an erect axis upwardly. Several main branches may arise from the base of the plant. The largest axial cells (about 190x70μ) are in the central region. The axis

branches several times by means of lateral branches borne on the upper side of the basal cells of whorl-branchlets, usually only a few cells below the apex. Female plants are more profusely branched due to the production of lateral branches from whorl-branchlets below the carposporophytes.

(2) Development, Arrangement and Branching of Whorl-branchlets: — Whorl-branchlet initials occur on the cell below the apex of axes, and a whorl of four whorl-branchlets may be formed on the 3rd or 4th cell (Fig. 31C). Whorl-branchlets do not occur on the lower cells of the axes and, in young plants, whorl-branchlet initiation does not commence immediately. The first whorl-branchlets formed may be single or in twos rather than in a complete whorl of four (Fig. 31B). Mature whorl-branchlets are 9-12 cells (up to 320µ) long, usually unbranched with the longest whorl-branchlets in the central parts of the axes. Whorl-branchlets are shorter towards the base of the plant, the lowest ones being 4-6 cells (140µ) long.

Occasionally whorl-branchlets may bear 1-3 short simple branches (1-5 cells long) on the upper side.

Gland-cells: — Gland-cells are ovoid, appear pitted on the surface, are 18-24µ long and sessile on the 3rd or 4th (-5th) cells of whorl-branchlets (Fig. 31D); occasionally they may also occur on the terminal cell of a whorl-branchlet. When this occurs there is often a degenerate gland-cell lower on the branchlet. (Fig. 31F).

Most gland-cells occur in the upper parts of the plant and are often lacking or degenerate in the central to lower regions.

Attachment Organs: — Sparingly-branched rhizoids arise from the base of the plant and penetrate into the tissues of the host. The cells of the rhizoids are elongate and irregular in form (Fig. 31B).

Tetrasporangia.

Tetrasporangia are borne on the upper side of the cells of the whorl-branchlets (Fig. 31F). A protrusion develops on the whorl-branchlet cell (Fig. 31G) and a tetrasporangium initial is cut off terminally from it. (Fig. 31H). The tetrasporangium is thus formed on a distinct stalk cell (Figs. 31 I,J). A second tetrasporangium may be cut off later (either obliquely or laterally) from the upper part of the stalk cell (Fig. 31J). Occasionally this cell, instead of forming a tetrasporangium develops into a sterile cell which produces further tetrasporangia (Fig. 31F - on third cell of whorl-branchlet).

Two tetrasporangial groups (stalk cell and derivatives) may occur on a single cell of a whorl-branchlet.

Each tetrasporangium is 30-40µ diam. within a thick gelatinous sheath, and divides tetrahedrally.

Spermatangia: — Spermatangial mother-cells are borne on special short branches on the upper side of the cells of the whorl-branchlets or on cells of the occasional branches of whorl-branchlets. Each special branch consists of a basal cell which bears a whorl of 4 cells from its outer end. Each of these cells usually bears a further whorl of 4 cells, each of which produces 1-2 (-4) spermatangial mother-cells (Fig. 31E). Occasionally there is a short rachis of 2-4 cells, each cell of which bears a whorl of cells from its upper end. Each cell of this whorl then produces either spermatangial mother-cells directly or one further sterile whorl which in turn bears the spermatangial mother-cells.

Development of Procarp and Carposporophyte: — The procarp is borne on the second (rarely the third) axial cell below the apex (Fig. 31K). The apical cell bearing the procarp is very much smaller than the next axial cell below (Fig. 31K) and does not develop other whorl-branchlets.

Only one (rarely 2-3) procarp occurs on the one branch apex. A supporting cell is cut off from the upper part of the axial cell and the 4-celled carpogonial branch is borne from the lower side of the supporting cell (Fig. 31K). A small sterile cell occurs on the outer end of the supporting cell and the two cells together may be analogous to a young 2-celled pinna. A distinct capping-cell, as commonly seen in Crouanieae, occurs at the apex of the carpogonium and the trichogyne (about 60µ long) develops beyond it (Fig. 31L). The capping-cell remains after the trichogyne disintegrates. Fusion between the carpogonium and auxiliary cell, which is cut off from the upper side of the supporting cell, takes place by means of a tube-like connecting cell (Fig. 31M - connecting cell attached to the auxiliary cell). The auxiliary cell divides to give a lower foot-cell and an upper central cell (Fig. 31N). At about this stage the connection between the residual-supporting-cell and the sterile cell elongates to a fine cytoplasmic strand (Fig. 31N).

The first gonimolobe develops terminally on the central cell and is followed by successive formation of two lateral gonimolobes (Fig. 31 O). Each gonimolobe, by successive divisions of cells, forms a rounded group of carposporangia borne on the outer end of an elongate sterile cell. As the gonimolobes develop, the connections between axial cell, residual supporting cell, foot-cell and central-cell become broader with probable fusions occurring between the cells. Further axial growth occurs from lateral branches on the axial cell below that bearing the carposporophyte.

Discussion: —

Heterothamnion muelleri occurs only on Cystophora platylobium, and is easily confused superficially with Heterothamnion sessile on the same host. The latter, however, is quite distinct in having (i) whorl-branchlets usually branched rather than simple as in H. muelleri and (ii) sessile tetrasporangia borne mainly on the cells of the branches of the whorl-branchlets. Tetrasporangia of H. sessile are also slightly smaller (25-30μ) than those of H. muelleri (30-40μ).

Kylin (1956) regarded Perithamnion arbuscula J. Ag. as a synonym of Heterothamnion muelleri, and Perithamnion ceramioides as being very closely related. Types of these species (Herbarium [J.] Agardh, 18201 and 18202) have not been examined, but Australian plants, considered by Womersley (unpublished data) to be identical with the type specimens, ~~are synonomous with one another and~~ rightly belong to a separate genus, Perithamnion.

HETEROTHAMNION SESSILE n. sp.

Thallus usque ad 0.5 cm altus, cristatus in thallo Cystophorae platylobii (Mert.) J.Ag. Axes ad basin attenuati, rhizoideis ad textum hospitis adfixi. E quoque cellula 4 vortico-ramuli ramosi, in thallo centrale usque ad 380μ longi, inferne breviores. Cellulae glandulosae in cellulis centralibus ramulorum sessiles. Tetrasporangia tetrahedralia in vortico-ramulis sessilia. Spermatangia ignota. Procarpus singulus in ramuli 2-cellulato in cellula axiale secunda vel tertia adapicem rami positus.

TYPE Locality: — Victor Harbour, South Australia.

HOLOTYPE: — AD, A 29,304.

DISTRIBUTION : — Known only from the type locality. Epiphytic on Cystophora platylobium.

(Fig. 31 P - S).

General Features: — The plant occurs in tufts on the receptacles of the host and consists of an erect, branched thallus, to 0.5 cm. high attached by rhizoids which penetrate between the cells of the host. Whorl-branchlets occur in whorls of four from the upper part of each axial cell (except at the tapered base of the axis), and are shorter and less branched toward the lower part of the plant (Fig. 31P).

Structure of the Thallus: —

(1) Form and Development of the Main Branches: — Apical development occurs as in Heterothamnion muelleri and produces main axes in which the largest cells (to 190 x 70µ) are in the central thallus region. Axial cells at the base of the tapering axis are small and about as broad as long (approx. 25µ). Lateral branches are borne from the outer upper part of basal cells of whorl-branchlets in the upper parts of the thallus (Fig. 31Q).

(2) Development, Arrangement and Branching of Whorl-Branchlets: — Whorl-branchlets are initiated on the second cell of branch apices and the young whorl-branchlets curve upward around the growing apex. The longest, most branched whorl-branchlets occur in the upper to central thallus (Fig. 31 Ra) while those toward the base decrease in length and branching (Fig. 31 R, b,c), and the number per whorl is often reduced to one or two. The lowest smallest axial cells do not bear whorl-branchlets.

Mature whorl-branchlets (to 380µ long) have a rachis of 5-8 cells and are borne at 45-90° to the main axis (sometimes with the tips curved downward) and usually bear 1-6 simple branches each 1-5 cells long, which may be alternately, irregularly or unilaterally placed. Branching usually does not occur from the basal cells of whorl-branchlets (in contrast to the branching habit of Tetrathamnion).

Gland-cells: — Gland-cells are sessile (about 20µ long) on the central cells of the whorl-branchlets and their branches. They are cut off laterally from cells of young whorl-branchlets but are sparsely distributed over the plant and often degenerate lower down on the thallus.

Tetrasporangia: — Tetrasporangia are sessile on cells of the whorl-branchlets (Fig. 31S). Several may arise successively on one cell and a second may develop within the sheath of a previous tetrasporangium. Each tetrasporangium is spherical, 20-30µ diam. and divides tetrahedrally. The gelatinous sheath remains after the sporangia are shed (Fig. 31 S).

Spermatangia: — Not recorded.

Development of Procarp and Carposporophyte: — As in *Heterothamnion muelleri*, procarps are borne on the second or third cell below the branch apex and each consists of a supporting cell which bears a 4-celled carpogonial branch and a small sterile cell. The supporting cell and sterile-cell are probably analogous to two cells of a modified whorl-branchlet. The procarp and development of the carposporophyte is identical with that of *Heterothamnion muelleri* which has already been described.

Discussion: —

Heterothamnion sessile occurs as does *H. muelleri*, on *Cystophora platylobium* and the two species are thus easily confused.

As already pointed out (see discussion on *H. muelleri*) the species are however undoubtedly distinct.

HETEROTHAMNION EPISILIQUOSUM n. sp.

Thallus usque ad 0.5 cm altus in cristis confertis in receptaculis Cystophorae siliquosae J. Ag. positis. Axes ad basin attenuati, rhizoideis ad textum hospitis adfixi. E quoque cellula 4 vortico-ramuli usque ad 200μ longi; in thallo superiore ei 1-5 ramis simplicibus, inferne non ramosi brevesque aut nulli. Cellulae glandulosae sessiles in cellulis exterioribus vortico-ramulorum. Tetrasporangia tetrahedralia, sessilia in vortic-ramulis. Spermatangia in ramis specialibus brevibus in vortico-ramulis posita. Procarpi (usque ad 4) in ramulis 2-cellulatis in cellula axiale tertia ad apices ramorum positi.

TYPE Locality: — Robe, South Australia.

HOLOTYPE: — AD, A 10,935.

DISTRIBUTION : — Common on Cystophora siliquosa from south coast of Kangaroo Island and from Robe, South Australia, to Cape Schlanck, Vic.

(Fig. 32 A-O; Plate 8).

General Features: — Plants about 0.5 cm in height, occurring in dense tufts near the apices of receptacles of Cystophora siliquosa J. Ag. Attachment is by rhizoids which are developed from axial cells at the base of the plant and which penetrate deeply between the cells of the host tissue (Fig. 32B).

Each plant of Heterothamnion episiliquosum is divided at the base into several erect branches, each of which consists of a main axis with several shorter lateral branches in the upper part. The axis tapers toward the base and the whorl-branchlets, which occur in whorls of 4, become shorter and are sometimes completely unbranched (Fig. 32C) in this region. Whorl-branchlets are usually absent from the several lowest cells of the erect axis.

There is no axial cortication.

Structure of the Thallus: —

(1) Form and Development of Main Branches: — Axial elongation occurs by transverse divisions of a dome-shaped apical cell with the largest mature axial cells at about the centre of the thallus. These cells are 3 to 5 times longer than broad and are about 200μ x 50-70μ. The axis tapers toward the base with smaller cells which become proportionately shorter until their length about equals their breadth (Fig. 32 B).

Lateral branches are borne on the outer, upper part of the basal cells of whorl-branchlets in the upper parts of the plant and each erect axis bears only one to several branches.

(2) Development, Arrangement and Branching of Whorl-branchlets: — Whorl-branchlets are initiated close to the branch apex, usually on the cell below the apical cell, and when very young curve upward and protect the growing apex of the branch. As they mature they become set at about 45^{o} to the axis and towards the lower part of the plant are almost horizontal. Mature whorl-branchlets are evenly spaced in whorls of 4 from the upper part of axial cells.

The oldest whorl-branchlets at the base of the axes are unbranched, or with only one short branch, and about 80-120μ long. Mature whorl-branchlets in the central to upper parts of the plant bear 1-5 simple or simply branched pinnules of 1-4 cells in length on the upper side, and are up to 200μ long (Fig. 32C). Tips of mature whorl-branchlets, particularly in the lower parts of the plant, are often curved slightly downward.

Gland-cells: — Gland-cells occur directly on cells of the whorl-branchlets and their branches (Fig. 32D-I) and are up to 25µ in diameter. They are cut off obliquely from cells of the young whorl-branchlets (Fig. 32D). A protuberance often develops from fully developed gland-cells (Fig. 32 G,H) which forms a smaller second gland-cell associated with and attached to the original gland-cell (Fig. 32I). This has not been observed in other species of Heterothamnion.

Attachment Organs: — Rhizoids develop from cells near the base of the erect axis and penetrate between cells of the host tissue. Within the host the rhizoids may branch sparingly (Fig. 32B) and even when deeply embedded within the host tissues are pigmented and distinctly red in colour. The restriction of tufts to the tips of the receptacles of the host suggests that the rhizoids are only able to penetrate young tissues where the gelatinous cover is thin.

Tetrasporangia: — Tetrasporangia are borne successively on cells of the whorl-branchlets either on the rachis or its branches. Several may occur on one cell, usually 3 or 4 on each of the inner cells and 1 or 2 on the outer cells of each whorl-branchlet (Fig. 32, O). Each tetrasporangium is sessile, pear-shaped when young and spherical, 25-35µ diam., when mature. Division is tetrahedral. The sporangia are liberated terminally from the gelatinous sheath.

Spermatangia: — Spermatangial mother-cells occur terminally on special short branches borne on the cells of the rachides of whorl-branchlets. Young stages in the formation of the special fertile branches are often present on the outer cells of the whorl-branchlets (Fig. 32J).

Each special branch consists of a basal cell which bears from its outer, upper end a whorl of 3-4 cells each of which bears a further similar whorl. The spermatangial mother-cells are borne in groups of 2-4 from the outer end of these cells.

Development of Carpogonial Branches and Carposporophyte: Procarps are developed in a whorl of up to 4 on the third axial cell below the apex (Fig. 32 K,L). No further elongation of the axis occurs and there is a considerable change in size between the axial cell bearing the procarps and the one below. Each procarp consists of a supporting cell (equivalent to the basal cell of a whorl-branchlet which bears a small sterile cell, possibly derived from a second (terminal) whorl-branchlet cell) and a 4-celled carpogonial branch. The cells of the carpogonial branch are formed as in *Antithamnion* by three successive divisions (2 transverse, followed by 1 oblique).

The supporting cell cuts off an auxiliary cell on the upper side (Fig. 32M) and, following fertilization, this divides transversely to give a lower foot-cell and upper central-cell (Fig. 32N). Fusion occurs between the axial cell, residual supporting cell and foot-cell while the connection between foot-cell and central-cell is considerably broadened. The first gonimolobe is developed terminally from the central-cell and is followed by several successively-developed lateral gonimolobes.

Each gonimolobe consists of an elongate sterile cell (Fig. 32N) from which a rounded group of carposporangia is developed.

Thallus growth is continued by lateral branch(es) borne on the axial cell below the carposporophyte.

Discussion: —

Heterothamnion episiliquosum is distinct from other species of the genus particularly in:

(1) Occurring exclusively on Cystophora siliquosa J. Ag.

(2) Bearing shorter pinnae (-200µ) than in H. muelleri or H. sessile, in which pinnae are over 300µ long.

(3) Initiation of up to 4 procarps in one whorl on a single axial cell. In both other species usually only one occurs or, occasionally, two.

TETRATHAMNION Nov. gen.

Thallus irregulariter ramosus, ad textum hospitis rhizoideis adfixus. E quoque cellula 4 vortico-ramuli, vorticibus sequentibus cellularum ramosi. Cellulae glandulosae in cellulis exterioribus vortico-ramulorum positae. Tetrasporangia in cellulis exterioribus vortico-ramulorum sessilia. Spermatangia ignota. Procarpi (2-3) in ramulis 2-cellulatis cellulis pluribus infra apices ramorum natis positi. In quoque carposporophyto 4-6 globi rotundati carposporangiorum vortice ramulorum longorum cincti positi.

The genus is intermediate between Heterothamnion and Perithamnion with some features in common with each genus. The name suggests the characteristic whorls of four branchlets developed on each axial cell. Characters which distinguish the genus and at the same time indicate its similarities with either Heterothamnion or Perithamnion are: —

(1) Lateral Branching: — Numerous lateral branches occur which are limited in growth as in Perithamnion. The main axis is, however, also limited

and is not capable of indefinite elongation as may occur in Perithamnion. In the female plant procarps are initiated on main axes as well as on laterals and thallus elongation is continued by lateral branches developed below the carposporophyte.

(2) Form of Whorl-Branchlets: — Whorl-branchlets are branched, as in Perithamnion, by whorls of 2 (-3) cells from the outer end of each successive cell. This is distinct from the single main rachis bearing lateral branches as occurs in Heterothamnion. Reduction in branching of whorl-branchlets occurs towards the base of the plant and consists in Heterothamnion of the development of fewer pinnules together with a shortening of the rachis. In this genus reduction consists of the development of fewer orders of cell-whorls which are made up of smaller constituent cells.

(3) Position of Gland-cells: — Gland-cells occur on the short chain of cells which forms the final branching of each whorl-branchlet. This position of gland-cell is also found in Perithamnion. In Heterothamnion gland-cells occur on the 3rd-5th cell of the rachis of each whorl-branchlet usually in the central region of the rachis; occasionally they may occur terminally.

(4) Attachment to Host: — No prostrate axis develops, as sometimes occurs in Perithamnion, and attachment is by rhizoids from the lower cells of the erect axes. The plant lacks, however, the marked host specificity characteristic of species of Heterothamnion.

(5) *Position of Tetrasporangia*: — Tetrasporangia are sessile on the outer cells of the branchings of the whorl-branchlets. In *Heterothamnion*, although also sessile on cells of whorl-branchlets, they tend to be concentrated on the inner cells of the branchlet and in *Perithamnion* are produced on special short branches borne in place of a lateral branch.

A new genus is justified on the basis of these features, and three distinct species fall within the generic limits defined above. Of these species, *Tetrathamnion ramosum* is perhaps the most advanced phylogenetically and comes closest to *Perithamnion*. In lateral branch organization in particular, there is indication of a trend from *Tetrathamnion lineatum* to *T. pyramidatum* to *T. ramosum*. There is no evidence of any evolutionary line of development in reproduction within the group.

TYPE species: — *Tetrathamnion lineatum* n. sp.

Key to the Southern Australian Species of Tetrathamnion

1. Lateral branches elongate, rarely more than one from each whorl of branchlets and adjacent branches often separated by several axial cells. Mature tetrasporangia 50µ diam. Procarps usually in whorls of 3 on the 3rd cell below the apex... ... ... *T. lineatum*

1. Lateral branches shorter with often more than one from each whorl of branchlets... ... ... Mature tetrasporangia up to 49 µ. diam. Procarps usually 1-2 on second cell below apex... 2

    2. Thallus bushy with axes covered by numerous short lateral branches and upwardly curved whorl-branchlets.. ... ... *T. ramosum*

    2. Thallus open usually with not more than two lateral branches per whorl. Axes exposed between whorls of almost horizontal whorl-branchlets.. ... ... *T. pyramidatum*

TETRATHAMNION RAMOSUM nov. sp.

Thallus ca. 1.0 cm. altus, ramis lateralibus numerosis. Axes ad basin attenuati rhizoideis ad textum hospitis adfixi. E quoque cellula 4 vortioo-ramuli, ca 300μ longi, interdum pilis terminalibus vestiti, verticibus sequentibus cellularum 2-3 ramosi. Cellulae glandulosae in cellulis exterioribus vortico-ramulorum positae. Tetrasporangia tetrahedralia 35-40μ diametro, sessilia in cellulis exterioribus vortico-ramulorum. Spermatangia ignota. Procarpi (1-2) in ramulis 2-cellulatis in cellula axiale secunda ad apices ramorum positi.

TYPE Locality: — Port Noarlunga, South Australia.

HOLOTYPE: — AD, A 24,580, growing on Sargassum sp.

DISTRIBUTION: — Known only from the type locality.

(Fig. 32 P - U).

General Features: — The plant is small, to 1.0 cm. high, occasionally more, and is bushy in appearance due to the development of numerous lateral branches (Fig. 32P). In female plants carposporophytes are produced near the apices of lateral branches and, with the many laterals produced, occur abundantly.

Whorl-branchlets occur in whorls of 4 from each axial cell and branch by whorls of three, or two, cells, from the outer end of each successive cell. Gland-cells are prominent near the ends of whorl-branchlets (Fig. 32Q).

Structure of Thallus: —

(1) Form and Development of Main Branches: — Growth occurs by transverse divisions of a dome-shaped apical cell. Axial cells enlarge quickly and only a short chain of immature cells, well protected by the surrounding,

upwardly-curved young whorl-branchlets, occurs at each branch apex. Mature axial cells are often broader in the upper part and are up to 250 x 65µ. Cells of about this dimension occur only in the central region of the thallus, as the erect axes taper towards the base and the cells gradually become smaller and proportionately shorter for their breadth. Small basal cells are about 60-80µ in both length and breadth.

Lateral branches are produced on the outer upper ends of basal cells (occasionally 2nd cell) of whorl-branchlets. Most of these laterals must be limited in growth as few of them develop into long lateral axes.

(2) Development, Arrangement and Branching of Whorl-branchlets: — Whorl-branchlets are initiated on the cell below the apical cell and develop rapidly. Whorl-branchlets only several cells below the apex have developed the mature form of cell branchings. A whorl-branchlet when fully elongated is about 300µ long and branched by successive whorls of 3-2 cells from the outer end of each cell. Usually the first whorl consists of 3 cells and the following 2-4 whorls of 2 cells each. The final branchings consist of short chains of 2-3 cells which bear prominent gland- cells and often a terminal hair (to 120µ long) (Fig. 32Q).

Gland-cells: — Gland-cells are abundant on the final branchings of whorl-branchlets. Each gland-cell is sessile, rounded in form and about 15µ long (Fig. 32 S).

Attachment Organs : — Branched rhizoids, which are at first enclosed within the gelatinous sheath of the axis, arise from the cells at the tapered base of the erect axes and penetrate between cells of the host-tissue (Fig. 32R).

Tetrasporangia: — Tetrasporangia are borne from the outer upper ends of whorl-branchlet cells of the outer several branchings. Each tetrasporangium is sessile, about 35-40μ diam. when mature and divides tetrahedrally at an early stage (12-20μ diam.) (Fig. 32Q).

Abundant tetrasporangia are produced successively on each branch.

Spermatangia:-not recorded.

Development of Procarp and Carposporophyte: — One or two procarps are borne on the second cell (the cell below the apical cell) at branch apices (Fig. 32T). The supporting cell bears a small sterile cell as well as the 4-celled carpogonial branch which develops from its lower side and curves upward (Fig. 32 Ta). On initiation of procarps the branch ceases to elongate and the apical cells always remain small. Further branch elongation may take place from lateral branches produced on whorl-branchlets below the fertile axial cell. Only one carposporophyte matures at any one branch apex.

The auxiliary cell is cut off from the upper side of the supporting cell (Fig. 32Tb) and, presumably after fusion with the carpogonium, divides to form a lower foot-cell and an upper central-cell. Fusion occurs between axial cell, residual-supporting-cell and foot-cell. Rounded groups of carposporangia are formed from buds developed on the central cell. The first group to mature is terminal and is followed successively by two lateral groups (Fig. 32U).

Discussion: —

The species is known from only one locality but is distinct from other species of the genus in its dense, bushy thallus in which the main axes are completely covered by the lateral branches and upward curvature of the whorl-branchlets.

The plant agrees well with other species of the genus in development of lateral branches, form of whorl-branchlets, attachment to host, position of gland-cells, development and position of tetrasporangia and features of carposporophyte development.

The dense production of lateral branches of limited growth suggests a close link with the genus Perithamnion which is, however, more specialised in position of reproductive organs.

TETRATHAMNION LINEATUM nov. sp.

Thallus usque ad 1.5 cm altus rhizoideis ad textum hospitis adfixus. E quoque cellula 4 vortico-ramuli, ca. 300µ longi, horizontales, saepe pilis terminalibus vestiti, verticibus sequentibus cellularum ramosi. Cellulae glandulosae in cellulis exterioribus vortico-ramulorum. Tetrasporangia tetrahedralia, 50µ diametro, sessilia in vortico-ramulis. Spermatangia ignota. Procarpi 3 (aut pauciores) in ramulis 2-cellulatis in cellula axiale tertia ad apices ramorum positi.

TYPE Locality: — White Beach, Wedge Bay, Tasmania.

HOLOTYPE: — AD, A 27,686.

DISTRIBUTION : — Known only from the type locality. Epiphytic on Sargassum verruculosum (Mert.) Ag.

(Fig. 33, A-P).

General Features: — Plants are up to 1.5 cm. long and consist of a laterally-branched erect axis attached by penetration of rhizoids between the cells of the host tissue (Fig. 33A).

Axial cells are elongate, 6-8 times as long as broad and each bears a whorl of four whorl-branchlets from its upper part (Fig. 33F). Whorl-branchlets are at right angles to the axis with upturned tips, and are apparently dichotomously branched, usually 4-6 times.

The axis tapers towards the base of the plant with smaller, proportionately shorter cells and whorl-branchlets reduced in size and branching.

Gland-cells are prominent on the outer parts of whorl-branchlets and terminal hairs are well-developed (Fig. 33F).

Structure of the Thallus: —

(1) Form and Development of Main Branches: — Growth occurs by transverse divisions of a dome-shaped apical cell and a whorl-branchlet several cells in length may occur on the second axial cell (Fig. 33G).

Mature axial cells are about (300-380) x (40-50) μ and are largest in the central part of the thallus. The erect axis tapers towards the base and the axial cells become comparatively shorter and are finally about as long as broad.

Lateral branches are borne on the outer, upper part of the basal cells of whorl-branchlets and are obliquely to upwardly directed. Usually only one occurs from each whorl. Lateral branches are irregularly scattered along the axis, often several occurring successively from adjacent whorls. Usually the older branches are at the base of the plant, giving the thallus a pyramidal form, but not as consistently developed as in T. pyramidatum (Fig. 33A).

(2) Development, Arrangement and Branching of Whorl-branchlets: — Whorl-branchlets are initiated, and often reach several cells in length, on the second cell of axes. At this stage a gland-cell is often present (Fig. 33G). As the whorl-branchlet elongates the early-formed gland-cells disintegrate and new ones are developed on outer cells of the whorl-branchlets. A mature whorl-branchlet (about 300μ long) appears to be dichotomously branched (Fig. 33F) but is not truly dichotomous in formation (Fig. 33 B-E). The final branching consists of a short chain of 1-3 (-4) cells in length often terminated by a hair to 275μ long (Fig. 33H). Although two branches usually occur from the outer end of the basal cell, occasionally a whorl of three cell-branches is formed in this position.

Gland-cells: — Gland-cells occur on cells of the outer branchings of whorl-branchlets and most commonly on cell-branches in a terminal or sub-terminal position (Fig. 33H). Each gland-cell is flattened against its mother cell, is rounded above and up to 14μ long. Several gland-cells may occur on the ends of young immature whorl-branchlets (Fig. 33I) and the older ones disintegrate as the whorl-branchlet matures.

Attachment Rhizoids: — At the base of the erect axes rhizoids are produced from the lower end of axial cells and also by modification of the axial cells themselves (Fig. 33J). Each rhizoid consists of elongate cells and grows downward between the cells of the host tissue.

Tetrasporangia: — Tetrasporangia occur singly from the outer upper end of cells of the pinnae (Fig. 33K) and two or three may develop successively within the gelatinous sheath of a previous tetrasporangium (Fig. 33L). Each tetrasporangium is sessile and pear-shaped when young but spherical and up to 50μ diameter when mature. Division occurs early, at about 24μ diam. and is tetrahedral, or sometimes appears cruciate.

Spermatangia: — Not recorded.

Development of Procarp and Carposporophyte: — Procarps are borne usually in whorls of 3 on the 3rd cell below the apex of branches (Fig. 33M). Apical growth ceases and further branch elongation takes place from laterals produced on the whorl-branchlets of the whorl below the procarps. Occasionally a gland-cell develops on the apical cell of the original axis (Fig. 33 N,O). A procarp initial consits of a supporting cell with a small sterile cell on the outer side (Fig. 33M) — probably equivalent to a 2-cell initial of a whorl-branchlet in which the basal cell bears the carpogonial branch. The carpogonial-branch initial is cut off from the outer, lower side of the supporting cell (Fig. 33 Na) and develops into a 4-celled, upwardly-curved carpogonial branch (Fig. 33 O). Only one carposporophyte develops from each whorl.

An auxiliary cell is cut off from the upper part of the supporting cell (Fig. 33 Nb) and divides, presumably after fusion with the carpogonium, to give a lower foot-cell and upper central-cell. The central cell gives rise to three gonimolobes, each of which finally produces a rounded mass of carposporangia. The terminal group develops first, followed by the successive lateral development of the second and third groups (Fig. 33P).

Discussion: —

Lateral branching in this species lacks the density found in other species of Tetrathamnion both in number of branches produced and in the comparatively greater length of individual branches. It differs particularly in having usually more elongate thallus cells, seldom more than one lateral branch formed from a single whorl of whorl-branchlets, and in procarps usually produced in whorls of 3 on the 3rd axial cell below the branch apex. The axial cell which bears the procarps tends to be rectangular in form, rather than triangular as it is in Tetrathamnion pyramidatum.

TETRATHAMNION PYRAMIDATUM nov. sp.

Thallus 2-3 cm altus rhizoideis ad textum hospitis adfixus, pyramidalis, e quoque cellula 1-2 (-3) ramos laterales producens. E quoque cellula 4 vortico-ramuli, 200-300μ longi, horizontales, verticibus sequentibus cellularum ramosi, ad basin attenuatam axis redacti aut nulli. Cellulae glandulosae in cellulis exterioribus vortico-ramulorum positae. Tetrasporangia tetrahedralia, 36μ diametro, in vortico-ramulis sessilia. Spermatangia ignota. Procarpi plerumque oppositi in ramulis 2-cellulatis in cellula secunda ad apicem rami positi.

TYPE Locality: — Pennington Bay, Kangaroo Is., South Australia.

HOLOTYPE: — AD, A 19,745.

DISTRIBUTION: — Known only from the type locality and Stanley Beach, Kangaroo Is. Epiphytic on drift Encyothalia cliftoni Harvey.

(Fig. 33 Q - X).

General Features: — Plants 2-3 cm. high, erect and attached by rhizoids which penetrate between the filaments of the tufted branch apices of Encyothalia. The plant is pyramidal in outline due to the development of 1 or 2 (-3) lateral branches from most of the nodes (except at the extreme base) of the main axes (Fig. 33Q). Carposporangial plants tend to be more branched than other plants. Lateral branches are further laterally branched from the outer ends, but usually bear few laterals on the inner part. A whorl of four almost horizontal whorl-branchlets occurs from the upper part of each axial cell. Each whorl-branchlet is about 200-300µ long, except at the tapered base of the plant where they are reduced or completely absent. Mature whorl-branchlets consist of several successive apparent dichotomies (Fig. 33 S) the branches of which are not, however, developed simultaneously. Gland-cells occur on the outer cells of the whorl-branchlets.

Structure of the Thallus: —

(1) Form and Development of Main Branches: — Growth occurs by transverse divisions of a dome-shaped apical cell and the youngest 4-10 axial cells are rounded, densely protoplasmic and covered by the rapidly developing young whorl-branchlets which, while immature, are curved upward.

Mature axial cells are cylindrical and about 230-320 x 100µ. Occasionally they may reach about 500 x 150µ in the central region of a well developed thallus. At the tapering base the cells of the erect main axis become smaller and about as long as broad and finally bear rhizoidal attachment filaments (Fig. 33 V).

Lateral branches are borne from the outer, upper part of the basal cells of whorl-branchlets (Fig. 33R) and are formed successively with the elongation of the main axis. In this way those at the base of the plant are further developed than those in the upper parts and so contribute to the pyramidal plant form.

(2) Development, Arrangement and Branching of Whorl-branchlets: — Whorl-branchlets are initiated on the 2nd to 4th axial cell at branch apices and develop successively in each whorl. The initial cell bears two cells, one after the other, from its outer end, which when mature, appear dichotomous. The mature whorl-branchlet consists of several, often 4, successive orders of cell branches each of which terminates with a small 2-celled branch (Fig. 33S).

Occasionally a short third branch is formed on the outer upper end of the basal cell on whorl-branchlets which do not bear lateral branches.

Gland-cells: — Gland-cells occur on the inner cells of the short 2-celled branches which terminate the whorl-branchlets. Usually only one of the two branches of the final dichotomy bears a gland-cell. Gland-cells are sessile and about 10-14µ long (Fig. 33S,T).

Attachment Rhizoids: — Filamentous rhizoids consisting of elongate cells occur at the base of the erect thallus axis and penetrate between the closely packed cells at the base of the filamentous tufts of Encyothalia. Axial cells at the base of the plant are modified to form elongate rhizoidal cells and each bears a further two rhizoidal initials from its lower part. The rhizoidal initials may bear two or three rhizoidal cells from their lower end (Fig. 33V).

The initial production of rhizoids occurs within the gelatinous sheath of the basal axial cells and, at this stage, rhizoidal cells are approximately equal in length. They soon become separated as they penetrate between the host cells and this formation is obscured.

Tetrasporangia: — Tetrasporangia are sessile on the outer upper ends of cells of the whorl-branchlets (Fig. 33U). Mature tetrasporangia are about 36μ within a thick, often double, gelatinous sheath and are tetrahedrally divided (or occasionally appear cruciate). Division occurs when the tetrasporangium is about 15-18μ diam. and must occur rapidly as few stages of division have been observed. Sporangia are liberated laterally from the gelatinous sheath, and, although the common occurrence of double sheaths surrounding the developing sporangia and the presence of only one tetrasporangium on each cell, suggest successive development of tetrasporangia within the old sheath, no initial stages have been found to support this suggestion. It is possible, therefore, that the gelatinous sheath may normally consist of two distinct layers.

Spermatangia: — Not recorded.

Development of Procarp and Carposporophyte: — Procarps occur in pairs, opposite one another, on the cell below the apical cell (rarely on the 3rd cell) at a branch apex. Axial elongation ceases and a very great size difference occurs between the cell bearing the procarps and the axial cell below (Fig. 33W). Thallus growth continues by 1-3 lateral branches borne on the branchlets of the whorl below the procarps. Only one of the two procarps matures a carposporophyte. A supporting cell is cut off laterally from the axial cell and bears a further small sterile cell outwardly. These two cells may be analogous to a short 2-celled whorl-branchlet in which the basal cell acts as a supporting cell.

The 4-celled carpogonial branch develops from the lower side of the supporting cell and curves upward. An auxiliary cell develops on the upper side of the supporting-cell and after fertilization apparently fuses with a projection from the carpogonium. A distinct small cell close to the supporting cell (Fig. 33X) suggests that fusion probably occurs by means of a small connecting cell.

After fusion a foot-cell and central-cell are formed and the first gonimolobe develops terminally (Fig. 33X). A second and third gonimolobe occur laterally one after the other. The mature carposporangial group is rounded and about 150-200μ in diameter.

Discussion: —

Tetrathamnion pyramidatum resembles T. lineatum but differs in usually having denser lateral branching leading to a more distinctly pyramidal plant form and in developing 2, rather than 3, procarps on the second instead of the third cell of the branch apex. Also the axial cell which bears the procarps is triangular rather than rectangular in form.

PERITHAMNION J. Agardh 1892

The genus Perithamnion J. Agardh (1892) is probably closely related to Heterothamnion. Perithamnion ceramioides and P. arbuscula have indeed both been included as synonyms of Heterothamnion muelleri by Kylin (1956). Unfortunately details of structure and reproduction of all three species of Perithamnion described here must await fresh collections, and until this time their identity must remain somewhat in doubt.

It is clear, however, that Perithamnion ceramioides J. Ag. and P. arbuscula J. Ag. are synonomous, and are distinct from Heterothamnion muelleri (Sonder) J. Ag. Perithamnion ceramioides is a larger plant (to 6 cm) with much-branched whorl-branchlets and 1-3 lateral branches arising from most whorls, particularly in the central to lower parts of the thallus. Heterothamnion muelleri grows only to 0.5 cms. in height, bears simple or sparingly-branched whorl-branchlets and comparatively few lateral branches.

At least until further details of the plants are known it seems best to retain the genus Perithamnion for the three species, P. ceramioides J. Ag., P. densum n. sp. and P. dispar (Harv.) nov. comb., on the basis of the following similarities:

(1) Thallus consisting of a main central axis bearing 1-4 distinctly smaller laterals, of limited rate of growth, from basal cells of the whorl-branchlets of the majority of mature whorls.

(2) Branching of whorl-branchlets by whorls of 2-3 cells from the outer end of each successive cell with terminal branches consisting of a chain of 2-3 small cells. Prominent gland-cells occur on cells of final or sub-terminal order of branching.

(3) Attachment to host by rhizoids from the base of plant, and sometimes from the under side of a prostrate axis.

(4) Tetrasporangia borne on special branches developed from the outer, upper part of the basal, and occasionally the second, cells of the whorl-branchlets. (Probably some tetrasporangia occasionally occur directly on cells of the whorl-branchlets in P. ceramioides).

(5) Carposporophyte borne on 2nd-4th cell below apex of a lateral branch. The lateral branch is very much reduced in length in P. densum. Apical elongation of the main axis continues in all species.

Perithamnion most closely resembles Heterothamnion but is distinguished from it by the branching habit of whorl-branchlets, position of tetrasporangia and continued elongation of main axes in female plants, while carposporophytes are borne on lateral branches only.

Features of probable phylogenetic significance occur within the genus. A change in thallus form occurs from the regular development of 4 equal branchlets per whorl in Perithamnion ceramioides to the rather less stable occurrence of 4-5 unequal branchlets in P. dispar. This character may be considered to represent an upward trend in the opposite direction from usual as generally reduction in number and regularity and consistency of form are considered more advanced than increase in number and inconsistency in form. In arrangement of lateral branches, however, P. dispar shows greater organization than found in other species. There is at first a definite alternate-distichous pattern in development of lateral branches in P. dispar (although more may later be produced lower on the thallus) which appears to be linked with the changes occurring in the whorl-branchlets of each whorl, so that as a lateral branch develops from each whorl the opposite 1 or 2 whorl-branchlets become very much reduced in size. In this way P. dispar possibly represents an intermediate form in the development of a Callithamnion-like plant in which main branches are developed alternately on adjacent cells of the axes. Another trend towards this type of plant form occurs in the limited growth of lateral branches in all species of Perithamnion, and which is most highly organized in P. dispar. Tetrasporangia and spermatangia (known only for P. densum) occur on short modified branches borne in the position of lateral branches; carposporophytes occur near the apex of lateral branches which develop normally in P. ceramioides and P. dispar, but which always remain short in P. densum. In this species 2-3 procarps occur on one axial cell at a greatly reduced branch apex (Fig. 34F). Only one procarp and comparatively more sterile cells are produced at fertile branch apices in P. dispar (Fig. 34M). It is thus possible that reproductive organs have reached the highest level of organization in P. densum, while vegetative adaptations have become most specialized in P. dispar.

This suggests possible separate lines of vegetative and reproductive development (especially in the carposporophyte) within the genus.

TYPE Species: — Perithamnion ceramioides J. Ag.

The following descriptions of species of Perithamnion are based on inadequate material for detailed study and are hence abbreviated in form.

Key to the southern Australian species of *Perithamnion*

1. Main axes bearing whorls of 4 equal branchlets from each axial cell. Lateral branches irregularly arranged on axes in all parts of thallus... 2

1. Main axes bearing whorls of 5 (occasionally only 4) branchlets of which 2 (or 1 in whorls of 4 branchlets) are very much reduced. Lateral branches at first alternate-distichous in arrangement ... ... *P. dispar*

   2. Whorl-branchlets short (200-250µ), axis distinctly exposed between whorls. Gland-cells 12-20µ long. Tetrasporangia on a special branch (not much different from a branch of the whorl-branchlet) and also on cells of the whorl-branchlet... ... ... *P. ceramioides*

   2. Whorl-branchlets slightly longer (250-320µ), axis not exposed due to development of lateral branches. Gland-cells 24-30µ long. Tetrasporangia always on special short small-celled branches ... ... *P. densum*

PERITHAMNION CERAMIOIDES J. Agardh 1892: 30.

Perithamnion arbuscula J. Agardh 1892: 31.

TYPE Locality: — Pt. Phillip Heads, Victoria.

HOLOTYPE: — LD. Herbarium J. Agardh No. 18202 (J.B. Wilson).

DISTRIBUTION : — Figure-of-Eight Island, Recherche Archipelago, W.A., to Pt. Phillip Heads, Victoria. Epiphytic on species of Cystophora (e.g. C. siliquosa J. Ag., C. intermedia J. Ag., C. brownii (Turn.) J.Ag., C. moniliformis (Esper.) Wom. & Niz. and one specimen on Polysiphonia nigrita Sonder.

(Fig. 35 A-C)

General Features: — The plant grows to about 6 cm in height and consists of several main axes which bear lateral branches from the basal cells of whorl-branchlets. Lateral branches are usually less robust than main axes and most are limited in rate of growth. One to three (-4) may arise from each whorl of whorl-branchlets in the lower and central parts of the plant. The upper parts are usually less densely branched (Fig. 35A). Cells of the main axis are about 320 x 130μ but may at times be much larger; cells of the axes of lateral branches are about 230 x 90μ. The main axis tapers towards the base. Attachment is by rhizoids from the base of the plant. Slight enlargement of the host tissues forms a small raised area at the point of attachment and some penetration of rhizoids occurs between cells of the outer layer of host tissue. Whorl-branchlets which lie against the host tissue may be modified and attach to the host so that an occasional prostrate axis is thus formed.

Whorl-Branchlets: Whorl-branchlets occur in whorls of 4 from the upper end of each axial cell. Each branchlet is short, about 200-250µ long and horizontal to oblique in the central and lower parts of the thallus and sometimes with tips upturned. Towards branch apices the whorl-branchlets are shorter and at the tips grow upward and cover the apical cell. Towards the base of the erect axes the whorl-branchlets are shorter and simpler in form as in species of Heterothamnion. All whorls are widely spaced so that the axis is conspicuous in all parts of the thallus. Whorl-branchlets consist of a large basal cell branched by several orders of smaller cells from its outer end. The first branching usually consists of a whorl of three cells but thereafter varies in individual branches. Several prominent gland-cells (12-20µ diam.) occur on the final branchings (usually a chain of several cells) of each whorl-branchlet and the final cell is often terminated by a hair (Fig. 35B).

Tetrasporangia: — Tetrasporangia are borne on the upper, outer part of the cells of the outer branchings of whorl-branchlets, and often on a branch borne in the position of a lateral branch. Tetrasporangia are sessile, spherical and about 34µ diam. when mature (Fig. 35C). Division is cruciate-tetrahedral with divisions not always simultaneous.

Spermatangia: — Not recorded.

Carposporophyte: — The carposporophyte is developed on an axial cell near the apex of a lateral branch which ceases to elongate further. At least three rounded groups of carposporangia are formed successively from the central cell with the terminal group being the first developed. Female plants have only been available as herbarium specimens and it has not been possible to follow stages of development of the procarp and carposporophyte.

Discussion: —

The material used was mainly herbarium specimens which were difficult to restore and observations need careful checking from fresh collections. The features used in classifying the plant are, howevér, fairly easily recognized and hence reasonably well established.

PERITHAMNION DENSUM nov. sp.

Thallus ca. 1.5 cm altus ramis lateralibus numerosis. E quoque cellula 4 vortico-ramuli, 250-320μ longi, horizontales apicibus curvato-adscendentibus, verticibus cellularum ramosi. Cellulae glandulosae in cellulis exterioribus vortico-ramulorum. Tetrasporangia tetrahedralia, 36μ diametro, sessilia in ramis specialibus in cellulis infimis (aut sub-basalibus) vortic-ramulorum. Spermatangia in ramis similibus terminalia. Procarpi (2-3) in ramulis 2-cellulatis in cellula axiale secunda vel tertia ad cacumina ramorum brevium lateralium positi.

TYPE Locality: — Pennington Bay, Kangaroo Island, South Australia.

HOLOTYPE: — AD, 27,009.

DISTRIBUTION : — Wanna and Sleaford Bay, Eyre Peninsula, Pt. Noarlunga, and Pennington Bay, Kangaroo Is., South Australia.

(Fig. 34 A-G).

General Features: — The plant is small, about 1.5 cm in height and is usually densely laterally branched in the central part of the thallus (Fig. 34A). The lateral branches arise from the outer upper end of the basal cells of whorl-branchlets and 3-4 may often occur from one whorl. Immature axial cells are rounded, but when mature, are cylindrical and 2-3 times as long as broad (about 250-300 x 130-150µ). The axis tapers towards the base and axial cells are shorter in proportion to breadth.

Attachment is by rhizoids from the base of the thallus. In the specimen from Wanna, Eyre Peninsula, the rhizoids form a tuft and penetrate the conceptacles of the host plant (Sargassum sp.) .

Whorl-Branchlets: — Whorl-branchlets occur in whorls of 4 from the upper end of each axial cell and branch several times in whorls of 2-3 cells initiated one after another from the outer end of each successive cell. The basal cell usually bears two, occasionally three, cell-branches and a lateral branch (Fig. 34B). In fertile plants this lateral branch may remain short and bear procarps, spermatangial mother-cells or tetrasporangia. Cells of the outer 1-3 whorls of each whorl-branchlet may bear prominent ovoid gland-cells 24-30µ long (Fig. 34 B,C). Whorl-branchlets are about 250-320µ long, usually set horizontally to the axis and often with upturned tips. The final branching usually consists of a short 2-celled chain and only occasional terminal hairs are developed. Cells of the central mature axis are exposed between adjacent whorls of branchlets but are often hidden by development of lateral branches. At branch tips and in lateral branches the whorls of branchlets are close together and form a dense cover over the axes (Fig. 34A)

Tetrasporangia: — Tetrasporangia are borne on the outer ends of cells of special short branches developed from the basal cells of . whorl-branchlets in the position of lateral branches (Fig. 34E). The special branch branches profusely with small cells and may bear 10-18 tetrasporangia at various stages of development at the one time. Further similar special short branches bearing tetrasporangia may also develop from the outer upper end of the cells of the second orderof branching of the whorl-branchlet.

Each tetrasporangium is developed in place of one of the branch cells (Fig. 34E) and is sessile, spherical, about 36µ diam. when mature andappears tetrahedrally divided although all divisions may not be completed simultaneously.

Spermatangia: — Spermatangial mother-cells are borne on special short branches on the outer upper end of the basal cell and the cells of the first and second orders of branching of whorl-branchlets. Each special branch, 60-75µ long, consists of several successive orders of whorls of cells. The outermost of these form the spermatangial-mother-cells, each 5-7µ long (Fig. 34D). The spermatangial-mother-cells are initiated as protrusions from the outer end of the terminal cells.

Procarp and Carposporophyte: — Procarps are initiated in whorls of 2 or 3 on the second or third cell below the apex of special short branches borne in the position of lateral branches. The special branches are similar in form to a normal lateral branch, but are determinate in growth with the initiation of procarps and do not develop beyond 4-7 axial cells in length. Each procarp consists of a supporting cell and small outer sterile cell (Fig. 34Fa) which is probably analogous to a short 2-celled initial of a whorl-branchlet. A 4-celled carpogonial branch is borne on the outer, lower side of the supporting cell (Fig. 34F,b).

An auxiliary cell is cut off from the upper side of the supporting cell and, after fusion with the carpogonium, divides into a lower foot-cell and an upper central-cell. A small cell is cut off after fertilization from the lower, inner corner of the carpogonium and this cell presumably acts as a connecting cell (Fig. 34Fc). A terminal group followed by two lateral groups of carposporangia develop from the central cell (Fig. 34G).

Discussion: —

Only a small amount of material was available for study. The plant is, however, distinct from other species of Perithamnion.

The shape of cells of the whorl-branchlets, the comparatively large and conspicuous gland-cells, the denser lateral branching and the shortened laterals which bear carposporophytes distinguish this species from P. ceramioides.

The regular whorls of 4 branchlets are alone sufficient to distinguish this species from P. dispar which has whorls of 5 (-4) unequal branchlets.

PERITHAMNION DISPAR (Harv.) nov. comb.

Callithamnion dispar Harvey 1860: 335; 1862: pl. 227. J. Agardh 1876: 27. Wilson 1892: 186.

Antithamnion dispar J. Agardh 1892: 20. De Toni 1897: 1405. De Toni & Forti 1922: 54. Lucas 1909: 51; 1929a: 25. Lucas & Perrin 1947: 353.

TYPE Locality: — East Coast, Tasmania.

TYPE: — TCD, Herbarium Harvey (Gunn) on Mychodea disticha Harvey.

DISTRIBUTION: — From the south coast of Kangaroo Is. (Pennington Bay and Vivonne Bay) and Robe, South Australia, to Bridgewater Bay, Victoria, and from east coast of Tasmania. Epiphytic on a variety of hosts. (e.g. *Gigartina crassifolia* (J.Ag.) S. & G., *Perithalia inermis* (R.Br.) J. Ag., *Cystophora siliquosa* J. Ag., *Mychodea disticha* Harvey).

(Fig. 34 H - P).

General Features: — The thallus consists of elongate main axes (to 8 cm. long) bearing shorter lateral branches, limited in rate of growth, and developed in the first place alternately from adjacent nodes (Fig. 34H). The distichous pattern may, however, be lost by the irregular development of further laterals. The plant attaches by a prostrate axis from which erect unattached axes arise (Fig. 34H). Some lateral branches usually from the lower parts of the thallus may develop into comparatively long axes. Mature cells of the main axes (prostrate and erect) are about $1\frac{1}{2}$-2 times as long as broad (about (160-260) x (100-200)µ). Growing tips are always covered and protected by the young whorl-branchlets.

Whorl-Branchlets and Lateral Branch Arrangement: — Each axial cell of the main axis bears a whorl of 5 (occasionally reduced to 4) whorl-branchlets from its upper end. In mature, upper parts of the thallus the usual arrangement of whorl-branchlets is as in Fig; 34P,a. Numbers 1 and 2 represent equal branchlets (320-380µ long), 3 represents a third branchlet equal in length to 1 and 2, but bearing a lateral branch (about 1000-1200µ long) from the outer end of the basal cell, and 4 and 5 are two very small-celled branchlets each about 60-90µ long. This arrangement is reversed on adjacent cells to give a distichous arrangement of lateral branches. Fully developed whorls in younger parts of the thallus have 3 equal branchlets (1, 2 and 3), usually 2 short branchlets (4 and 5) but lack the lateral branch which develops after the pinna is fully formed. Variations of this arrangement may occur, such as Fig. 34 Pb,c,d, but are not usually frequent.

Lower down on the thallus it is usual for further lateral branches to develop particularly from the one or two short branchlets or, occasionally, from all branchlets. The usual whorl arrangement thus becomes as in Fig. 34Pe in which lateral branches are shown on branchlets 3,4 and 5. There is often reduction in length and branching of whorl-branchlets towards the base of the axes. Whorls of branchlets are also developed on the upper part of each axial cell of the short lateral branches. A full whorl consists of 4 equally spaced branchlets, each about 220-260μ long. In the lowest whorl of the branch the fourth branchlet (4), facing the axis, is usually absent (Fig. 34 Oa), and, in the following one or two whorls it is reduced in length (Fig. 34, Ob,c). Thus a gradation in whorl arrangement occurs from the base toward the upper part of the branch (Fig. 34 Oa-c; "A" represents the position of the main axis). Whorl-branchlets are not rotated on adjacent cells and occur always one directly under the other.

Branching of Whorl-branchlets: — Whorl-branchlets are branched several times by whorls, usually each of 2 cells, developed from the outer end of each successive cell (Fig. 34I). The final branching consists of a short chain of 1-3 cells ending in an acute tip. Gland-cells, 25-28μ long, are prominent near the branch apices (Fig. 34 I,J).

Attachment organs on prostrate axes are formed from the basal cells of whorl-branchlets in contact with host tissue. Initially one to several unbranched rhizoids develop, but these soon branch profusely and attach firmly to the host, and the normal cells of the whorl-branchlet are completely lost (Fig. 34L). Young plants attach by a basal cluster of branched rhizoids, which may penetrate the outer layers of host tissue and from which several erect axes arise. The prostrate axis is a secondary development.

<u>Tetrasporangia</u>: — Tetrasporangia occur on special small-celled short branches which are borne on the upper outer end of the basal cells of whorl-branchlets, and, occasionally, on cells of the second order of branching. The branches consist of small rounded cells, and are profusely branched and up to 200µ long. Each tetrasporangium occurs in place of a cell-branch on the outer end of a cell and as many as 12–18 tetrasporangia in various stages of development may occur on a branch at one time. Each tetrasporangium is sessile, spherical, 40–48µ diam. within the gelatinous sheath when mature. Division occurs at an early stage (diam. 20–30µ) and is tetrahedral with divisions usually completed together (Fig. 34K).

Tetrasporangial development is most concentrated at the outer ends of lateral branches.

<u>Spermatangia</u>: — Unrecorded.

<u>Procarp and Carposporophyte</u>: — Available female material provided mature carposporophyte stages. The only carpogonial branch found (Fig. 34M) had probably not been fertilized. The carpogonial branch was borne on the lower

side of the basal cell (supporting cell) of a young 2-celled whorl-branchlet on the third cell below the branch apex and only one procarp was developed from the axial cell. Carposporophyte development always occurs near the apex of a lateral branch and growth continues from the apex of the main axis of the thallus.

Maturing carposporophytes show fusions between the axial cell, residual supporting cell, foot cell and central cell. The terminal group of carposporangia develops first, but is followed rapidly by a succession of 5-8 further groups from lateral positions (Fig. 34N). A mature group of carposporangia is about 150-200μ diam.

Discussion: —

The species varies in form e.g. in density of lateral branching in the lower parts of the plant and in the development of a prostrate axis. It is sufficiently consistent, however, in form and organization of whorls of branchlets, in position of lateral branches, in position, size and division of tetrasporangia and in form of carposporophyte to be regarded as a ~~single~~ separate species.

The instability of form, particularly in the variations and inequality found in arrangement and length of whorl-branchlets, suggests possible phylogenetic significance.

The species is separated from Antithamnion on these features: —

1. Unequal whorl-branchlets (2 of the 5 being very much reduced).
2. Lateral branches of limited growth.

3. Tetrasporangia borne on special short small-celled branch. (Tetrasporangia are borne on cells of the whorl-branchlets or their branches in Antithamnion).

4. Procarps single near apex of lateral branch. In Antithamnion procarps, usually more than 8, are borne successively at the axial apex.

TRICHOTHAMNION nov. gen.

Thallus erectus; rami dichotomi ut videtur. E quoque cellula 3-5 vortico-ramuli, saepe impares, saepe e cellula basale grande 3 ramis productis. Vortico-ramuli pilis binis in cellulis parvis stipitatis instructi. Cellulae glandulosae nullae vel in cellulis exterioribus vortico-ramulorum positae. Tetrasporangia cruciato-tetrahedralia, in vortico-ramulis sessilia. Spermatangia in ramis specialibus brevibusque e cellulis basalibus vortico-ramulorum crescentibus. Procarpi (1-3) in vortico-ramulis redactis prope cacumina ramorum positi. Carposporophyti globis rotundatis carposporangiorum, globo terminale primum crescente, instructi.

Trichothamnion includes three southern Australian species characterised by the following features: —

1. An erect thallus with no prostrate axis and attached by means of branched rhizoids which do not penetrate the host tissue.

2. Axes apparently dichotomously branched. Details of branching have been described for each species ~~but~~ and is often not truly dichotomous as, even when two apical initials occur, one branch is initiated before the other.

3. Whorls of 3-5 (variable) whorl-branchlets often with 1 (-2) of the branchlets longer than others in the whorl. Each whorl-branchlet consists of a larger basal cell bearing usually three branches, which may vary in form. Two of these are usually shorter than the central one. Small stalk cells bearing (or without) terminal hairs, occur, often in pairs, on whorl-branchlets of all species. The genus is named in reference to these structures.

4. Procarps 1 (or more), borne several cells below the branch apex on a cell which usually bears 1-several initials of whorl-branchlets.

Superficially species of the genus show similarities with those of *Tetrathamnion*. They are, however, distinct in:

(i) Branching of the thallus to give equivalent axes (the lateral branches of *Tetrathamnion* are always distinctly less robust and remain in the position of lateral branches).

(ii) Attachment to host - some penetration always occurs in *Tetrathamnion*.

(iii) Structure of whorl-branchlets in having often one central dominant branch of the three occurring on the basal cell.

(iv) Frequent irregularity in number and size of branchlets in a whorl.

(v) Having small cells, often in twos, equivalent to short stalk cells bearing hairs.

(vi) Position of procarps.

(vii) Tendency to produce more than three groups of carposporangia consistently occurring in *Trichothamnion minimum*.

These features suggest that the genus is probably more closely related to *Antithamnionella* than to *Tetrathamnion* and possible phylogenetic trends within ~~the~~ *Trichothamnion* itself indicate an intermediate position between *Antithamnionella* and *Trithamnion*. Affinities with *Antithamnionella* are suggested ~~in:~~ by:

(a) Position of lateral branch initiation either on the basal cells of whorl-branchlets or directly on an axial cell in place of a whorl-branchlet (see Fig. 36B,C).

(b) ~~In~~ the inconsistency in number and form of whorl-branchlets per whorl even in individual plants, and

(c) particularly, in position of procarp development.

Procarps in *Antithamnionella* are developed successively ~~(to 4-8 procarps)~~ on the basal cells of whorl-branchlets at branch apices and although there is reduction in number of procarps formed in *Trichothamnion*, there is little specialization in vegetative development at the apex of the fertile branch. The branch apex above the procarp consists of several cells bearing initials of whorl-branchlets and the whorl-branchlet bearing the procarp may be several cellslong (*T. planktonicum*) and occasionally branched (*T. minimum*) or reduced to only one cell beyond the procarp (*T. elongatum*). Several procarps may occur on the basal cells of whorl-branchlets near the branch apex in *T. elongatum* and this probably represents a transition from a more primitive condition.

Within the genus *Trichothamnion* trends of probable evolutionary significance occur, and point towards the development of the more stable form found in *Trithamnion*.

Lateral Branching: — occurs (a) on the basal cells of whorl-branchlets (T. elongatum), (b) in place of a whorl-branchlet and in this case initiated from immature axial cells at the branch apex (T. elongatum), (c) from the apex of a cell above the whorl of branchlets (T. planktonicum, T. minimum and occasionally T. elongatum). When this occurs the initial cell of the lateral branch is a separate cell and is not necessarily developed simultaneously with the axial initial and thus branching is not truly dichotomous. The trend probably goes from (a) to (b) to (c) and in this respect T. elongatum, with mainly (a) to (b) type branching, is the most primitive.

Structure of Whorl-Branchlets: — Each species is characterised by having a large basal cell to each whorl-branchlet. In T. planktonicum this basal cell is particularly large compared with subsequent cells, rounded and may bear either one simple central whorl-branchlet of several cells in length and 2 short hair-bearing branches (T. planktonicum, Fig. 35I) or branched whorl-branchlets may occur in place of the 2 hair-bearing branches (T. planktonicum Fig. 35H). In T. elongatum it is common to find three more or less similar branches developed on each basal cell. These vary in form but are usually branched one to several times, bear prominent gland-cells and branches terminate with small hair-bearing cells. Gland-cells and hairs are more numerous on the outer branches while the central one tends to be the longest of the three.

Whorl-branchlets of T. minimum are perhaps the most advanced in form, and most closely approach the form from which whorl-branchlets of Trithamnion have probably evolved. The basal cell is elongate (Trichothamnion minimum Fig. 36S,T) and bears a well developed central branch. This central cell bears two further cells and usually two small cells similar to stalk cells of hair-bearing branches (T. minimum Fig. 36S). The development of a series of similarly branched central cells from the outer end of each successive central branch would produce a major branchlet of the form found in Trithamnion (for example, in T. tetrapinnum, Fig. 38D).

Development of Carposporophyte: — As already described, Trichothamnion elongatum is the species probably most closely allied to Antithamnionella in position of procarps and hence is probably the most primitive species in this respect. On the other hand T. minimum probably most nearly approaches the genus Trithamnion in consistently producing more than 3 successively-formed groups of carposporangia from each carposporophyte. In this feature the species is equivalent to Trithamnion, but due to its obvious differences in vegetative structure is left in the genus Trichothamnion. Both T. planktonicum and T. elongatum may very occasionally produce at least a fourth carposporangial group from a carposporophyte.

In summary, the features exhibited by T. elongatum indicate that it is probably the most primitive species while T. minimum is the most advanced species of the genus.

TYPE species: — Trichothamnion planktonicum nov. sp.

<u>Key to the southern Australian Species of Trichothamnion.</u>

1. Cells of the central part of main axes not much longer than broad (about (150-200) x (120-150)μ). Whorl-branchlets with large conspicuously rounded basal cells usually bearing a central simple branch 3-5 cells long which terminates in an abrupt acute tip. Gland-cells not recorded... ... ... <u>T. planktonicum</u>

1. Cells of main axis distinctly longer ($2\frac{1}{2}$-5 times) than broad. Whorl-branchlets with rounded, but not conspicuous or elongate basal cells bearing branched central whorl-branchlets without obviously abruptly acute tips to its branches. Gland-cells present... ... ... 2.

2. Axial cells of central main axes about 4-5 times as long as broad (500 x 120μ). Longest whorl-branchlets up to 75μ long. Tetrasporangia (65μ diam.) borne on an upward projection from basal cells of whorl-branchlets. Usually only 3 groups of carposporangia seen on carposporophyte at one time. Gland cells prominent.... <u>T. elongatum.</u>

2. Axial cells of central main axes about $2\frac{1}{2}$ times as long as broad (170 x 70μ). Whorl-branchlets (10-170μ long). Tetrasporangium (36μ diam) sessile on lower (1st, 2nd and 3rd) cells of whorl-branchlets. More than 3 groups of carposporangia occur on carposporophyte at one time ... ... <u>T. minimum</u>

TRICHOTHAMNION PLANKTONICUM n. sp.

Thallus 1.5 cm altus, ramosus dichotome. E quoque cellula 4 (-5) vortico-ramuli usque ad 80µ longi, apicibus acutis, plerumque non ramosi; cellulae basales magnae rotundatae pilis stipitatis vestitae. Cellulae glandulosae nullae. Tetrasporangia cruciato-tetrahedralia, 45-55µ diametro, in cellulis basalibus vortico-ramulorum sessilia. Spermatangia in ramis specialibus brevibus in cellulis basalibus vortico-ramulorum. Procarpi singuli in ramis brevibus prope cacumina ramorum positi.

TYPE Locality: — Sports Beach, Bridgewater Bay (near Portland), Victoria.

HOLOTYPE: — AD, A 29,292.

DISTRIBUTION : — Dongarra, Western Australia; Pennington Bay and Stanley Beach, Kangaroo Is., South Australia; and Bridgewater Bay, Cape Nelson Bay and Port Fairy, Victoria. Epiphytic on other algae (e.g. species of Hypnea, Monospora, Spongoclonium), on rocks, and as a free-floating "bloom" under suitable conditions (Womersley & Norris, 1959).

(Fig. 35 D-Q; Plate 9)

General Features: — The plant grows to 1.5 cm. in height from a basal rhizoidal holdfast. The thallus is apparently dichotomously branched at short intervals and, in the free-floating form, develops into rounded balls 1-1½ cm in diameter. Axial cells are about 1-2 times as long as broad and each bears from the uppər end, a whorl of 4-5 short whorl-branchlets (to 80µ long) which taper abruptly to an acute tip (Fig. 35D).

Hairs supported on one (or two) stalk cells occur particularly in the upper parts of the branches.

Structure of the Thallus: —

(1) Form and Development of Main Branches: — Growth takes place by transverse divisions of a dome-shaped apical cell and axial cells enlarge quickly so that only a few small immature cells occur at each branch apex (Fig. 35 E,F). Mature axial cells vary in size and proportion; those of the central thallus are about 150-200 x 120-150µ.

Branching occurs usually at intervals of 2-4 cells from a pair of apical cells formed above the position of the whorl of branchlets (Fig. 35F). In female plants, apical growth ceases with the development of the carposporophyte and axial growth is continued by lateral branches. These are produced on the basal cells of whorl-branchlets on the axial cell below that bearing the carposporophyte (Fig. 35Q) and a whorl of 4 or 5 new branches may develop. Lateral branches from the basal cells of whorl-branchlets may also occur in other parts of the plant, especially near the base. As the upper axes elongate new growth occurs lower down and it seems likely that the upper branches are detached to form the "blooms" reported by Womersley and Norris (1959) while regeneration occurs from the base of the plant.

Development, Arrangement and Branching of Whorl-branchlets: — Whorl-branchlets are initiated on cells immediately below the apical cells and develop successively to form whorls of 4 (or 5) simple, short whorl-branchlets (to 80µ in length) of 3-5 cells. The basal cell is the largest (25-35µ diam.) and the whorl-branchlets taper to an abrupt, usually acute tip. A whorl-branchlet is often lacking from the inner side of the lowest axial cell of a dichotomy while, on the same cells, the outer whorl-branchlet is often larger than the others. Short hair-bearing branches occur usually in twos on the upper side of the basal cells of whorl-branchlets thus making a total of three branches from a basal cell. Hairs may occur on other cells of whorl branchlets also (Fig. 35I). Each hair is up to 60 µ long with an expanded tip and is borne on one (or two) cylindrical stalk cells each 6-10µ long. Towards the base of the thallus short branches occur on the basal cells of the whorl-branchlets in place of simple hair-bearing branches (Fig. 35J). These bear terminal hairs, or, in place of a hair, a small cell may be cut off laterally from the stalk cell (Fig. 35J). This lateral cell development is similar to the production of gland-cells in other genera of the Antithamnieae but in this case the small cell produced does not appear different from other vegetative cells of the thallus.

Gland-cells: — Not known for this species (see note above).

Attachment Organs: — At the base of the plant dichotomously branched rhizoids of elongate cells develop from the base of the lowest whorl-branchlet and also directly from the axial cells below the whorls of whorl-branchlets. The rhizoids grow downward and attach in a mass to form a much-branched rhizoidal holdfast (Fig. 35G).

There is no creeping base formed on the plant, although the production of rhizoids occurs from a number of the erect basal cells of the thallus.

Tetrasporangia: — Tetrasporangia are borne usually singly, on the upper side of the basal cells of whorl-branchlets on the upper part of the thallus. Each tetrasporangium is sessile, spherical when mature and usually 45-55µ diameter within the thick gelatinous sheath. Division is cruciate although it often appears tetrahedral. All divisions may commence at the same time at the periphery, but the one central transverse or partly-oblique division is completed first (Fig. 35H).

Spermatangia: — Spermatangial mother cells occur terminally on short special branches borne on the upper side of the basal cells of whorl-branchlets in all parts of the plant. Several branches may occur on the basal cell of ~~the~~ a whorl-branchlet, each one consisting of a single stalk cell which bears a whorl, usually of 4 cells, on its upper end. Each of these cells bears a terminal whorl, usually of 4 spermatangial mother-cells, each about 4-5 μ long (Fig. 35K).

Development of Procarp and Carposporophyte: — Procarps occur singly near branch apices and elongation of the branch ceases soon after initiation of the carpogonial branch. The carpogonial branch is borne on the basal cell of a whorl-branchlet several cells in length and 2- several cells below the apex (Fig. 35L), which is deflected away from the carpogonial branch. The axial cell bearing the procarp remains very much smaller than the cell below and does not produce further whorl-branchlets. It may however occasionally develop a small hair-bearing branch of 1-2 cells (Fig. 35M). The 4-celled carpogonial branch is formed by successive divisions, 2 transverse and 1 oblique, as in Antithamnion, and a comparatively short trichogyne (40-60μ long) is developed from the carpogonium (Fig. 35M,N). The supporting cell (the basal cell of the whorl-branchlet) elongates upward prior to cutting off the auxiliary cell from its upper side (Fig. 35N). Presumably fusion then occurs between the auxiliary cell and the carpogonium and, following this, there is an upward development of the auxiliary cell before it divides to form the foot-cell and the upper central cell (Fig. 35 O). Carposporangial buds develop from this cell, the first being produced terminally (Fig. 35 P,Q) and the following ones laterally (Fig. 35Q). As the carposporophyte develops fusions occur between the axial cell, the residual supporting cell and the foot-cell while the connection between the foot-cell and the central-cell is considerably broadened (Fig. 35Q). The developing carposporangia are somewhat protected by the upward growth of 3-5 lateral branches which are borne on whorl-branchlets of the axial cell below the carposporophyte and which continue. further upward growth of the thallus. These branches are still short when the carposporangial buds are initiated, but are well above the carposporophyte by the time the first rounded group of carposporangia is mature.

Discussion: —

This plant is undoubtedly the species recorded by Womersley and Norris (1959) as occurring in a free-floating form in sufficient quantities to produce, when cast ashore, a red band up to 25 ft. broad, several hundred yards long and 1-10 inches thick on the beach and also in the sea off the Victorian coast at Bridgewater Bay. Mr. C. Beauglehole, a local resident, had previously recorded a similar "bloom" of a red alga in the vicinity, and following Womersley and Norris' record, noted it again at Cape Nelson Bay and at Port Fairy on later occasions.

The habit of the plant allows the upper branches to be liberated, while regeneration occurs from near the base of the plant. There must, however, be considerable and rapid growth in the free-floating form to produce the vast masses of alga reported in these "blooms".

TRICHOTHAMNION ELONGATUM nov. sp.

Thallus usque ad 3 cm altus, tenuis; cellulae axiales quater vel quinquies longiores quam latae. E quoque cellula 4 vortico-ramuli 40-50µ longi dichotome ramosi, saepe pilis terminalibus praediti, e cellula magna basale nonnulli rami producti. Cellulae glandulosae in cellulis exterioribus vortico-ramulorum. Tetrasporangia cruciato-tetrahedralia, 65µ diametro, in processis e cellulis basalibus vortico-ramulorum posita. Spermatangia ignota. Procarpi in ramulis 2-cellulatis prope apices ramorum positi.

TYPE Locality: — Pennington Bay, Kangaroo Island, South Aust.

HOLOTYPE: — AD, A 13,032.

DISTRIBUTION : — Known from the type locality only. Drift, on Sargassum bracteolosum J. Ag.

(Fig. 36 A-Q).

General Features: — The thallus is very fine and delicate, up to 3 cm. long with elongate axial cells bearing from their upper end whorls of 4 very short whorl-branchlets. Branching may appear dichotomous from the apex of the axes, or lateral from the basal cells of the whorl-branchlets (Fig. 36A). Branch apices usually consist of a chain of immature cells which is often curved near the tip. Gland-cells are numerous and conspicuous on the whorl-branchlets.

Structure of the Thallus: —

(1) Form and Development of Main Branches: — Growth occurs by transverse divisions of a dome-shaped apical cell. The transition from young rounded cells to those which are elongate in form is often pronounced, with a sudden

change between two adjacent cells. Whorl-branchlet initials with gland-cells are conspicuous at immature branch apices (Fig. 36B,C).

Mature axial cells are cylindrical in form and about 4-5 times as long as broad. Cells of the central thallus are about 500x120μ (Fig. 36I).

The thallus may appear dichotomously branched from the apex of axial cells above the whorls of whorl-branchlets at intervals of about 5-8 cells. Lateral branches are, however, usually initiated in place of a whorl-branchlet on an axial cell and grow upward to appear dichotomous with the main axis (Fig. 36C,A). Lateral branches may also be produced on the basal cells of whorl-branchlets (Fig. 36Ia). In carposporangial plants, elongation of the thallus beyond the procarp is continued by a whorl of lateral branches. These are produced on the basal cells of the whorl-branchlets on the axial cell below that bearing the carposporophyte.

(2) Development, Arrangement and Branching of the Whorl-Branchlets: — Whorl-branchlets are initiated from 2 to several cells below the branch apex (Fig. 36B,C) from a chain of immature axial cells. At this stage they are large in proportion to the axial cells as compared with their mature proportions (Figs. 36I). Gland-cells are developed early, often when initials of whorl-branchlets are only 2 cells long.

Mature whorl-branchlets occur in whorls of 4, having one whorl-branchlet sometimes longer than the others. They are usually 40-50μ long with the longer one to 75μ long. Whorls may be reduced at bases of branches with the whorl-branchlets lacking on the inner side, adjacent to the other axis. The basal cell produces several, usually 3, branches, each of 2-4 cells in length; each branch bears one or more further cell branches. Usually gland-cells are borne laterally on terminal cells and often a terminal hair (up to 60µ long) with an expanded tip is developed (Fig. 36J).

Gland-Cells: — Gland-cells are borne on the terminal (or sub-terminal) cells of the branches of the whorl-branchlets and are initiated early in the development of the whorl-branchlets near branch apices (Figs. 36C,J). Each gland-cell is 12-14µ long with a groove on the lower side where it fits against its parent cell.

Attachment Rhizoids: — Fine dichotomously branched rhizoids develop from the basal cells of whorl-branchlets in the lower part of the plant. These are small, delicate and easily broken and have only been discerned with difficulty.

Tetrasporangia: — Tetrasporangia are borne on upward projections from the basal cells of whorl-branchlets, with occasionally two forming on the one projection (Fig. 36D,E).

Each tetrasporangium is spherical when mature, up to 65µ in diameter, within the gelatinous sheath and cruciately divided, although often appearing tetrahedral. The central transverse division is completed first (Fig. 36F,G,H).

Spermatangia: — Not recorded.

Development of Procarp and Carposporophyte: — A single procarp is borne on an axial cell near a branch apex, but occasionally one or more further carpogonial branches may occur irregularly spaced, on basal cells of other whorl-branchlets. Normally the basal cell of a young 2-celled whorl-branchlet acts as a supporting cell and no further cells of the whorl-branchlet are developed. Frequently a gland-cell occurs on the terminal (second) cell of the whorl-branchlet (Fig. 36K) and the branch apex ceases further growth when the procarp develops.

The carpogonial branch is four-celled and is formed, as in Antithamnion, by successive divisions, 2 transverse and 1 oblique, of the initial formed on the lower side of the supporting cell (Fig. 36 K,L). The trichogyne is up to 60µ long with a small swelling near the base (Fig. 36M). Numerous stages showing the development of a projection from the lower part of the carpogonium, after loss of the trichogyne, and development of a connecting cell toward the auxiliary cell were found. The auxiliary cell is cut off from the upper side of the supporting cell (Fig. 36N) and this cell divides transversely to give a lower foot-cell and an upper central-cell (Fig. 36 O). The first gonimolobe is formed terminally on the central cell, with carposporangial cells cut off from the initial cell which remains vegetative (Fig. 36P,Q). The second and third gonimolobes are lateral, and formed one after the other. Possibly further groups of carposporangia are formed but usually only 3 are seen at one time. As the carposporangial groups develop, fusions occur between the axial cell, the residual supporting cell and the foot-cell, while the connection between foot-cell and central-cell is considerably widened (Fig. 36Q).

Further elongation of the axis takes place from lateral branches as previously described.

Discussion: —

Although only the type collection is known, this species is clearly distinct from Trichothamnion planktonicum:

(1) The thallus is much finer and more delicate, although it is longer and bears shorter and more branched whorl-branchlets.

(2) Gland-cells are developed prominently.

(3) Branching occurs at intervals of 5-8 cells rather than 1-3 cells.

(4) Tetrasporangia are borne on elongate protrusions from the basal cells of whorl-branchlets.

(5) Usually one cell only develops beyond the procarp on the whorl-branchlets which bear carpogonial branches.

TRICHOTHAMNION MINIMUM nov. sp.

Thallus usque ad 0.5 (-1) cm altus, dichotomus ut videtur. E. quoque cellula 4-5 vortico-ramuli, ca. 110- (-170)μ longi, saepe binis cellulis parvis praediti, interdum impares, e cellula magna cylindricale basale ramosi, ad basin axis attenuati redacti. Cellulae glandulosae in cellulis exterioribus vortico-ramulorum positae. Tetrasporangia cruciato-tetrahedralia 36μ diametro, in cellulis interioribus vortico-ramulorum sessilia. Spermatangia ignota. Procarpi singuli in ramulis brevibus prope cacumina ramorum positi.

TYPE Locality: — Stanley Beach, Kangaroo Island, South Aust. Drift on *Wrangelia* sp.

HOLOTYPE: — AD, A 20,058.

DISTRIBUTION : — Known only from type locality and from Pennington Bay Kangaroo Is., S.A. Epiphytic on drift algae (e.g. *Wrangelia* sp. *Spongoclonium conspicuum* Sonder).

(Figs. 36 R-U, 37A-L).

General Features: — Thallus up to 1 cm. in height, usually less than 0.5 cm. and attaches to the host by rhizoids from the basal cells of the branched erect axis (Fig. 36R). Branching is apparently di- (or tri-) chotomous, but branches are initially developed one after another. Each axial cell bears a whorl of 4-5 whorl-branchlets which may be unequal in length. The basal cell bears a whorl of two or three short branched branches which terminate abruptly with an acute tip (Fig. 36S). Chromoplasts are irregular and elongate (Fig. 37B).

Structure of Thallus: —

(1) Form and Development of Main Branches: — Apical growth is by transverse divisions of a dome-shaped cell and immature axial cells are often rounded in form. Mature axial cells are cylindrical, 2-3 times as long as broad (about 170x70µ) and largest in the central region of the thallus. The base of the axis may taper and the axial cells become about equal inlength and breadth (Figs. 36R, 37C).

Branching occurs from the apex of axial cells above the whorls of branchlets. The two (or three) branches may not be developed simultaneously, although when mature branching may appear di-(or tri-) chotomous (Figs. 36R,37A).

(2) Development, Arrangement and Branching of Whorl-Branchlets: —Initials of whorl-branchlets occur on the second or third axial cell at the branch apex and are produced successively to form whorls of 4 or 5 branchlets.

Mature whorl-branchlets are about 110µ long or, where one (sometimes two) is longer than the other branchlets of the whorl, this one may be up to 170µ in length. Each whorl-branchlet consists of a basal cell, about

(70-80) x (16-20)µ in the larger whorl-branchlets and proportionally smaller in the shorter whorl-branchlets, which bear a whorl of 2-4 cell branches from its outer end. Several further successive whorls of cells less than 12µ long occur and the final branching consists of a short chain of 2-4 cells, and terminates in an abrupt point (Fig. 36S,T). The outer end of a cell often bears a pair of small densely staining cells (Fig. 36Sa,b). These are comparable with the small hair-bearing branches in T. planktonicum. Whorl-branchlets on cells of tapering axes at the base of the thallus are shorter and less branched than those above.

Gland-cells: — Gland-cells are small (8-10µ long) and sparsely distributed over the thallus. They occur on the cells of the terminal or subterminal order of branching of the whorl-branchlets (Fig. 36U).

Attachment Organs: — The thallus is attached by rhizoids, consisting of elongate cells, which arise from axial cells near the base of the plant. A digitate attachment process of slender, elongate cells forms on contact with the host (Fig. 37C).

Tetrasporangia: — Tetrasporangia are borne successively on the upper side of the lower (first, second, or, occasionally, third) cells of the whorl-branchlets. Each tetrasporangium is sessile, spherical and about 36µ diam. within the gelatinous sheath. A second tetrasporangium may occur within the sheath of a previous tetrasporangium.

Divisions may commence together (Fig. 37H,I) but usually the transverse division is completed first (Fig. 37K) and the sporangia arranged as when division is truly tetrahedral (Fig. 37J,L).

Spermatangia: — Not recorded.

Development of Procarp and Carposporophyte: — A procarp is developed on the basal cell of a young whorl-branchlet several cells below the branch apex. Frequently the procarp is borne on one of the two cells at the point of initiation of a pair of lateral branches; one of the laterals becomes fertile and bears the procarp and, later, the carposporophyte (Fig. 37Db), while the other continues axial elongation (Fig. 37Da).

At other times the procarp is borne several cells above the point of initiation of the two laterals; in this case one, bearing the procarp, ceases further growth and the other, as previously , continues thallus growth.

Axial growth above the procarp ceases and no further development occurs of the young vegetative cells. Any young whorl-branchlets (at this stage several cells long) on the axial cell bearing the procarp also cease further growth. The fertile whorl-branchlet is 2-3 cells long and the basal cell acts as a supporting cell and bears, from its lower side, the 4-celled carpogonial branch which curves upward (Fig. 37D,E).

After fertilization an auxiliary cell is cut off from the upper side of the supporting cell (Fig. 37E). This cell divides to give a lower foot-cell and an upper central-cell from which the terminal gonimolobe develops first (Fig. 37F). A further 3-5 lateral gonimolobes develop successively later (Fig. 37G). Connections between axial cell and supporting cell and between foot-cell and central-cell are broadened and complete fusion occurs between supporting cell and foot-cell of the carposporophyte (Fig. 37G).

Discussion: —

This plant is the smallest species of *Trichothamnion* but is probably the most advanced phylogenetically. It approaches *Trithamnion* in structure of whorl-branchlets and equals it in carposporangial ddvelopment and thus may form a link between these genera. It is retained in the genus *Trichothamnion* as it is comparable to species of this genus in length of whorl-branchlets and agrees also in other structural features such as attachment to host, branching habit and development of tetrasporangia.

TRITHAMNION nov. gen.

Thallus irregulariter ramosus. E quoque cellula 3 (interdum 4) vortico-ramuli, plerumque unus longior. Ramulus longior ramis brevibus jugatisque glanduliferis praeditus. Ramuli breves interdum non ramosi. Saepe in cellulis parvis stipitatis pili jugati adsunt. Tetrasporangia tetrahedralia in cellulis interioribus vortico-ramulorum brevium posita. Spermatangia ignota. Procarpi in ramulis 2-cellulatis cellulis pluribus infra apices ramorum natis positi. In quoque carposporophyto 4-6 globi rotundata carposporangiorum vortice ramulorum longorum cincti positi.

Trithamnion is morphologically, a well-defined genus particularly in having, characteristically, whorls of three unilaterally arranged whorl-branchlets from the upper end of each axial cell. The genus is named in reference to this feature. Whorls are rotated on adjacent axial cells and consist of one long central whorl-branchlet between two equal, but much shorter, lateral whorl-branchlets. Four whorl-branchlets sometimes occur in each whorl, particularly in T. tetrapinnum. This condition probably indicates instability in the development of the 3-branchlet whorl and, hence, phylogenetic relationship with an ancestor which normally bore whorls of 4 whorl-branchlets. Inconsistency in the lengths of whorl-branchlets making up the whorl (as in T. tetrapinnum) also signifies instability.

The central whorl-branchlet in all species consists of a main rachis, each cell (except the basal cell) of which bears a pair of short branches. These branches are usually terminated by small stalk cells, usually in two's or three's, and sometimes bearing terminal hairs. Gland-cells are also prominent on these branches. A whorl-branchlet of this form could be developed from one of the form occurring in Trichothamnion minimum, the development of a series of successive cells each similar to the central one of the whorl occurring on the outer end of the basal cell and each bearing two branches representative of the two other cells of the original whorl. This origin of the whorl-branchlets in Trithamnion also explains the shift in position of gland-cells from the near-terminal cell of the whorl-branchlet (as in Trichothamnion) to the branches of a whorl-branchlet (Trithamnion). The hair-bearing cells on the branches of the whorl-branchlets of Trithamnion are also comparable to those found in Trichothamnion and probably again denote evolution of the whorl-branchlet from a Trichothamnion-like ancestor.

Lateral whorl-branchlets are reduced in form as well as in length in Trithamnion. Least reduction in both features occurs in T. vulgare. Ratio for length of long whorl-branchlet (L) to length of short whorl-branchlet (l) for the three species indicates that most difference occurs in T. tetrapinnum. Thus (where a range of length occurs, these ratios are based on a mid-point value):—

<u>T. vulgare</u> $\frac{L}{l} = \frac{320}{250} \equiv 1.3$

<u>T. gracilissimum</u> $\frac{L}{l} = \frac{250-500}{130} \equiv 3.75$

<u>T. tetrapinnum</u> $\frac{L}{l} = \frac{550-700}{130} \equiv 4.8$

Thus, although <u>T. tetrapinnum</u> is the least stable of the species in arrangement of whorl-branchlets in each whorl, it has probably reached the highest degree of specialization of whorl-branchlets. Further increase in dominance of one branchlet per whorl with complete suppression of other whorl-branchlets might result in the production of a single branch from each axial cell.

This may indicate a primitive ~~form for~~ form of the tribes Antithamnieae and Heterothamnieae from which other tribes, having single branches from each axial cell, could have arisen. Specialization in carpospore production also occurs in the genus. The procarp is developed several cells below the apex of the branch on the basal (supporting) cell of a 2-celled whorl-branchlet so that one sterile cell of the whorl-branchlet occurs beyond the procarp. This cell is small and rounded. When mature the carposporophyte produces a succession of 4-6 rounded groups of carposporangia. This condition is not common in Heterothamnieae, although an increased number of carposporangial groups occurs in <u>Antithamnionella tasmanica</u> and in <u>Trichothamnion minimum</u>. <u>Trichothamnion minimum</u> is excluded from Trithamnion on account of its vegetative structure.

The carposporophyte in Trithamnion is surrounded by a whorl of long branchlets borne on the adjacent cell below. These whorl-branchlets are limited in length, as are normal whorl-branchlets, and the production of a complete whorl usually of about 4 long branchlets of limited growth suggests a link with an ancestor having whorls of 4 whorl-branchlets. This may also represent specialization in vegetative features associated with carposporophyte development and suggests a very early stage possibly leading to the development of a special protective involucre around the carposporophyte. In other genera where axial elongation ceases with procarp initiation, lateral branches may develop below the fertile apex and continue axial growth. These are not, however, specialized in any way and a similar development of lateral branches may occur at any time where apical growth is interrupted.

TYPE species: — Trithamnion vulgare n. sp.

Key to the southern Australian species of Trithamnion

1. Long whorl-branchlets with rachis of 8–11 cells (550–850µ) long. Axial cells about $2\frac{1}{2}$ times as long as broad. Whorls frequently consisting of 4 branchlets (instead of 3).... *T. tetrapinnum*

1. Long whorl-branchlets less than 8 cells (or 550µ) long, usually of 6–8 cells (250–500µ) long. Axial cells more than 3 times as long as broad. Whorls usually of only 3 branchlets.. ... 2

  2. Short whorl-branchlets about 250µ long often bearing opposite branches. Gland-cells 18–20µ long. Axial cells about $3\frac{1}{2}$–4 times as long as broad... ... *T. vulgare*

  2. Short whorl-branchlets about 100µ long, simple or bearing simple branches, not opposite. Gland-cells 12–15µ long. Axial cells about 6 times as long as broad... ... ... *T. gracilissimum*

TRITHAMNION VULGARE n. sp.

Thallus usque ad 0.4 (-0.7) cm altus. E quoque cellula 3 vortico-ramuli, unilaterales in 180° producti; ramulus centralis usque ad 320µ longus, ramuli ceteri ca. 250µ longi, ramis jugatis brevibus 1-3 cellulae longis ramosi. Pili in cellulis parvis stipitatis terminales. Cellulae glandulosae in ramis vortico-ramulorum positae. Tetrasporangia tetrahedralia, 24µ diametro, in ramis brevibus specialibus in cellulis infimis vortico-ramulorum posita. Spermatangia et carposporophyti ignoti.

TYPE Locality: — D'Estrees Bay, Kangaroo Is., South Australia.

HOLOTYPE: — AD, A 15,421, growing on Caulerpa simpliuscula (R.Br.) Ag.

DISTRIBUTION : — From Pearson Is., Kangaroo Is. (Pennington Bay and D'Estrees Bay), Port Noarlunga and Brighton, South Australia, to Laurence Rock and Bridgewater Bay, Victoria, and also from Bicheno, Tasmania. Often epiphytic on species of Caulerpa (C. flexilis, C. brownii, C. papillosa, C. simpliuscula), but also on other algae.

(Fig. 37 M-R).

General Features: — The plant may grow to 0.7 cm high, but is often much smaller (0.2 - 0.4 cm). It attaches by a group of branched rhizoidal filaments arising from the base of the erect axes (Fig. 37M). Each axial cell is rather broader towards the apex and bears from the upper part three whorl-branchlets unilaterally arranged within 180° of the circumference of each axial cell (Fig. 37N). The central whorl-branchlet is usually larger than the other two and may be replaced by a lateral branch. The unilateral whorls are rotated on adjacent axial cells, either alternately or irregularly and consequently cells of the axes may be arranged somewhat zig-zag, particularly in the upper parts of the plant. Whorl-branchlets bear short, simple branches in opposite pairs from the cells of their rachides. Terminal hairs about 70µ long and gland-cells are also borne on the branches of the whorl-branchlets (Fig. 37N). Occasionally "buds" similar to young lateral branches, are formed, usually near the apices of axes. These develop rhizoids from their lower axial cells and are presumably liberated as propagules and thus provide a means of vegetative reproduction (Fig. 37Q).

Structure of the Thallus: —

(1) Form and Development of Main Branches: — Growth occurs by transverse, or slightly oblique divisions of a dome-shaped apical cell and a short chain of 6-12 rounded, immature cells occurs at the branch apex. Mature axial cells are cylindrical, broader in the upper part and largest in the central region of the thallus (about 128 x 34µ). Towards the base of the axis they become proportionally shorter (e.g. about 40 x 30µ). Lateral branches arise in place of the larger whorl-branchlets on axial cells. Several may occur on an erect axis most commonly in the upper part of the thallus.

(2) Development, Arrangement and Branching of Whorl-Branchlets: — The first initial of a whorl-branchlet occurs on the first or second axial cell below the branch apex, and the rachis of the whorl-branchlet may develop to six cells in length before its branches are initiated. The basal cell of the rachis usually remains slightly shorter than other cells of the rachis. The central larger whorl-branchlet is 6-8 cells (about 320µ) long and bears

short opposite branches each 1-3 cells long. These branches are usually terminated, as also is the rachis of the whorl-branchlet by 1-3 (commonly 2) small cells sometimes bearing an elongate hair outwardly (Fig. 37N). The two lateral whorl-branchlets are usually shorter (about 250μ long) and with fewer pairs of branches. All whorl-branchlets curve upward and overlap the whorl above.

Gland-cells: — Gland-cells (18-20μ long) are borne on the upper side of the branches of the whorl-branchlets and often on the final cell of the rachis of a whorl-branchlet. When the branch bearing the gland-cell is more than one cell in length, the gland-cell occurs on the outer cell. Most whorl-branchlets bear several gland-cells which most frequently occur on the upper part (Fig. 37,O).

Attachment Organs: — The basal cells of the erect axes become elongated and form the upper cells of branched rhizoidal filaments which attach the thallus firmly to the host. The elongation of cells commences above the host surface and the rhizoids become more branched where in contact with host tissue (Fig. 37P).

Tetrasporangia: — Tetrasporangia are borne successively on the cells of a special short branch (consisting of only 1-several cells) borne on the upper side of the basal cells of whorl-branchlets.

Each tetrasporangium is sessile, spherical when mature, about 24μ diam. within the gelatinous sheath and tetrahedrally divided (Fig. 37R). Divisions commence when the tetrasporangium is small, sometimes less than 12μ diam. and are usually completed before the tetrasporangium is much enlarged.

The double gelatinous sheath which surrounds many tetrasporangia suggests that at least two may develop successively in the same position.

Spermatangial and Female Plants: -- Not recorded.

Discussion: —

The plant is distinctive in arrangement of whorl-branchlets, and also in occurring on species of *Caulerpa*. There are very few other records of *Caulerpa* as a host for algae in the tribes discussed here.

TRITHAMNION TETRAPINNUM n. sp.

Thallus usque ad 1 cm altus e base prostrata. E quoque cellula 3-4 vortico-ramuli, saepe unilaterales plerumque uno ramulo longo praediti. Ramulus longus 550-700 (-850)µ longus, curvato-adscendens, binis ramulis brevibusque ad 80µ longis ramosus. Ramuli breves 130 (-190)µ longi, plerumque ramosi. Cellulae glandulosae in ramis vortico-ramulorum positae. Tetrasporangia tetrahedralia, 42-48µ diametro, in cellulis interioribus vortico-ramulorum brevium sessilia. Spermatangia ignota. Procarpi in ramulis 2-cellulatis cellulis pluribus infra apices ramorum orientibus positi. In quoque carposporophyto 4-6 globi rotundati carposporangiorum vortice ramulorum longorum cincti positi.

TYPE Locality: — Pennington Bay, Kangaroo Island, South Australia.

TYPE: — AD, A 19,737.

DISTRIBUTION: — Known only from the type locality.

(Fig. 38 A-H).

General Features: — The plant consists of a prostrate axis attached to the host by rhizoids and bearing erect branches up to 1 cm. in height (Fig. 38A). Each cell of the axes bears a whorl of 3-4 whorl-branchlets which, when only 3 whorl-branchlets occur, is unilateral in position. Generally a whorl consists of one long whorl-branchlet, bearing pairs of short branches, and 2 or 3 short whorl-branchlets which are usually branched. This arrangement is not consistent and whorls may consist of any combinations of long and short (or occasionally of all long or all short) whorl-branchlets. Terminal hairs and gland-cells may occur on the branches of the whorl-branchlets.

Structure of the Thallus: —

(1) Form and Development of Main Branches: — Growth occurs by transverse divisions of a dome-shaped apical cell and a chain is formed at branch apices of about 12 rounded, immature axial cells.

Mature cells of the axis are cylindrical and usually about 250x 100μ. Occasionally they are proportionally longer for their breadth and in some axes are about 250 x 50μ. Lateral branches arise from the basal cells of whorl-branchlets, usually from short whorl-branchlets, and develop similarly to the main axes (Fig. 38B). The original whorl-branchlet often remains as a single branchlet on the basal cell of well-developed lateral branches. Lateral branching occurs most frequently in the upper parts of the thallus.

(2) Development, Arrangement and Branching of Whorl-branchlets: — Whorl-branchlets are initiated usually on the second axial cell at the branch apex, and its branches commence to form when the rachis of the whorl-branchlet is 6-8 cells long.

Mature whorl-branchlets may be comparatively long or short. Usually one branchlet of each whorl is considerably longer than the others, and, in whorls of three, the long branchlet usually occurs between two shorter branchlets (Fig. 38D). The long whorl-branchlets curve upward and are 8-11 cells (550-700(-850)μ) long. The basal cell of the rachis always remains slightly shorter than the cells immediately above it and the rachis tapers toward the outer end. Each long branchlet bears short branches up to 5 cells (80μ) long, which occur in pairs, either opposite, or more often directed slightly outwardly from each cell (except the basal cell). These branches sometimes themselves bear one short branch of 1-3 cells in length and commonly one gland-cell (Fig. 38D). On young whorl-branchlets the branches are often terminated by small, hair-bearing cells. In the lower parts of the thallus these occur less frequently and have probably been lost. Occasionally a third short branch occurs on the outer side between the two normally present on each cell of the rachis of a whorl-branchlet. Short whorl-branchlets are often branched one to several times and are about 130 (-190)μ long (Fig. 38B,D). In female plants the carposporophyte is surrounded by a whorl of 2-4 long whorl-branchlets which make up the whorl on the cell below that bearing the procarp. The lowest whorl of branchlets on a lateral thallus branch often consists of 4 short, whorl-branchlets and no longer ones.

Gland-cells: — Gland-cells (20µ long), are borne on the basal cell (occasionally the second cell) of the branches of the long whorl-branchlets and may also occur occasionally on the short whorl-branchlets (Fig. 38B,D) Six to ten gland-cells are commonly formed on one long whorl-branchlet (Fig. 38D).

Attachment Organs: — Rhizoidal attachment organs are borne on basal cells of whorl-branchlets on the prostrate axis. They are developed as elongate cells and on contact with the host a digitate attachment process forms (Fig. 38C).

Tetrasporangia: — Tetrasporangia occur on the basal and second cells of short whorl-branchlets and on the lower pairs of branches of the long whorl-branchlets. They are sessile on these cells (or on short branches of 1-several cells borne on these cells) and several may develop successively on each cell. Each tetrasporangium is ovoid, 42-48µ long when mature and divides tetrahedrally. Divisions occur rapidly at an early stage — while the tetrasporangium is 24-30µ long.

Young tetrasporangia are frequently attached laterally and are oblique or parallel to the cells upon which they occur (Fig. 38E).

Spermatangia: — Not recorded.

Procarp and Carposporophyte: — One procarp is developed several cells below the apex of a branch. The supporting cell and small sterile cell are probably analogous to a 2-celled initial of a whorl-branchlet in which the basal cell bears the carpogonial branch. The branch axis ceases to elongate on development of the procarp. A mature 4-celled carpogonial branch is about 15µ long and bears a trichogyne (60-70µ long) from the carpogonium (Fig. 38F).

An auxiliary cell is cut off from the upper side of the supporting cell and divides transversely to form a lower foot-cell and an upper central cell (Fig. 38G). Several, at least 4-6, rounded groups of carposporangia are produced from the central-cell. The terminal one is initiated first followed successively by several lateral ones (Fig. 38H).

Whorl-branchlets from the axial cell below that bearing the procarp grow around the maturing carposporophyte.

Discussion: —

There is only one record of this species. It is, however, distinct in habit and form from other species of Trithamnion. All measurements, are based on this one record and require careful checking when additional material is available. The plant differs from other species in having longer central whorl-branchlets, denser lateral branching, comparatively shorter, broader axial cells and whorls usually made up of four whorl-branchlets of which two may often be long in form.

TRITHAMNION GRACILISSIMUM n.sp.

Thallus prostratus ramis erectis usque ad 0.5 cm altis. E quoque cellula 3 (interdum 4) vortico-ramuli, unilaterales in 180°, ramulo centrale longo praediti. Ramulus longus 250-500µ, ramis jugatis brevibus 1-3 cellulae longis. Ramuli breves 100µ longi, interdum ramosi. Pili, saepe jugati, in cellulis brevibus. Cellulae glandulosae in ramis vortico-ramulorum positae. Tetrasporangia tetrahedralia, 30-36µ diametro, in cellulis infimis vortico-ramulorum brevium sessilia. Spermatangia ignota. Procarpi 1-2 in ramulis 2-cellulatis compluribus cellulis infra apices ramorum orientibus positi. Carposporophyti globis rotundatis carposporangiorum, globo terminale primum crescente, instructi.

TYPE Locality: — Saunder's' Beach, Kangaroo Island, South Australia.

HOLOTYPE: — AD, A 29,511. Growing on Chondria sp.

DISTRIBUTION : — Known from Middleton Beach, Albany, Western Australia and from the type locality and Pt. Willunga, South Australia. Epiphytic on species of Chondria, Dictyota and Hymenocladia.

(Fig. 38 I - P).

General Features: — The thallus is very small with erect parts up to 0.5 cm. high and a creeping prostrate basal axis. Cells of the axes are elongate and each one bears a whorl from its upper end consisting usually of three whorl-branchlets — two short ones and, between them, a central longer one. All three are unilaterally placed within 180° on the axis (Fig. 38, I). There is often an additional (fourth) whorl-branchlet (usually short, but sometimes long) and the long central branchlet may be replaced by a lateral branch.

Structure of the Thallus: —

(1) Form and Development of Main Axes: — Growth occurs by transverse or slightly oblique divisions of a dome-shaped apical cell (Fig. 38K) and a short chain of 4-10 rounded, axial cells occur at branch apices. Mature axial cells are cylindrical and elongate, about 6-8 times as long as broad and up to 250 x 40µ.

Lateral branches occur in place of long whorl-branchlets and are developed most frequently in the upper part of the thallus. Occasionally a lateral branch ceases further elongation after growing several nodes in length. Where a lateral branch is produced in place of a fourth whorl-branchlet, three remain in the whorl, one of which may be a long branchlet. The whorl may extend around the axis, occupying more than 180° as is usual in a normal 3-branchlet whorl arrangement. On prostrate axes erect branches equivalent to lateral branches may arise from the basal cells of a short whorl-branchlet.

(2) Development, Arrangement and Branching of Whorl-Branchlets: — Initials of whorl-branchlets occur on the third cell below the apex of branches. The long whorl-branchlet is initiated first followed by the development of the short whorl-branchlets, several cells lower down (Fig. 38K). The first branches on whorl-branchlets occur also at about this position. Long whorl-branchlets are initiated alternately on adjacent axial cells, but this arrangement is not consistent in mature whorls, due possibly to rotation between axial cells.

Long whorl-branchlets, when mature, are 250-500µ long with a rachis up to 7 cells long, and bear 2 (-3) short branches from each cell except from the shorter basal cell of the rachis (Fig. 38J). In female plants the carposporophyte is surrounded by 2-4 long whorl-branchlets developed from the whorl below. The branches of the whorl-branchlets are 1-3 cells in length, sometimes with simple branches of single cells, and are set between 90° and 180° to one another. Each branch is commonly terminated by a pair of small cells, often bearing hairs. The final cell of the rachis usually bears 2 or 3 similar small cells (Fig. 38J). When lacking a terminal hair these small cells probably represent stalk-cells of hairs which have been lost.

Short whorl-branchlets about 100µ long may be unbranched and 2-5 cells in length, or simply branched, and may bear hairs, gland-cells or small cells as found in the branches of the long whorl-branchlets (Fig. 38J).

Gland-cells: — Gland-cells (12-15μ long) occur on cells immediately behind the terminal cells of the branches of the whorl-branchlets. Often each branch consists of only one main cell, plus a pair of small, terminal cells and the large cell then bears the gland-cell (Fig. 38J). Several gland-cells may occur on one long whorl-branchlet and may also occur on cells of the rachis of short whorl-branchlets.

Attachment: — Attachment of the prostrate axis is by branched rhizoids which develop from the basal cells of whorl-branchlets. The rhizoids consist of elongate cells which broaden on contact with the host tissues, develop loose terminal branches which adhere to the host, and,, when host tissue is soft, may penetrate between the outer cells.

An erect branch of the thallus often develops from the upper side of the basal cell of the whorl-branchlet bearing rhizoids (Fig. 38L).

Tetrasporangia: — Tetrasporangia are borne on the basal cells of whorl-branchlets. The few recorded have been only on the short whorl-branchlets and have been developed from the outer, usually upper, part of the cell (Fig. 38M). Each tetrasporangium is sessile, probably tetrahedrally divided and when mature 30-36μ diam. within the gelatinous sheath.

Spermatangia: — not recorded.

Procarp and Carposporophyte: — Procarps are initiated several cells (often the third) below the branch apex and consist of supporting cell, sterile cell and 4-celled carpogonial branch. As in other genera of the group, the carpogonial branch develops from the lower side of the supporting cell which, with the small sterile cell, may be analogous to a short 2-celled whorl-branchlet (Fig. 38N).

Occasionally 2 procarps separated by 2 or 3 axial cells, occur on one branch apex. Only one, however, is borne on any one axial cell and only one carposporophyte develops per branch apex; growth of the axis ceases after initiation of the procarp.

The auxiliary cell is cut off from the upper side of the supporting cell and after fusion with the carpogonium, divides to form a lower foot-cell and an upper central cell. A terminal gonimolobe develops first from this central-cell (Fig. 38,O) and is followed by several further lateral gonimo-lobes. A total of at least 4-6 rounded groups of carposporangia may mature successively (Fig. 38P).

The carposporophyte is surrounded by a whorl of long whorl-branchlets from the axial cell below that bearing the procarp.

Discussion: —

The plant is delicate in form and on account of its size, may be easily overlooked. Probably due to this fact, it has only been recorded from widely separated localities. It is characteristic of the genus in plant habit, in arrangement and form of whorl-branchlets, in bearing pairs of small cells and terminal hairs on branches of the whorl-branchlets and in position of gland-cells.

Specifically it is distinct in proportion of long to short whorl-branchlets and in length of whorl-branchlets to their branches.

VI. THE CLASSIFICATION AND EXTENSION OF THE CROUANIEAE SCHMITZ.

Schmitz (1889) divided the Ceramiaceae into fifteen groups and included within the Crouanieae the genera *Ballia*, *Antithamnion*, *Crouania*, *Gulsonia*, *Gattya* and *Ptilocladia*. The latter three genera were originally described from southern Australia, and species of all six genera are widely distributed in this region.

Schmitz and Hauptfleisch (1897) added *Lasiothalia*, another Australian genus, to the tribe but removed *Gulsonia* to the Batrachospermeae of the Helminthocladiaceae on account of its thallus structure and the presence of a filamentous involucre surrounding the gonimoblast. They defined the tribe Crouanieae to include forms either filamentous or with dense axial cortication and cystocarps in which an involucre was absent or much reduced. De Toni (1924) added *Dohrniella*, *Hymenoclonium*, *Chalicostoma* (none of which is from southern Australia) and *Platythamnion* to Crouanieae. He recognized the original fifteen groups of Schmitz.

Feldmann-Mazoyer (1940) described only those species of the Crouanieae which occur in the Mediterranean and removed *Dohrniella* to a newly-erected tribe. Kylin (1956) removed both *Hymenoclonium* and *Chalicostroma* (the other two non-Australian genera included by De Toni) from the Crouanieae, but added *Grallatoria* Howe from the Bahamas. This is now the only genus remaining in the group which has not been recorded from southern Australia . Kylin (1956) also included the genera *Heterothamnion*, *Antithamnionella*, *Acrothamnion* and *Warrenia* in the Crouanieae. He defined the group to include species bearing whorls of 2-4 generally much-branched branchlets from each axial cell and procarps borne on the basal cell of a short branch.

Hommersand (1963) split the Crouanieae into

(i) *Crouanieae*, which he included in the sub-family Crouanioideae and

(ii) *Antithamnieae* placed in the Ceramioideae. Crouanieae, according to Hommersand, includes *Crouania*, *Gulsonia*, *Gattya* and *Gulsoniopsis* while Antithamnieae includes *Antithamnion*, *Ballia*, *Acrothamnion*, *Antithamnionella*, *Heterothamnion*, *Platythamnion*, *Ptilocladia*, *Grallatoria*, *Bracebridgea* and *Warrenia*.

Hommersand distinguished the Crouanioideae by: —

1. Whorls of whorl-branchlets which are not orthostichous, and which are superimposed on alternate axial cells, while the Ceramioideae has whorl-branchlets which are always orthostichous.
2. Procarps which entirely lack sterile groups in the Crouanioideae, but contain a single sterile group in the Ceramioideae.
3. A carpogonial branch initial which enlarges between divisions and produces a recurved carpogonial branch in Crouanioideae while in Ceramioideae the carpogonial branch initial does not enlarge between divisions and the cells of the carpogonial branch generally lie in a straight line.
4. A connecting cell in Crouanioideae which remains evident as a process containing its own nucleus, extending from the auxiliary cell after fusion with it while in Ceramioideae the connecting cell fuses completely with the auxiliary cell and is not recognisable as a process extending from it.

Detailed study of the southern Australian representatives of these genera (except Bracebridgea and Warrenia) reveals that Crouanieae and Antithamnieae cannot be thus separated and placed in these two sub-families on the four characteristics quoted by Hommersand and outlined above. Thus:

(1) Hommersand's classification of the Crouanieae does not include genera with orthostichous arrangement of whorls. The rotation of whorls varies however, so that whorls are superimposed on alternate cells, as given by Hommersand, only in Ptilocladia (≡ Gulsoniopsis) and in Gulsonia. In Crouania and Gattya which have 3 (not 4) whorl-branchlets per whorl, a rotation of 40° in adjacent whorls causes them to be superimposed on every 4th axial cell. Euptilocladia (≡ Ptilocladia of Hommersand 1963) has orthostichous arrangement of whorls and, in respect of this feature, Hommersand was correct in removing the genus from the Crouanieae as he defined it. In respect to other features, however, Euptilocladia is closely related to Ptilocladia. It possesses a highly specialised thallus structure and, because of its relationship to Ptilocladia, must be regarded phylogenetically as a highly advanced genus of Crouanieae. Of the genera placed by Hommersand in the Antithamnieae, Heterothamnion, some species of Antithamnionella and Macrothamnion (separated here from Antithamnion) all have whorls of branchlets which are not orthostichous.

(2) Sterile cells associated with procarp development may be:

(a) Formed before the procarp is initiated such as the cells of a whorl-branchlet (or pinna) which bears a carpogonial branch on its basal (supporting) cell. Such a fertile whorl-branchlet (pinna) may be equivalent to other whorl-branchlets (pinnae) of the vegetative parts of the thallus, or may be reduced to only one small cell besides the basal (supporting) cell (e.g. *Antithamnionella*, *Perithamnion*).

(b) Formed *after* initiation of the procarp such as occurs in some genera of other groups (e.g. *Ptilota*, *Plumaria* and *Gymnothamnion* of the Ptiloteae (Balakrishnan (1958)). All genera of Antithamnieae and Crouanieae (sensu Hommersand) may be classed as the (a) type.

Procarps in both groups occur in the position of a whorl-branchlet (pinna) but whereas the branchlet develops an elongate rachis of a number of cells in *Antithamnion*, it is reduced to 2 or 3 cells in *Trichothamnion*, to a single cell of normal size in *Antithamnionella*, to a very much reduced cell in *Heterothamnion* and *Trithamnion*, while sterile cells are absent in *Crouania* *Gattya* and *Ptilocladia* (occasionally a modified branch occurs in *P. vestita*). Origin of the procarp is thus closely related in both the Crouanieae and Antithamnieae and this factor strengthens indications shown by other features that the groups are closely allied to one another.

(3) In the genera *Crouania*, *Gattya*, *Ptilocladia* (≡ *Gulsoniopsis*) and *Euptilocladia* the 4 cells of the carpogonial branches are formed by three divisions of a large cell cut off outwardly from the supporting cell. Divisions are simultaneous (or follow in rapid succession) so that no enlargement of cells between divisions is observed. The cells do enlarge, however, while they partly straighten to form the upwardly-curved carpogonial branch. Observations on the genera included by Hommersand in Antithamnieae

(except Ptilocladia) show that the 4-celled carpogonial branch is formed by three successive divisions (2 transverse and one oblique) of the initial borne on the underside of the supporting cell. In this type of development there is some enlargement of the outer cell formed by one transverse division before the following division takes place. The fully formed carpogonial branch curves upwardly around the supporting cell.

These observations of southern Australian species are the reverse of those given by Hommersand. Even when fresh, fertile material is available it is difficult to determine the exact timing of divisions of the carpogonial branch-initial of genera of the Crouanieae. It is certain, however, that they occur almost, if not quite, simultaneously, while those in Antithamnieae follow one another independently and stages in the formation of the 4 cells are commonly observed. The four cells of the carpogonial branch of Crouanieae occur within the rounded initial cell and the carpogonial branch straightens out after the four cells are formed. The initial cell of genera of Antithamnieae is rather more elongate and divisions occur as the branch elongates to its mature curved form. In all genera the mature carpogonial branch is curved upward and none have been observed with cells in a straight line (cf. Hommersand). The curvature occurs necessarily in the Antithamnieae as the upwardly directed carpogonial branch is attached to the lower side of the rounded supporting cell.

(4) In discussing the retention of the connecting cell as a discrete cell Hommersand does not indicate how long it might remain as a distinguishable entity. In all southern Australian species the connecting cell, if recognizable at all, does not remain distinct for long. In most cases

the formation of a connecting cell is only known from rare observations of good fresh material and for many species the form of connection between carpogonium and auxiliary cell has not been accurately observed. In some species a distinct projection of the auxiliary cell towards the carpogonium is known to occur and in several species (Crouania mucosa, Ptilocladia pulchra and Gulsonia Annulata (Wollaston and Womersley (1959)), a connecting cell formed from the carpogonium fuses with this projection. There is no evidence, however, that the connecting cell remains distinct and, from numerous observations of later stages, it seems that it soon becomes completely fused with the lower part of the auxiliary cell (the foot-cell).

A permanent nucleated cell does not occur. Similar observations have been made for genera of the Antithamnieae and Heterothamnieae (e.g. Antithamnionella tasmanica).

Detailed investigation of genera and species from other tribes is necessary to determine the validity of the Crouanioideae and Ceramioideae as sub-families of the Ceramiaceae.

The above observations on species from the Crouanieae and Antithamnieae suggest that the features used by Hommersand are too variable to be satisfactory criteria for this separation.

VII. CLASSIFICATION OF SOUTHERN AUSTRALIAN GENERA

Sixteen genera, each (except Gattya, Gulsonia and possibly Platythamnion) including 2-8 species have been studied in detail and consequently three tribes are recognized. These are based particularly on features of thallus structure, procarp position and form of tetrasporangia. Probably two distinct lines of evolution are also represented with the Crouanieae having arisen independently of the Antithamnieae and Heterothamnieae. Heterothamnieae very likely evolved as an offshoot from the Antithamnieae line of development due to specialization in reproductive features, while Antithamnieae has developed greater organization of thallus structure.

Genera included in the tribes are:

Crouanieae Schmitz	Crouania J. Ag.
	Gattya Harvey.
	Gulsonia Harvey.
	Ptilocladia Sonder.
	Euptilocladia nov. gen.
Antithamnieae Hommersand	Antithamnion Naeg.
	Platythamnion J. Ag.
	Acrothamnion J. Ag.
	Ballia (Ag.) Mont.
	Macrothamnion nov.gen.

Heterothamnieae nov. tribus.

Antithamnionella Lyle
Heterothamnion J. Ag.
Tetrathamnion nov. gen.
Perithamnion J. Ag.
Trichothamnion nov. gen.
Trithamnion nov. gen.

(Note: — Warrenia and Bracebridgea (southern Australia) and Grallatoria (Bahamas) are included by Hommersand in the Antithamnieae. The former two genera are insufficiently known for inclusion in this review).

VIII. FEATURES AND COMPARISON OF TRIBES (CROUANIEAE, ANTITHAMNIEAE AND HETEROTHAMNIEAE).

CROUANIEAE Schmitz.

The Crouanieae includes genera having:

(1) a thallus consisting of an articulate axis either of prostrate and erect parts or erect with holdfast and with or without rhizoidal cortication. Each cell of these axes bears a whorl of 3 or 4 whorl-branchlets each cell of which bears a whorl of 2-3 (-4) cells from its outer end. A short chain of 2-10 cells develops terminally. Thallus branching may be monopodial or sympodial. In Crouania lateral branches arise, as in normal branching of monopodial species, from the basal cell of a whorl-branchlet. Also new sympodially-developed axes arise as distinct branches from axial cells near branch apices. Initials of these axial branches are formed above the whorl of branchlets on an axial cell. It is doubtful therefore whether this axial branch represents a fourth whorl-branchlet as suggested by Hommersand (1963, p. 331). This is particularly so as the three whorl-branchlets of the usual whorl are evenly-spaced in the normal way.

(2) Procarps are borne directly from axial cells close to branch apices and, after initiation of the procarps, axial elongation ceases (except in Ptilocladia australis which probably represents a primitive form). The procarp consists of a 4-celled carpogonial branch borne on a supporting cell which probably represents the basal cell of a whorl-branchlet but which does not produce further vegetative cells. This is suggested by occasional production of modified branches on the supporting cell in Ptilocladia vestita. Carpogonial branches are formed by almost simultaneous divisions of a rounded initial cell and although they curve upward when mature, could scarcely be described as "recurved" or "curved in a hook" as described by Hommersand (1963, p. 331).

(3) Spermatangia are terminal on the final cells of whorl-branchlets.

(4) Tetrasporangia are sessile on cells of the whorl-branchlets and are spherical and tetrahedrally divided (reported as cruciate for Crouania attenuata by Feldman-Mazoyer (1940) but previously reported as tetrahedral by Harvey(1846-1851)).

ANTITHAMNIEAE Hommersand.

On the basis of structure and phylogeny genera placed by Hommersand (1963) in Antithamnieae fall into two groups. Cohsequently a new tribe Heterothamnieae, has been separated from Antithamnieae. Genera remaining in the Antithamnieae are characterized by:

(1) A thallus of prostrate and erect parts or of an erect axis usually corticated densely with rhizoids and attached by means of a fibrous holdfast. Whorl-branchlets (usually in the form of pinnae) are in

whorls of 2, 3 or 4 from each axial cell and are usually simple or distichously branched with a distinct rachis.

(2) Procarps (4-) 8-20 are borne successively on the basal cells of whorl-branchlets at branch apices which cease to elongate after initiation of the carpogonial branches. Whorl-branchlets (pinnae) bearing procarps consist of an elongate chain of cells, sometimes with pinnules developed also. Only one carposporophyte matures at each branch apex. Hommersand (1963 p. 332 and 330) states that procarps in Antithamnion and in other primitive genera "are borne at intervals along the branches of unlimited growth", and in his tribe description, states "procarps not terminalized". These statements are misleading, as in all species of Antithamnion and all other genera (except Ballia for which procarp position is not known) the procarps occur at a reduced branch apex which ceases further elongation with the development of carpogonial branches. Carpogonial branches are formed by successive divisions of an initial cell in which the outer newly-formed cell enlarges prior to each division.

(3) Spermatangia are borne on special branches usually on the inner part of whorl-branchlets.

(4) Tetrasporangia are borne either directly on cells of whorl-branchlets or their branches, or on special branches usually on the inner part of whorl-branchlets and are ovoid or spherical and cruciately divided.

<u>HETEROTHAMNIEAE</u> nov. tribus.

Thallus sine pede retinente, saepe rhizoideis ad textum hospitis adfixus. Axes non corticato. E quoque cellula vortico-ramuli 2,3,4, aut 5, plerumque verticibus sequentibus cellularum ramosi, in thallo inferiore saepe redacti. Cellulae glandulosae adsunt. Tetrasporangia cruciato-tetrahedralia. Procarpi 1-3 (-4) in ramulis redactis (saepe 2-cellulatis) in cellulis axialibus prope cacumina ramorum positi. Carposporophyti globis rotundatis carposporangiorum, globo terminale primum crescente, instructi.

Heterothamnieae is based upon <u>Heterothamnion</u> which is a well-established genus representative of the tribe in all main features of thallus and reproduction. Distinctions between this group and the Antithamnieae are discussed in reference to the phylogeny of each group. The genera included in this tribe are separated from Antithamnieae on the following features:

(1) Thallus occasionally of prostrate and erect systems but usually of erect parts only which have axes without rhizoidal cortication. Attachment to the host usually involves some penetration by rhizoids between cells of the host tissue. There is no fibrous holdfast as occurs in Crouanieae and Antithamnieae. Whorl-branchlets, in whorls of 2-5, may be simple or branched, but are seldom distichous (in the form of a pinna) as in the Antithamnieae. They usually consist of whorls of 2-3 cells formed from the outer end of each successive cell and terminate in a short chain of 2-4 small cells. This form of branching

is comparable to that of the Crouanieae. Whorl-branchlets are often reduced in size and branching towards the base of the axes.

(2) A total of 1-3 (-4) carpogonial branches are formed on the basal cells of whorl-branchlets reduced to 2 (occasionally several) cells in length, borne on the second to fourth axial cells of very much reduced branch apices. The fertile whorl-branchlet usually consists of the basal (supporting) cell and one further cell which is much reduced in size. Axial cells of the fertile apex are much smaller than those of the normal thallus axes, and growth is usually continued by lateral branches produced below the axial cells bearing procarps. Carpogonial branches, as in Antithamnieae, are 4-celled and formed by similar successive divisions of the initial cell.

(3) Spermatangia, as in Antithamnieae, are borne on special branches towards the base of the whorl-branchlets.

(4) Tetrasporangia are usually spherical and borne directly on cells of the whorl-branchlets (on special branch in Perithamnion). In form they appear to have been tetrahedrally divided even when division is really cruciate.

Comparison of Tribes: — In summary, the three tribes are distinguished by the combination of features set out above. The most significant single feature of separation is the position and arrangement of procarps and this alone is probably sufficient to separate the groups. Relative taxonomic use of various features in separation of tribes, genera and species has already been discussed (Section IV) while features characteristic of individual tribes are enlarged upon in Sections VIII and IX.

Key to the Tribes Crouanieae, Antithamnieae and Heterothamnieae

1. Procarps (1-several) borne in place of whorl-branchlets directly on axial cells near branch apices. Whorl-branchlets in whorls of 3 or 4, branched by whorls of 2-4 cells from the outer end of each successive cell. Gland-cells usually absent, or, occasionally present and ovoid with crystal-like inclusions. Spermatangia terminal on final cells of whorl-branchlets... ... ... Crouanieae

1. Procarps (1-20) borne on basal cells of whorl-branchlets (usually reduced to 2 cells in length in Heterothamnieae) on axial cells near branch apices. Whorl-branchlets in whorls of 2-5 either unbranched, pinnately branched or branched by whorls of cells (as in Crouanieae). Gland-cells present (except in Ballia spp. and Trichothamnion planktonicum), usually prominent, densely homogenous or apparently porous without crystal-like inclusions. Spermatangia on special branches on whorl-branchlets.... 2

2. Procarps developed successively on basal cells of pinnae (4-) 8-20 occurring at each branch apex (unknown for Ballia). Whorl-branchlets distichously branched or unbranched. Tetrasporangia cruciately divided.. ... ...Antithamnieae

2. Procarps borne on basal cells of much-reduced (2-4 cells) whorl-branchlets, 1-3 (-4) occurring on one (or two) axial cells at much reduced branch apex. Whorl-branchlets usually not distichously-branched (except occasionally in species of Antithamnionella and Trithamnion). Tetrasporangia tetrahedrally divided or, if cruciate, usually appear to have been tetrahedrally formed..Heterothamnieae

IX. CROUANIEAE

Key to the Genera of Crouanieae.

1. Whorl-branchlets in whorls of 3. All lateral branch initials forming a chain 10-20 cells long before initiation of whorl-branchlets. Tetrasporangia on basal cells of whorl-branchlets. Carposporophyte developed in club-shaped branch apices with the first gonimolobe developed terminally on a rounded central cell... 2.

1. Whorl-branchlets in whorls of 4. Lateral branch initials 2-5 cells long before initiation of whorl-branchlets (except *Gulsonia*) Tetrasporangia on basal and/or outer cells of whorl-branchlets (never on basal cells only). Carposporophytes lateral on long or short branches with the first gonimolobes developed laterally on a transversely elongate central cell... ... ... 3.

    2. Axes of thallus terete. New axes formed sympodially and unilaterally at branch apices ... ... *Crouania*

    2. Axes of thallus flattened. Axial branching sympodial and bilateral forming pinnated thallus segments.. ... *Gattya*

3. Axes of thallus terete with more or less alternate-distichous arrangement of indeterminate lateral branches (irregular in *Ptilocladia australis*); determinate short branches scattered irregularly over thallus (absent in *P. australis*). 4

3. Axes of thallus flattened with indeterminate and determinate branches alternately-distichously arranged.. ... ... *Euptilocladia*

    4. Thallus spongiose and somewhat firm (flexuous in *Ptilocladia australis*). Branch initials 2-5 cells long before initiation of whorl-branchlets.... ... ... *Ptilocladia*

    4. Thallus slimy-mucilaginous and flexuous. Branch initials 10-20 cells long before initiation of whorl-branchlets. *Gulsonia*

Characteristics of Crouanieae.

The genus Crouania was established by J.G. Agardh (1842) for the Mediterranean species Crouania attenuata (Bonnem.) J. Ag. which became the type species of a genus well represented in the southern Australian region. J. Agardh (1876) presented a key to the species of Crouania recognized at that time and which comprised 6 species from southern Australia and 2 from Europe. The southern Australian species included by J. Agardh were, Crouania gracilis J.Ag., C. australis (Harv.) J. Ag., C. muelleri Harvey, C. vestita Harvey, C. wattsii Harvey, C. agardhiana Harvey and C. insignis Harvey. No further species of the genus from southern Australia have been described until the present study. Several of these species listed by J. Agardh (1876) have now been removed to various related genera. Crouania wattsii was taken by Schmitz as the type species for his genus Muellerena and later De Toni (1897) transferred both Crouania agardhiana and C. insignis to this genus. Hommersand (1963) separated M. insignis as a new genus Gulsoniopsis.

The present survey embraces a detailed morphological and taxonomic investigation of these species together with species of the closely related genera Gattya Harvey (1854), Ptilocladia Sonder (1845), Gulsonia Harvey (1855) and includes also several previously undescribed species. Muellerena wattsii (Harvey) Schmitz appears to be distinct, particularly in development of the carposporophyte, and has for the present been left in the Dasyphileae.

No fresh collections of Crouania gracilis J. Ag. have been available and a detailed investigation of this species awaits suitable material for further study. C. muelleri shows features of reproduction and gland-cell development more closely resembling those of the Heterothamnieae.

Diagram 1 (p.358) sets out the groupings of species into genera following detailed investigation of fresh material.

Each species has been compared with Crouania attenuata, the type species of the genus, taking mainly the description of this species given by Feldmann-Mazoyer (1940) as a basis for comparison. Southern Australian species fall firstly into two groups — Group A which has sympodial branching and Group B which develops monopodially.

Features of comparison used in grouping of Species.

Features discussed here have been selected as those of greatest taxonomic use particularly in grouping of species into genera. Significant features consist mainly of variations in detail of structure and development within the following characteristics, which are common to all species of the group:

(1) Plant Form:

(a) All species have a uniaxial, articulate axis each cell of which bears an evenly-spaced whorl of 3 or 4 whorl-branchlets and axial growth occurs by transverse divisions of a dome-shaped apical cell.

(b) Cortication of axis occurs in most species and consists of the downward development of rhizoidal filaments and occasionally (e.g. Ptilocladia vestita and Euptilocladia spp), upward and downward extension of the whorl-branchlets. Axial cortication is never cellular.

(2) Reproduction:

(a) Procarp and Carposporophyte:- upwardly curved, 4-celled carpogonial branches initiated near branch apices and borne on the outer part of a supporting cell developed on an axial cell in place of a whorl-branchlet. A single auxiliary cell is cut off from the upper part of the supporting cell and divides transversely to produce a smaller inferior foot-cell and a larger superior central cell. Rounded, successively-developed, groups of carposporangia are protected by the surrounding whorl-branchlets which may elongate due to elongation of the individual cells. No special involucral structure is formed.

(b) Tetrasporangia: — Sessile on cells of whorl-branchlets. Usually tetrahedrally divided and scattered in younger parts of the thallus.

Detail of spermatangial development is omitted because insufficient material is available for significant comparison.

Individual features used in separating genera and species: —

A. Vegetative Features.

1. Plant Form and Habit: — Species belonging to Crouanieae are usually erect plants only occasionally showing a tendency towards a prostrate habit e.g. *Gattya pinnella* and *Crouania shepleyana*. This is in direct contrast to some genera of Antithamnieae and Heterothamnieae in which species show a well-developed prostrate system from which the erect branches arise. Only two species, *Crouania mucosa* and *Gulsonia annulata*, are distinctly mucilaginous and this feature, used by J. Agardh (1842) in the type description for the genus *Crouania*, cannot be retained as a useful generic character. In spite of the spongiose southern Australian species (e.g. *Crouania australis*, *C. vestita*) later added to the genus, Kylin (1956) still used the gelatinous nature of the thallus as a generic character for *Crouania*. J. Agardh (1876) remarked on the spongiose character of species from Australia.

Flattening of the thallus is distinctive of the genera *Gattya* and *Euptilocladia* and is associated with a high degree of thallus organization. The terete form is, however, characteristic of most species within the group.

2. Branching: — Lateral branching shows several trends of possible phylogenetic significance which can be broadly interpreted as representing two lines of development each leading toward a more highly organized thallus structure:

(i) The tendency toward the development of a sympodium.

(ii) The gradation from a completely irregular initiation of lateral branches to a more or less defined development, usually from about every fourth cell of the axis. With this is coupled a tendency toward an alternate-distichous arrangement of lateral branches. There is also an increasing tendency toward the production of short, determinate, often unbranched, branches between the long indeterminate laterals. These features reach their greatest development in *Euptilocladia* where both determinate and indeterminate laterals are distichously arranged at more or less regular intervals from the edges of the flattened axis.

Firstly, both monopodial and sympodial branching occurs within the group and in both forms there is a tendency toward a cessation of axial elongation. In monopodial growth the main axes continue to elongate and lateral branches are comparatively slow in development (e.g. *Ptilocladia vestita* and *Ptilocladia pulchra*) thus giving rise to a pyramidal thallus form. Short determinate lateral branches, distinct from the whorl-branchlets also occur in all species of *Ptilocladia* (except *P. australis*) and *Euptilocladia*.

Sympodial branching appears to be developed from a monopodial system in which the main axes, rather than lateral branches, are limited in elongation. The irregular, lax branching habit of *Crouania shepleyana* occasionally develops sympodial branching of a partial, supposedly-primitive form in that occasionally axial dominance of a lateral branch occurs when it takes over from a main axis. This is the usual form of branching found in *Crouania mucosa* and it is common for several lateral branches, initiated near the apex of a main axis, to become dominant. In *Gattya pinnella* there is a high degree of thallus organization with a definite, almost consistent, regular sympodial branching pattern. New, alternate, pinnately-arranged branches develop from a succession of axial branches which have been overtopped alternately to right and left by lateral branches developed at approximately equal intervals. The possibilities of phylogenetic upgrades and downgrades within this series are discussed later with reference to other features of possible evolutionary significance.

The gradations, within Crouanieae, from irregular to somewhat regular distichous - alternate branching is developed in both the monopodial and sympodial forms of thallus development.

In Ptilocladia australis the branching is irregular and the lateral branches form comparatively long, lax axes without the development of short intermediate determinate laterals. Carposporophytes are produced at intervals along the axes, without inhibition of axial growth even in association with carpospore development. Other southern Australian monopodially developed species all show some limitation of lateral growth and, except for Ptilocladia agardhiana and Gulsonia annulata which are usually irregularly branched, show a gradation from Crouania attenuata through Group B (Diagram 1) to Euptilocladia villosa in the development of an alternate-distichous lateral branch arrangement. This is well represented in Ptilocladia vestita and Ptilocladia pulchra and occurs strongly in Euptilocladia. This character may be linked with a spiral rotation of 45° and 90° respectively in whorl-branchlet initiation in the two genera. Any tendency toward sympodial branching has not been mentioned for Crouania attenuata by previous authors. The figures of Newton (1931 p. 393) however, suggest branching similar to that found in the southern Australian species.

3. Initiation of Branches.

Two forms of young branch development occur within Crouanieae,

(a) An elongate form in which the branch initial divides transfersely to form a chain of up to 20 cells before whorl-branchlet initiation commences, and in which the whorl-branchlets are slow in growth and do not cover the growing point until the branch is well protruded beyond the mature whorl-branchlets of the main axis. This form is found in the three southern Australian species of Crouania, in Gattya pinnella, in Crouania attenuata and in Gulsonia annulata.

In southern Australian species, therefore, this character is found in the group in which sympodial development can occur, with Gulsonia as the only exception. Gulsonia is intermediate between the sympodial and monopodial groups in some other characters also.

(b) A short form of branch development in which only a few axial cells are formed before whorl-branchlets are produced. These are again produced in spiral sequence, but develop comparatively rapidly so that the apical cell of the axis is covered and protected by the young whorl-branchlets.

In both forms the young whorl-branchlet initials develop from a protrusion of the axial cell which becomes cut off to form the new branch initial. The whorls of cell branches of the whorl-branchlet are developed successively from the apex of the previously formed cell, so that the whorls are not true di-, tri- or quadri-chotomies and only appear as such when fully developed.

In all species, except Gattya pinnella, lateral branches are developed from the outer end of the basal cell of a whorl-branchlet. Hommersand (1963) suggests that short laterals bearing carposporophytes in Gulsoniopsis insignis may occur on the "supra-basal" cell, but no evidence of this has been found in further investigation of the species. In the sympodially branched group (e.g. Crouania mucosa, C. shepleyana) branches destined to become new main axes are produced directly from the axial cells and occur just above the whorl of whorl-branchlets and are additional to these branchlets. In this way it is easy to determine which branches will become part of the sympodium and which will remain as true lateral branches. In Gattya pinnella all branch initials develop directly on the axis as an additional branch above the whorl. Possible phylogenetic significance may also be attached to this character and is discussed below.

Feldmann-Mazoyer (1940) and Wollaston and Womersley (1959) used the position of initiation of lateral branches of indeterminate growth in separating Crouania and Gulsonia (Crouaniopsis). Details are not available for Crouania attenuata, the species upon which Feldmann-Mazoyer based her comparison, but since branch initials occur both on the basal cells of whorl-branchlets and directly on axial cells in southern Australian species of Crouania, this feature cannot be retained as a character of separation at the generic level.

4. Whorl-branchlets.

These are initiated spirally in all species. Hommersand (1963, p. 171) has placed some significance on the order of development in relation to lateral branch initiation for Gulsoniopsis insignis (≡ Ptilocladia pulchra); he describes the alternate-distichous arrangement of lateral branches which are produced on each 4th axial cell, as consequent upon their initiation from the first-developed branchlet of a whorl; this branchlet is spirally rotated on successive axial cells. Certainly the rotation of 90° on adjacent axial cells in Euptilocladia is responsible for the apparent "orthostichous" arrangement of the whorl-branchlets referred to by Hommersand, but is not here considered sufficient evidence for removing the genus from this group. Three whorl-branchlets are developed in all southern Australian sympodially-branched species, and four in the monopodial species. It is impossible to compare the initiation pattern of a three-branch whorl with the situation found in the Rhodomelaceae, as there are no two opposite initials. Initiation must, therefore, be in a simple spiral sequence. In all monopodial species, in which four whorl-branchlets are formed, a similar spiral sequence of initiation occurs.

The terminal cells of the whorl-branchlets may or may not divide transversely to give a short chain of small cells. In the monopodially developed species of the group there is a tendency towards the development of a short terminal chain, which becomes well developed in Euptilocladia (up to 10 cells in length). In the sympodial group of species there is usually a single terminal cell to each final branch of the whorl-branchlet and seldom more than two cells in the chain. In Gattya pinnella the terminal cells are embedded in a firm gelatinous matrix which forms a distinct outer layer over the thallus, and which can be easily separated from the inner thallus structure.

5. Cortication.

Axial cortication in Crouanieae is characteristically of rhizoidal filaments and this feature has been used in classification of the Ceramiaceae (Schmitz and Hauptfleish 1897, p. 484).

In all species where axial cortication occurs it is built up from elongate, sometimes branched, multicellular rhizoids borne on the lower part of the basal cells of whorl-branchlets. The degree of cortication varies greatly, but is always more densely developed towards the lower parts of the plant and often forms a dense interwoven mat completely masking the annular appearance of the thallus. This rhizoidal development contributes largely to the spongy texture of those species in which it is strongly developed (e.g. Ptilocladia vestita).

In Ptilocladia vestita and Euptilocladia spp. there is also an elongation of the whorl-branchlets in the plane of the axis in the lower parts of the plant. Where this occurs the thallus is given added rigidity, so that the branching pattern becomes more readily recognized.

Ptilocladia agardhiana and P. pulchra develop a more complex arrangement of rhizoids. In both species the rhizoidal filaments consist of larger upper cells and narrower more elongate cells further away from the point of attachment. The smaller cells overlie the shorter, broader cells and in this way two distinct layers occur. Short horizontal, unbranched projections of several small cells in length extend outward from the rhizoid cells. This arrangement of cortical filaments together with the horizontal projections is also found in the Dasyphileae.

In Crouania shepleyana, Ptilocladia australis (except var. cortica) and Gattya pinnella rhizoids occur mainly as attachment organs.

6. Gland-cells.

Wollaston and Womersley (1959) describe pyriform gland-cells for Gulsonia annulata and these, they note, could represent the "monospores" referred to by Schmitz and Hauptfleish (1897). No other reference to gland-cell-like structures within this group is known. In G. annulata they are borne on the inner cells of the whorl-branchlets, but in Ptilocladia australis and P. vestita, in which similar gland-cells are found, they occur in place of one of the cells of the final branching of the whorl-branchlets.

These gland-cells are unicellular with a thick wall and enclose crystal-like bodies of various but definite forms. The axial cells of Ptilocladia agardhiana and P. pulchra, particularly in the younger parts of the plant, contain similar crystal-like inclusions. The function of such gland-cells is unknown, but the presence of similar inclusions in axial cells of some species suggests that their formation may be in some way associated with accumulation of substances either as storage or waste products.

The gland-cells of *Antithamnieae* and *Heterothamnieae* are structurally different. They are cut off laterally from cells, are apparently densely homogeneous (or diffuse with small pores) and never contain obvious inclusions.

B. *Reproductive Features.*

1. *Tetrasporangia:* --

In all species of *Crouanieae* the tetrasporangia are sessile on the upper side (usually toward the outer ends) of cells of the whorl-branchlets, and are usually developed successively. All are divided tetrahedrally by simultaneous divisions starting at the periphery of the tetrasporangium and extending toward the centre. Feldmann-Mazoyer (1940) reports cruciate division for *Crouania attenuata*. This is not consistent with the pattern of division found in the southern Australian species, but may have developed independently in the European region. Harvey (1846-51) describes tetrasporangium division in this species as "tripartite" and his figure shows distinct tetrahedral division. Newton (1931) also states and figures tetrahedral division of tetrasporangia for *C. attenuata*. Hommersand (1963) reports cruciate arrangement of spores in *Ptilocladia pulchra*, although divisions are simultaneous. It is thus necessary to observe actual stages of division to distinguish between cruciate and tetrahedral division.

Sympodial species, including Gattya pinnella, all produce tetrasporangia from the basal cell of the short branch. In the monopodial species, however, there is a tendency (excluding Gulsonia) for tetraspore initiation to occur on cells progressively further removed from the base of the whorl-branchlet.

Gulsonia annulata is again intermediately placed in respect to this feature.

2. Development of the Carposporophyte.

The development of the carposporophyte follows a characteristic pattern and varies only in comparatively minor, although possibly taxonomically useful, features:

(a) Position: — In all species the carpogonial branches are produced close to the apex of a branch. In the sympodial species there is no further elongation of the axis and the carpospore groups appear to develop "terminally". Further growth takes place from a lateral axial branch initiated below the fertile branch apex. The cells of the surrounding whorl-branchlets enlarge slightly, and the branches grow upward surrounding the carposporophyte and a more or less club-shaped branch apex is formed.

In the monopodial species the carpospore groups are formed on determinate lateral branches. Actually the carpogonial branches are again borne a few cells from the branch apex, but after initiation, branch elongation becomes limited and further development of the branch ceases.

In most species a succession of carpogonial branches is produced from axial cells before branch growth is arrested, but only one, usually the first formed, develops Due to this limited continuation of branch elongation the short, carpospore-bearing branches vary in length and form in respective species. In Group B (Diagram 1) there again appears to be a gradation towards the production of shorter branches. Ptilocladia australis shows no limitation of branch axes after the initiation of the carpogonial branch, and mature carposporophytes are developed successively along the axes. In P. vestita the branch axis elongates for some distance while in P. agardhiana, P. pulchra and Euptilocladia there is very little elongation.

In Gulsonia annulata the branch bearing the carposporophyte is modified due to almost complete cessation of growth above the carpogonial branch initials. No whorl-branchlets are produced beyond the carpogonial branches and the terminal cells of the fertile branch remain immature in form. As carpogonial branches are produced early in the development of the branch, it always remains short and somewhat specialized in form.

In all species some protection for the carposporophyte is formed simply by elongation of the surrounding whorl-branchlets. No special involucral structure is formed.

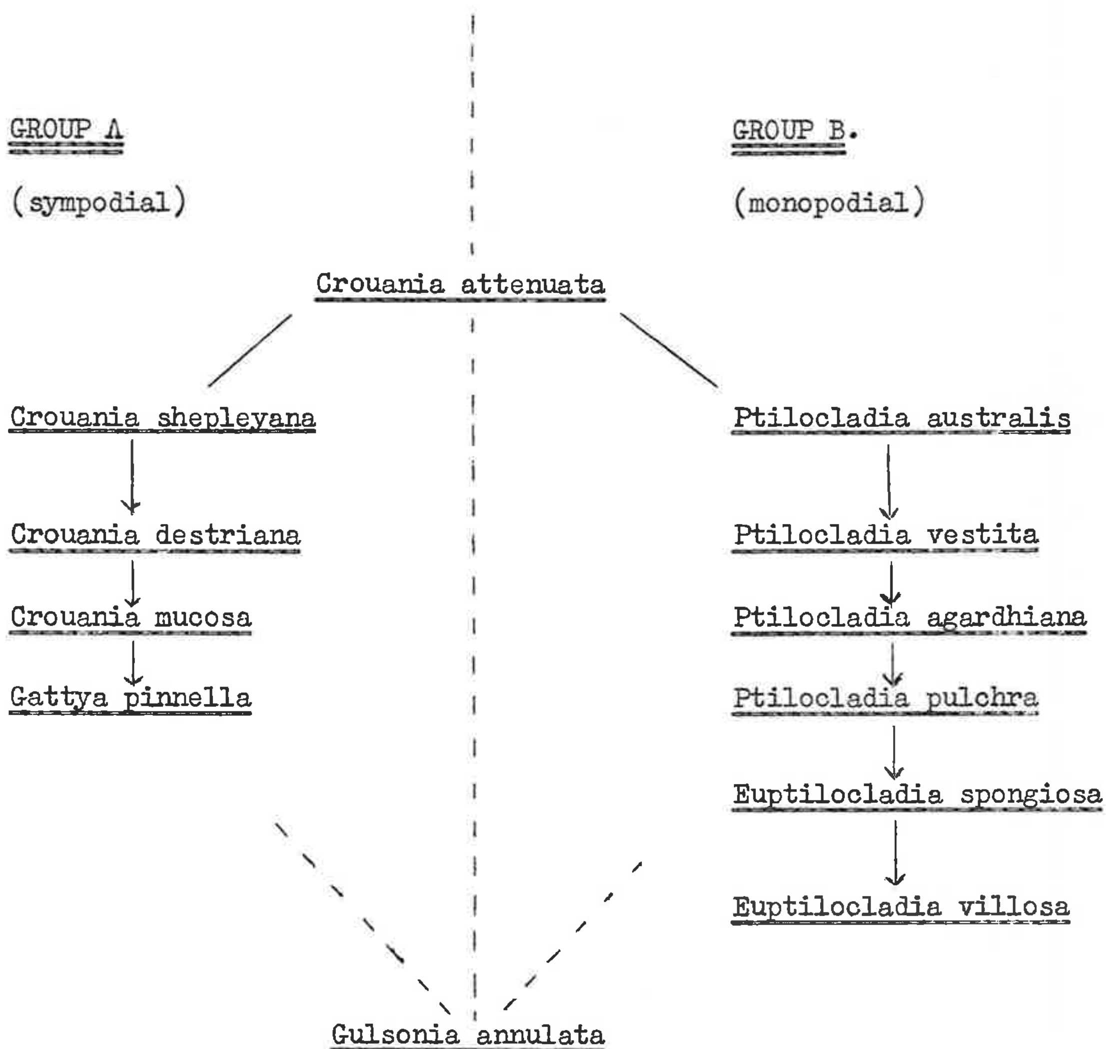
(b) Carposporophyte:

The carposporophyte varies mainly in the extent of fusion between cells, in the form of the central cell and in the position of the first-formed carpospore groups.

Fusion between cells of the carposporophyte is greater in the monopodial species, except Gulsonia, than in the sympodial species. In Gattya pinnella and species of Crouania there is fusion between the axial cell and the residual supporting cell while further fusions may or may not develop. Stronger fusions develop in the monopodial group and it is usual to find a fusion also between the residual supporting cell and the foot-cell. These fusions are particularly well developed in Ptilocladia agardhiana. Widening of pit-connections occurs commonly, but it is usually difficult to distinguish whether an actual fusion has taken place with complete breakdown of membranes separating the cells. Gulsonia annulata shows a widening of the connections between cells but there are seldom marked fusions between cells as sometimes occur in Ptilocladia agardhiana and P. pulchra.

The central-cell may be rounded in form as in the sympodial group of species, or elongate as in the monopodial species. The rounded form develops the first gonimolobe in a terminal position while in the elongate form lateral carpospore groups are produced first.

DIAGRAM I. Grouping of species of Crouanieae based on comparison with Crouania attenuata.



NOTES ON DIAGRAM I.

The features discussed above and summarized in Diagram I form the basis for the classification of the group.

All previously recorded plants (except Gattya, Gulsonia and Euptilocladia) were originally placed in the genus Crouania.

Broadly the southern Australian species thus fall into two main groups which are tabulated to the left and right respectively of Crouania attenuata. Species in the group to the left (Group A) show similarities in: —

1. A tendency towards a sympodial form of branching in which axial growth ceases at intervals and further elongation takes place by means of main lateral branches developed directly from the axial cells above the normal whorl (in contrast to lateral branches borne on the outer ends of the basal cells of whorl-branchlets). These occur occasionally in Crouania shepleyana, more or less consistently in C. mucosa and show a high degree of organization in Gattya pinnella. In this species all lateral branches (of both axial and irregular form) are initiated directly from the axial cells and the sympodium formed is regular, distichous and pinnately-branched. In all species the new branch initials are elongate in form.

2. The development of a whorl of three whorl-branchlets from the upper part of each axial cell. These branches in each plant are themselves di- tri- or quadri-chotomously branched from the outer end of each cell with whorls of progressively smaller cells toward the exterior. In Gattya the terminal cells are firmly embedded in a gelatinous matrix to form a distinct outer sheath over the thallus.

3. Axial cortication, where developed, of sparingly branched multicellular downwardly projecting rhizoids from the basal cells of the whorl-branchlets. In _Crouania shepleyana_ and in _Gattya pinnella_ these are developed mainly as attachment organs from the basal parts of the plant and in both species there is a prostrate part of the lower thallus.
4. Tetrasporangia are borne on the basal cell of the whorl-branchlets. In those species to the right (Diagram I) tetrasporangia are borne progressively further out on the whorl-branchlets.
5. The carposporophyte in each case is similar in:
   (a) its close to terminal position when mature, surrounded by upwardly directed whorl-branchlets to form a blunt club-shaped apex to the branch axis. Further axial growth takes place from a lateral branch developed below the carposporophyte.

   (b) A similar pattern of fusions between the cells of the carposporophyte. These are never predominant and may or may not occur. There is usually a widening of the connection between the axial and residual supporting cells but seldom any further fusions.

   (c) The central cell is rounded and develops the first gonimolobe in a terminal position. In all species in Group B the gonimoblast cell is elongate and produces the first carpospore buds laterally.

In all these features (except in axial cortication which is basically similar throughout the tribe) the four species of Group A are distinct from species of Group B. _Ptilocladia australis_ is an exception in Group B with its irregular, lax form of branching; in other features, however, it resembles Group B more closely than Group A. An organized distichous habit such as is developed in Gattya may develop along with greater thallus organization in both developmental lines.

Crouania attenuata, as described by Feldmann-Mazoyer (1940), shows close similarity with Group A. In branching habit there is, however, no mention by Feldmann-Mazoyer or other authors of a tendency toward sympodial thallus development although position of lateral branch initiation is described as direct from the axis. This suggests that new axial branches are probably developed and, because they occur near axis apices, are those most likely to have been observed. The diagram given by Newton (1931) of the thallus structure of C. attenuata also indicates a probable similarity in branching habit to the southern Australian group.

C. attenuata also apparently differs from the southern Australian group in having the first carpospore buds developed laterally. Feldmann-Mazoyer does not mention this in her description, but her figure (1940 p. 196) definitely indicates this condition.

Crouania shepleyana, C. destriana and C. mucosa thus fall reasonably naturally into the genus Crouania, but differ from one another sufficiently in form, degree of sympodial development, proportion of axial cortication, and size of tetrasporangia to be regarded as distinct species.

The present monotypic genus Gattya differs from the other three species in its flattened, highly-organized thallus structure and well-defined sympodial development and, on the basis of these features, is retained as a separate genus. Thallus organization is taken to include, as well as the flattened form and pinnate sympodium, the development of a distinct outer layer of cohering cells, the distichous branching and the stabilization of one position of lateral branch initiation.

Species of Group B (excluding Gulsonia which will be dealt with separately) show a series of gradations in features rather than a group of well-defined characteristics as occurs in Group A. This gradation follows from

Ptilocladia australis ⟶ P. vestita ⟶ P. agardhiana ⟶ P. pulchra ⟶ Euptilocladia spp.

Thallus development is monopodial and lateral branches with axial initials formed of short chains of cells are produced from the basal cells of whorl-branchlets. Fusions between cells of the carposporophyte are often strongly developed and the first carpospore buds are lateral. A gradation also occurs in –

(1) A tendency towards the development of an alternate-distichous branch system with long laterals developed at regular intervals and short determinate laterals produced between the longer ones.

(2) Elongation of terminal filaments of whorl-branchlets from 2-3 cells in Ptilocladia australis to about 10 cells in Euptilocladia spp.

(3) More elaborate axial cortication with the elongation of whorl-branchlets parallel to the axes in Ptilocladia vestita and Euptilocladia, differentiation of cells of the rhizoids to form two layers in Ptilocladia agardhiana and P. pulchra and production of short horizontal projecting filaments from the rhizoids in P. agardhiana and P. pulchra.

(4) Position of tetraspore initiation from inner to outer cells of whorl-branchlets.

(5) A gradation towards earlier cessation of axial elongation in laterals bearing carposporophytes, so that the mature carpospore groups occur progressively closer to the apex of short lateral branches.

These characteristics present a group of gradually changing features. The group also presents a number of consistently similar features in a terete, spongiose thallus, monopodial branching, the position of initiation of lateral branches, the "short" form of lateral initials, whorls each consisting of four whorl-branchlets, tetrahedral division of tetrasporangia and similar carposporophyte development. On the basis of the consistency of these characteristics it is proposed to unite all these species, with the eexception of Euptilocladia, into the one genus, which on a basis of priority must revert to Ptilocladia with P. pulchra Sonder as the type species. Euptilocladia, with two species, is sufficiently distinct to be regarded as a separate genus. The plant form is highly organized, particularly in the form of whorl-branchlets which produce the flattened axis, in distichous branching from the edges of the axis (seen in both indeterminate laterals which are more or less regularly alternately spaced and in short determinate lateral branches) in the form of lateral branch initial, and in having rhizoids, forming an axial cortication, developed from other cells besides the basal cells of the whorl-branchlets.

In main features, however, it corresponds with the Crouanieae and is rightly placed in this tribe.

The genus Gulsonia, with one Mediterranean and one southern Australian species, is intermediate between Crouania and Ptilocladia, in a number of features.

It is distinct however, in its very specialized form of short, fertile branches bearing the carposporophytes and on the basis of this feature together with its other intermediate characters, is retained as a separate genus.

Possible Phylogenetic trends within the Crouanieae of southern Australia.

In Diagram I it has been shown that species of Crouanieae show probable developmental sequences along two lines — Group A which includes Crouania shepleyana to Gattya pinnella (the sympodial group) and Group B from Ptilocladia australis to Euptilocladia villosa (the monopodial group). This excludes Gulsonia annulata which is intermediate between the two groups.

This arrangement accepts increase in thallus organization as being probably phylogenetically more advanced.

Reversal of the direction of development in either line would involve a downgrade from a more highly-organized thallus to a comparatively less complex structure. This would be contrary to the generally accepted theory of phylogenetic advance from the primitive plant form and also to the hypothesis that the Crouanieae is the most primitive tribe of the Ceramiaceae which in turn is less advanced than other families of the Ceramiales such as Delesseriaceae and Rhodomelaceae in which there is comparatively greater thallus organization.

With the acceptance of an upgrade series along two lines, one sympodial and one monopodial, towards elaboration and stabilization of thallus structure a possible phylogenetic sequence can be set out as in Diagram 2 (page 368).

The main features are:

(1) A separation between the northern and southern species for convenience in consideration of the southern Australian group as an entity.

(2) Two strong lines of development one sympodial (*Crouania* - *Gattya*) and one monopodial.

(3) The inclusion of the genus *Gulsonia*, intermediate in characters between the two lines, as closely related to, but probably somewhat more highly developed than a common ancestor of the two lines.

Notes on the *Crouania - Gattya* line: —

This line is distinct in the following ways: —

1. Irregular sympodial branching ⟶ definite sympodium.
2. Terete axis (spongiose or mucous) ⟶ flattened axis.
3. Two positions of lateral branch initiation (*Crouania* spp.) ⟶ a single position only introduced in this line (*Gattya*) and not found in the monopodial species.
4. Lack of gland-cell development (gland-cells present in *Gulsonia annulata*).
5. Terminal initiation of first gonimolobe from a rounded central-cell.
6. Cessation of axial growth at branch apex bearing procarp. New axial branch produced below the fertile apex.
7. Tetrahedrally-divided tetrasporangia borne on basal cells only of whorl-branchlets.

These features suggest a direct phylogenetic line of development from the lax irregular form of *Crouania shepleyana* to the more highly organized thallus of *Gattya pinnella*.

Notes on the Monopodial line: —

Features characteristic of the group are: -

1. Monopodial axial growth.
2. A spongiose non-gelatinous thallus.
3. Irregular to more or less regular alternate-distichous branching.
4. All laterals (except in *Euptilocladia*) initiated similarly.
5. Gland-cells developed in some species.
6. Fusions between cells of the carposporophyte with lateral gonimolobes developed first from an elongate central-cell.
7. Indeterminate (*Ptilocladia australis*) to determinate growth of lateral branches bearing carposporophytes.
8. Tetrahedrally-divided sessile tetrasporangia borne on cells of the whorl-branchlets.

There is a division between species of this line in characters of cortication and in the presence of gland-cells. Two secondary lines of development incorporating these features can be visualised to develop from *Ptilocladia australis* and terminate respectively in *P. pulchra* and *Euptilocladia* species. *Ptilocladia australis* develops gland-cells which are carried on in *P. vestita*. Cortication in *P. australis* is of simple branched rhizoids, but *P. vestita* and *Euptilocladia* both have elaborate cortication including elongation of whorl-branchlets. In the other line *Ptilocladia agardhiana* and *P. pulchra* have developed a specialised rhizoidal cortication consisting of layers of filaments having large and small cells respectively.

Several features of this group are also found in the Dasyphileae as, for example: —

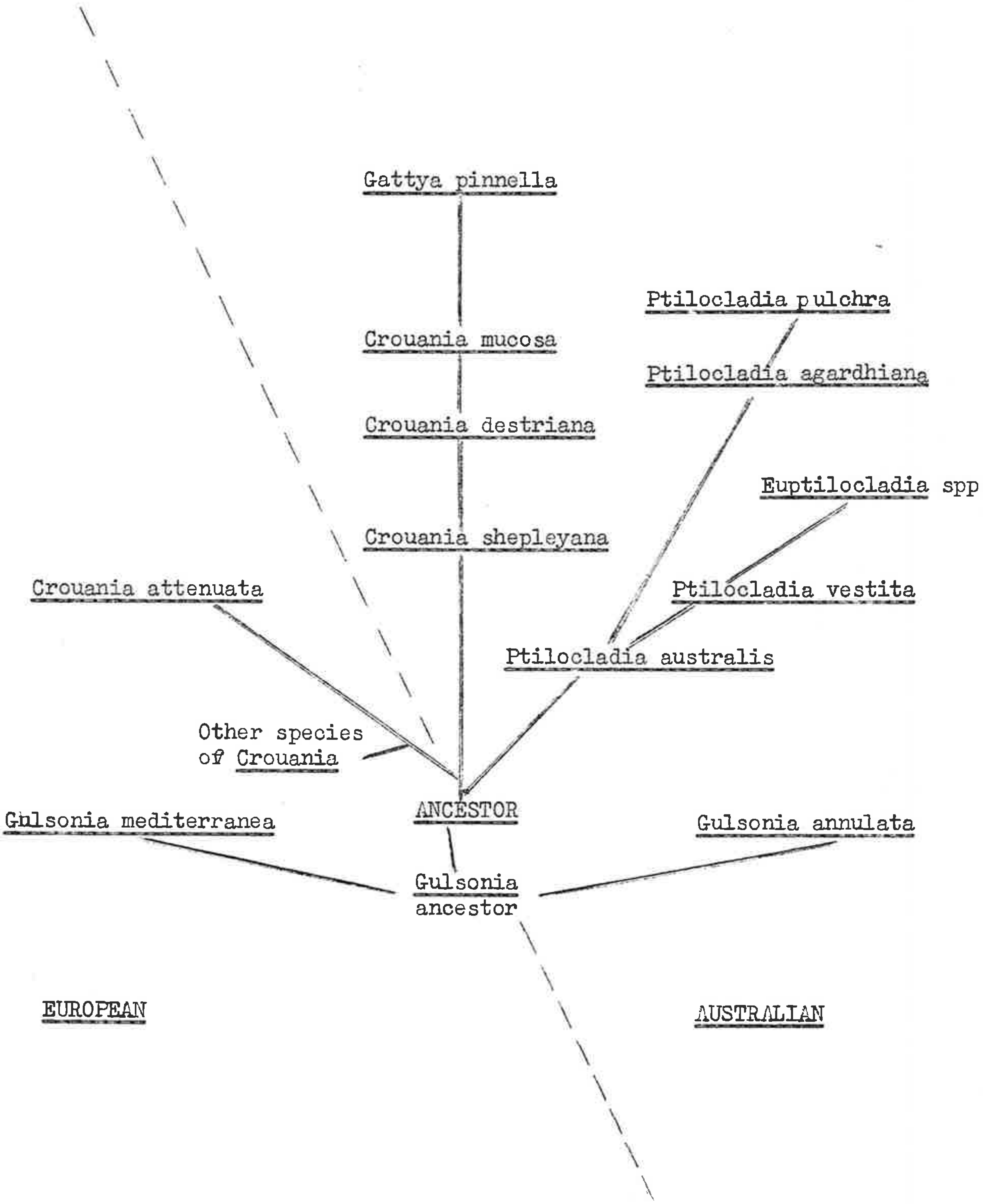
(1) Orthostichous arrangement of whorl-branchlets, as occurs in *Euptilocladia* and which is probably the result of a 90° or 180° rotation in position of initiation of branchlets (instead of the usual 45° rotation) on adjacent axial cells.

(2) Cortication similar to that found in *Ptilocladia pulchra* and *P. agardhiana*.

(3) Alternate-distichous branching (more regularly developed in the Dasyphileae).

A thorough revision of the Dasyphileae in relation to this group is necessary to clarify possible phylogenetic affinities of the tribes.

DIAGRAM 2. Possible Phylogenetic trends within the Crouanieae (Southern Australia).



X. ANTITHAMNIEAE AND HETEROTHAMNIEAE

Antithamnieae and Heterothamnieae are closely related and are here considered in relation to one another and separately from Crouanieae which has probably evolved independently.

The eleven genera included in Antithamnieae and Heterothamnieae clearly fall into two groups, both of which could have evolved from a common ancestor which was characteristically unstable and variable in form. In Antithamnieae there have been significant changes in thallus structure, while in Heterothamnieae evolution has occurred most pronouncedly in procarp position and carposporophyte development. Balakrishnan (1958) recognized this distinction when he wrote "species of *Antithamnion* are clearly divisible into two groups, (1) in which the procarp is borne on the basal cell of a fully developed branchlet (*A. plumula* (Ellis) Thur., *A. occidentale* Kylin, *A. tenuissimum* (Hauck) Sch.), (2) in which the fertile branchlet is reduced and is one to three cells long (*A. pacificum* (Harv.) Kylin and *A. spirographidis* Schiff.)".

A. spirographidis is here transferred to *Antithamnionella*.

Key to Genera of Antithamnieae.

1. Thallus consisting of prostrate and erect parts usually < 3 cm. high. Axes without rhizoidal cortication... ... ... 2.

1. Thallus erect 8-40 cm. usually with distinct fibrous holdfast. Axes densely corticated with rhizoids. (*Macrothamnion pectenellum* is sparsely corticated and up to 4 cm. high).... ... ... 3.

  2. Whorl-branchlets (pinnae) in 2's, equal and opposite on each axial cells Gland-cells on special short 2-4 celled branch. *Antithamnion*.

  2. Whorl-branchlets (pinnae) in whorls of 4 (occasionally reduced to 3) on each axial cell, equal or unequal. Gland-cells terminal on rachides of whorl-branchlets.... ... *Acrothamnion*

3. Whorl-branchlets in whorls of 4 (opposite pairs long and short respectively). Gland-cells sessile on rachides of whorl-branchlets. *Platythamnion*

3. Whorl-branchlets in whorls of 2 or 3 (or not whorled). Gland-cells absent or on special short branches... ... ... 4.

  4. Whorl-branchlets evenly-spaced in whorls of 3 (occasionally 2 in *Macrothamnion pectenellum*). Gland-cells on special short branches... ... ... *Macrothamnion*

  4. Whorl-branchlets distichously arranged in opposite pairs *or* with 1 long whorl-branchlet opposite 2 short whorl-branchlets *or* axial cells without whorls. Gland-cells absent.. *Ballia*

Genera and Phylogeny of Antithamnieae.

Three main lines of development occur in group A terminating respectively in *Platythamnion*, *Ballia* and *Macrothamnion*. *Acrothamnion* is probably not as highly evolved as the other three genera. It is unstable in thallus form and probably represents an actively developing line between *Antithamnion armatum* and *Ballia* spp. (Diagram 3, p. 377).

Platythamnion, *Ballia* and *Macrothamnion* have in common:

1. A large thallus with densely corticated axes attached by well-developed fibrous holdfasts. *Ballia* is the most specialized genus, and includes 6 species, all of which are highly organized. *B. callitricha* and *B. pennoides* have developed, in particular, specialization of axial cells, and *B. scoparia* and *B. hirsuta* are most advanced in pattern of growth and branching. *Platythamnion* is represented in southern Australia by only one species of large thallus size and *Macrothamnion* shows marked evolutionary development within the genus.

2. Procarp and carposporophyte development (unknown for *Ballia* sp.) similar to that in *Antithamnion*. After the first procarp is initiated the branch apex continues growth until up to 20 procarps are formed on the basal cells of successive whorl-branchlets. At this stage axial elongation ceases and only one carposporophyte matures. Fertile whorl-branchlets develop elongate rachides in contrast to the reduced branchlets which bear the procarps in Heterothamnieae.

3. Cruciate division of tetrasporangia as also occurs in Antithamnion. This feature is consistent throughout the group, although in the most highly evolved species (e.g. Ballia spp.) tetrasporangia are borne on special branches and not directly on the whorl-branchlets as in Antithamnion.

The three evolutionary lines probably diverge from a simpler Antithamnion-type ancestor and differ finally in elaboration of whorl-branchlets, branching and growth habit. Antithamnion shows marked evolutionary trends within the genus and it is probable that the three major lines have originated from different points within this sequence. The name Antithamnieae of Hommersand is thus appropriate for the tribe although it contains a rather different assemblage of genera from those ascribed to it by Hommersand (1963).

Comparatively primitive features of Antithamnion are:

(a) Small plant size (usually much less than 3 cm high) consisting of erect and prostrate systems in which the erect branches are formed from the unattached apices of prostrate axes. In more highly developed systems (such as Acrothamnion) the erect axes are distinct lateral branches and not apices of prostrate axes.

(b) There is a complete lack of axial cortication, which develops only in larger plant forms, but with rhizoidal filaments borne on the basal cells of whorl-branchlets and serving as attachment organs rather than corticating filaments.

(c) Whorl-branchlets which vary in form in the more primitive species (e.g. *A. cruciatum*) but remain constant in more advanced species. Whorl-branchlets with alternate branching are usually less stable than oppositely branched forms and hence alternate branching is considered to be more primitive than opposite branching.

Evolutionary lines of Antithamnieae (Diagram 3).

Changes which have occurred within the respective lines of evolution are:

1. Platythamnion line: — *P. nodiferum* is probably much advanced from *Antithamnion*, while some of the north Pacific species represent intermediate evolutionary stages. These are smaller plants, without axial cortication of rhizoids and with variously and rather irregularly branched whorl-branchlets. Gland-cells occur on whorl-branchlets or their branches. *P. nodiferum* has consistently pectinately branched whorl-branchlets with sessile gland-cells borne in place of a branch on the 3rd - 5th cell of the rachis. The occasional occurrence of gland-cells on the first or second branch of a whorl-branchlet provides a possible link with less highly evolved species.

Lateral branching in *Platythamnion* is distinct in the rapid growth of the new branch which quickly overtops the main axis and causes the axial apex to be deflected away from the young lateral branch. This gives a characteristic somewhat dichotomous appearance to the mature thallus with consistent divergence between main and branch apes.

2. Ballia Line: -- probably represents the most highly evolved line of the Antithamnieae with particular elaboration in form of whorl-branchlet, cortication and growth pattern. Details of these structures and probable trends between species are discussed with the genus. Ballia scoparia and B. hirsuta completely lack the whorls of branchlets characteristic of other species and most of the branchlet-like branches are capable of continued growth as occurs in the main axes. A diffuse form of thallus is thus formed which is unlike the characteristic monopodial development of other Antithamnieae. Apical cells are much larger than in other genera and the highly elaborate form of axial cells which occurs in B. callitricha and B. pennoides is not known elsewhere. Lateral branches borne on the rhizoidal corticating filaments are larger and more specialized in form than those which occur in certain genera of other tribes (e.g. Crouanieae, Compsothamnieae and Dasyphileae) and which are not present in other genera of the Antithamnieae. Modification of branches into corticating filaments is another form of cortical specialization which occurs only in B. scoparia.

Gland-cells are lacking in all species of Ballia, even in young growth where they occur most abundantly in Antithamnion.

Acrothamnion is included as a side branch of the main Ballia line for several reasons --

(a) The plant form is unstable with variation in form and number of whorl-branchlets and, hence, probably represents a line of active evolution.

(b) There is a reduction in number of procarps (4-8) formed at each branch apex. This could indicate a new line involving a change in the pattern of reproduction as well as in vegetative features. This, however, may be better understood when reproduction of *Ballia* is known.

(c) The thallus consists of prostrate and erect axes and is very much smaller than that of *Ballia* spp. This form of thallus is more primitive than that of *Ballia* and may indicate either a stage of evolution in the *Ballia* line or in a second line of similar origin.

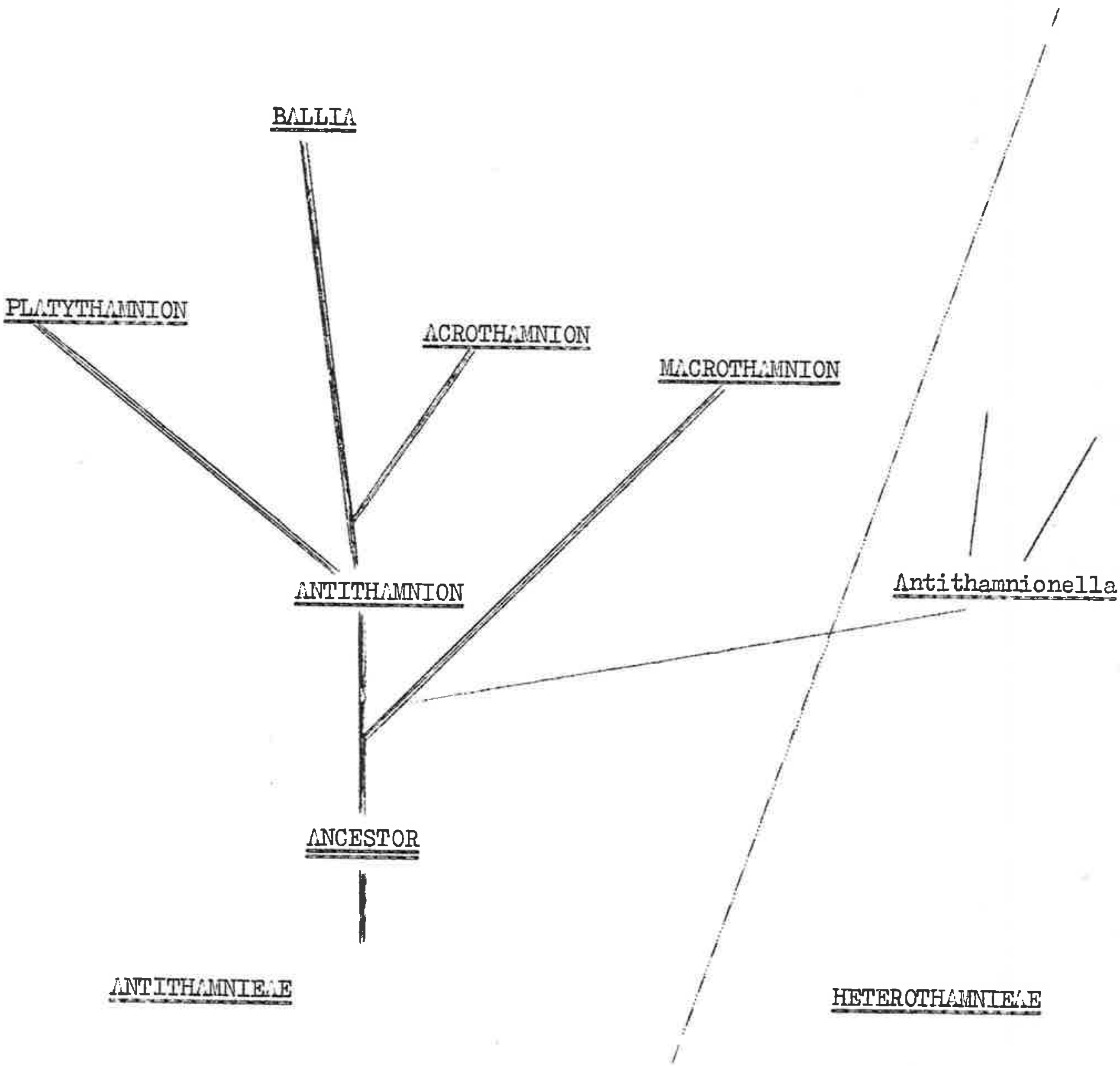
In *Acrothamnion preissii* tetrasporangia are borne on elongate protrusions of the basal cells of whorl-branchlets. This could represent an early stage in the formation of special branches which produce tetrasporangia as occur in some other genera (e.g. *Ballia*).

The placing of *Acrothamnion* depends largely upon a better knowledge of reproduction for both this genus (for which procarp development is known only for *A. preissii*) and for species of *Ballia*.

3. *Macrothamnion line*: —

Although reproductive features are similar to those of other species of Antithamnieae, the line probably does not arise directly from *Antithamnion* as the genus is known at the present time. It seems probable that *Antithamnion* itself arose from an unstable ancestor, not far removed from *A. cruciatum*, but which was variable in the number of whorl-branchlets arising in each whorl as well as in branching of whorl-branchlets. *Antithamnion* then developed along a line in which 2 whorl-branchlets per axial cell became stabilized, while the *Macrothamnion*-*Antithamnionella* line arose as a second line in which whorls consisted of 2 or 3 whorl-branchlets per cell. *Antithamnionella* retained a variable number of branchlets per whorl but underwent marked reduction in procarp development, while *Macrothamnion* became vegetatively stable. *M. pectenellum* is a small plant with 2 or 3 branchlets in each whorl and is probably close in thallus form to both *Antithamnionella* and to the *Antithamnion*-like ancestor form of thallus. *Macrothamnion mucronatum*, on the other hand, is highly-evolved and consistently produces 3 whorl-branchlets from each axial cell. Gland-cells in *Macrothamnion* are borne on short 2(-4) celled branches as in *Antithamnion* although in *Macrothamnion mucronatum* the special branches may be extended, branched and produce up to 14 gland-cells.

DIAGRAM 3 - Possible Evolutionary Lines within Antithamnieae.



HETEROTHAMNIEAE.

Key to Genera of Heterothamnieae.

1. Thallus with prostrate and erect axes. Whorls of branchlets variable in number (up to 4) and form of whorl-branchlets. Branching of whorl-branchlets often increasing toward base of thallus... ... ... Antithamnionella

1. Thallus of erect axes only. Whorl-branchlets in whorls of 4 (3 in Trithamnion) usually decreasing in length and branching towards base of axes... 2

2. Whorls of 3 (-4) whorl-branchlets unilaterally placed on each axial cell and usually with central whorl-branchlet longer than the other 2.
Carposporophyte surrounded by evenly-spaced whorl of 4 long branchlets (not lateral branches).... ... ... Trithamnion

2. Whorls of 4 evenly-spaced whorl-branchlets approximately equal in length (except on main axes of Perithamnion dispar). Carposporophyte surrounded by normal whorl-branchlets and/or lateral branches from axial cell below... 3

3. Tetrasporangia on special short branches borne on basal (and 2nd) cells of whorl-branchlets
Lateral branches often numerous and limited in growth.. Perithamnion

3. Tetrasporangia sessile on normal cells of whorl-branchlets. Lateral branches scattered and not obviously restricted in growth 4

4. Plants occurring in tufts on receptacles of <u>Cystophora platylobium</u> and <u>C. siliquosa</u>. Species confined to single host plant. Whorl-branchlets simple or branched, but without branches from basal cells. Gland-cells sessile on 3rd-5th (rarely on terminal cell) of rachis hf whorl branchlet... ... ... <u>Heterothamnion</u>

4. Plants not in discrete tufts nor confined to single host plant. Whorl-branchlets usually branched, including branches from basal cells. Gland-cells terminal or sub-terminal on final branchings of whorl-branchlets. 5

5. Thallus attached by rhizoids which do not penetrate host tissues... ... ...
Lateral branches forming an apparent dichotomy with main axes. Whorl-branchlets usually with a whorl of 3 unequal branches from the outer end of a large basal cell. Small hair-bearing stalk cells, with or without terminal hairs, usually present in pairs on whorl-branchlets ... ... <u>Trichothamnion</u>

5. Thallus attached by rhizoids which usually penetrate outer tissue of host. Lateral branches not equivalent nor appearing dichotomous with axes. Whorl-branchlets with two equal branches from basal cell. Small hair-bearing stalk cells absent, although hairs may occur on normal terminal cells of whorl-branchlets... ... ... <u>Tetrathamnion</u>

Genera and Phylogeny of Heterothamnieae.

Antithamnionella displays an unstable thallus structure in having variable whorls of branchlets and sessile gland-cells which are not always constant in position on the one plant (e.g. *A. glandifera*). These features indicate an instability which is likely to give rise to more stable thallus forms and thus *Antithamnionella* probably represents a link between an ancestor form and other genera of the tribe (Diagram 4, p.384). Heterothamnieae, in contrast to Antithamnioneae has: —

1. Small thallus forms which lack axial cortication and which do not form discrete holdfasts. *Antithamnionella* consists of prostrate and erect axes, while more advanced genera consist of erect axes only. Where the prostrate axis has been lost, particularly in the *Perithamnion* line, attachment by rhizoidal penetration between cells of the host tissues has evolved.
2. Procarp and carposporophyte development much reduced from that in Antithamnieae. Characteristically only 1-3 (-4) procarps develop at each branch apex. These are formed on the basal cells of whorl-branchlets, often in a single whorl, and are borne on an axial cell close to the branch apex. Fertile whorl-branchlets are much reduced in length and consist of only 1 (-3) cells beyond the basal (supporting) cell. When only one cell occurs it is usually small and stains densely.
3. Tetrahedral divison of tetrasporangia. Occasionally division is cruciate, but the resultant tetrad is spherical and the sporangia are formed as if division had been tetrahedral.

4. Branching of whorl-branchlets which is rarely distichous (except in a few species of Antithamnionella and Trithamnion) and a distinct rachis is seldom formed (except in some species of Antithamnionella and Heterothamnion). Usually branching occurs by whorls of cells developed from the outer end of each successive cell with the final order of branching consisting of a short chain of 1-3 cells. In this form of branching whorls arise from the basal and following cells of whorl-branchlets, whereas in Heterothamnion branches do not occur on basal cells and are produced randomly on other cells of a definite rachis.

Evolutionary Lines of Heterothamnieae (Diagram 4).

Within Heterothamnieae two lines of development can be traced.

1. The Trithamnion line has probably evolved from an Antithamnionella-like ancestor with Trichothamnion represdnting an intermediate phase of evolution. In Trichothamnion the prostrate axis, as present in Antithamnionella, has been lost, whorl-branchlets are still variable in number (3-5) per whorl and some may be longer or more branched than others. The basal cell of each whorl-branchlet is enlarged and usually bears three branches of which one is often longer than the others. The procarp is borne on the basal cell of a whorl-branchlet several cells in length and occasionally more than 3 carpogonial groups develop successively from one central cell of the carposporophyte.

These features are represented in Trithamnion in a comparatively more advanced form. Whorl-branchlets are concentrated into unilaterally placed whorls of 3 which are probably derived from a whorl of 4 with the loss of one branchlet (3 or 4 whorl-branchlets may occur in each whorl in T. tetrapinnum). The central whorl-branchlet is much longer than the 2 equal lateral branchlets and, when whorls are unilaterally opposite on adjacent axial cells, further reduction in number by the elimination of lateral branchlets could lead to an alternate arrangement of branchlets. The form of the central whorl-branchlet resembles an extended form of the branching developed in Trichothamnion, especially T. minimum. Each whorl-branchlet which bears a procarp is only 2 cells in length, one of which is the basal (supporting) cell, and there are always more than 3 groups of carposporangia produced by the carposporophyte. Specialization is also evident in the development of a whorl of usually 4 long whorl-branchlets surrounding the carposporophyte, and suggests an early stage in the formation of a special involucre.

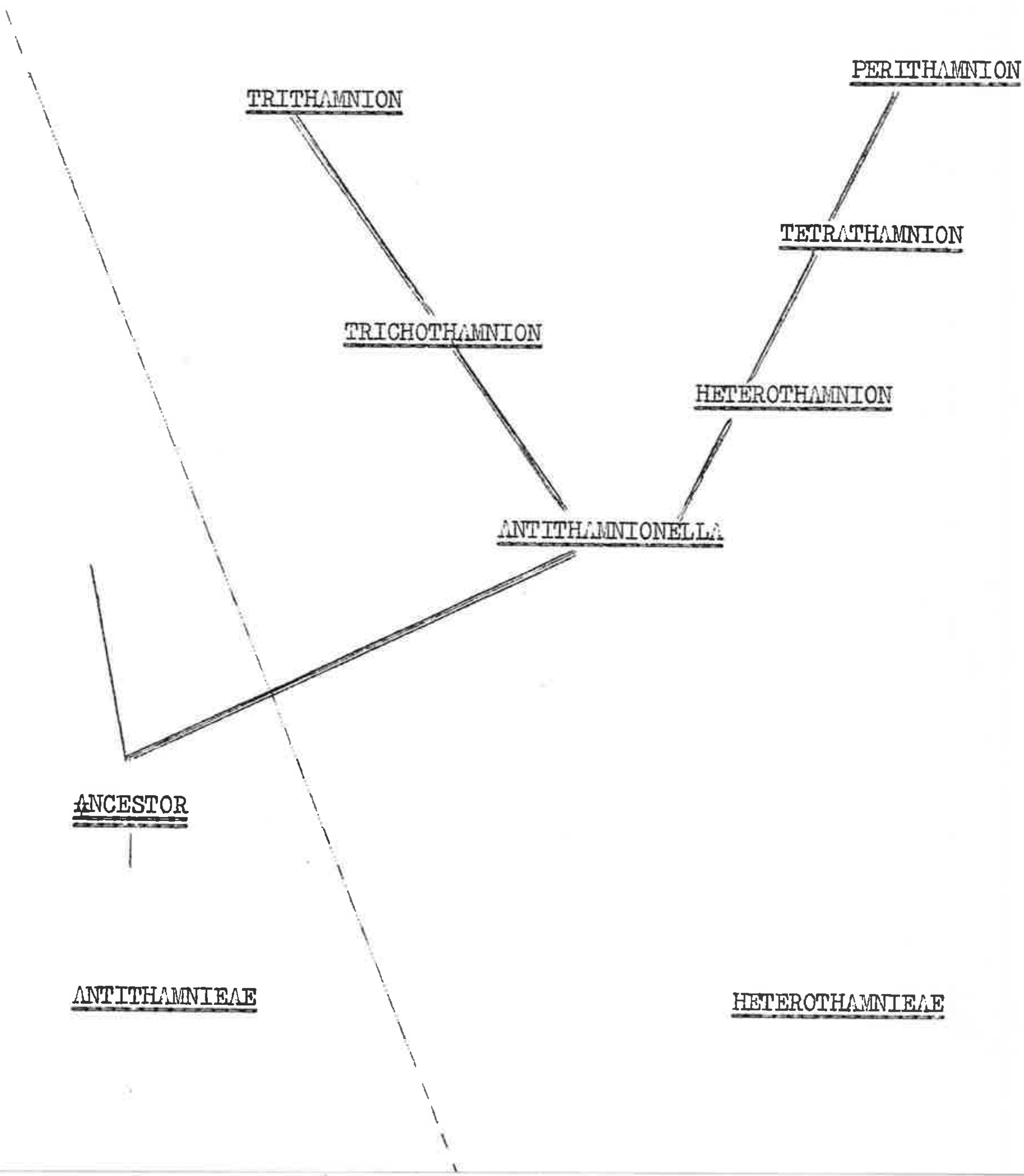
2. Perithamnion Line: —

Relationships of the genera Heterothamnion, Tetrathamnion and Perithamnion are discussed in notes on the respective genera. Heterothamnion is probably the least advanced genus of the three, and differs from Antithamnionella in having well developed erect axes without trace of a prostrate system. It retains, however, whorl-branchlets which may be simple or branched (similarly to

A. glandifera) and which may form whorls in which the branchlets are reduced in both number and branching. Such whorls are not randomly distributed as in Antithamnionella but occur only towards the bases of axes. Gland-cells, as in some species of Antithamnionella, are sessile in the central region of whorl-branchlets. The form of branching of the whorl-branchlets is better defined in Tetrathamnion which develops successive whorls of cell-branches and lacks development of a central rachis. Each whorl consists of 4 equal branchlets with gland-cells borne close to the tips of the branchlets. Occasionally gland-cells occur terminally in Antithamnionella, and A. glandifera, in which they are numerous on each branchlet, offers a variety of possibilities for evolutionary stabilization. Perithamnion is elaborate in thallus structure culminating in the development in P. dispar of alternate-distichous lateral branches borne opposite 1 or 2 much-reduced branchlets in each whorl. This arrangement does not occur in other genera and produces a very specialized thallus form. A tendency toward the development of larger forms is indicated by the continuous elongation of axes, which is not limited even in female plants where carposporophytes occur only on lateral branches.

Specialization occurs also in the position of tetrasporangia and spermatangia which are borne on special branches rather than directly on cells of whorl-branchlets as in Heterothamnion and Tetrathamnion. These distinct evolutionary trends within the genus suggest that the line is actively evolving.

DIAGRAM 4 - Possible Evolutionary Lines within Heterothamnieae.



XI. GEOGRAPHIC DISTRIBUTION OF SPECIES IN SOUTHERN AUSTRALIA

Collections in general are too scanty to give significant indications of the distribution of the species studied or to attempt any biographical inferences for these groups of the Ceramiaceae.

The accompanying table sets out the known limits of distribution for each species. Much of the southern Australian coastline is, however, poorly known and many collections have been confined to localized areas as, for example, Port Phillip Heads, Victoria, Robe, South Aust., and Pennington Bay and Vivonne Bay, Kangaroo Is., South Aust. In many instances locality data has been based on early collections such as those of Preiss, Harvey, von Mueller and Bracebridge Wilson during the previous century. Long sandy stretches such as occur in the Great Australian Bight, the ocean beach of the Coorong in South Aust., and the eastern Victorian coast, may be expected to form barriers in distribution.

Interpretations of the table are based mainly on ecological studies of the coast line made, in particular, by Womersley. The limits of southern Australia are taken as approximately Rottnest Island in Western Australia to about the Victorian - New South Wales Border in the east, and includes Tasmania. Because of the small number of records available from Western Australia, the whole region of south-west Western Australia (from Rottnest Island to Esperance) has been included under the one heading. Womersley and Edmonds (1958) have shown that similar sea temperatures exist along the whole of the southern Australian coast, in both winter and summer, from about Cape Naturaliste in the west to the Victorian - New South Wales border in the east and that the waters around Victoria are only about $2^{O}C$ lower than those in the Great Australian Bight, while those in Tasmania are only $1-2^{O}C$ lower again.

Knox (1960) pointed out that distribution of plants and animals coincided with littoral subdivisions into areas defined on water types and Womersley and Edmonds (1958) and Womersley (1959) have given evidence for changes in the composition of algal associations associated with the cooler temperatures recorded from Robe eastward around the Victorian coast. A sub-antarctic influence reaches the southern part of Tasmania. The table has, therefore, been set out especially to compare distributions for areas where other ecological differences are known to occur. The column "notes" points out areas included in the distribution which are of particular significance in the following discussion.

1. Only five species are known from only S-E South Australia and Victoria. Two of these (*Macrothamnion pectenellum* and *Antithamnionella tasmanica*) are each based on records from two localities only and a third (*Ballia ballioides*) extends north of Robe to Victor Harbour. *Heterothamnion muelleri* and *H. episiliquosum* occur only on *Cystophora platylobium* and *C. siliquosa* respectively. Their range of distribution is not, however, controlled by that of the host plant as both species of *Cystophora* extend westward to Western Australia (Womersley 1964).

2. Two species (*Antithamnion armatum* and *Trithamnion gracilissimum*) occur only in the western part of southern Australia (i.e. from W.A. to Robe) and both these species occur also on Kangaroo Island. No species are known from Western Australia only.

3. Another two species (*Euptilocladia villosa* and *Macrothamnion secundum*) are recorded only in the Victor Harbour - Kangaroo Island - Robe region. Both these species, however, have been separated from widely distributed species (*Euptilocladia spongiosa* and *Macrothamnion mucronatum* respectively) and are likely to have a wider distribution than shown in records.

4. The richness of the Kangaroo Island flora is indicated with thirty-six of the total forty-eight species occurring there. Seven of these are recorded from Kangaroo Island only. Of these seven species there is only one record of each of *Crouania destriana* and *Acrothamnion arcuatum*. *Antithamnion diminuatum* and *Trichothamnion minimum* are small plants which may be easily overlooked while *Trichothamnion elongatum* probably does occur on the mainland although there is no official record of its distribution beyond Kangaroo Island.

5. The occurrence of twelve species from both the Victorian coast and the north coast of Tasmania probably indicates a similarity between the floras of these regions. Further similarities may be found as the Tasmanian coast becomes better known.

6. Two species (*Ballia hirsuta* and *Tetrathamnion lineatum*) occur only in southern Tasmania. *Ballia hirsuta* is also recorded from New Zealand and Stewart Island, and is probably representative of colder seas. *Tetrathamnion lineatum* needs further collections to establish the range of its distribution.

7. The high proportion (75%) of species occurring in Kangaroo Island is indicative of a rich marine flora and of intensive collecting from the area. The proportion is comparatively considerably higher than the 56.3% which occurs in the long stretch of coastline between Elliston and Port Willunga and in which only one species (Trithamnion vulgare) is recorded from more than one locality. This figure may indicate the need for a better knowledge of the flora of this region. 48% and 46%, recorded respectively from Pt. Phillip and Robe represent better known and richer floras as each figure is obtained from a comparatively concentrated locality. The low percentages for Western Australia and Tasmania are probably due to a lack of knowledge of these areas.

Other comparisons, such as species inhabiting calm bays versus species occurring on rough coasts are not possible from the data available. It seems likely that the slightly cooler temperatures of the eastern part of southern Australia have little, if any, effect on the distribution of these species. It is possible that the greater temperature difference which occurs in southern Tasmania may be sufficient to limit the distribution of these species in that area, but too little information is available as yet.

SPECIES	Western Australia (W.A.) (S.W.)	West. S. Aust (Elliston - Pt. Willunga) (Pt. W.)	Victor Harbour region (V.H.)	Robe region.	Kangaroo Island (K.I.)	Western Victoria* (Vic.)	Port Phillip region** (Pt.P)	Northern Tasmania (N. Tas.)	Southern Tasmania (S. Tas.)	NOTES
CROUANIEAE										
Crouania mucosa		+		+	+		+	+		Vic. + N. Tas.
C. destriana					+					K.I. only
C. shepleyana		+						+		
Euptilocladia spongiosa	+	+	+	+	+		+			
E. villosa			+	+	+					
Gattya pinnella	+	+	+	+	?		+			V.H. + Robe + K.I.
Gulsonia annulata		+	+		+		+	+		Vic. + N. Tas.
Ptilocladia australis	+	+			+			+		
P. vestita	+	+	+	+	+	+	?	+		
P. agardhiana	+	+			+		+			
P. pulchra	+	+		+	+	+	+	+		Vic. + N. Tas.
ANTITHAMNIEAE										
Acrothamnion preissii	+	+		+	+		+			
A. arcuatum					+					K.I. only.
Antithamnion divergens	+	+			+		+	+		Vic. + N. Tas.
A. gracilentum	+	+	+	+	+	+	+	+		Vic. + N. Tas.
A. hanowioides	+	+	+	+	+	+	+	+		Vic. + N. Tas.
A. verticale	+	+		+	+	+	+			
A. armatum	+	+		+	+					W.A.→ Robe + K.I.
A. pinnafolium		+			+					
A. diminuatum					+					K.I. only.
Ballia callitricha	rare	+	+	+	+	+	+	+	+	Vic. + N. Tas.
B. ballioides			+	+	+	+	+	+		V.H.→ Pt. P; Vic. + N.Tas.
B. mariana		+		+	+	+	+			
B. pennoides				+						Robe only.
B. scoparia		+		+	+	+	+	+		Vic. + N. Tas.
B. hirsuta									+	Cold regions
Macrothamnion secundum			+	+	+					V.H. + Robe + K.I.
M. mucronatum	+	+	+	+	+	+	+	+		Vic. + N. Tas.
M. pectenellum							+		+	
Platythamnion nodiferum	+			+		+	+			W.A. + Robe — Pt. P.

SPECIES	Western Australia (S.W.) (W.A.)	West. S. Aust. (Elliston - Pt. Willunga) (Pt. W.)	Victor Harbour region. (V.H.)	Robe region.	Kangaroo Island (K.I.)	Western Victoria (Vic.)	Port Phillip region (Pt.P).	Northern Tasmania (N. Tas.)	Southern Tasmania (S. Tas.)	NOTES
HETEROTHAMNIEAE										
Antithamnionella tasmanica						+ —	+	+		Vic. + N. Tas.
A. spirographidis		+								
A. glandifera		+						+		
Heterothamnion muelleri				+ —	+ —	+ —	+			K.I. + Robe → Pt.P
H. sessile			+							V.H. only
H. episiliquosum				+ —	+ —	+ —	+			K.I + Robe → Pt P
Perithamnion ceramioides	+ —	+ —	—	—	+ —	—	+			
P. densum		+			+					
P. dispar				+ —	+ —	+	?			K.I. + Robe → Pt.P
Tetrathamnion lineatum									+	
T. ramosum		+								
T. pyramidatum					+					K.I. only
Trichothamnion planktonicum	+				+	+				
T. elongatum					+					K.I. only
T. minimum					+					K.I. only
Trithamnion vulgare		+			+		+	+		Vic. + N. Tas.
T. tetrapinnum					+					K.I. only.
T. gracilissimum	+ —	+			+					W.A. → Pt. W. + K.I.
Species recorded (out of 48)	18	27	12	22	36	16	23	16	4	
% of Total Species.	37.5	56.3	25	46	75	33.3	48	33.3	8.3	

Notes:

Collections from eastern Victoria are too scarce to record the region separately.

+ Actual records from regions marked there.

——— Probable continuous distribution.

? Likely occurrence although not recorded.

"Notes" point out features commented on in discussion on distribution.

Distribution of species included in genera as "doubtful species" are not included in this table.

FUTURE WORK AND EXTENSION OF THIS REVISION.

This study has concentrated on southern Australian species of genera already ascribed to the Crouanieae Schmitz (including Hommersand's tribe Antithamnieae). The morphology and taxonomy of these species has been revised and several new concepts, particularly of the relationships and phylogeny of the group, are suggested. Although taxa have been compared with those from other parts of the world, the scope of the work has necessarily been limited.

In order to consolidate the interpretations suggested here, particularly in regard to relationships and phylogeny, it is hoped to extend the study to

(1) Compare southern Australian species with other related species and genera recorded outside Australia, e.g. *Grallatoria* and non-Australian species of *Crouania*, *Antithamnion*, *Platythamnion*, *Ballia* and *Antithamnionella*.

(2) Clarify the taxonomic position of other genera possibly closely related, e.g. *Muellerena*, *Dasyphila*, *Lasiothalia*, *Warrenia*, *Bracebridgea*, *Spongoclonium* and some species of *Callithamnion*.

(3) Revise certain tribes such as Dasyphileae, Compsothamnieae and possibly Callithamnieae and Ptiloteae. Features of the Crouanieae in common with these tribes have been referred to in the text.

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FIGURES AND PLATES

FIGURE 1

Gattya pinnella Harvey

A. Thallus composed of branched segments (a, b,c) terminal on pinnate branches of previous segment.

B. Lax terminal growth from pinnate branches of thallus. Lateral branch(a) may form a new segment of thallus.

C. Surface of thallus. Terminal cells of whorl-branchlets cohere to form a gelatinous sheath over thallus.

D. Thallus composed of prostrate and erect axes.

E. Lateral branch initial produced from apex of axial cell following breakage of the axis.

F. Pinnate branches (1-5) of sympodium formed from successive axial apices overtopped by alternately-developed lateral branches. Lateral branch (a) produced later.

FIGURE 1

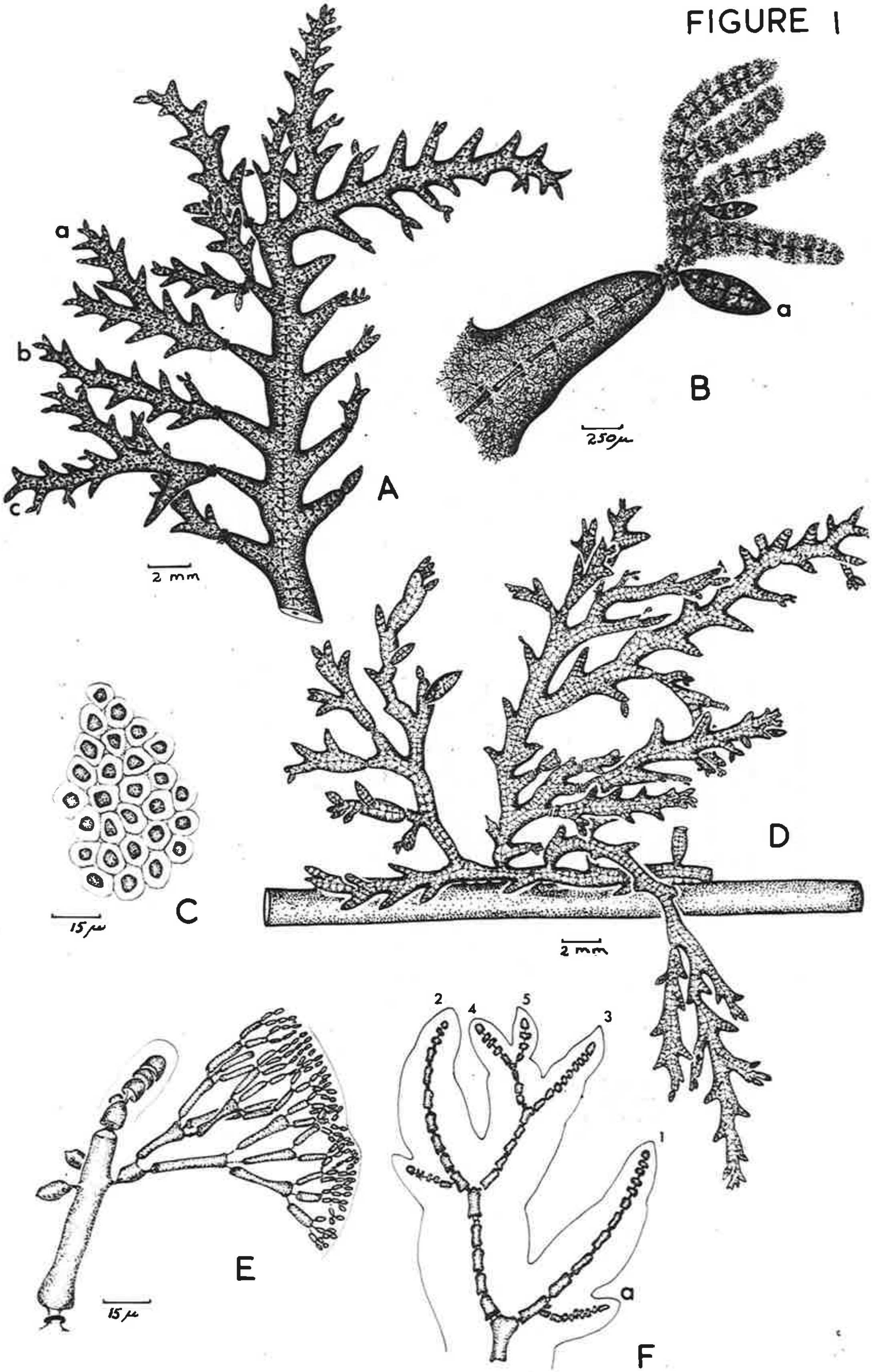

FIGURE 2.

Gattya pinnella Harvey

A - D. Stages in development of young lateral branch. Initial (a) borne directly on axial cell above whorl of branchlets.

E - J. Rhizoidal filaments borne on lower side of basal cells of whorl-branchlets. E - H. Initial stages, J. digitate attachment process terminating rhizoid in lower part of thallus.

K. Tetrasporangia borne on pinnate branches in younger parts of thallus.

L. Tetrahedrally-divided tetrasporangia borne on basal cells of whorl-branchlets.

M. Sequence of initiation of whorl-branchlets (1-3) on adjacent axial cells (a) - (d), showing respective branches superimposed on each 4th axial cell ~~(see text - p. 47).~~

FIGURE 2

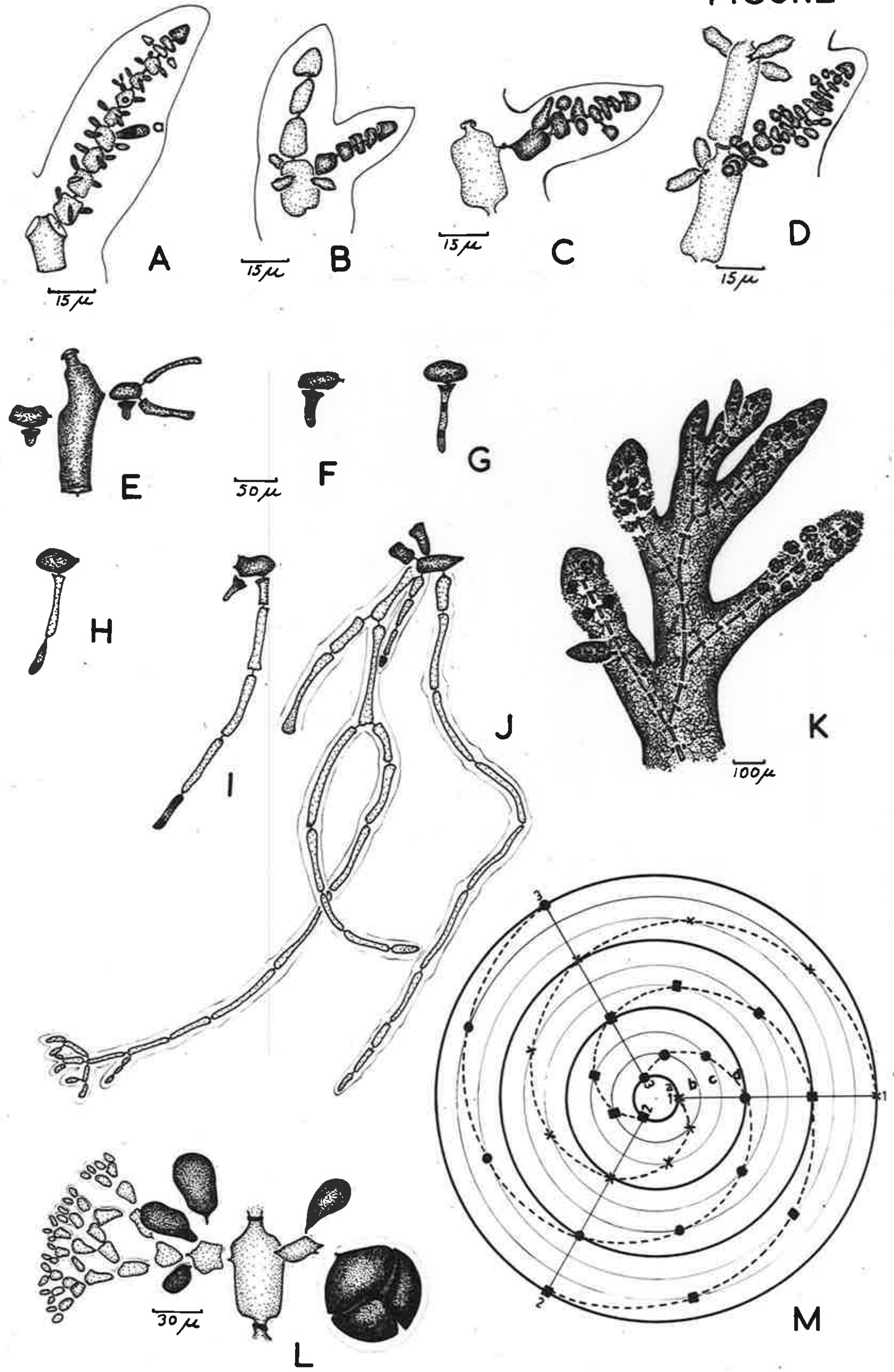

FIGURE 3.

Gattya pinnella Harvey.

A. Carposporophytes borne in club-shaped branch apices. Axial growth continued from branch produced laterally on axial cell below the fertile apex.

B. 4-celled curved carpogonial branch produced outwardly from supporting cell borne directly on axial cell near branch apex.

C. Carpogonial branch with terminal trichogyne.

D. Auxiliary cell, cut off from upper part of supporting cell, prior to formation of foot cell and central cell.

E. Carposporophyte consisting of residual supporting cell, foot-cell and central cell with initials of three groups of carposporangia.

F. Similar to E, with enlarging terminal group of carposporangia.

G. Carposporophyte with maturing groups of carposporangia surrounded by whorl-branchlets from axial cells below.

H. Spermatangial mother cells borne outwardly on terminal cells of whorl-branchlets.

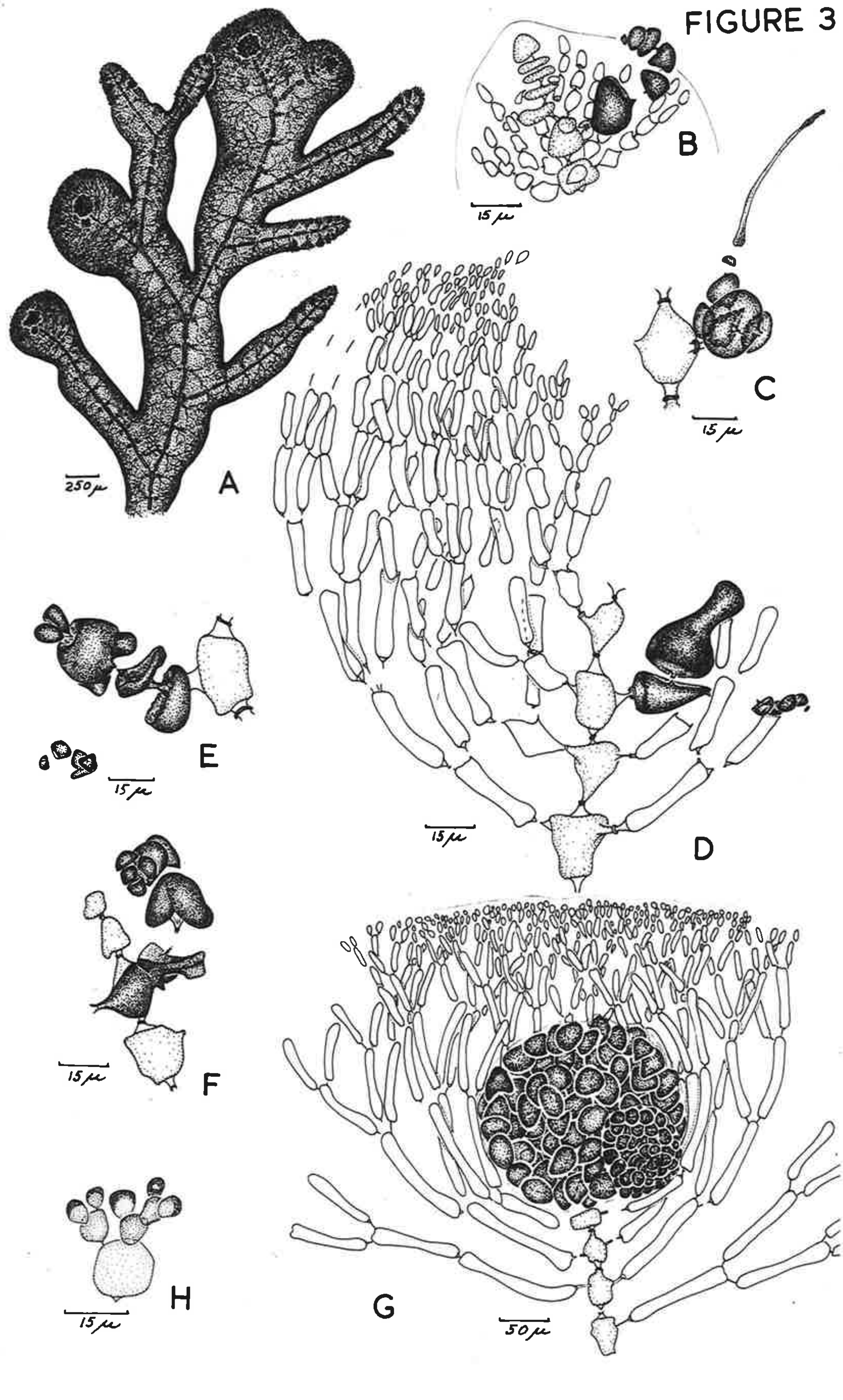
FIGURE 3
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FIGURE 4.

Crouania mucosa n. sp.

A. Thallus with new axial branches arising near apices of previous axes (e.g. (a) and (b)).

B. Whorl-branchlet with terminal hairs and rhizoidal filaments arising from basal cell.

C. Rotation of whorls (1-4 respectively) on adjacent axial cells allows whorl-branchlets to be superimposed on each 4th axial cell, (axial cells represented by circles) --(see text, p. 59-60).

D. Initiation of lateral branch on basal cell of whorl-branchlet.

E. Spiral initiation of whorl-branchlets on young lateral branch.

F - G. Early stages in growth of axial branch initiated directly from axial cell above whorl-branchlets.

H. Spermatangial mother-cells borne terminally on whorl-branchlet.

I. Spermatangial mother-cells in whorls of 3-4 with concentration of protoplast in median part of cell.

FIGURE 4

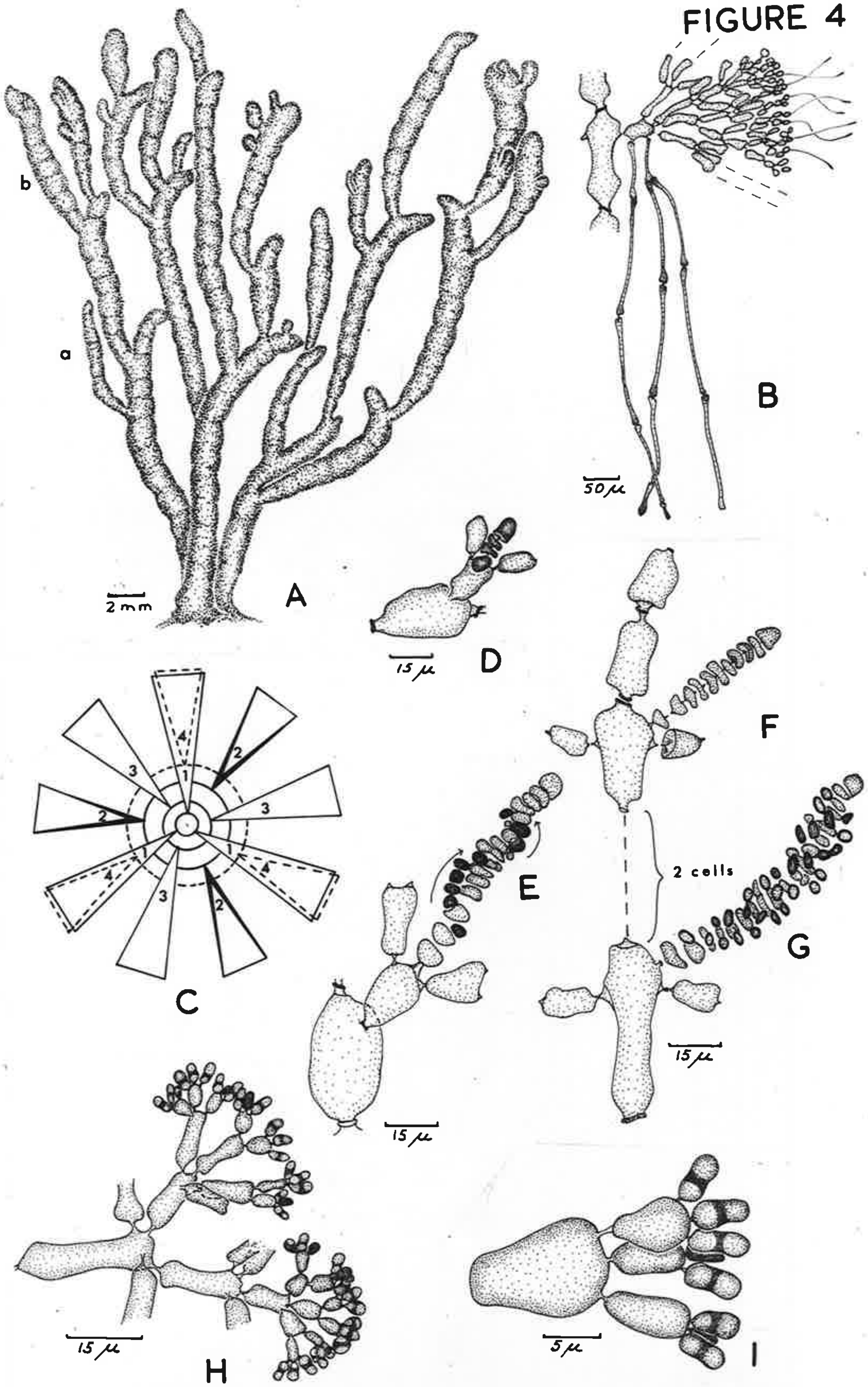

FIGURE 5

Crouania mucosa n. sp.

A. Carposporophytes borne in club-shaped branch apices.

B. Initiation of procarps (on adjacent cells) near branch apex.

C. Procarp initial with commencement of formation of carpogonial branch initial on outer side.

D. Division of carpogonial branch-initial to give 4 cells of carpogonial branch. Borne outwardly on supporting cell.

E-F. Young carpogonial branch shortly after division of initial cell (as in D).

G-I. Stages in development of trichogyne borne terminally from carpogonium.

J. Spermatium attached to tip of trichogyne at stage of fusion.

K. Connecting cell forming from carpogonium and enlargment of upper part of supporting cell prior to cutting off of auxiliary cell.

L. Shortly after fusion of carpogonium with auxiliary cell. Connecting cell attached to auxiliary cell.

M. Enlargment of upper part of auxiliary cell before dividing to form lower foot cell and upper central cell.

N. Initial of terminal carposporangial group developed from central cell. Carpogonial branch disintegrating.

/

FIGURE 5

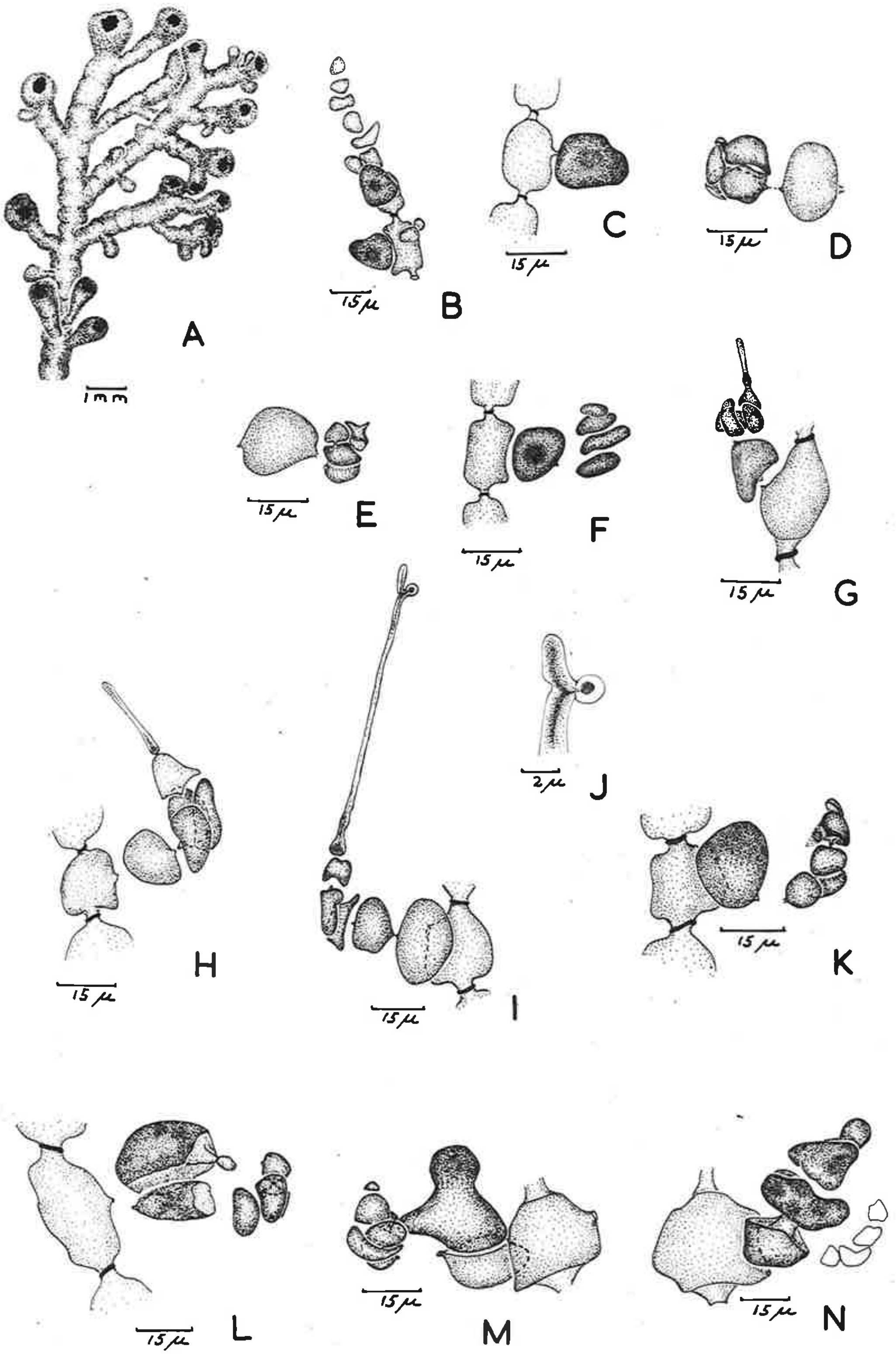

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FIGURE 6

Crouania mucosa n. sp.

A. First divisions of terminal carposporangial group in formation of carposporangia. Second carposporangial bud developed laterally.

B. Further development of terminal carposporangial group. Two lateral buds developed.

C-D. Later stages in formation of groups of carposporangia from central cell of carposporophyte.

E. Mature carposporangia.

F. Tetrasporangia borne on young branches of thallus.

G. Successive development of tetrahedrally-divided tetrasporangia from basal cells of whorl-branchlets.

FIGURE 6

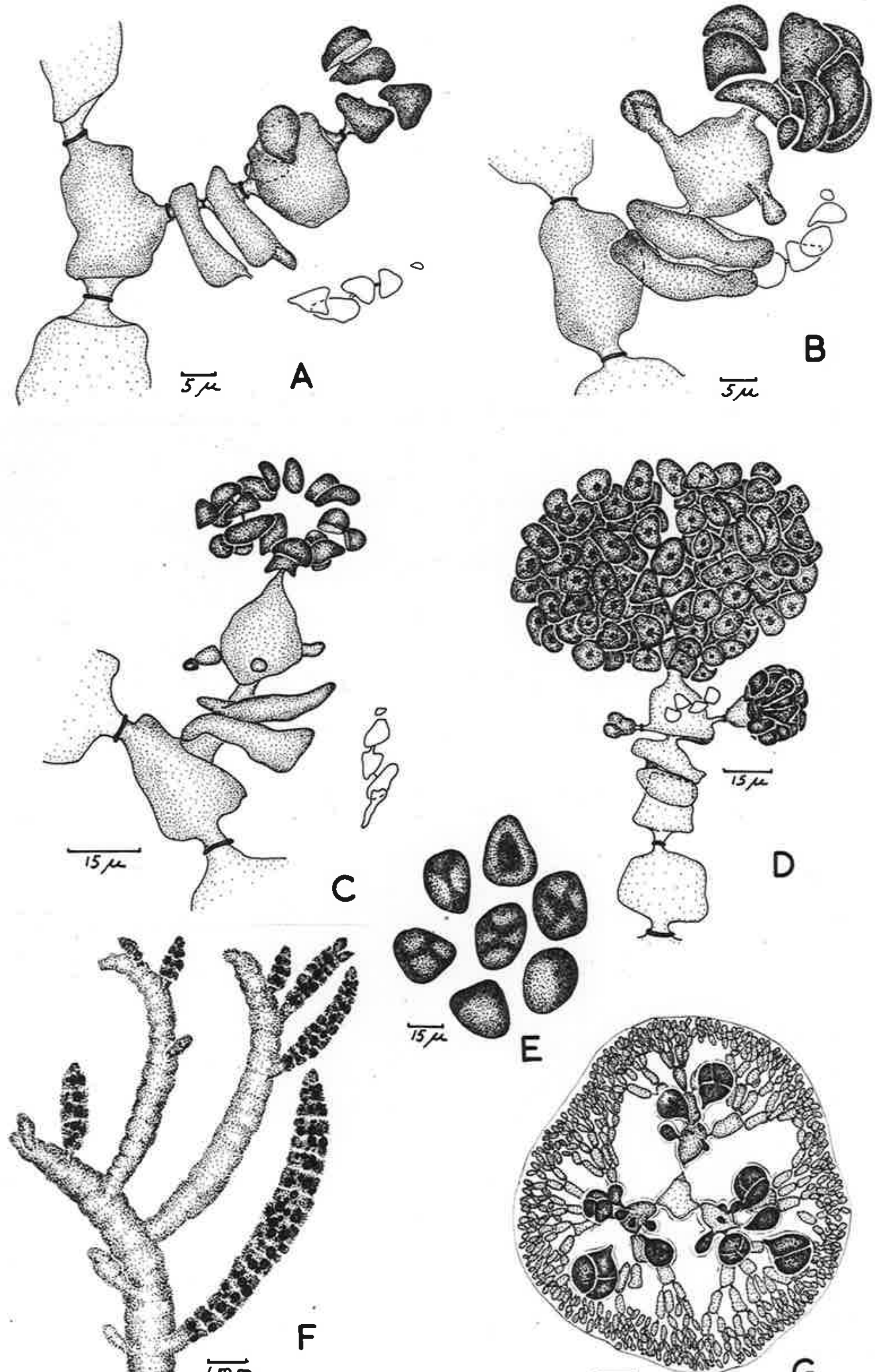


FIGURE 7

Crouania shepleyana n. sp.

A. Plant habit with new axial branches becoming dominant ($a + a_1$) and old axis (a_2) continuing growth beyond branches $b + B_1$ (see text, p. 67).

B. Carposporophyte at rounded branch apex; new axial branch developed from lower axial cell.

C. Procarp initials near branch apex.

D. 4-celled carpogonial branch borne on outer side of supporting cell.

E-F. Development of trichogyne terminally from carpogonium. Small capping-cell at base of trichogyne in F.

G. Connecting cell developed, after fertilization, from carpogonium and auxiliary cell cut off from upper side of supporting cell.

H. Carposporophyte showing fusion between axial cell and residual supporting cell and formation of terminal group of carposporangia; first lateral carposporangial bud also initiated.

I. On right — well developed carposporophyte.
On left — stage just prior to cutting off of auxiliary cell from supporting cell. Connecting cell developing from carpogonium.

J. Whorl-branchlets bearing tetrasporangia on basal cells.

FIGURE 7

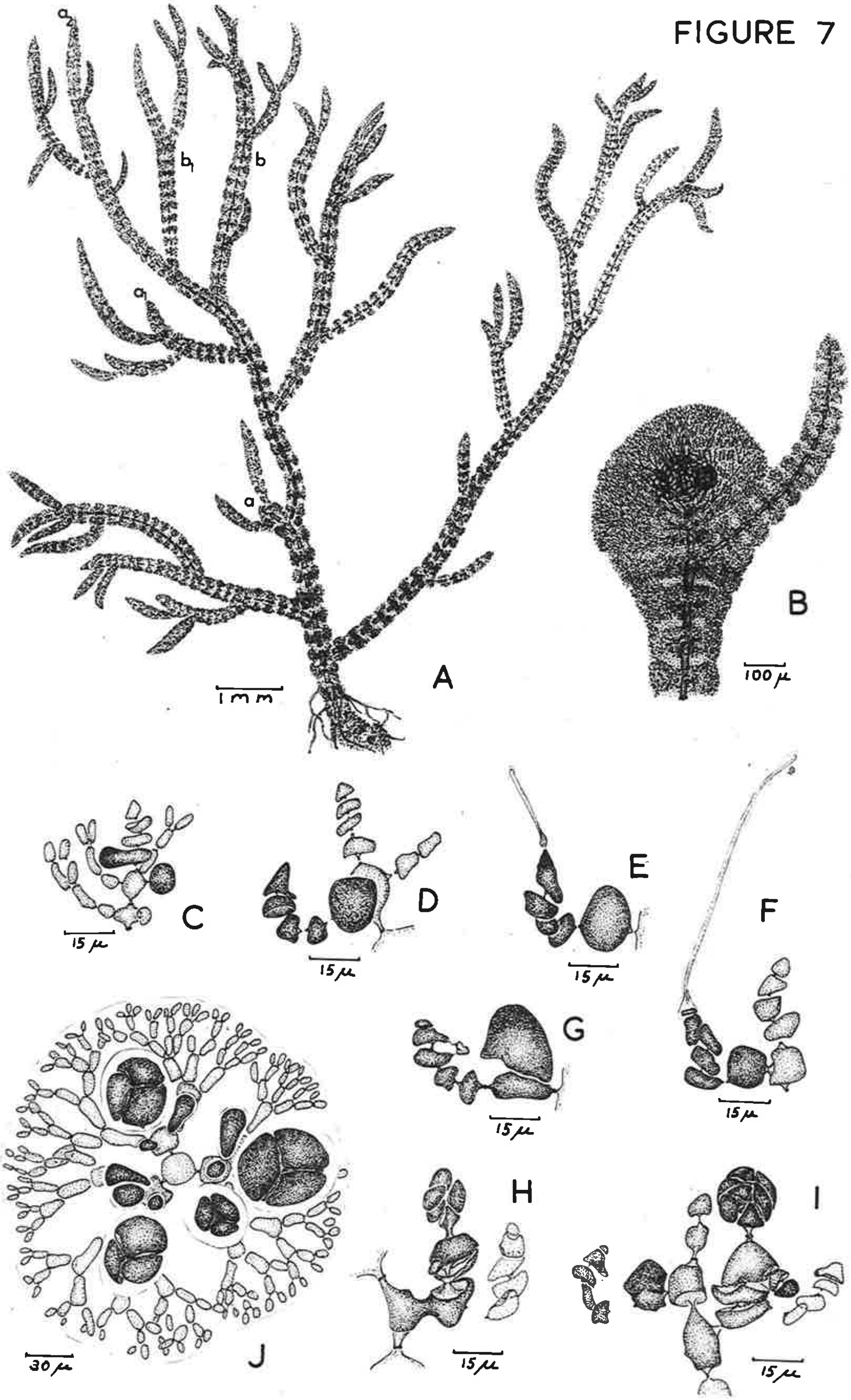


FIGURE 8

Crouania destriana n. sp.

A. Capping-cell and connecting cell associated with carpogonium; upward enlargment of supporting cell prior to cutting off of auxiliary cell.

B. Commencement of division of auxiliary cell to form a lower foot-cell and an upper central cell. Protrusion forming in position of terminal carposporangia group from central cell.

C. Carposporophyte with terminal group of carposporangia and initiation of two lateral carposporangial buds.

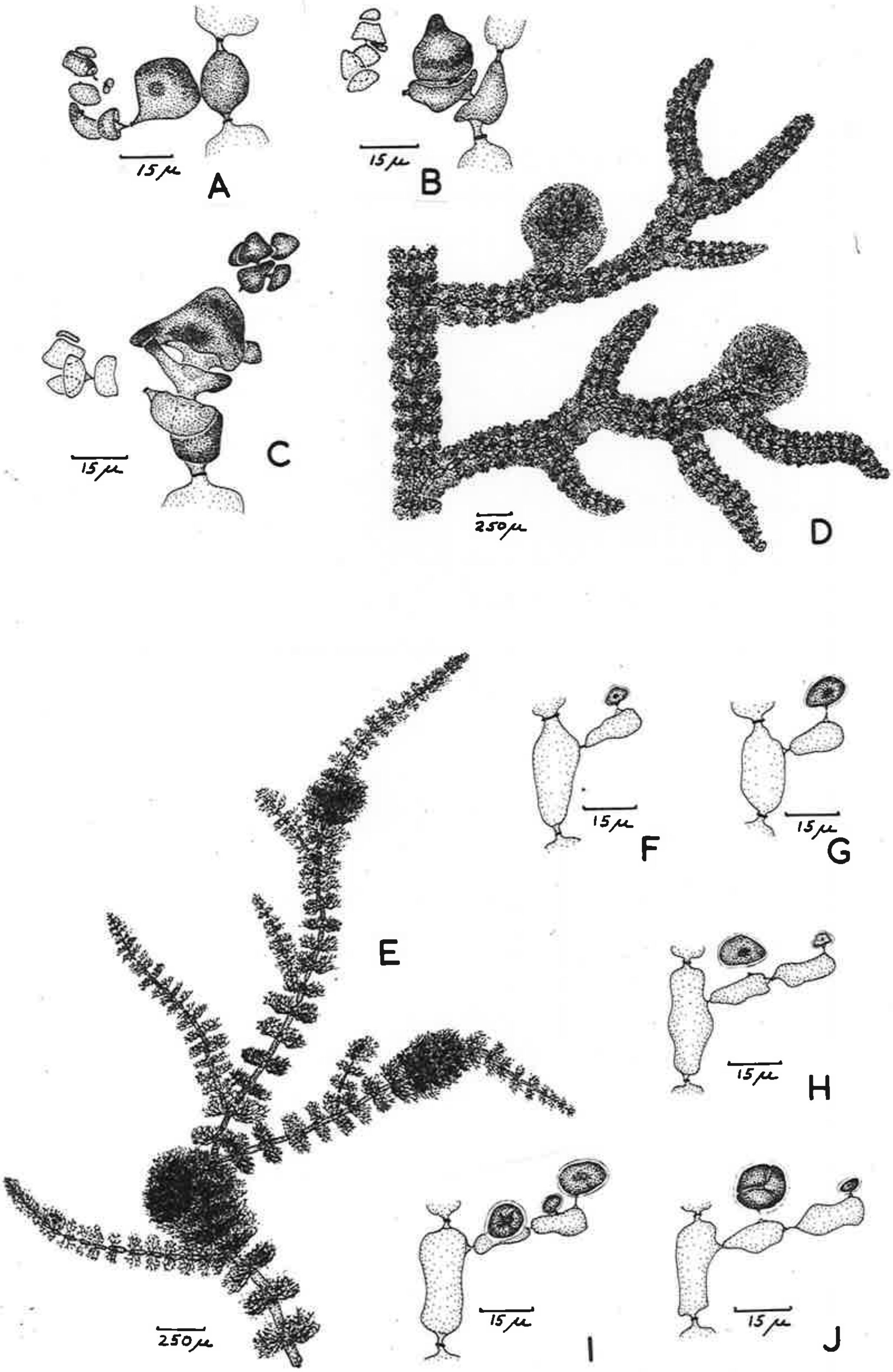
D. Part of female thallus with carposporophytes formed in rounded branch apices and new axial branches developed in pairs from axial cells below apices.

Ptilocladia australis n. comb.

E. Thallus showing continued axial elongation after development of carposporophytes.

F-J. Stages in development of tetrasporangia borne on outer end of basal and second cells of whorl-branchlets.

FIGURE 8



<u>FIGURE 9</u>

<u>Ptilocladia australis</u> (Harv.) n. comb.

A.- C Early development of lateral branch borne on basal cell of whorl-branchlet.

D. Supporting cell with outwardly-developed carpogonial branch initial borne near branch apex.

E. Young 4-celled carpogonial branch with developing trichogyne.

F. Branch apex continuing to elongate after procarp development. Ovoid 'gland-cell' with crystal - like inclusions on young whorl-branchlets.

G. Mature carpogonial branch; spermatia adhere to trichogyne.

H. Carposporophyte with two lateral carposporangial buds. Carpogonial branch disintegrating.

I. Carposporophyte with strong fusions between cells and maturing groups of carposporangia. Filaments (f) developed from cells near carposporophyte.

FIGURE 9

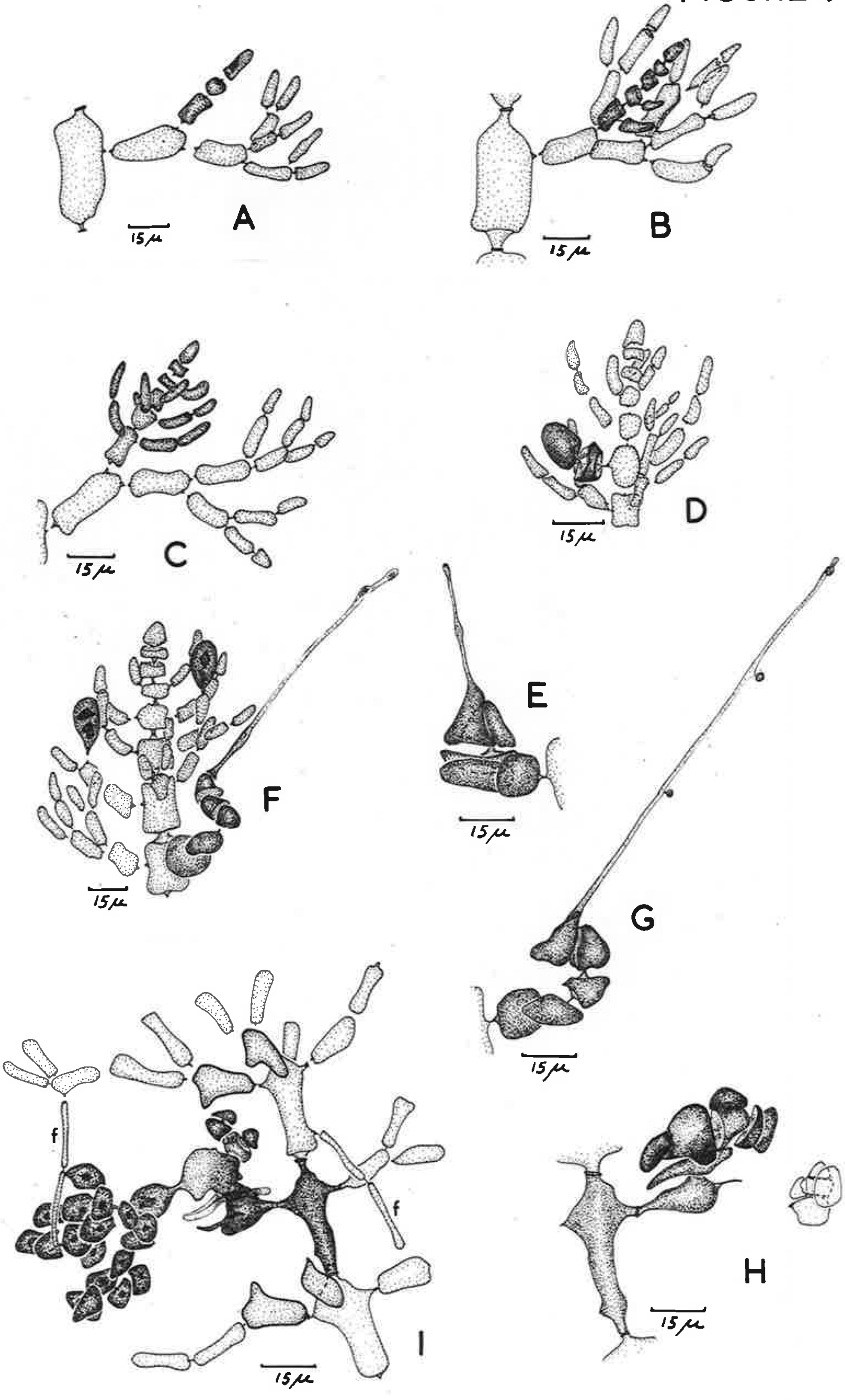


FIGURE 10

Ptilocladia vestita (Harv.) n. comb.

A. Alternate-distichous arrangement of lateral branches from axis; some elongation of branch axes after initiation of procarps.

B. Axial cortication of rhizoidal filaments and elongation of whorl-branchlets parallel to axis.

C. Procarps initiated near branch apices.

D. Just before initiation of first lateral carposporangial group from central cell of carposporophyte.

E. Maturing groups of carposporangia. Filaments (f) and protrusions developed from surrounding thallus cells.

F Aborted procarps developed at intervals along elongated axis beyond carposporophyte.

G. Aborted carpogonial branch borne on basal cell of whorl-branchlet in place of a normal vegetative branch of the branchlet.

FIGURE 10

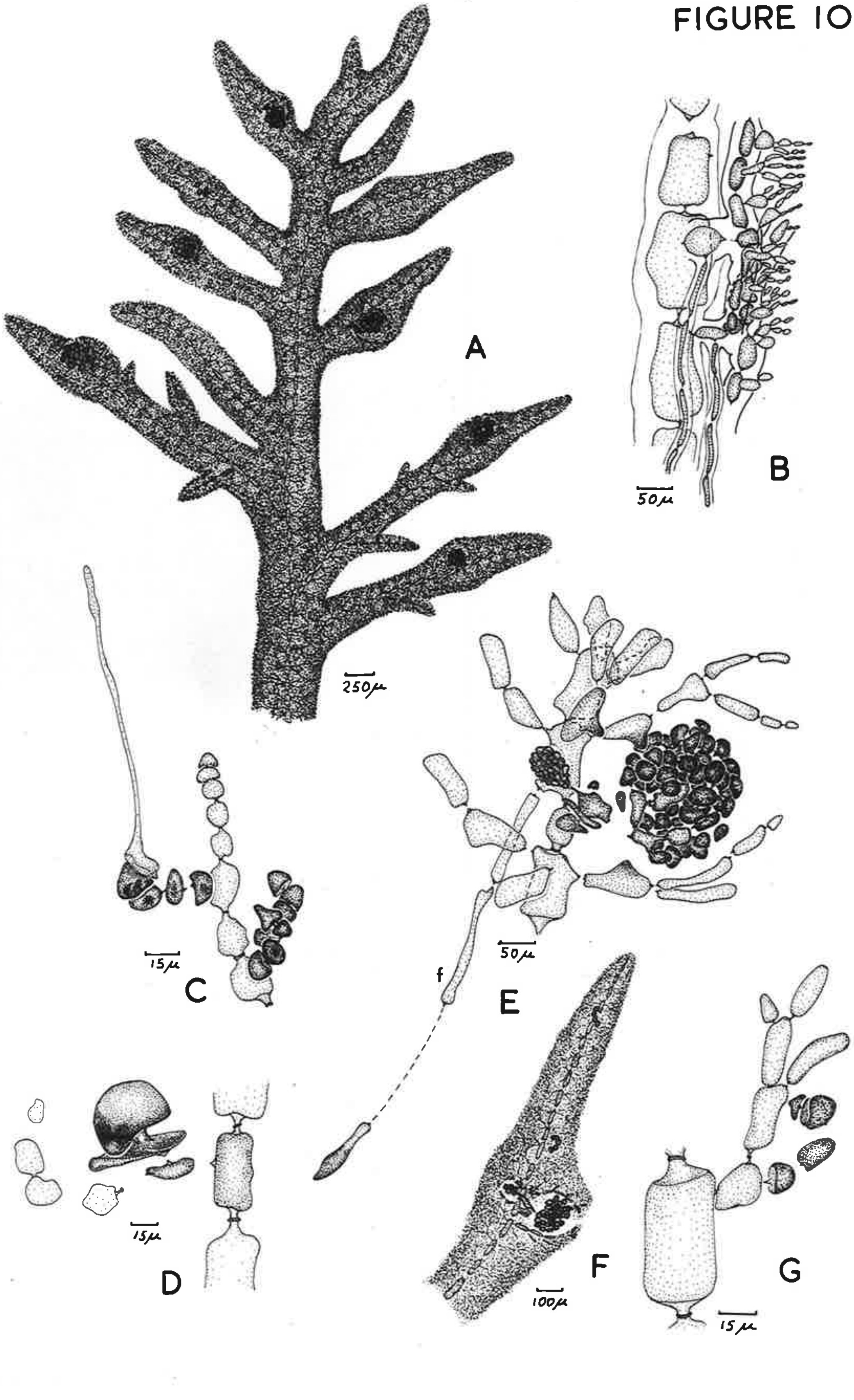


FIGURE 11

Ptilocladia agardhiana (Harv.) n. comb.

A. Crystal-like inclusions in axial cells.

B. Procarp consisting of supporting cell and 4-celled carpogonial branch.

C. Spermatangial mether-cells borne terminally on whorl-branchlets.

D. Carposporophyte with pronounced fusions between cells and maturing groups of carposporangia.

E. Tetrasporangia borne on cells of whorl-branchlets.

Ptilocladia pulchra Sonder ~~n. comb.~~

F. Carposporophytes borne near apices of short branches.

G-I Early development of lateral branch borne on basal cell of whorl-branchlet.

J. Young rhizoidal filaments - three branches from cell borne on basal cell of whorl-branchlet.

K. Branching of rhizoidal filaments to form an axial cortication of two layers - larger inner cells and smaller outer cells.

L. Transverse section of axis with two layers of cortical filaments.

M. Hairs and ovoid cells terminating whorl-branchlets.

N-S Series of stages in development of an apparent dichotomy in branching of whorl-branchlet.

FIGURE II

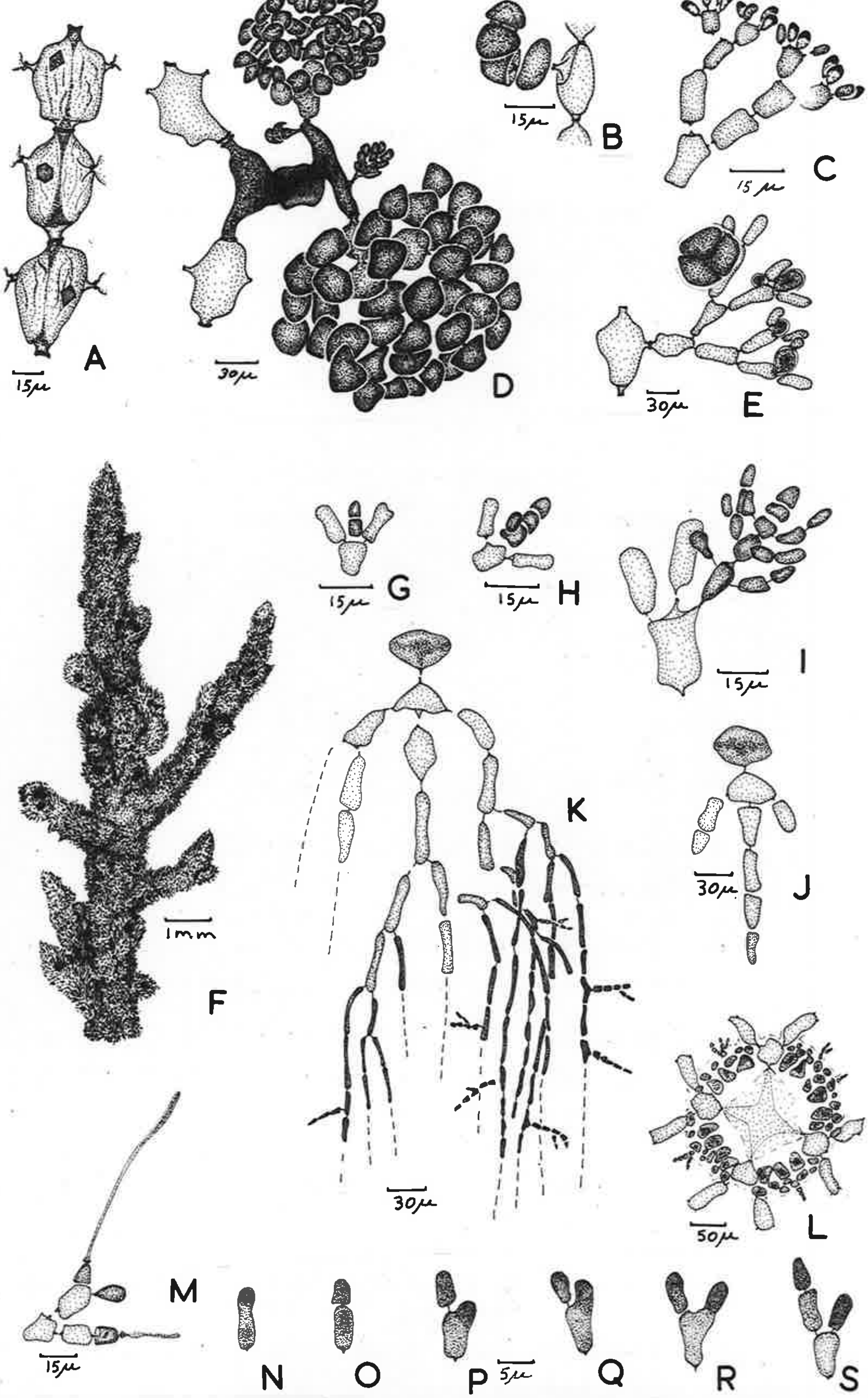

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FIGURE 12.

Ptilocladia pulchra Sonder n. comb.

A. Transverse section of thallus with tetrasporangia borne on cells of whorl-branchlets.

B. Tetrasporangia borne on young branches of thallus.

C. Procarp initial produced in place of a whorl-branchlet.

D. Carpogonial branch initial developed outwardly from supporting cell.

E. Division of carpogonial branch initial into 4 cells.

F. Mature carpogonial branch with trichogyne terminal on carpogonium. A second procarp initiated towards branch apex.

G. Auxiliary cell cut off from upper side of supporting cell and connecting cell developed from protrusion of carpogonium.

H. Auxiliary cell divided into lower foot-cell (with connecting cell evident as a process attached to it) and upper central cell.

I. Fusions occurring between cells of carposporophyte and development of first lateral carposporangial group.

J. Carposporophyte with maturing groups of carposporangia.

K-M Production of carposporangia by successive longitudinal and transverse divisions of initial cells.

FIGURE 12

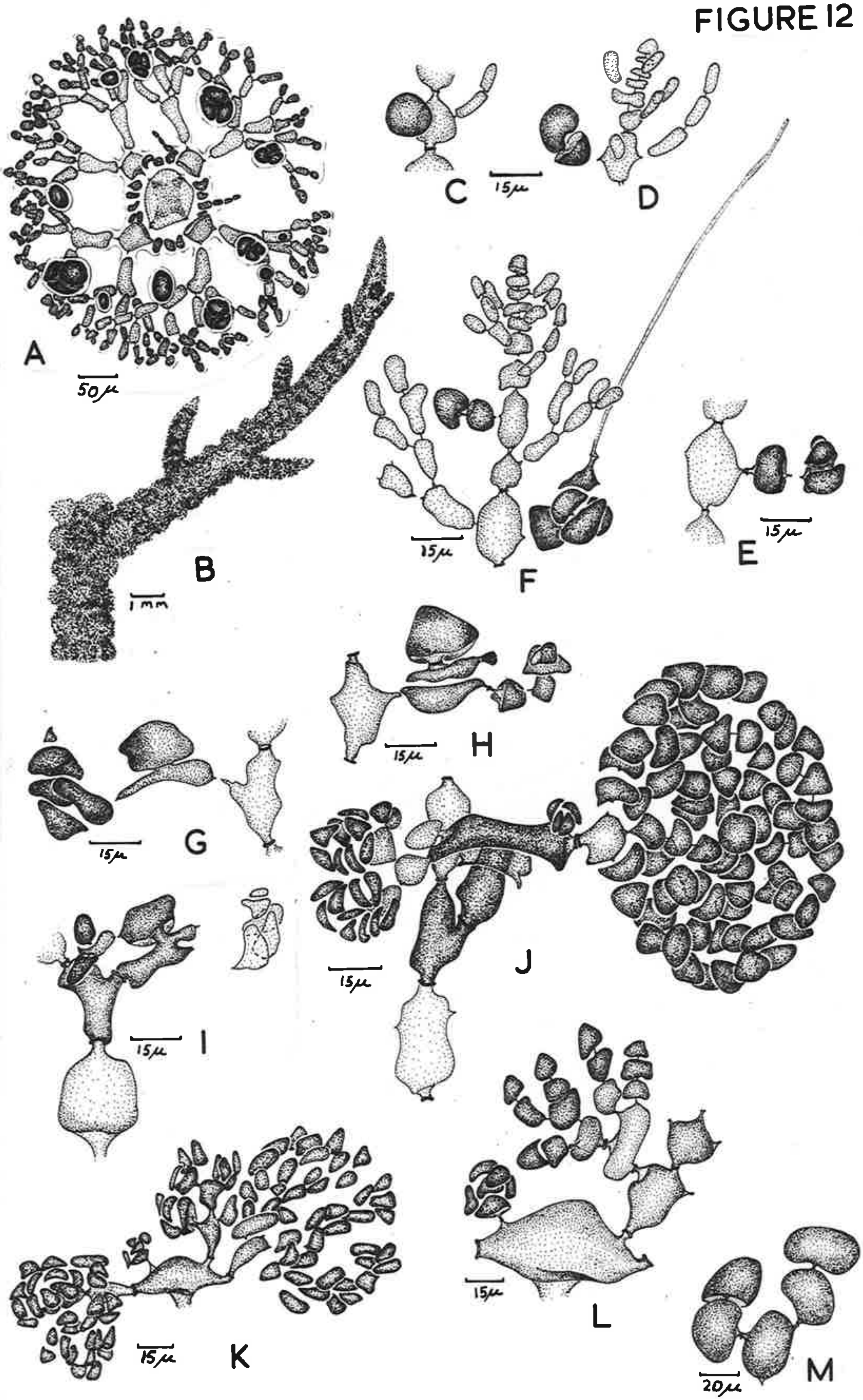


FIGURE 13

Gulsonia annulata Harvey.

A. Portion of thallus. Carposporophytes developed at intervals on special reduced branches.

Euptilocladia spongiosa n. sp.

B. Flattened thallus, alternately-distichously branched with carposporophytes borne near apices of short branches.

C. Whorl-branchlet bearing tetrahedrally-divided tetrasporangia and terminal chains of small cells.

D. Tetrasporangia scattered over thallus.

E. Whorl-branchlets initiated on second axial cell at branch apex.

F. Branching pattern of whorl-branchlet in upper terete parts of thallus.

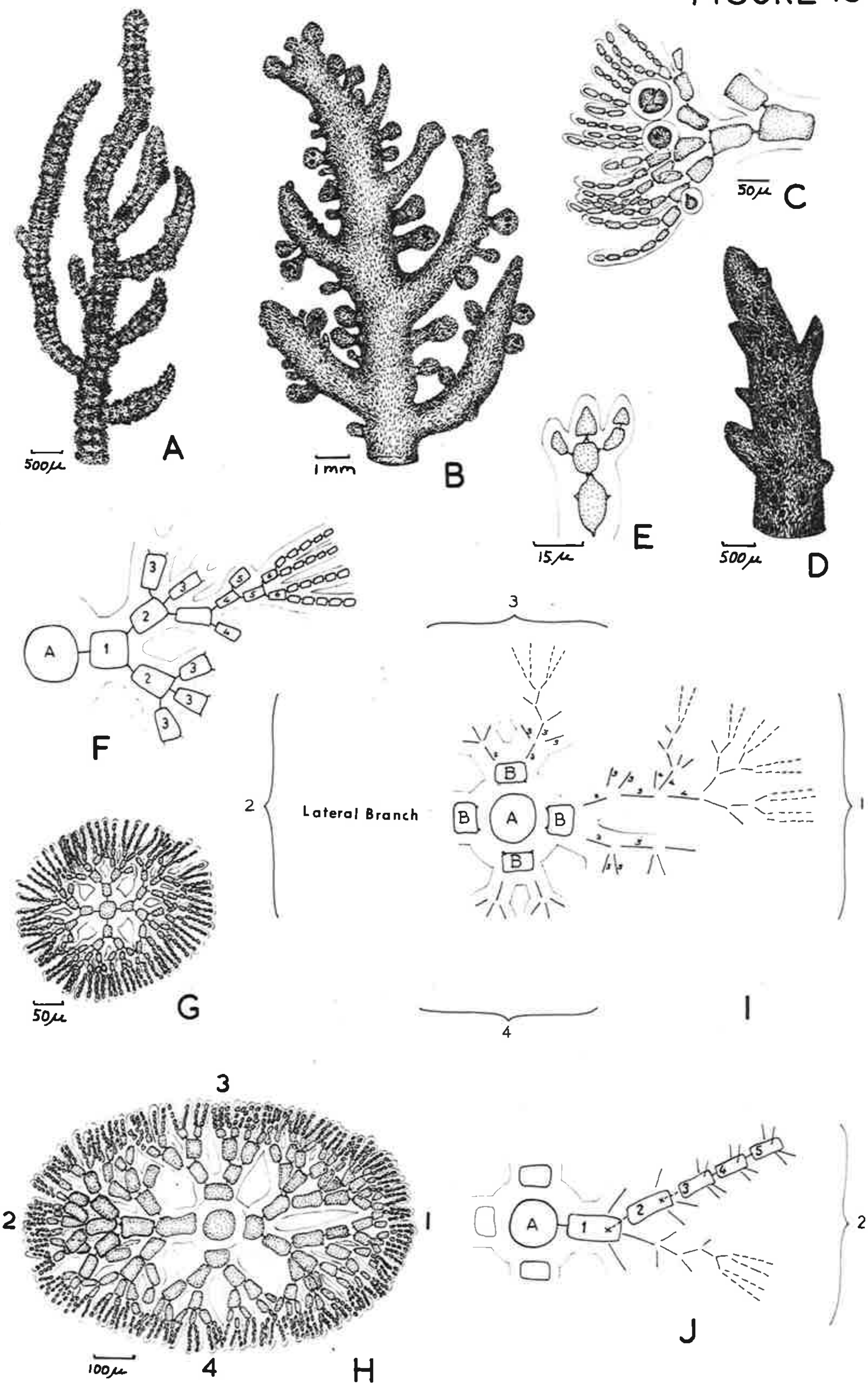
G. Transverse section of upper terete part of thallus.

H. Transverse section of flattened part of thallus with young lateral branch (2).

I. Branching pattern of whorl-branchlets in flattened parts of thallus (Branch (1) of H.)

J. Lateral branch (cells 2-5) borne on basal cell of whorl-branchlet (Branch (2) of H.).

FIGURE 13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2
Lateral Branch
B
A
1
50μ
G
4
I
3
2
1
100μ
4
H
1
2
3
4
5
6
J
2

FIGURE 14

<u>Euptilooladia spongiosa</u> n. sp.

A. Initiation of rhizoidal filaments on basal cells of whorl-branchlets.

B. Rhizoidal filaments borne on inner cells of whorl-branchlets (not restricted to basal cells only).

C. Axial cortication of rhizoidal filaments and extension of whorl-branchlets parallel to axes.

D. Procarp borne on axial cell in place of whorl-branchlet.

E. Procarp initial.

F. Supporting cell with carpogonial branch initial on outer side.

G. Prooarp of supporting cell and 4-celled carpogohial branch.

H. Carposporophyte showing fusions between cells and maturing groups of carposporangia.

<u>Euptilocladia villosa</u> n. sp.

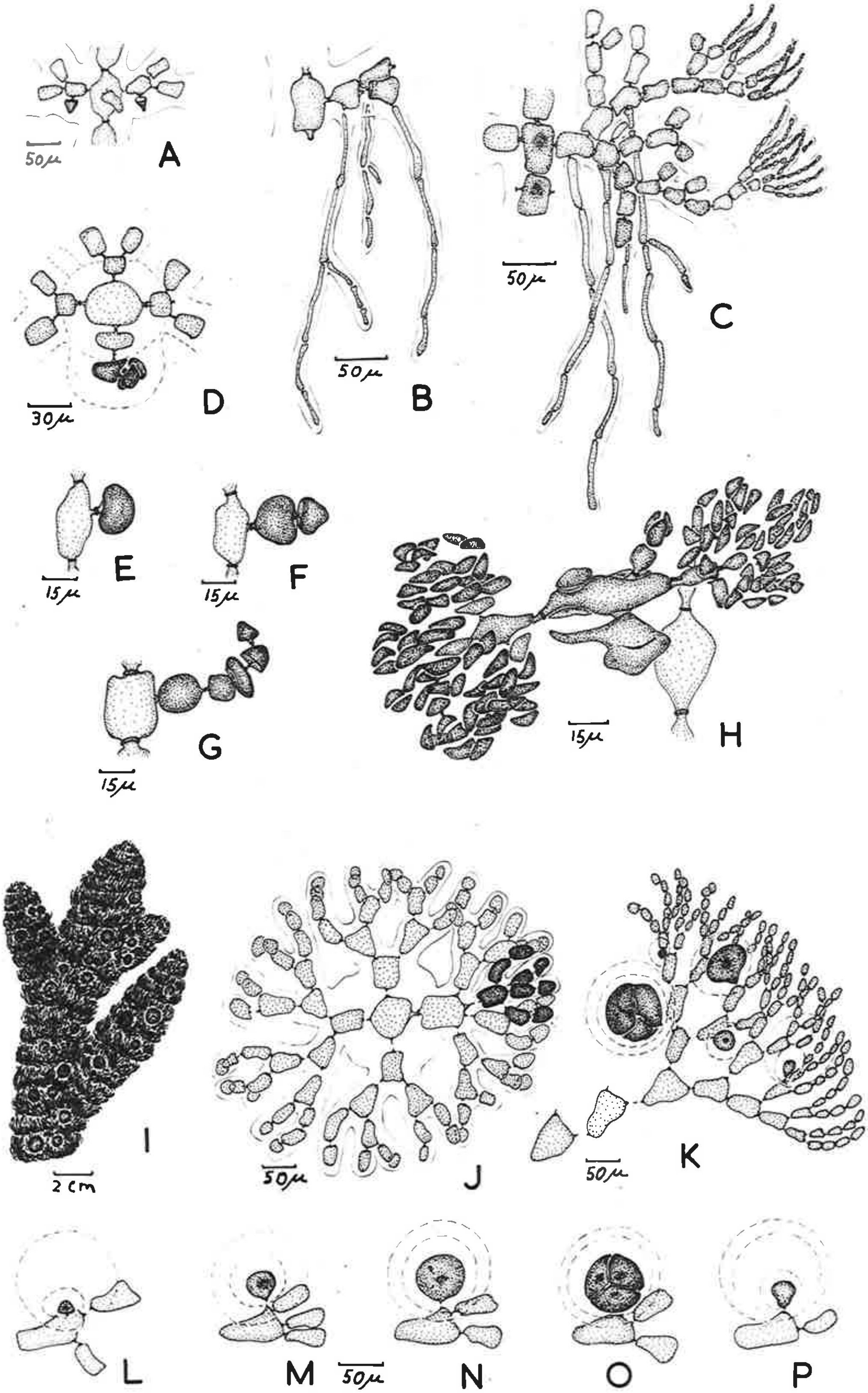
I. Tetrasporangia scattered on thallus.

J. Transverse section of terete part of thallus with young lateral branch.

K. Whorl-branchlet with tetrasporangia and terminal chains of small cells.

L-P Successive stages in development of a seoond tetrasporangium (L-O), and initial of a third (P) on cell of whorl-branchlet.

FIGURE 14


50μ
A
50μ
B
50μ
C
30μ
D
15μ
E
15μ
F
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G
15μ
H
2 cm
I
50μ
J
50μ
K
L
M
50μ
N
O
P

FIGURE 15

Antithamnion divergens (J.Ag.) J.Ag.

A. Rhizoidal attachment organs and lateral branch borne on basal cells of whorl-branchlets on prostrate axis.

B-C Young lateral branch initiated on basal cell of whorl-branchlet.

D. Ovoid tetrasporangia borne on cells of pinnules of pinna-like whorl-branchlets.

E. Gland-cells on special short 2-3 celled branches borne on cells of the rachis or pinnules of pinnalike whorl-branchlet.

F. Series of procarps borne on basal cells of pinnae at branch apex.

G. Auxiliary cell prior to division into lower foot-cell and upper central cell . Enlargement of second pinna cell (beyond carposporophyte).

H. Carposporophyte with marked fusions between cells and development of terminal group of carposporangia.

I. Carposporophyte with maturing groups of carposporangia.

FIGURE 15

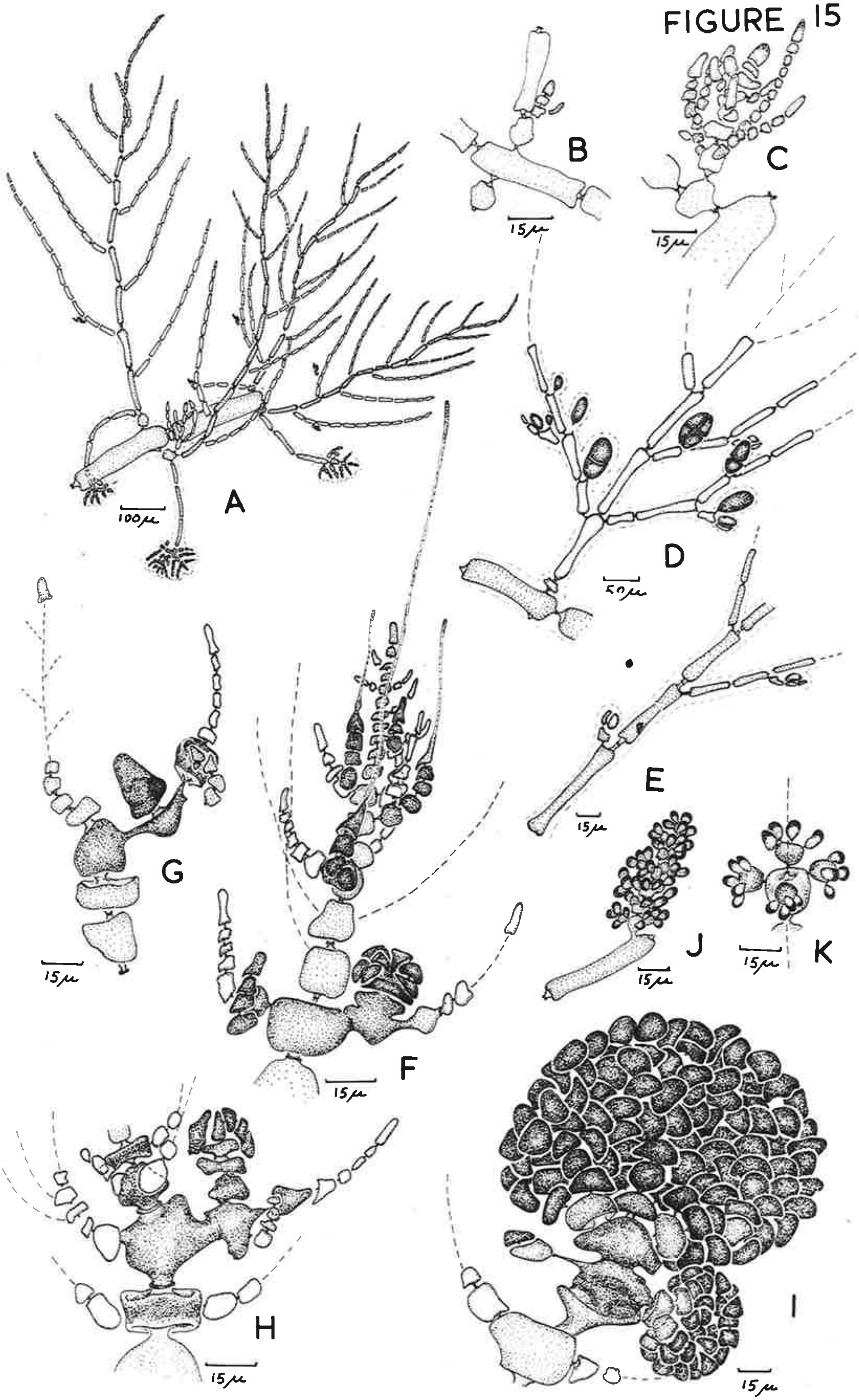


FIGURE 16

Antithamnion gracilentum (Harv.) J. Ag.

A. Thallus of prostrate axes with unattached tips and lateral branches borne alternately on about every 3rd cell.

B. Branch apex with young pinnae and lateral branch initials (a, b and c).

C. Young lateral branch borne in place of a pinna.

D. Pinna with small basal cell and pinnules opposite below and alternate above.

E. Elongate chromoplasts in axial cell of thallus.

F-G Gland-cells borne on special 2-4 celled branches.

H-K Development of branched rhizoidal attachment organs borne on basal cells of pinnae.

FIGURE 16

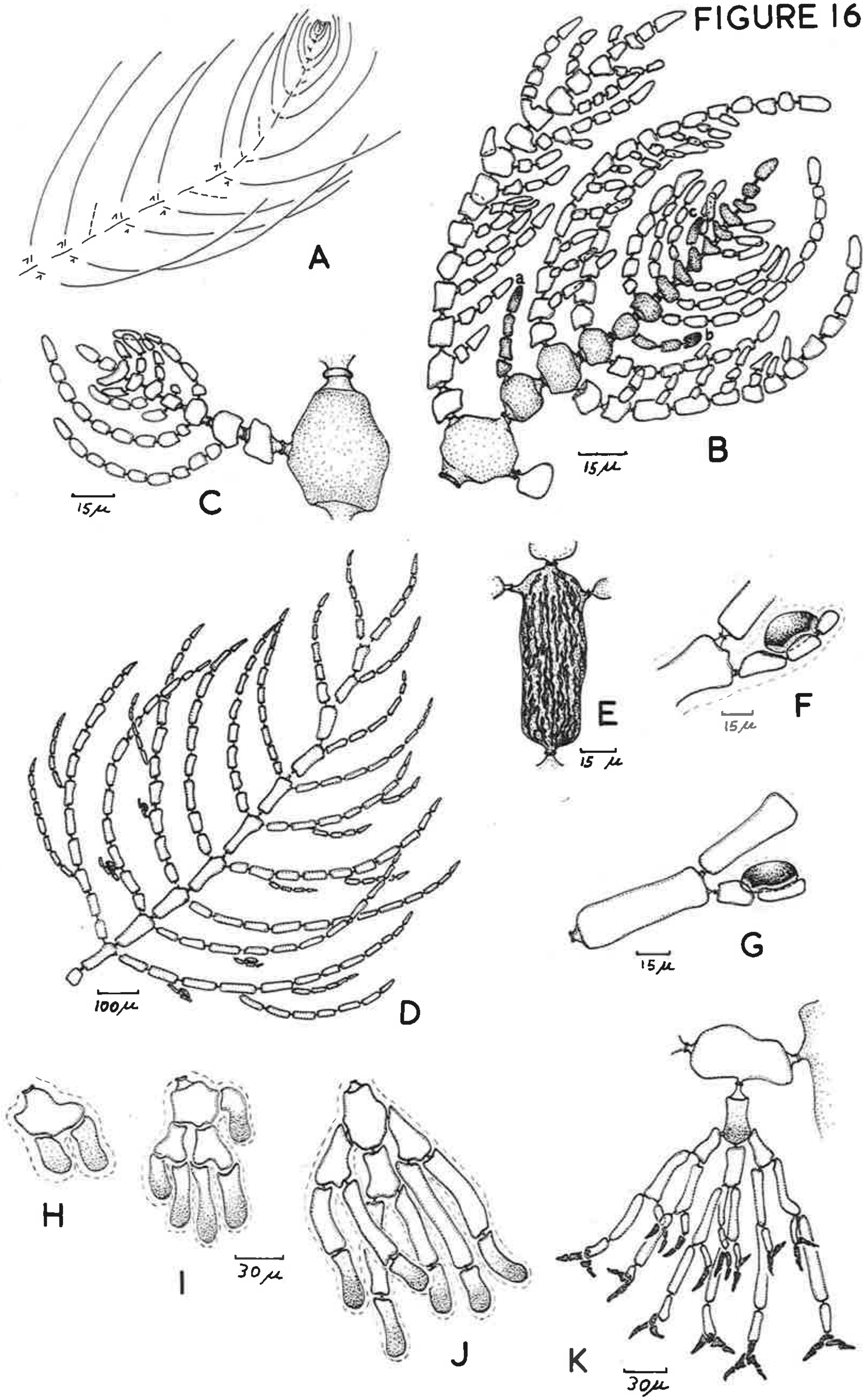


FIGURE 17

Antithamnion gracilentum (Harv.) J. Ag.

A. Tetrasporangia borne on lower cells of pinnules.

B. Spermatangial clusters borne on pinnules usually towards lower part of pinnae.

C. One branch of a spermatangial cluster with terminal whorls of spermatangial mother-cells.

D. Procarps borne on basal cells of pinnae near branch apices.

E. Mature carpogonial branch with spermatium attached to trichogyne.

F. Carposporophyte with marked fusions between cells; branch apex (a) deflected to left and pinnae (b) on fertile axial cell remaining under-developed.

G. Carposporangia produced by successive divisions of initial cells.

Antithamnion pinnafolium n.sp.

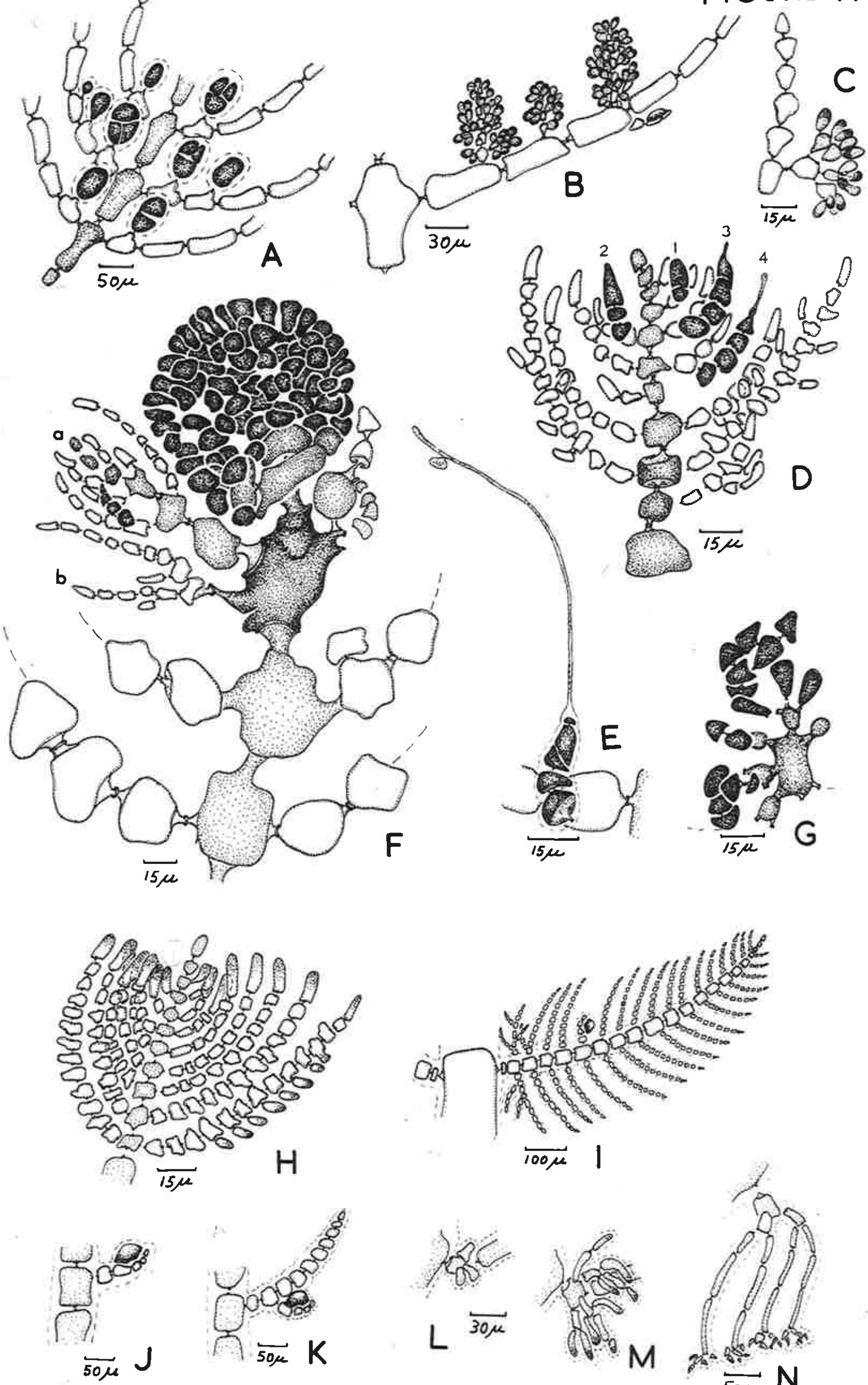
H. Branch apex and development of pinnae.

I. Pinnae with branches on basal pair of pinnules and gland-cell on short branch in place of a pinnule.

J-K Gland-cells borne respectively on short branch directly from cell of rachis of pinna and on lower side of pinnule.

L-N Stages in development of rhizoidal attachment organs.

FIGURE 17


A
50µ
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30µ
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2
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15µ
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b
F
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15µ
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15µ
I
100µ
J
50µ
K
50µ
L
30µ
M
N
50µ

FIGURE 18

Antithamnion armatum (J.Ag.) De Toni.

A. Branching of thallus.

B. Distichous arrangement of pinnae bearing unilateral pinnules and gland-cells.

C. Gland-cells borne on short-branches from cells of pinnules.

D. Lateral branch formed near branch apex in place of a pinna.

E. Initiation of pinnae and pinnules near branch apex.

F-I. Stages in development of rhizoidal attachment organs.

J. Tetrasporangia borne on special gland-cell-bearing branches of pinnules.

Antithamnion diminuatum n. sp.

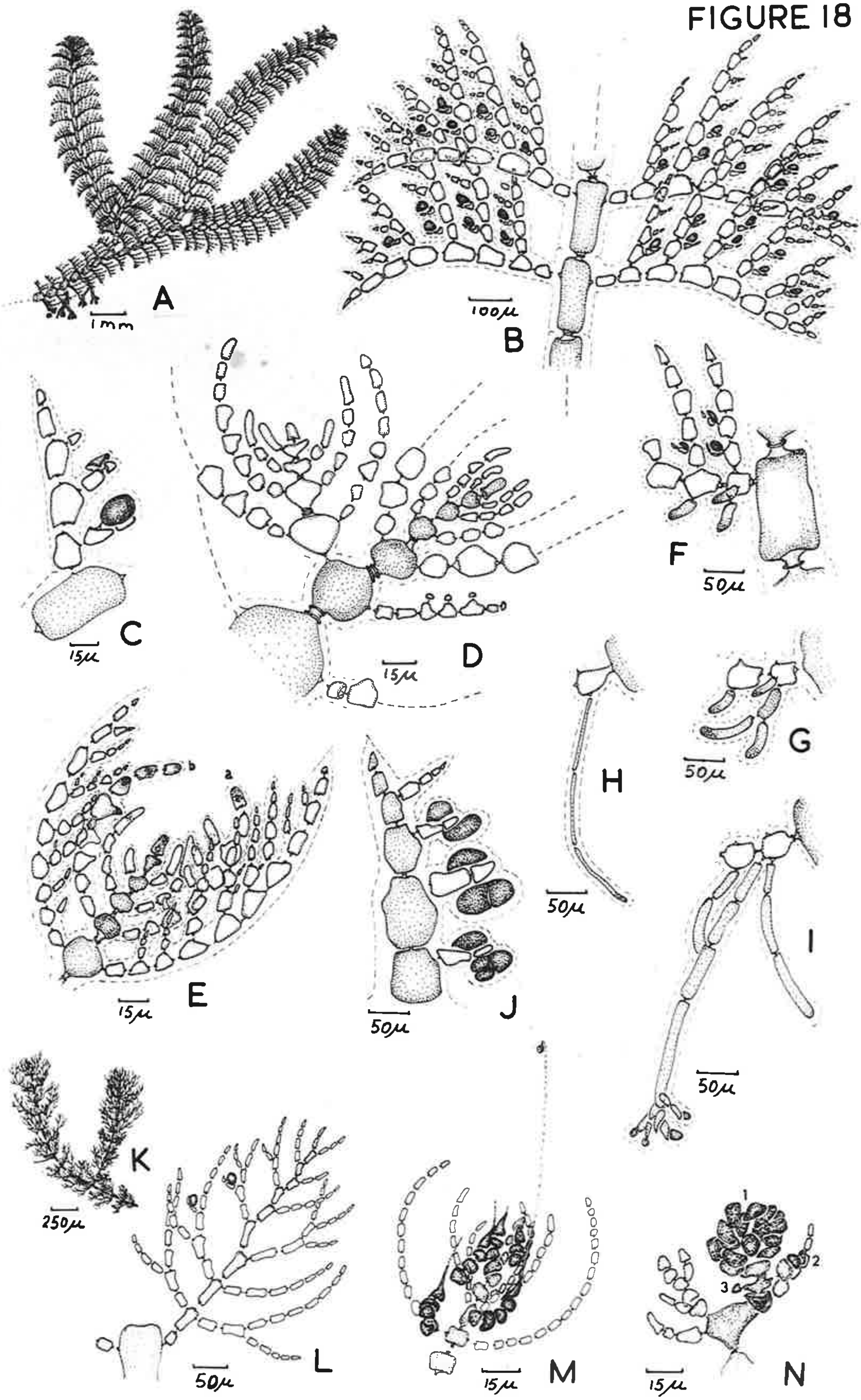
K. Portion of thallus with upcurved pinnae.

L. Pinna with branched pinnules and gland-cells.

M. Procarps borne on basal cells of successive pinnae near branch apex.

N. Groups of carposporangia (1,2 and 3) developing on carposporophyte near branch apex which is deflected to the left.

FIGURE 18



A
1mm
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100μ
C
15μ
D
15μ
F
50μ
H
50μ
G
50μ
a
b
E
15μ
J
50μ
I
50μ
K
250μ
L
50μ
M
15μ
1
2
3
N
15μ

FIGURE 19

Antithamnion hanowioides (Sond.) De Toni.

A. Thallus with decussate upwardly-curved pinnae.

B. Lateral branch on basal cell of pinna.

C. Mature pinna with branched pinnules and gland-cells.

D. Gland-cell on special short branch.

E. Group of developing attachment rhizoids.

F-G. Terminal digitate attachment organs on rhizoids.

H. Tetrasporangia borne on branches of pinnules.

I. Special branch, with lateral branch (a), bearing terminal whorls of spermatangial mother-cells.

J. Carpogonial branch initial borne on basal cell of pinna.

K-L. Formation of 4-celled carpogonial branch.

M. Procarps near branch apex; lowest one with enlargement of supporting cell before cutting off auxiliary cell.

N. Beginning of separation of auxiliary cell from supporting cell. Connecting cell forming from carpogonium.

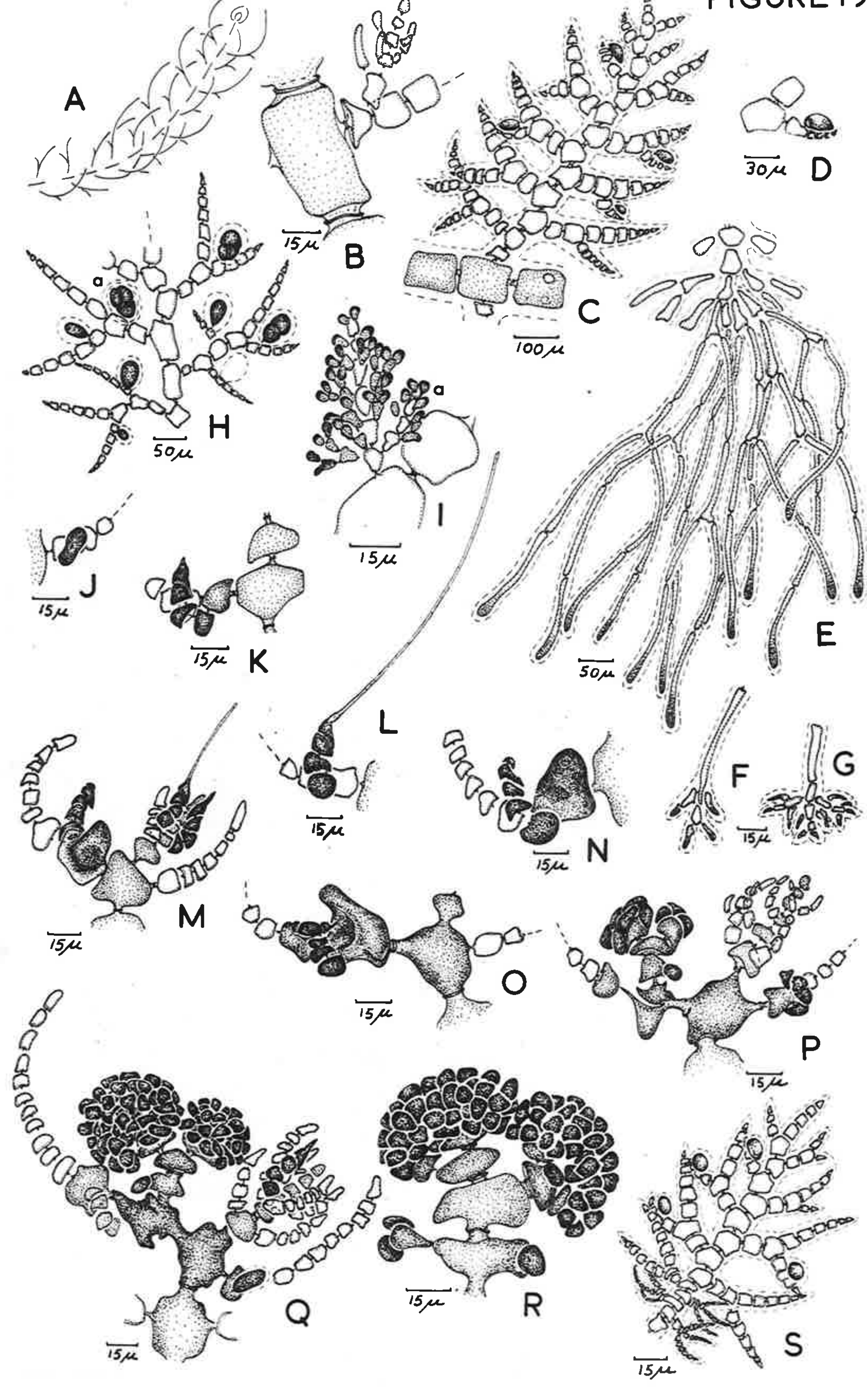
O. Stage near fusion of carpogonium with auxiliary cell via the connecting cell.

P-Q. Terminal bi-lobed group of carposporangia developing on carposporophyte.

R. Central cell of carposporophyte with initials of two lateral carposporangial groups and terminal group consisting of 2 lobes borne on large vegetative cells.

S. Pinna, with small-celled basal branches, at fertile branch apex.

FIGURE 19



A
15μ
B
C
100μ
30μ
D
E
50μ
a
H
50μ
a
I
15μ
J
15μ
K
15μ
L
15μ
M
15μ
N
15μ
F
G
15μ
O
15μ
P
15μ
Q
15μ
R
15μ
S
15μ

FIGURE 20

Platythamnion nodiferum (J.Ag.) n. comb.

A. Portion of thallus.

B. Main axis (A_1) bearing lateral branches (B_1, B_2 and B_3).

C. Spine-like processes on tip of pinna.

D. Gland-cell cut off laterally from cell of rachis of pinna.

E. Axial cells each bearing a whorl of 2 long + 2 short pinnae.

F. Rhizoidal filaments borne on inner cells of pinnae.

G. Digitate process borne terminally on attachment rhizoid.

H. Tetrasporangia on branches at base of pinnae.

I. Procarps borne near branch apices.

J-M. Stages in development of 4-celled carpogonial branch from initial borne on basal cell of pinna.

N. Group of procarps at fertile branch apex.

O. Carposporophyte with groups of carposporangia borne on central cell.

P-Q. Spermatangial mother-cells borne terminally on special branches.

R-V. Stages in development of a tetrasporangium.

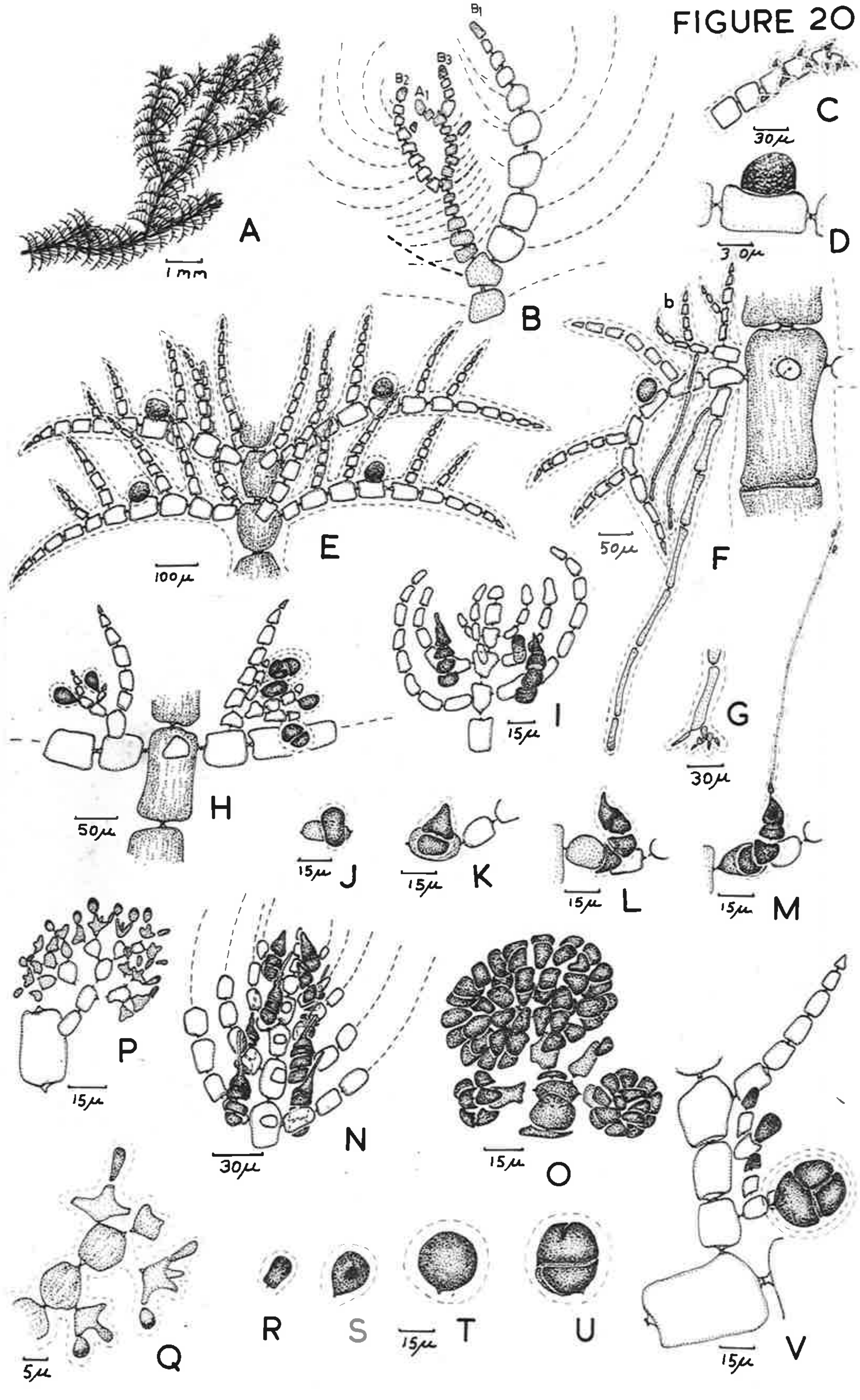


FIGURE 20
A
1 mm
B1
B2
B3
A1
B
C
30μ
D
30μ
b
E
100μ
F
50μ
G
30μ
H
50μ
I
15μ
J
15μ
K
15μ
L
15μ
M
15μ
P
15μ
N
30μ
O
15μ
Q
5μ
R
S
T
15μ
U
V
15μ

FIGURE 21

Ballia mariana Harvey

A. Axial cells of thallus bearing whorls composed of 1 long branchlet opposite 2 short branchlets.

B. Branching of minor pinna.

C. Short branches and rhizoidal filaments borne on basal cells of whorl-branchlets.

D. Tetrasporangia on short branches at base of whorl-branchlets.

E. Spermatangial mother-cells in terminal whorls on special branches of whorl-branchlets.

Ballia ballioides (Sond.) n.comb.

F. Axial cell bearing whorl of 1 long (major) branchlet (1), opposite 2 short (minor) branchlets (2 and 3).

G. Arrangement of whorl-branchlets of axial cell.

H. Development of branchlets at branch apex.

I. Tetrasporangia borne on short branches at base of branchlets.

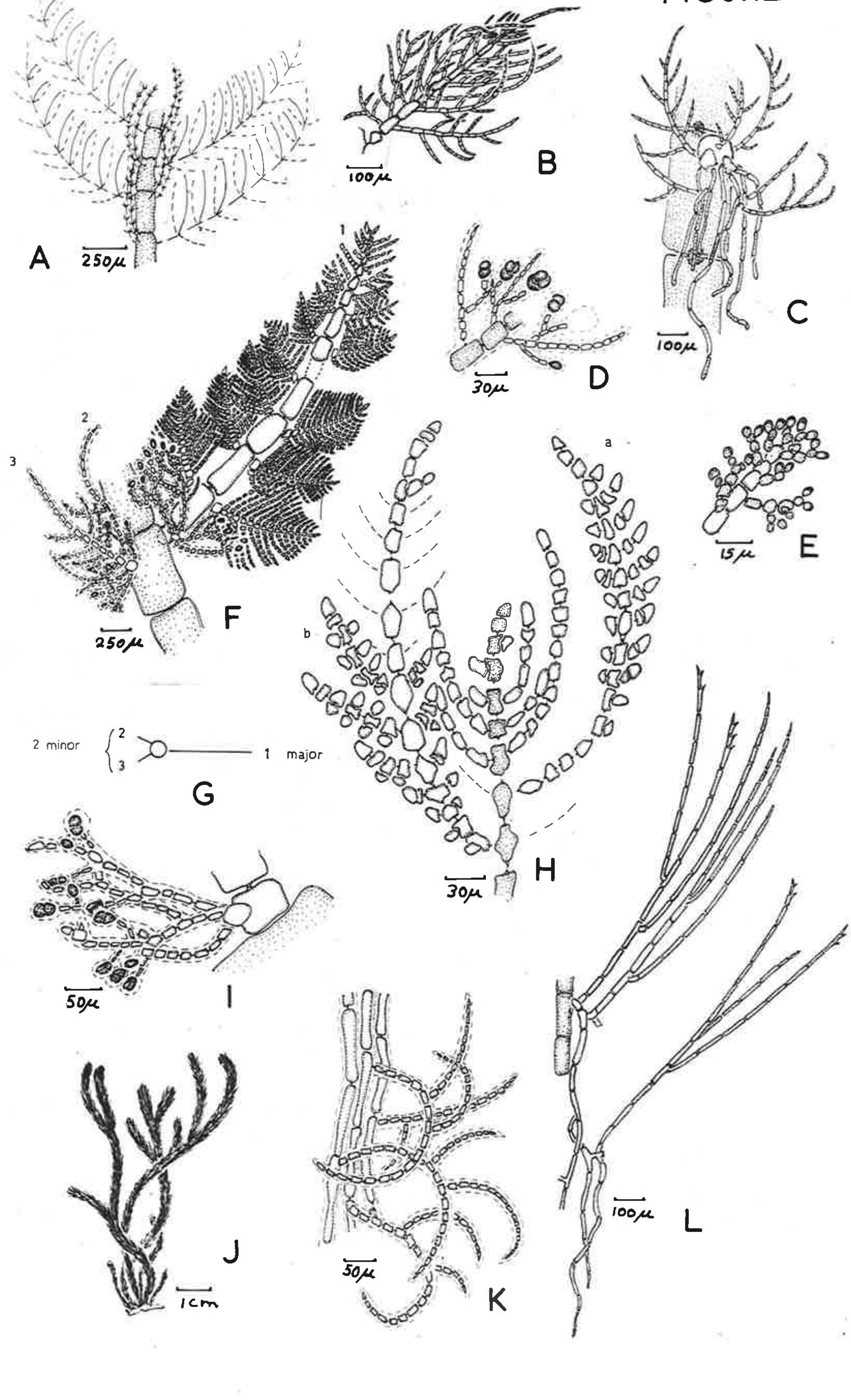
Ballia hirsuta n. sp.

J. Shaggy, erect branches of thallus.

K. Curved lateral branches on cells of rhizoidal filaments.

L. Determinate branches produced from cells of rhizoidal filaments.

FIGURE 21



A
250µ
B
100µ
C
100µ
D
30µ
E
15µ
F
250µ
1
2
3
G
2 minor
2
3
1 major
H
a
b
30µ
I
50µ
J
1cm
K
50µ
L
100µ

FIGURE 22

Ballia callitricha (Ag.) Mont.

A. Long branchlet with development of short branches at base.

B. Branch apex with large apical cell.

C. Axis showing elaboration of cell junctions in face-view.

D. Long branchlets showing elongation of rachides and consequent loss of pinnules.

E. Tetrasporangia borne on short branches at base of branchlet .

F-G. Apical cell showing development of elaboration of cell-junction.

H. Mature cell junction in lateral view.

I. Capping structure from one side of pit-connection at cell junction.

Ballia pennoides n. sp.

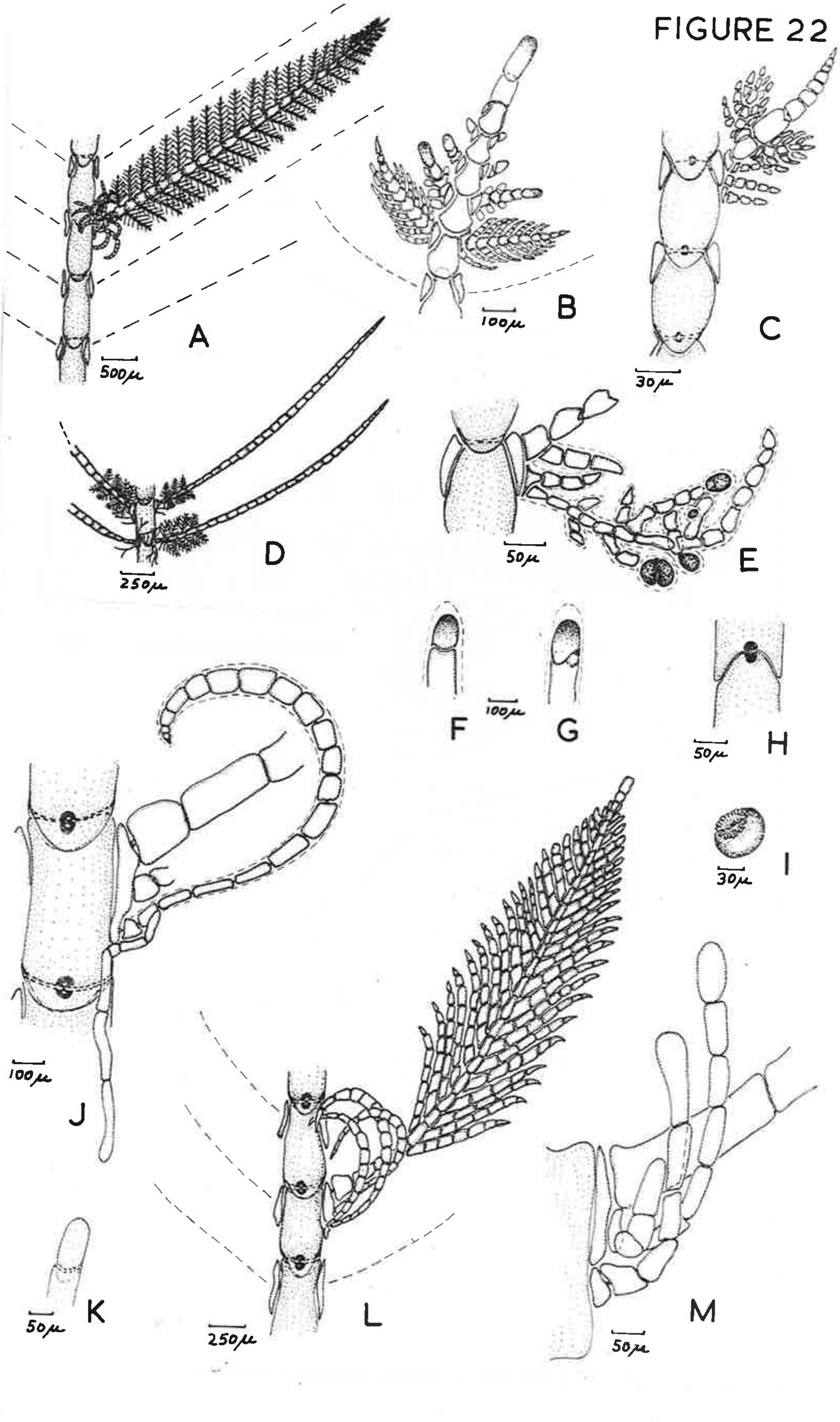
J. Unbranched short branch and rhizoidal filament borne on basal cells of branchlet.

K. Large apical cell of branch axis.

L. Pinna having unbranched pinnules.

M. Developing short branches at base of pinna.

FIGURE 22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E
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50μ
I
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J
100μ
K
50μ
L
250μ
M
50μ

FIGURE 23

Ballia scoparia Harvey.

A. Portion of thallus with apical growth from branches as well as from main axis.

B-E. Initiation of lateral branch from axial cell near branch apex.

F. Part of thallus showing determinate acute-pointed branchlets and intertwining corticating filaments of axis.

G. Spine-like processes on cells near tip of determinate branch.

H-I. Tetrasporangia terminal on cells of special branches near base of thallus-branches.

J-L. Origin and development of rhizoidal filaments corticating the axis.

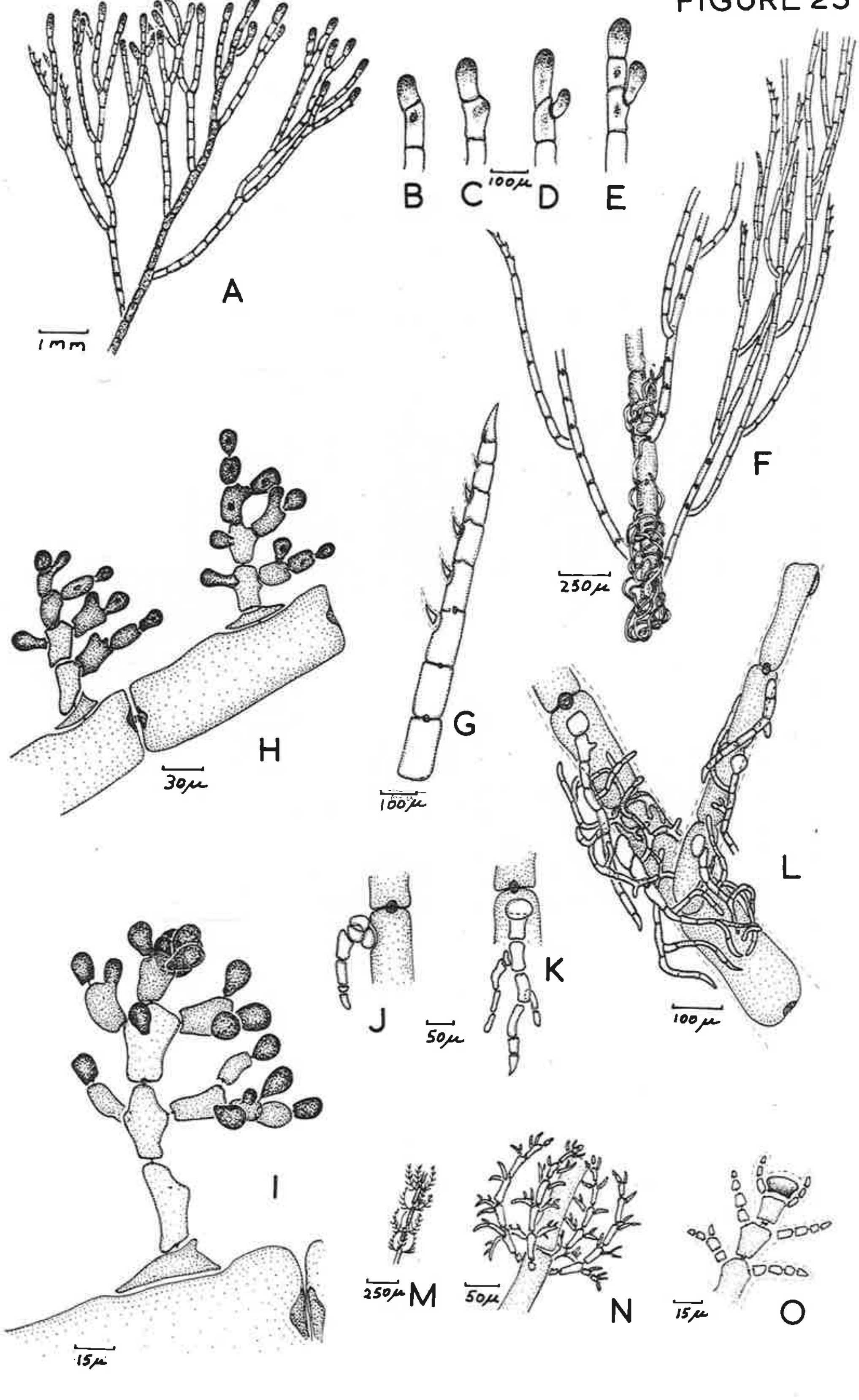
Acrothamnion arcuatum n. sp.

M. Part of thallus with upcurved whorl-branchlets.

N. Axial cell bearing whorl of 4 branchlets.

O. Gland-cell terminal on rachis of whorl-branchlet.

FIGURE 23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K
L
100μ
M
250μ
N
50μ
O
15μ

FIGURE 24

Acrothamnion preissii (Sond.) n. comb.

A. Erect axes of thallus arising from prostrate portion.

B. Axial cells bearing whorls of major and minor pinna-like branchlets. Lateral branch (a) arising from basal cell of pinna.

C. Spermatangial mother-cells borne in clusters on short branches replacing pinnules of pinnae.

D. Part of prostrate axis with erect lateral branches (a and c) and attachment rhizoids (b and d) borne on basal cells of pinnae.

E-I. Various forms of minor pinnae with or without terminal gland-cells.

J. Tetrasporangia borne on upward protrusions of basal cells of pinnae.

K. Tip of pinna without gland-cell.

L. Tip of pinna bearing gland-cell terminally on rachis.

M. 4-celled carpogonial branch borne on basal (supporting) cell of pinna.

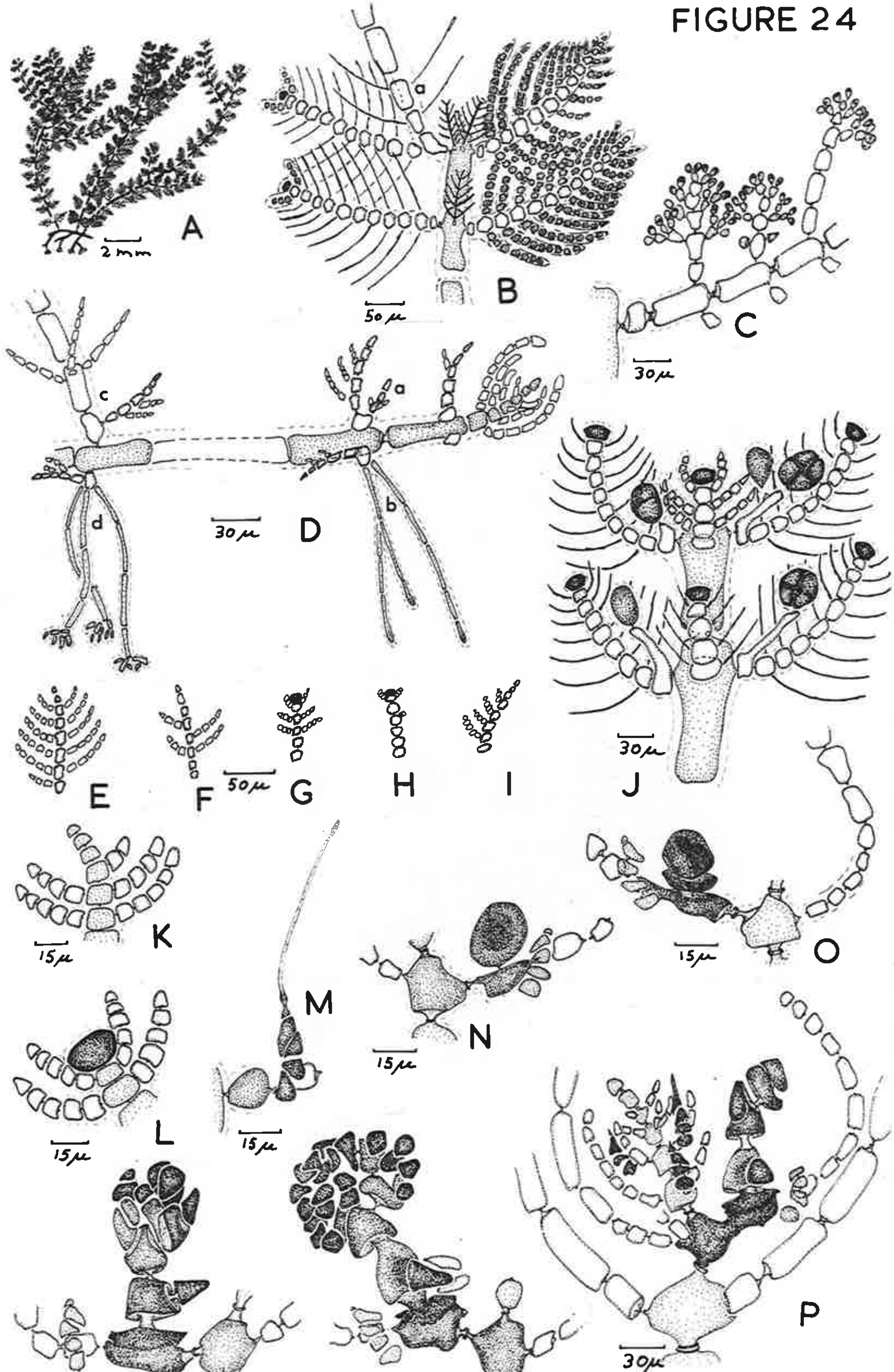
N. Auxiliary cell cut off from upper side of supporting cell.

O. Auxiliary cell divided to form lower foot cell and upper central cell.

P. Procarps near branch apex; lowest one with carposporo-sporophyte showing fusion between cells and development of carposporangial groups from central cell.

Q-R. Carposporophytes with central cells bearing lateral carpo-sporangial bud and maturing terminal groups composed of carposporangial lobes borne on sterile cells.

FIGURE 24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J
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K
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L
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M
15 μ
N
15 μ
O
15 μ
P
30 μ
Q
15 μ
R
15 μ

FIGURE 25

Macrothamnion mucronatum (J.Ag.) n. comb.

A. Portion of thallus.

B. Rotation of position of initiation of whorl-branchlets on adjacent axial cells (1-4) represented by circles.

C. Branch apex showing initiation of whorl-branchlets.

D. Mature whorl-branchlets bearing gland-cells.

E. Young gland-cell produced on special branch on branchlet.

F-G. Gland-cells on special branches of whorl-branchlet.

H. Spine-like processes on cells at tip of whorl-branchlet.

I. Tetrasporangia on branches of special branch bearing gland-cell.

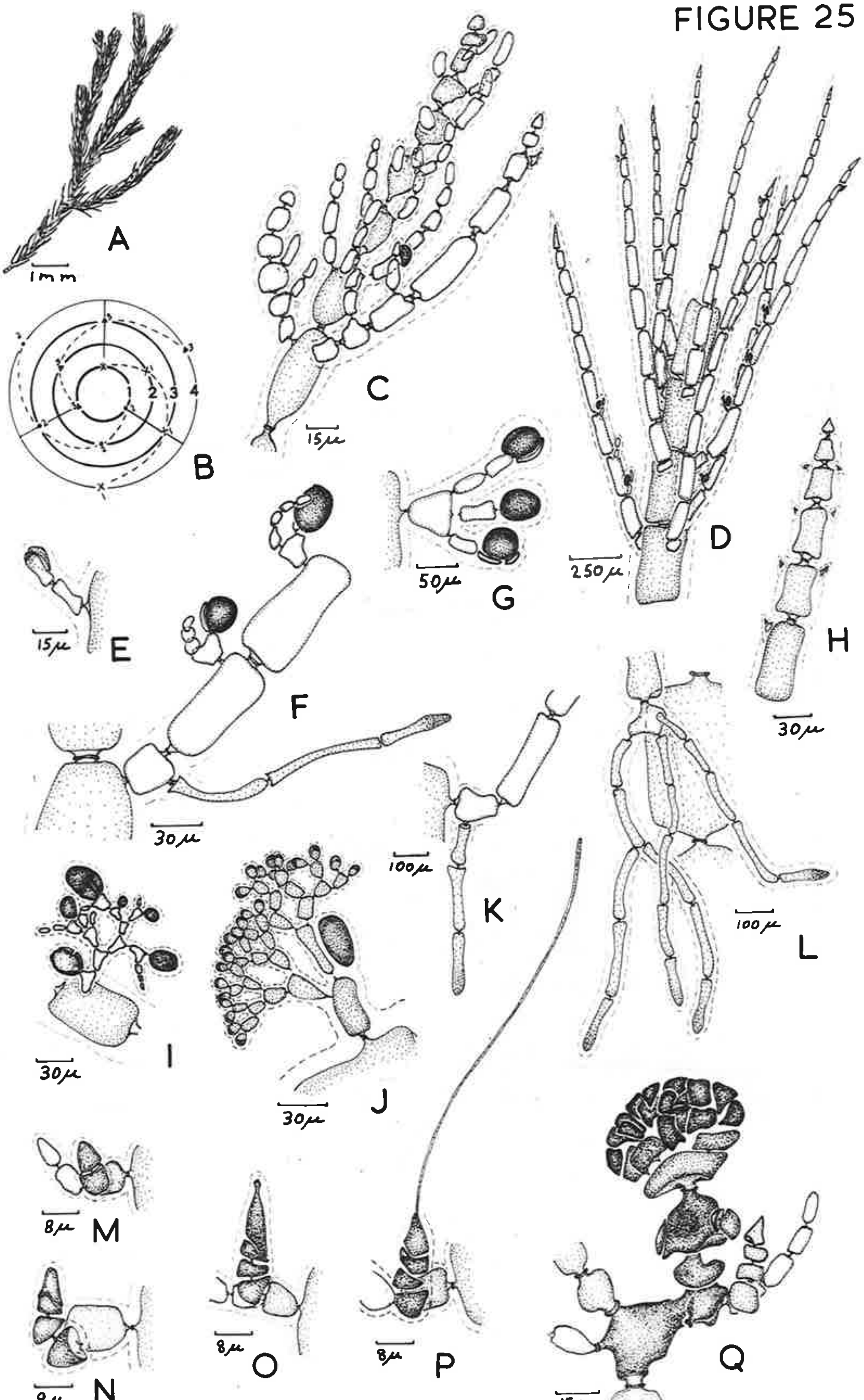
J. Spermatangial mother-cells in terminal whorls on special branches of gland-cell-bearing branch.

F,K-L. Development of rhizoidal filaments from basal cells of whorl-branchlets.

M-P. Stages in development of 4-celled carpogonial branch borne on basal (supporting) cell of whorl-branchlet.

Q. Carposporophyte showing fusions between cells and having central cell with two lateral carposporangial buds and terminal group consisting of carposporangia produced from sterile cells.

FIGURE 25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K
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L
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M
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N
8μ
O
8μ
P
8μ
Q
15μ

FIGURE 26

Macrothamnion secundum n. sp.

A. Portion of thallus.

B. Branch tip with procarps borne on basal cells of young whorl-branchlets.

C. Whorl-branchlets, in whorls of 3 from each axial cell, unilaterally branched and bearing gland-cells.

D. Acute tip of young mature whorl-branchlet.

E. Whorl-branchlet with acute apices and gland-cells on special branches toward base of branchlet.

F-G Development of rhizoidal filaments from basal cells of whorl-branchlets; attachment organs borne terminally on filaments.

FIGURE 26

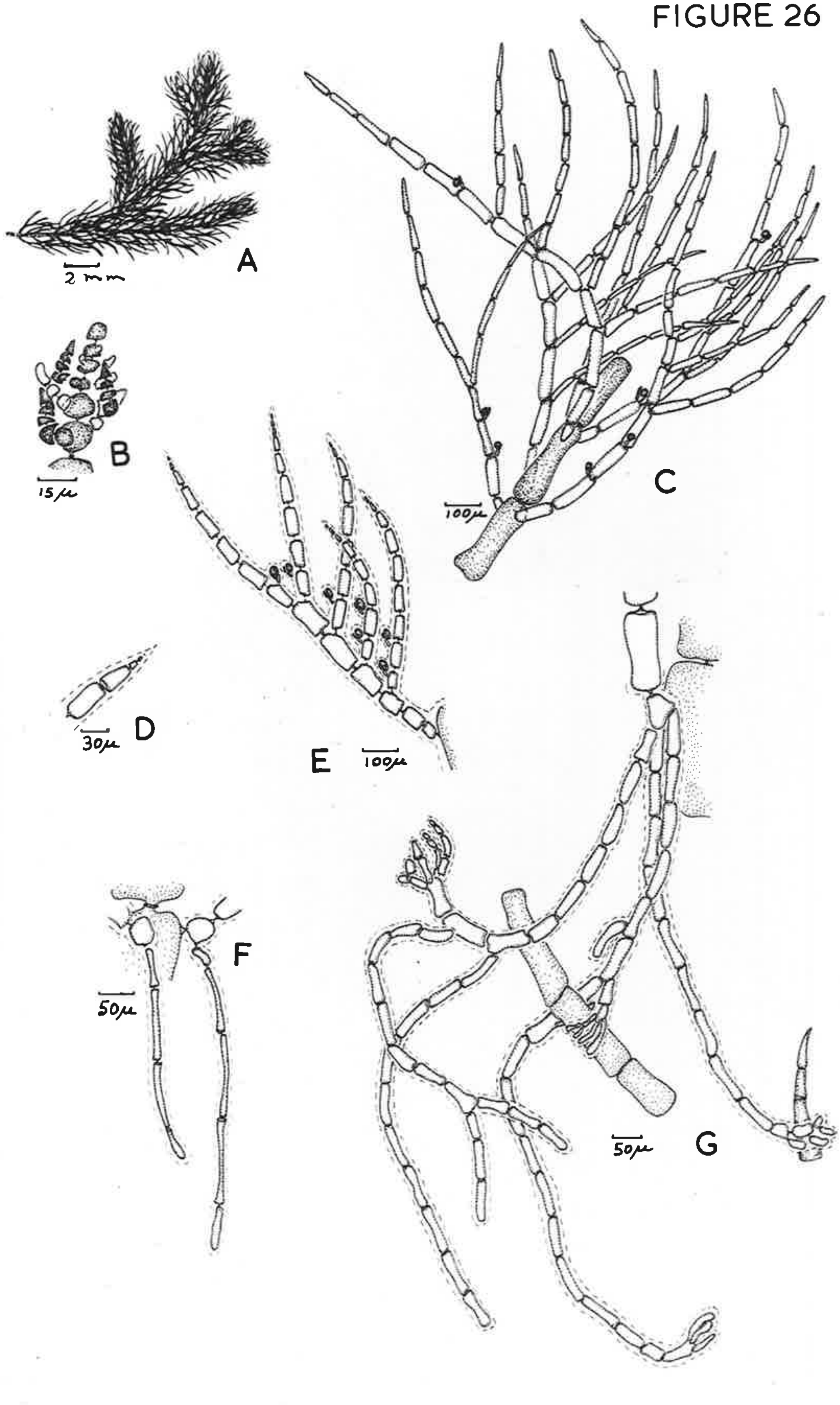


FIGURE 27.

Macrothamnion secundum n. sp.

A - D. Developmeht of gland-cells showing disintegration of the first formed gland-cell after formation of a second gland-cell on the same branch.

E-I. Development of tetrasporangia on the special gland-cell-bearing branches.

J. Spermatangial cluster formed as a branch of a special gland-cell-bearing branch.

K. Procarps produced on basal cells of whorl-branchlets near branch apex.

L. Enlargement of supporting cell prior to cutting off of auxiliary cell; connecting cell forming from base of carpogonium.

M. Stage immediately following fusion of the auxiliary cell and carpogonium via a connecting cell.

N. Maturing groups of carposporangia borne on sterile cells produced from the central cell of the carposporophyte;

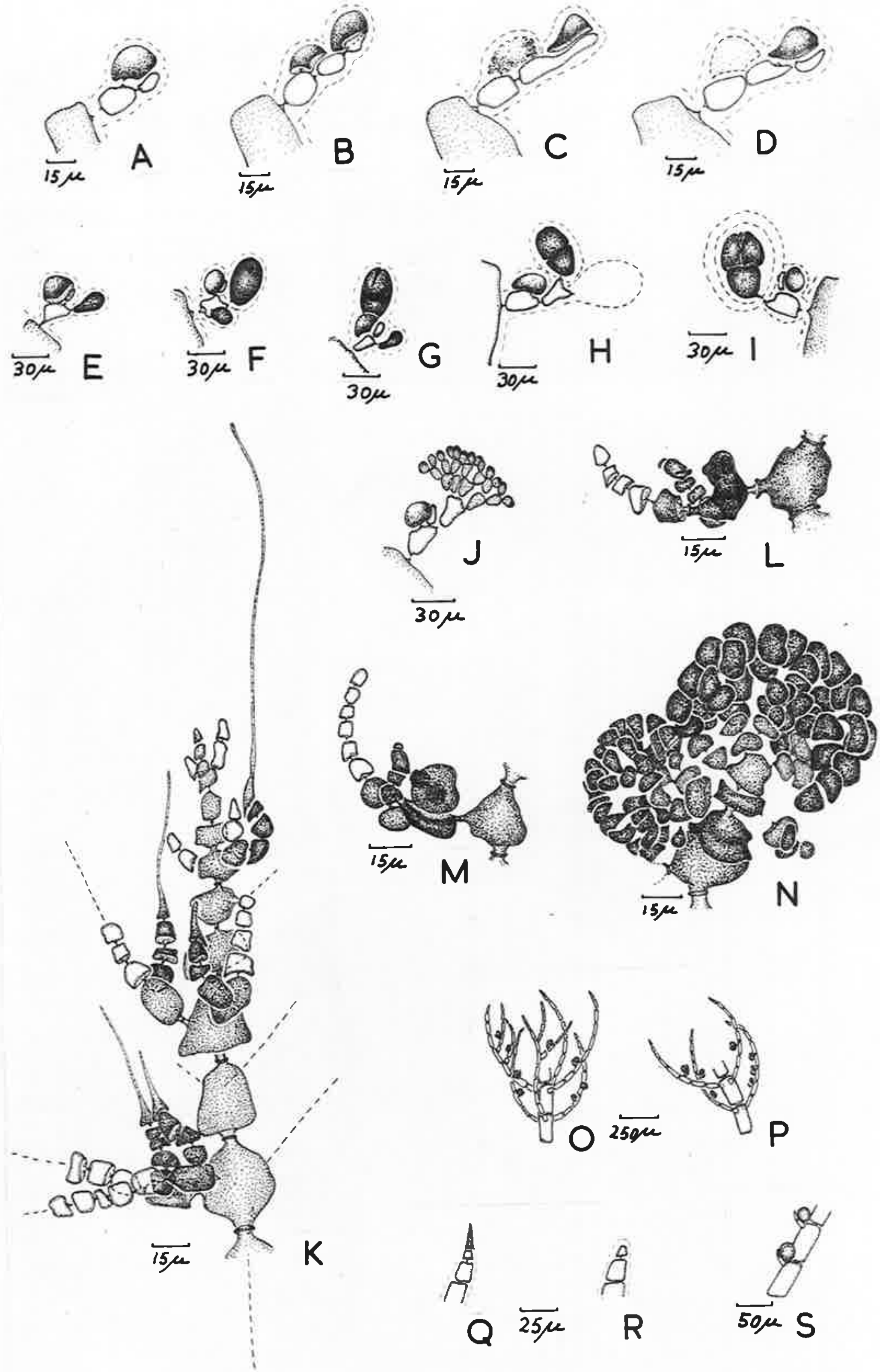
Macrothamnion pectenellum n. sp.

O-P. Axial cells bearing whorls of 2-3 whorl-branchlets.

Q. Acute tip of whorl-branchlet.

R. Tip of whorl-branchlet after loss of acute terminal cell.

S. Gland-cells borne on special short branches from cells of whorl-branchlet.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J
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L
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M
15μ
N
15μ
K
O
250μ
P
Q
25μ
R
50μ
S

FIGURE 28

Antithamnionella tasmanica n.sp.

A. Thallus of prostrate and erect axes.

B. Branch apex showing initiation of whorl-branchlets.

C-D. Whorl-branchlets, branched or unbranched, in whorls of 3-4 on each axial cell.

E. Gland-cells borne on 4th cell and tetrasporangia from basal cells of whorl-branchlets.

F-G. Rhizoidal attachment filaments and young lateral (erect) branch borne on basal cells of the whorl-branchlets of the prostrate axis.

H. Spermatangial clusters on cells of whorl-branchlet.

I. Young spermatangial branch showing initiation of spermatangial-mother-cells on the central axis.

J. Procarp borne on axial cell near branch apex.

K. Procarp close to fusion of auxiliary cell with carpogonium via a connecting cell.

L. Immediately after fusion; auxiliary cell cut off from upper side of supporting cell.

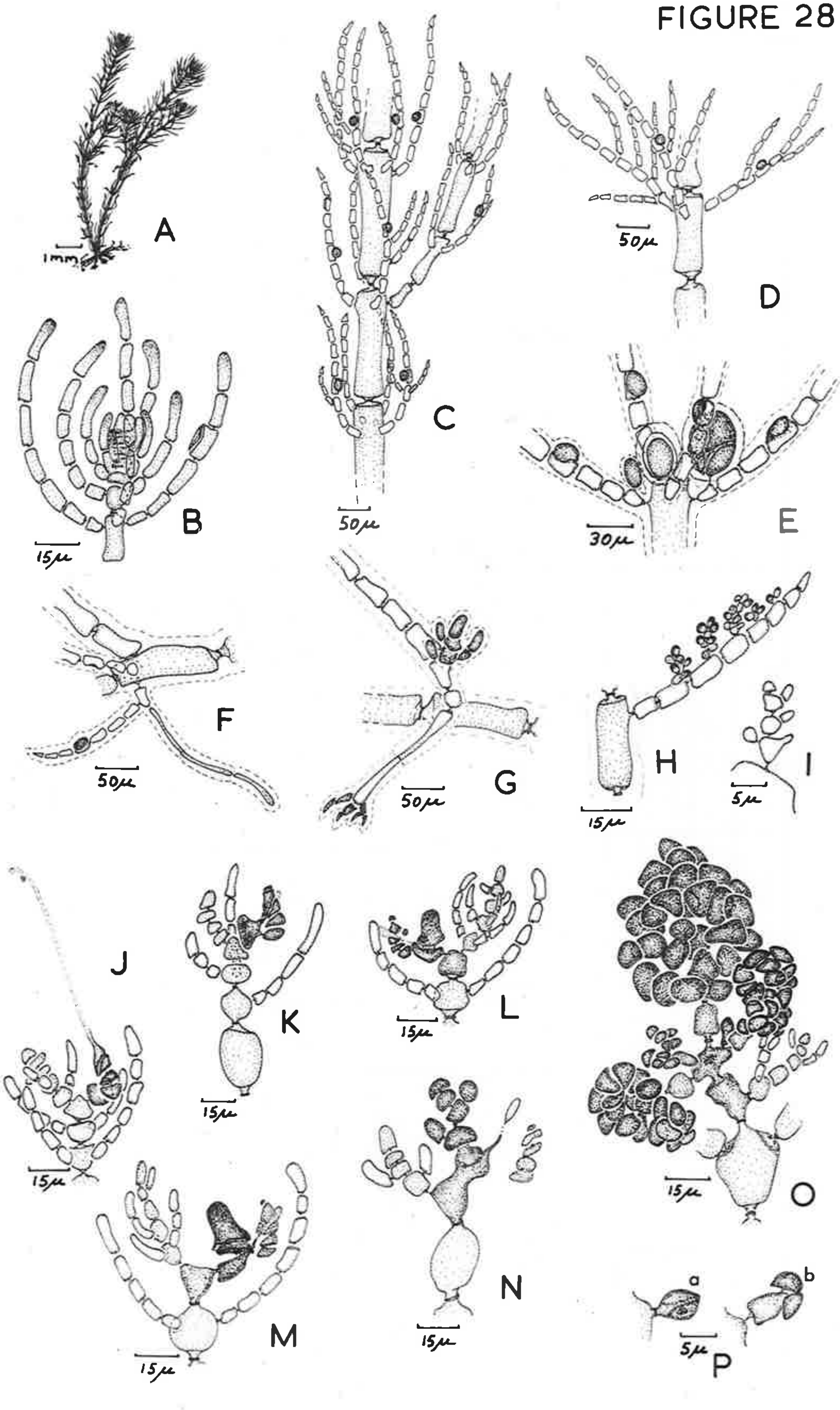
M. Division of auxiliary cell to form a lower foot-cell and an upper central-cell.

N. Carposporophyte with marked fusions between cells and developing terminal group of carposporangia.

O. Carposporophyte with 5 developing groups of carposporangia from the central cell.

P. First divisions of carposporangial bud.

FIGURE 28



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K
15μ
L
15μ
M
15μ
N
15μ
O
15μ
P
a
b
5μ

FIGURE 29

Antithamnionella spirographidis (Schiff) nov. comb.

A-B. Thallus of prostrate and erect portions showing distribution of whorl-branchlets and lateral branches.

C. Initiation and development of whorl-branchlets and lateral branches (1,2 & 3) at branch apex.

D. Development of gland-cells (a,b and c).

E-F. Attachment rhizoids borne on basal (or second) cell of whorl-branchlet.

G. Erect axis developing from a cell of the digitate attachment process.

H-K. Development of 4-celled carpogonial branch from basal (supporting) cell of young 2-celled whorl-branchlet.

L. Stage near fusion of carpogoium with auxiliary cell (cut off from upper side of supporting cell) via a connecting cell.

M-O. Groups of carposporangia formed from buds developed on the central cell of the carposporophyte. Fusions between cells of carposporophyte (O).

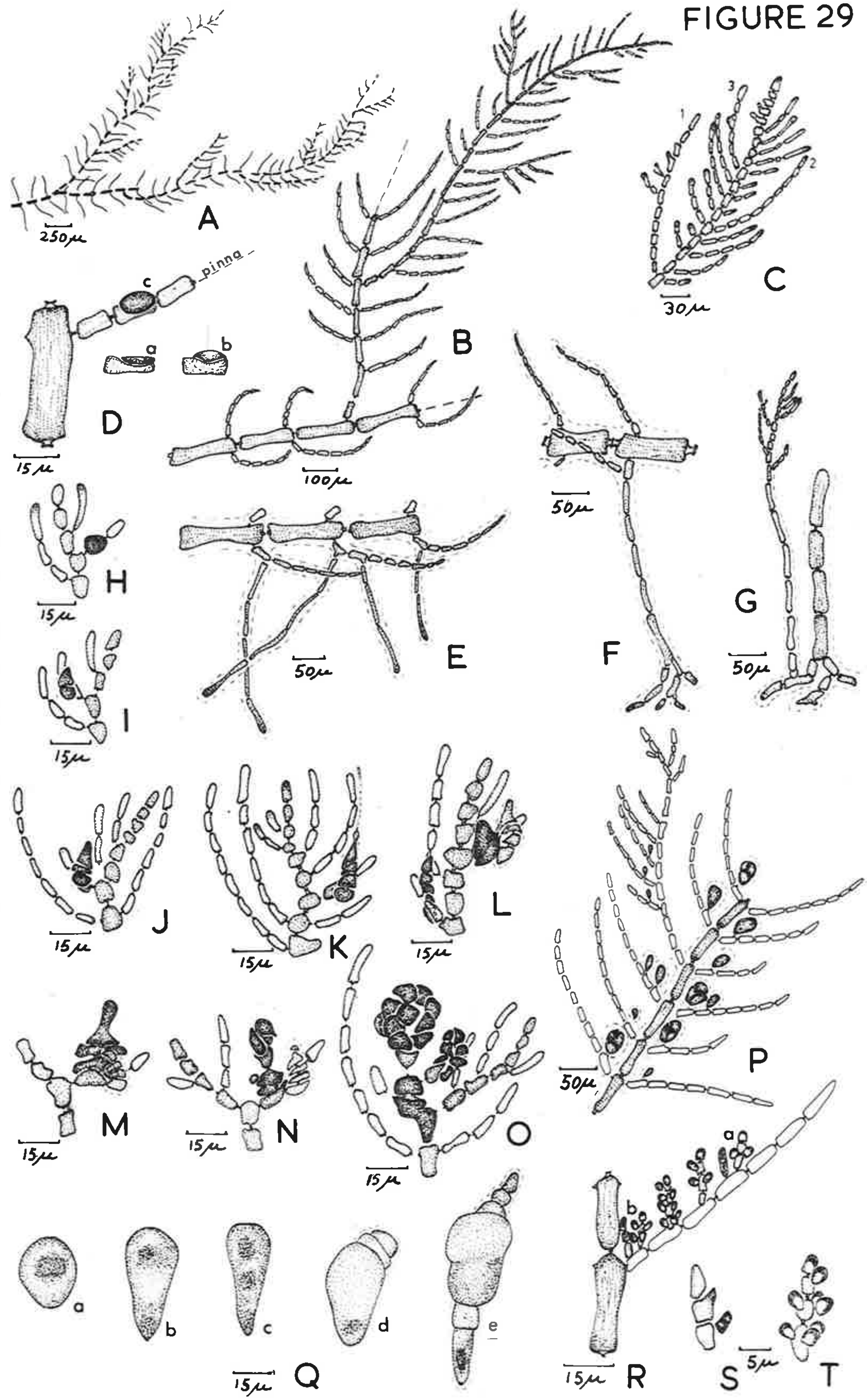
P. Tetrasporangia borne on lower cells of whorl-branchlets.

Q. Stages of spore germination during first 48 hrs. of development.

R. Spermatangial clusters on lower cells of whorl-branchlet.

S-T. Development of spermatangial-mother-cells from axis of special short branch.

FIGURE 29


A
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C
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3
D
15μ
pinna
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b
c
E
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F
50μ
G
50μ
H
15μ
I
15μ
J
15μ
K
15μ
L
15μ
M
15μ
N
15μ
O
15μ
P
50μ
Q
15μ
a
b
c
d
e
R
15μ
S
T
5μ

FIGURE 30.

Antithamnionella glandifera n. sp.

A. Branching habit of thallus. "a" shows intermal at base of new branch before branching commences.

B. Lateral branchex (a, b,c and d) and whorl-branchlets developing at branch tip.

C. Lateral branch borne on basal cell of whorl-branchlet.

D. Mature whorl-branchlets, irregularly branched.

E-G. Increased branching of whorl-branchlets from upper to central parts of thallus.

H. Gland-cells curved around parent-cell of whorl-branchlet.

I. Whorl-branchlet often with two gland-cells borne on a single parent cell.

J. Gland-cell with pitted surface appearance.

K-L. Attachment rhizoids borne on basal cells of whorl-branchlets.

M-O. 4-celled carpogonial branches borne on basal (supporting) cell of 2-celled whorl-branchlet near branch apex.

P-Q. Groups of carposporangia produced from buds borne on central cell of the carposporophyte.

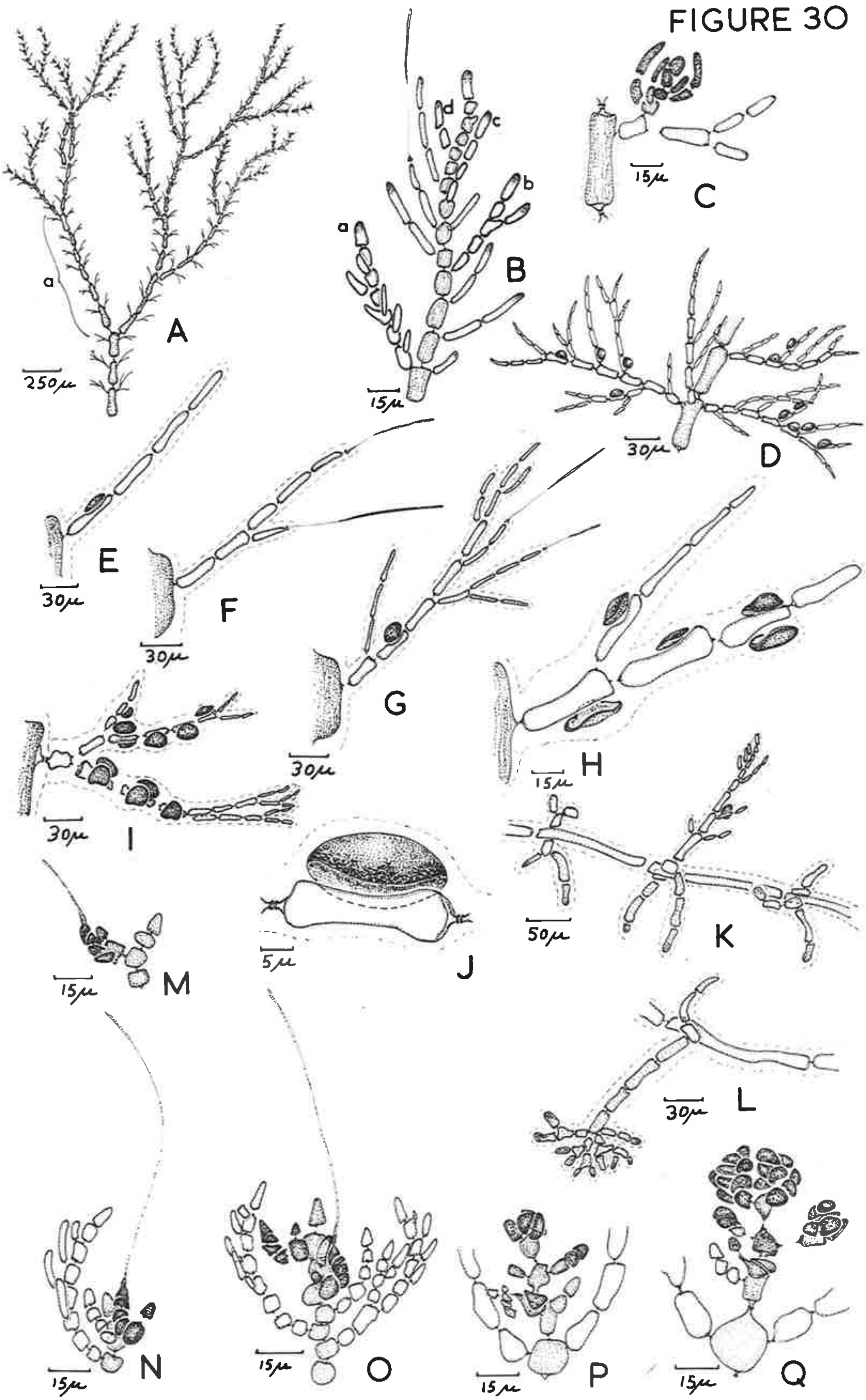
FIGURE 30
a
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Q

FIGURE 31

Heterothamnion muelleri (Sonder) J. Ag.

A. Thallus of branched erect axes.

B. Young thallus attached by penetration between cells of host-tissue.

C. Growing apex of branch and initiation of whorl-branchlets.

D. Mature whorl-branchlets borne in whorls from axial cells.

E. Spermatangial mother-cells borne terminally on cells of special short branches.

F. Tetrasporangia with stalk-cells borne on cells of whorl-branchlets.

G-J. Development of tetrasporangium and stalk-cell from initial cell.

K. 4-celled carpogonial branch borne on basal (supporting) cell of 2-celled whorl-branchlet near branch apex.

L. Auxiliary cell cut off from upper side of supporting cell after fertilization. Trichogyne disintegrating.

M. Connecting cell attached to base of auxiliary cell after fusion with carpogonium.

N. Auxiliary cell divided into a lower foot-cell and an upper central cell.

O. Carposporophyte with carposporangial groups developed from central cell.

Heterothamnion sessile n.sp.

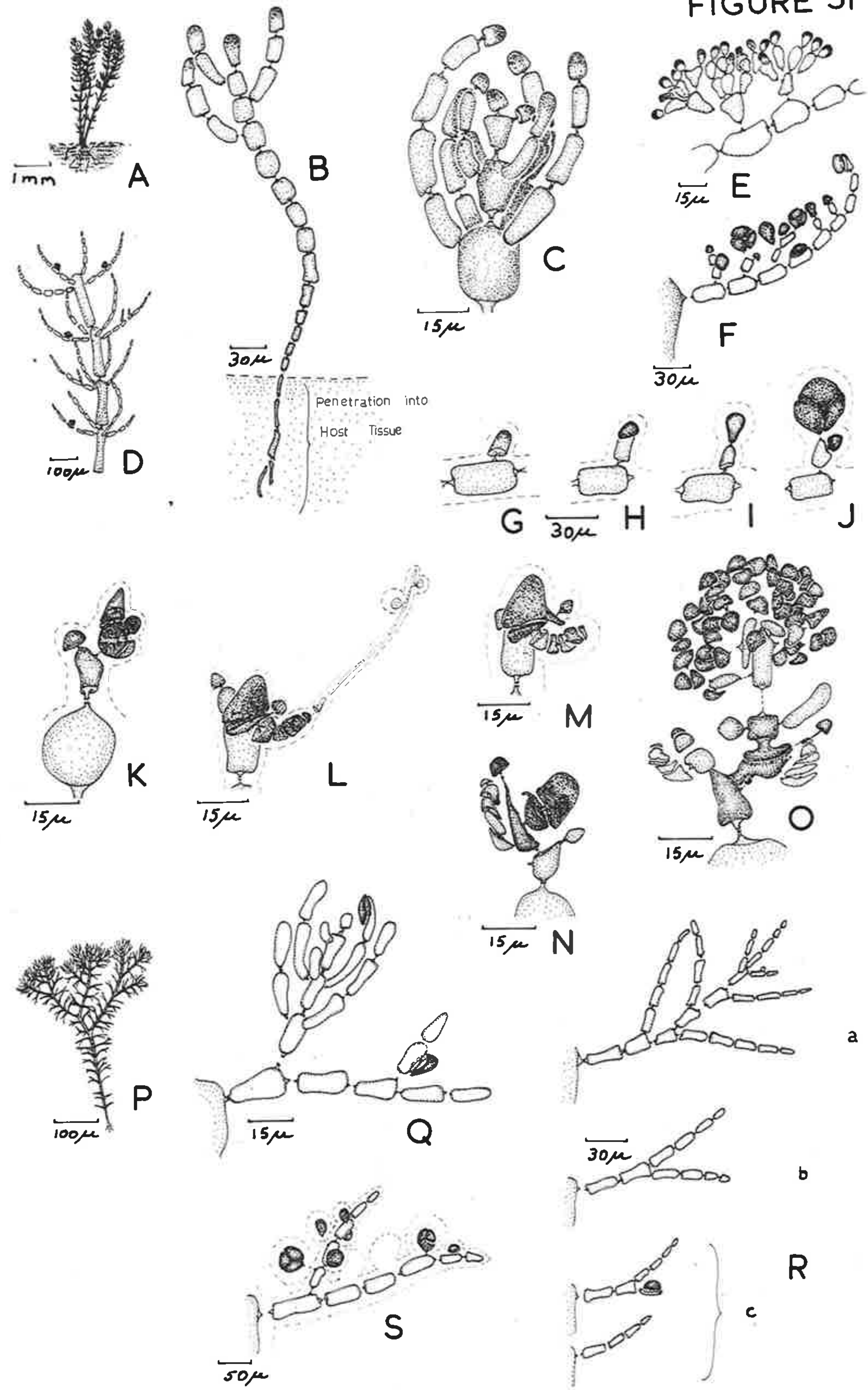
P. Branched erect axis of thallus.

Q. Lateral branch borne on basal cell of whorl-branchlet.

R. a-c shows decrease in length and branching of whorl-branchlets towards base of axis.

S. Tetrasporangia sessile on cells of whorl-branchlets.

FIGURE 31


1mm
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Penetration into
Host Tissue
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R
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FIGURE 32

Heterothamnion episiliquosum n.sp.

A.8 Thallus of branched, erect axes.

B. Attachment of axes by penetration of rhizoids between cells of host tissue.

C. Basal part of erect axis showing reduction in form of whorl-branchlets and in size of axial cells.

D-I. Gland-cell development with a second swollen gland-cell produced from the original gland-cell.

J. Special branches bearing spermatangial mother-cells produced successively on inner to outer cells of whorl-branchlet.

K-L. 4-celled carpogonial branches borne on basal (supporting) cell of 2-celled whorl-branchlets in whorls of up to 4 from the one axial cell.

M. Auxiliary cell cut off from upper side of supporting cell.

N. Carposporophyte showing fusions between cells and 4 groups of carposporangia developing from the central cell.

O. Tetrasporangia borne on cells of whorl-branchlet.

Tetrathamnion ramosum n. sp.

P. Thallus of densely branched erect axes.

Q. Whorl-branchlet bearing tetrasporangia, gland-cells and terminal hairs.

R. Attachment rhizoids penetrating host tissue.

S. Gland-cell on final branching of whorl-branchlet.

T. a. Carpogonial branch on basal (supporting) cell of 2-celled whorl branchlet.

b. Formation of auxiliary cell from upper part of supporting cell.

U. Carposporophyte with 3 carposporangial groups developing from central cell.

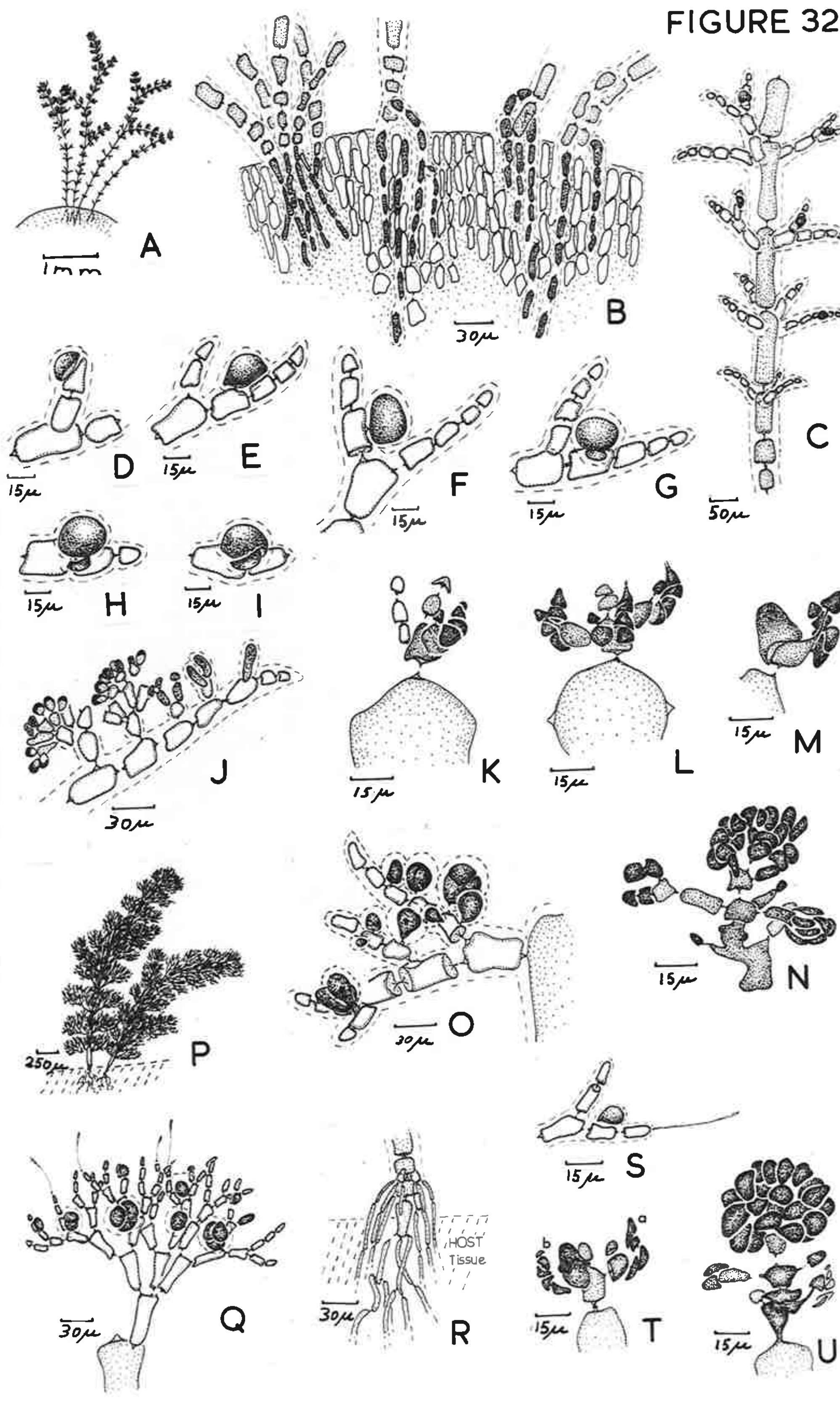
FIGURE 32
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Q
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30μ
R
15μ
S
b
a
15μ
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FIGURE 33

Tetrathamnion lineatum n. sp.

A. Portion of branched thallus.

B-F. Stages in development of a whorl-branchlet.

G. Initiation of whorl-branchlets at branch apex.

H-I. Final branchings of whorl-branchlets with gland-cells and terminal hairs.

J. Attachment rhizoids arising from base of erect axis.

K-L. Stages in formation of tetrasporangia.

M. Whorl of 2-celled whorl-branchlets prior to formation of carpogonial branches from basal cells.

N. a. Initial of carpogonial branch borne on supporting cell.
b. Auxiliary cell developed from upper side of supporting cell.

O. Carpogonial branches developed on basal (supporting) cells of whorl-branchlets.

P. Carposporophyte with maturing carposporangial groups.

Tetrathamnion pyramidatum n.sp.

Q. Portion of thallus.

R. Lateral branch borne on basal cell of whorl-branchlet.

S. Mature whorl-branchlet.

T. Gland-cells on final branch of whorl-branchlet.

U Tetrasporangia borne on outer ends of cells of whorl-branchlet.

V. Attachment rhizoids arising from cells at base of axis.

W. Fertile branch apex. Right - 4-celled carpogonial branch borne on basal cell of 2-celled whorl-branchlet; left - auxiliary cell cut off from supporting cell near time of fusion with carpogonium.

X. Carposporophyte with developing group of carposporangia.

FIGURE 33

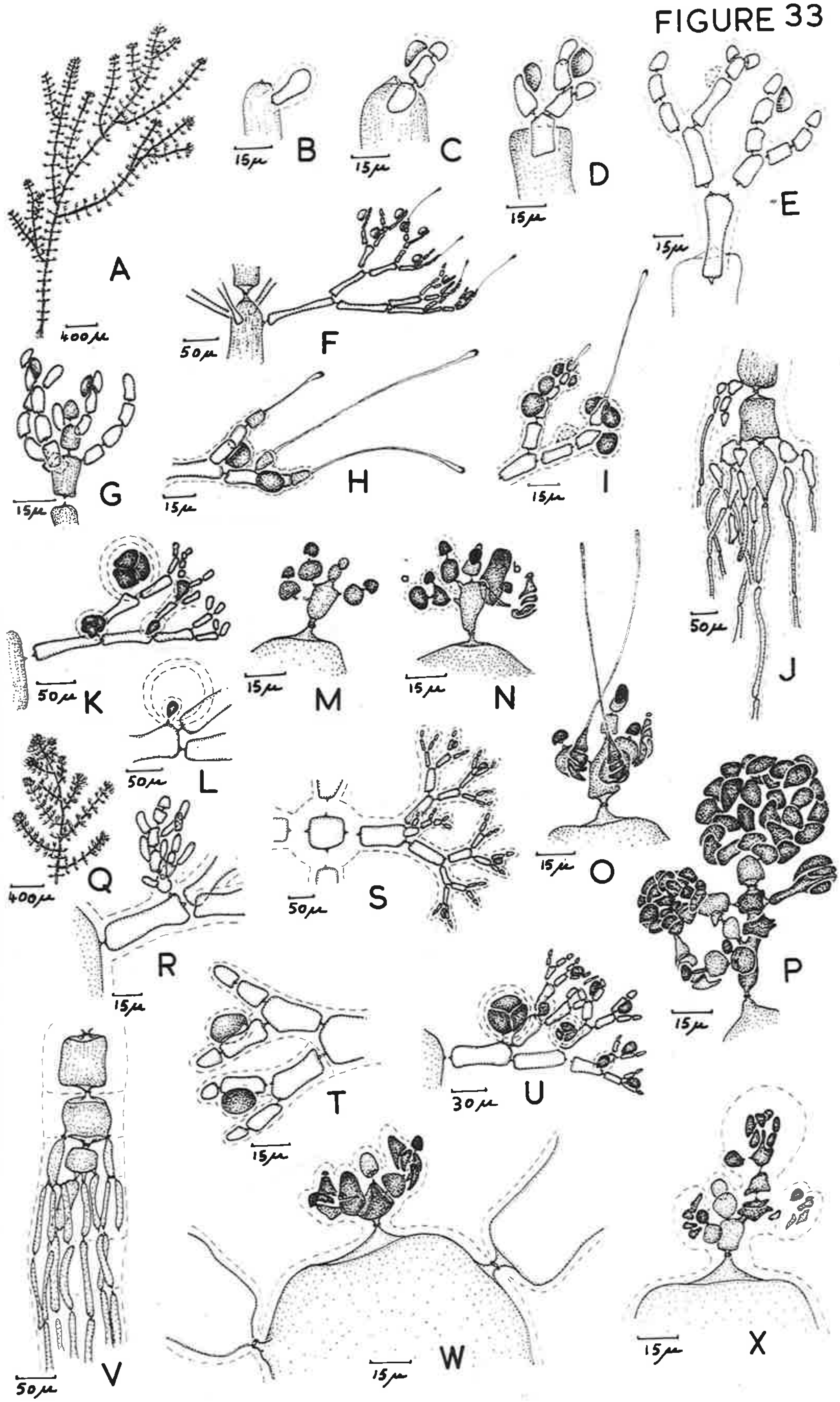
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FIGURE 34

Perithamnion densum n. sp.

A. Portion of densely-branched thallus.

B. Whorl-branchlet with lateral branch borne on basal cell.

C. Gland-cells on outer cells of whorl-branchlet.

D. Spermatangial-mother-cells borne on special branch in position of lateral branch.

E. Tetrasporangia on special branch borne in position of lateral branch.

F. a. 2-celled whorl-branchlet prior to formation of carpogonial branch from basal cell.
   b. carpogonial branch developed from basal (supporting) cell of whorl-branchlet.
   c. Carposporophyte development with auxiliary cell divided into lower foot cell and upper central cell.

G. Carposporophyte with maturing carposporangia.

Perithamnion dispar (Harv.) n. comb.

H. Portion of branched thallus.

I-J. Gland-cells borne on outer cells of whorl-branchlets.

K. Tetrasporangia on special small-celled branches.

L. Attachment rhizoids initiated from basal cell of whorl-branchlet.

M. Carpogonial branch borne on basal (supporting) cell of 2-celled whorl-branchlet.

N. Carposporophyte showing fusions between cells and 5 groups of carposporangia.

O. Positions of whorl-branchlets (1,2,3 and 4) in whorls on three lowest successive cells (a,b and c) of lateral branch in respect to axis A.

P. Various arrangements of whorl-branchlets showing comparative lengths and positions found on different axial cells.

FIGURE 34

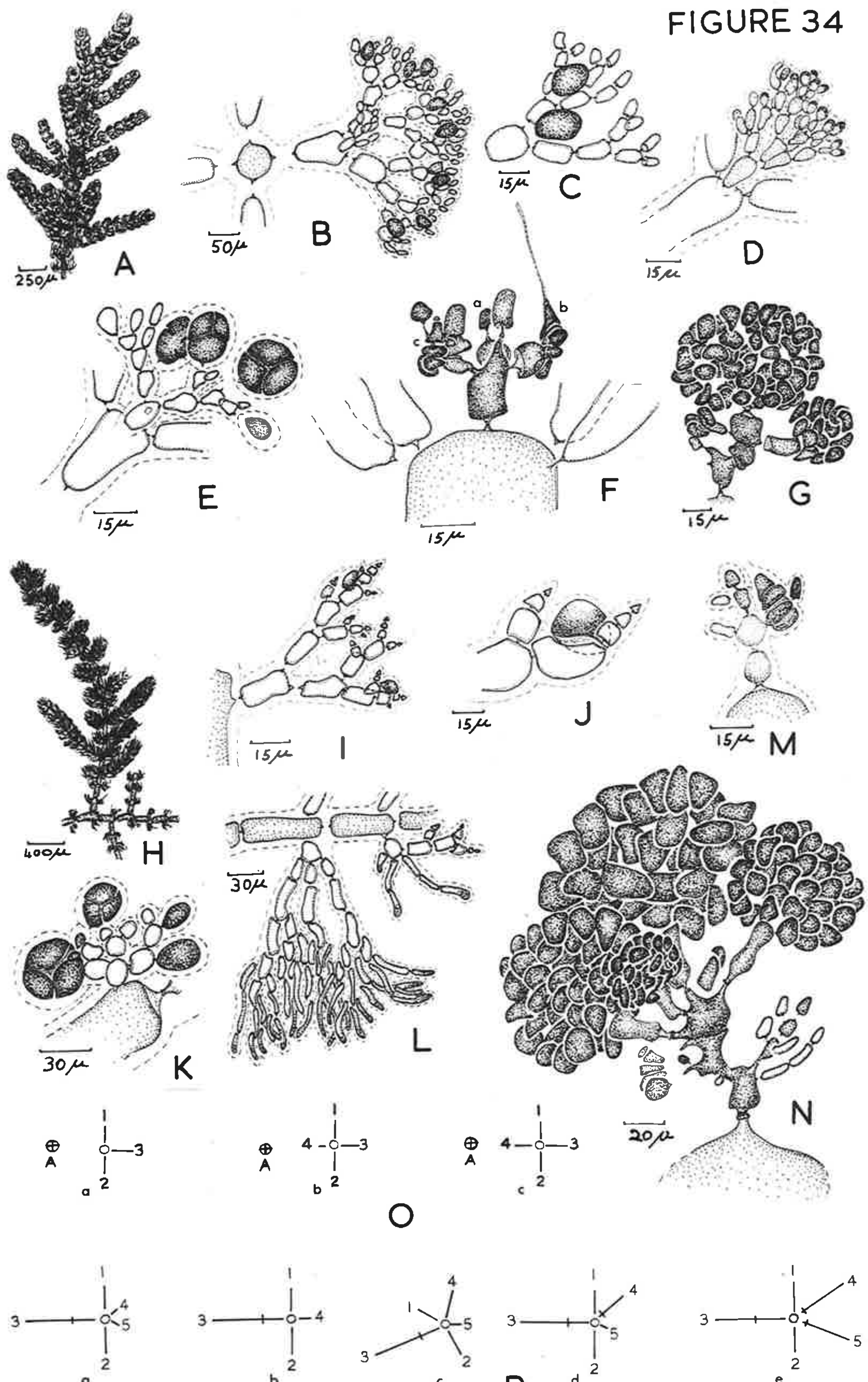
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FIGURE 35.

Perithamnion ceramioides J. Ag.

A. Portion of branched thallus.

B. Whorl-branchlet bearing gland-cells and terminal hairs.

C. Tetrasporangia on cells of whorl-branchlet.

Trichothamnion planktonicum n.sp.

D. Portion of thallus apparently dichotomously-branched.

E. Initiation of whorl-branchlets near branch apex.

F. Development of two apical cells at branch apex giving rise to a dichotomy of branches.

G. Attachment rhizoids borne on basal cells of whorl-branchlets.

H. Tetrasporangia borne on basal cells of whorl-branchlets.

I-J. Whorl-branchlets with large basal cells and bearing stalked hairs.

K. Three stages of development of special spermatangial branches on basal cell of whorl-branchlet.

L-M. Carpogonial branches borne on basal (supporting) cells of whorl-branchlets several cells in length near branch apices.

N. Enlargement of upper side of supporting cell prior to formation of auxiliary cell.

O. Auxiliary cell cut off from upper side of supporting cell.

P. First carposporangial buds ddveloping from central cell of carposporophyte.

Q. Carposporophyte with fusion between cells and 4 groups of carposporangia forming from central cell.

FIGURE 35

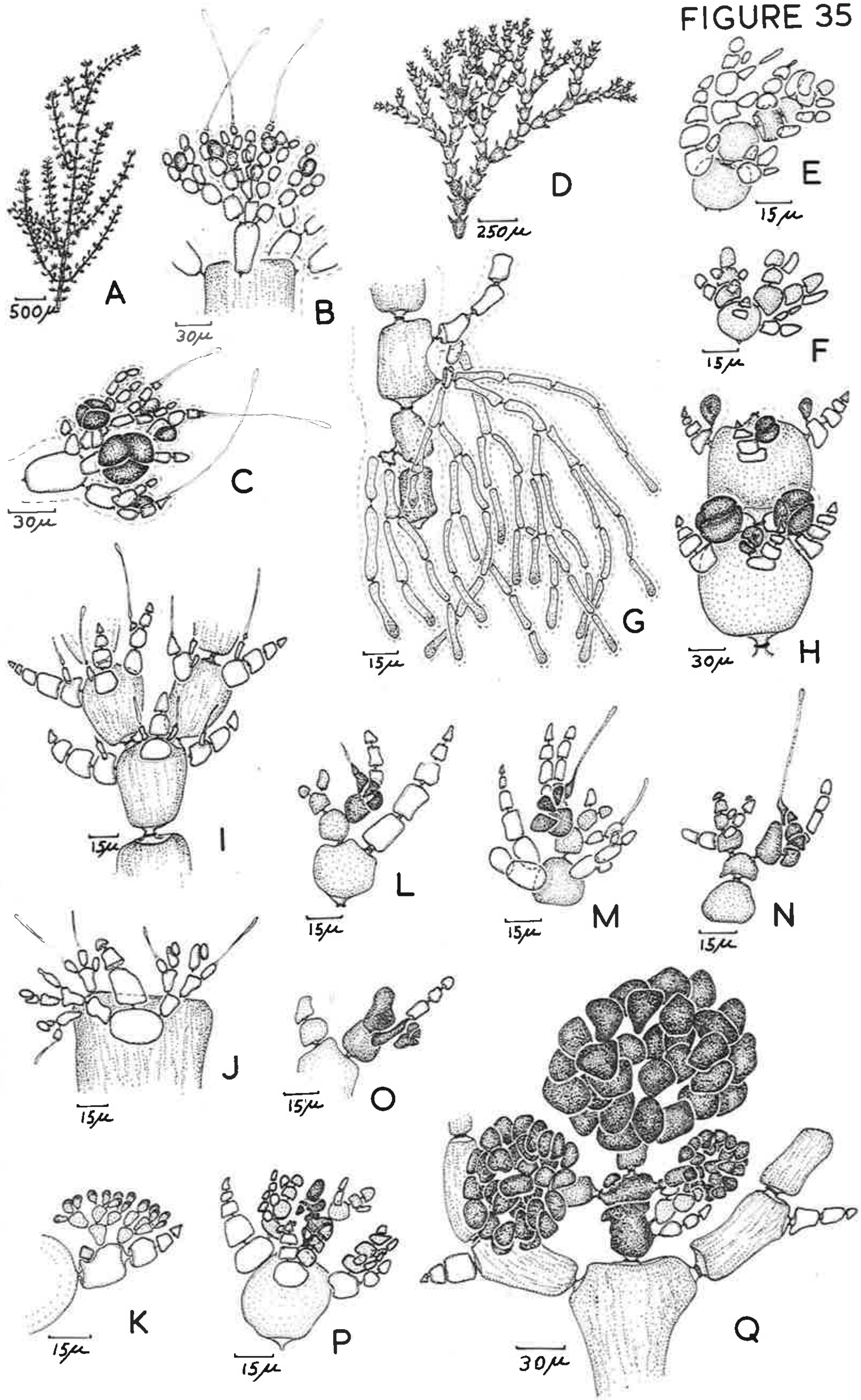
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FIGURE 36.

Trichothamnion elongatum n. sp.

A. Thallus showing apparent dichotomous branching and short whorl-branchlets.

B-C. Initiation of whorl-branchlets, often bearing large gland-cells, near branch apices.

D-H. Stages in development of tetrasporangia on protrusions of the basal cells of whorl-branchlets.

I-J. Whorl-branchlets with large basal cells and conspicuous gland-cells.

K-M. Carpogonial branch development from basal cell of 2-celled whorl-branchlet bearing a terminal gland-cell.

N. Auxiliary cell formed from supporting cell.

O. Auxiliary cell divided into lower foot cell and upper central cell. Gland-cell prominent on terminal cell of fertile whorl-branchlet.

P. First carposporangial bud formed terminally on central cell of carposporophyte.

Q. Carposporophyte with 3 carposporangial groups developing from central cell.

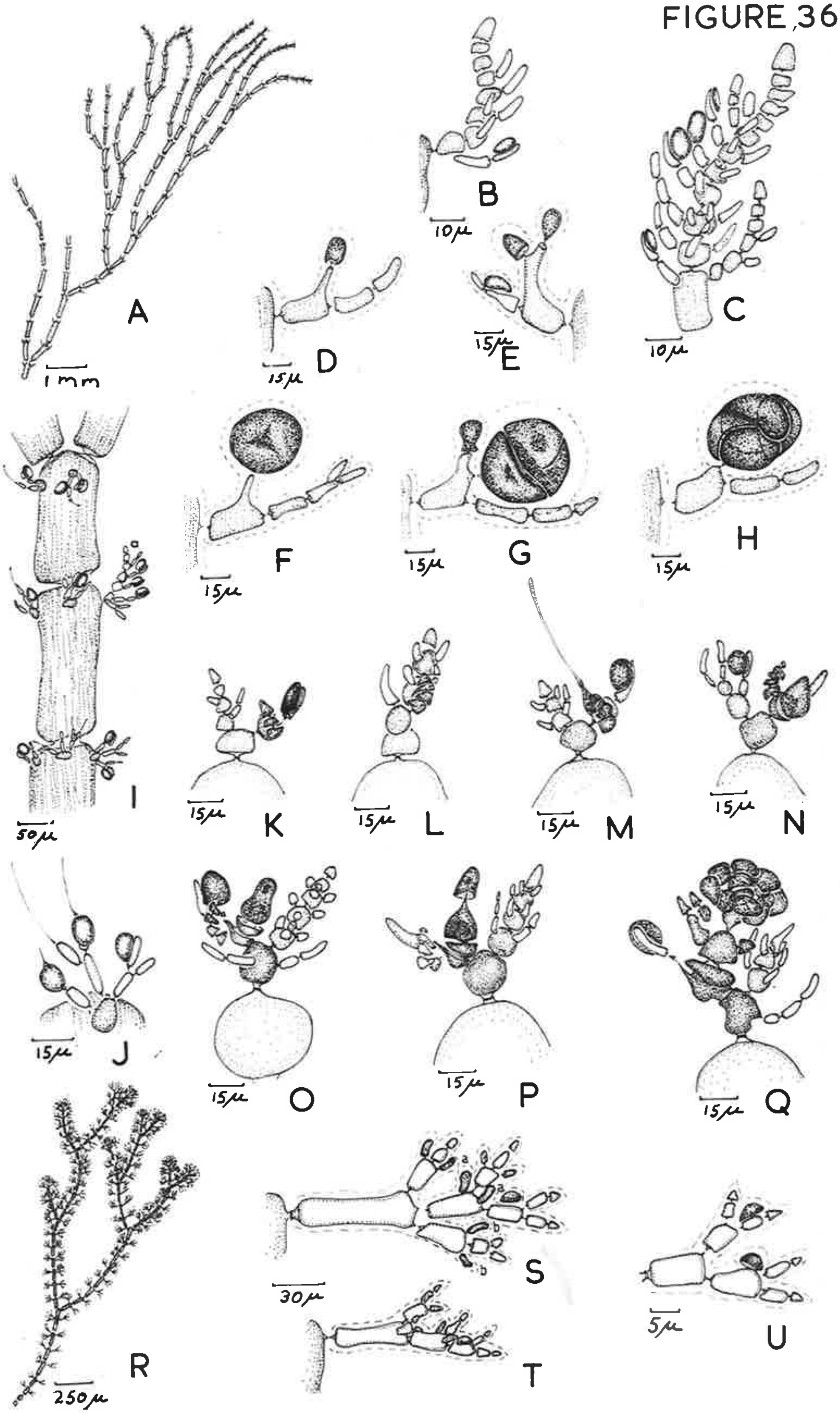
Trichothamnion minimum n. sp.

R. Portion of thallus showing branching.

S-T. Long and short whorl-branchlets bearing pairs of small cells (a,b).

U. Gland-cells on outer cells of whorl-branchlets.

FIGURE 36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U
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FIGURE 37

Trichothamnion minimum n. sp.

A. Branching at apex of axis to give apparent dichotomy.

B. Irregular, elongate chromoplasts in an axial cell.

C. Attachment rhizoids arising from cells near base of axis.

D. A pair of apical branches, one of which (b) bears a carpogonial branch while the other (a) continues to elongate.

E. Auxiliary cell formed from supporting cell (= basal cell of short branched whorl-branchlet).

F. Carposporophyte with first carposporangial bud terminal on central cell.

G. Carposporophyte with 4 developing groups of carposporangia.

H-L. Development and division of tetrasporangium.

Trithamnion vulgare n. sp.

M. Thallus of branched erect axes.

N. Whorl-branchlets in whorls of three consisting of a longer central branchlet and two shorter lateral branchlets.

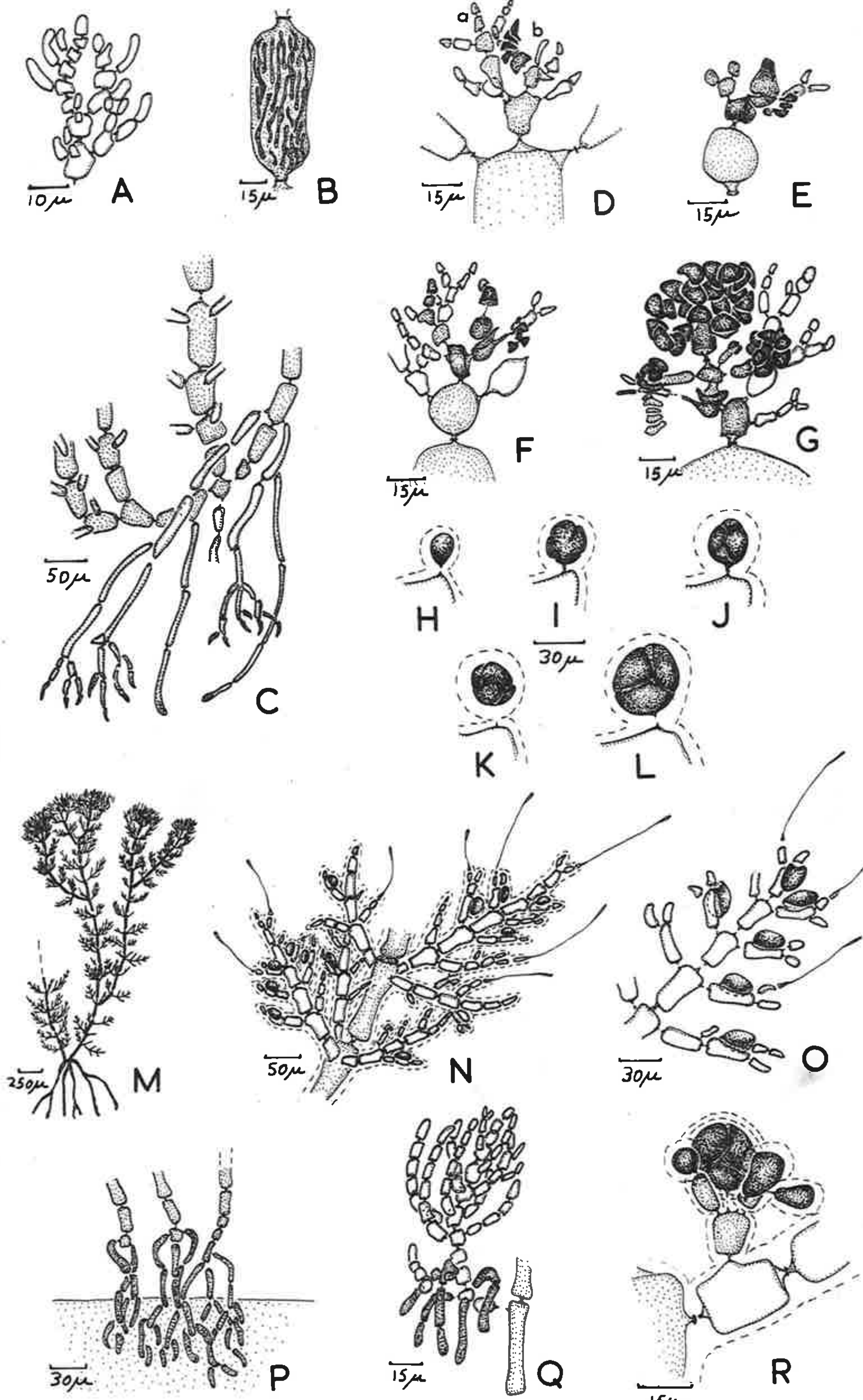
O. Branching of whorl-branchlet bearing gland-cells and terminal hairs.

P. Attachment by rhizoids which penetrate outer part of host tissue.

Q. Propagule consisting of a branched formation with basal rhizoids before liberation from parent plant.

R. Tetrasporangial branch on basal cell of whorl-branchlet.

FIGURE 37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O
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FIGURE 38

Trithamnion tetrapinnum n. sp.

A. Portion of thallus with carposporophytes near branch apices surrounded by a whorl of long branchlets.

B. Lateral branch borne on basal cell of whorl-branchlet.

C. Attachment rhizoid borne on basal cell of whorl-branchlet.

D. Unilaterally placed whorl consisting of one long whorl-branchlet and two short branchlets.

E. Tetrasporangia borne on lower cells of whorl-branchlets.

F. Carpogonial branch borne on basal (supporting) cell of 2-celled whorl-branchlet-near branch apex.

G. Auxiliary cell formed from upper side of supporting cell.

H. Carposporophyte showing fusions between cells and 3 developing groups of carposporangia from the central cell.

Trithamnion gracilissimum n. sp.

I. Portion of female thallus; carposporophyte surrounded by a whorl of 4 long branchlets.

J. Whorl-branchlets arranged in unilateral whorls consisting of one long branchlet and two short branchlets.

K. Development of whorl-branchlets at branch apex.

L. Lateral branch and attachment rhizoids developing from basal cell of short whorl-branchlet.

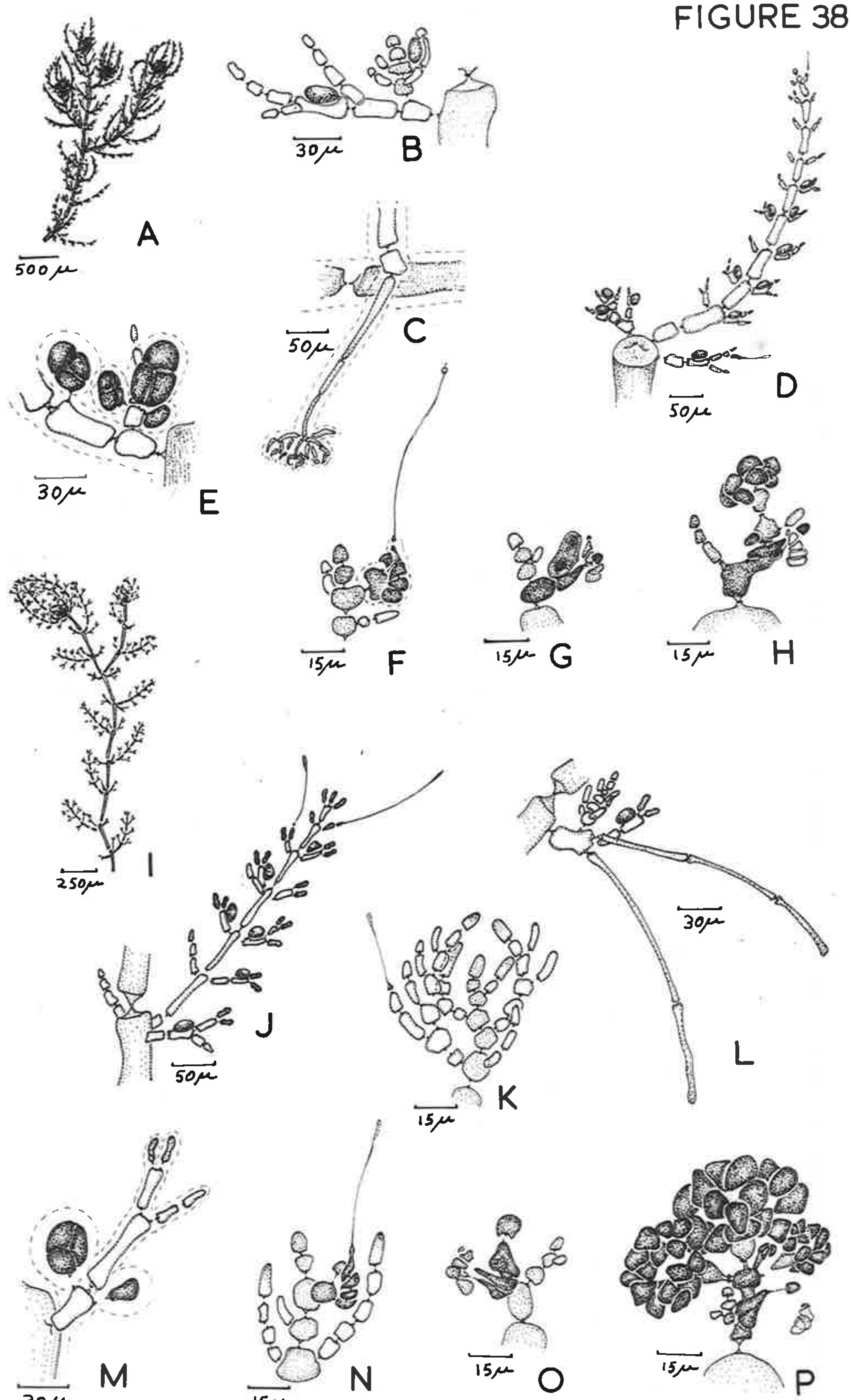
M. Tetrasporangia on short whorl-branchlet.

N. Carpogonial branch borne on basal(supporting) cell of 2-celled whorl-branchlet.

O. Terminal carposporangial bud developed on central cell of carposporophyte.

P. Carposporophyte with 4 developing groups of carposporangia.

FIGURE 38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PLATES.

Photographs are included only of type specimens of newly-described species of macroscopic dimensions.

PLATE 1. *Crouania mucosa* (Crouanieae) - female plant.

PLATE 2. *Crouania shepleyana* (Crouanieae)

PLATE 3. *Euptilocladia spongiosa* (Crouanieae) — portion of female plant.

PLATE 4. *Euptilocladia villosa* (Crouanieae).

PLATE 5. *Ballia pennoides* (Antithamnieae).

PLATE 6. *Ballia hirsuta* (Antithamnieae)

PLATE 7. *Macrothamnion secundum* (Antithamnieae).

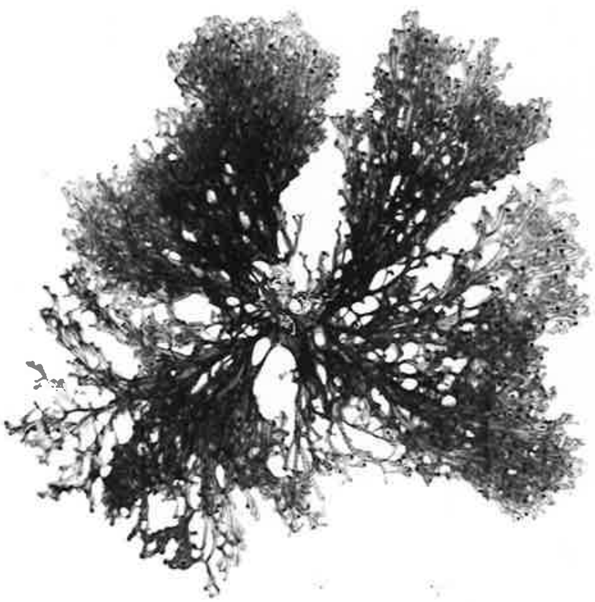
PLATE 8. *Heterothamnion episiliquosum* (Heterothamnieae) - occurring in dense tufts on receptacles of *Cystophora siliquosa* J.Ag.

PLATE 9. *Trichothamnion planktonicum* (Heterothamnieae)- floating form of thallus from type locality.

PLATE I

A 11,088a

TYPE



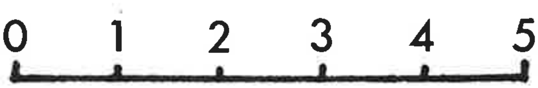
♀

Crouania mucosa n. sp.

Robe, S. Aus.

Littoral on reef, W. side

30/8/1949



Coll.

A28,382

TYPE

0 1 2 3 4 5 cm

Crouania ~~australis (Harv.) J.Ag.~~ shepleyana n.sp.

Pt. Willunga reef
Under ledges in drainage channels
Coll. H.B.S. Womersley 25-X-1964

PLATE 2

PLATE 3

A 27,925

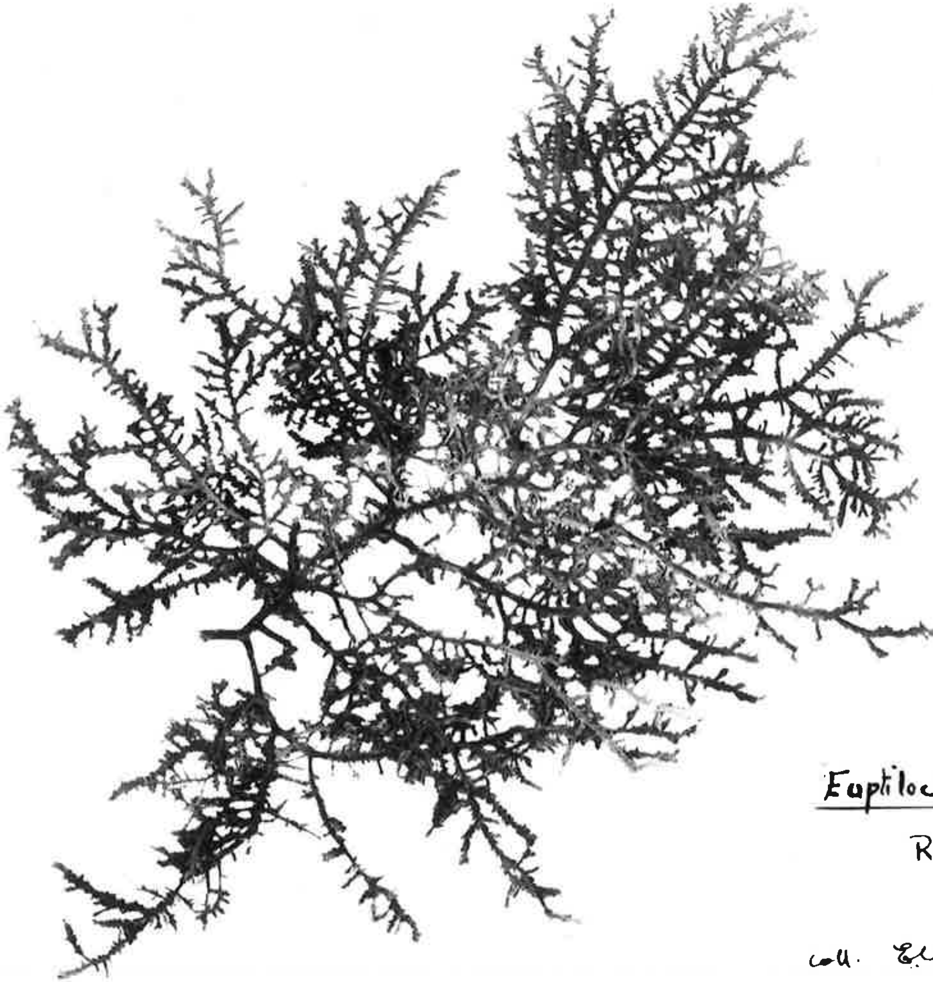
TYPE

0 1 2 3 4 5 cm

Euptilocladia spongiosa n. sp.
Robe S.A.
♀-C Drift
Coll. & Det. E.W. 18·V-1964

A29,282

TYPE



0 1 2 3 4 5 cm

Euptilocladia villosa n. sp

Robe S.A

Drift

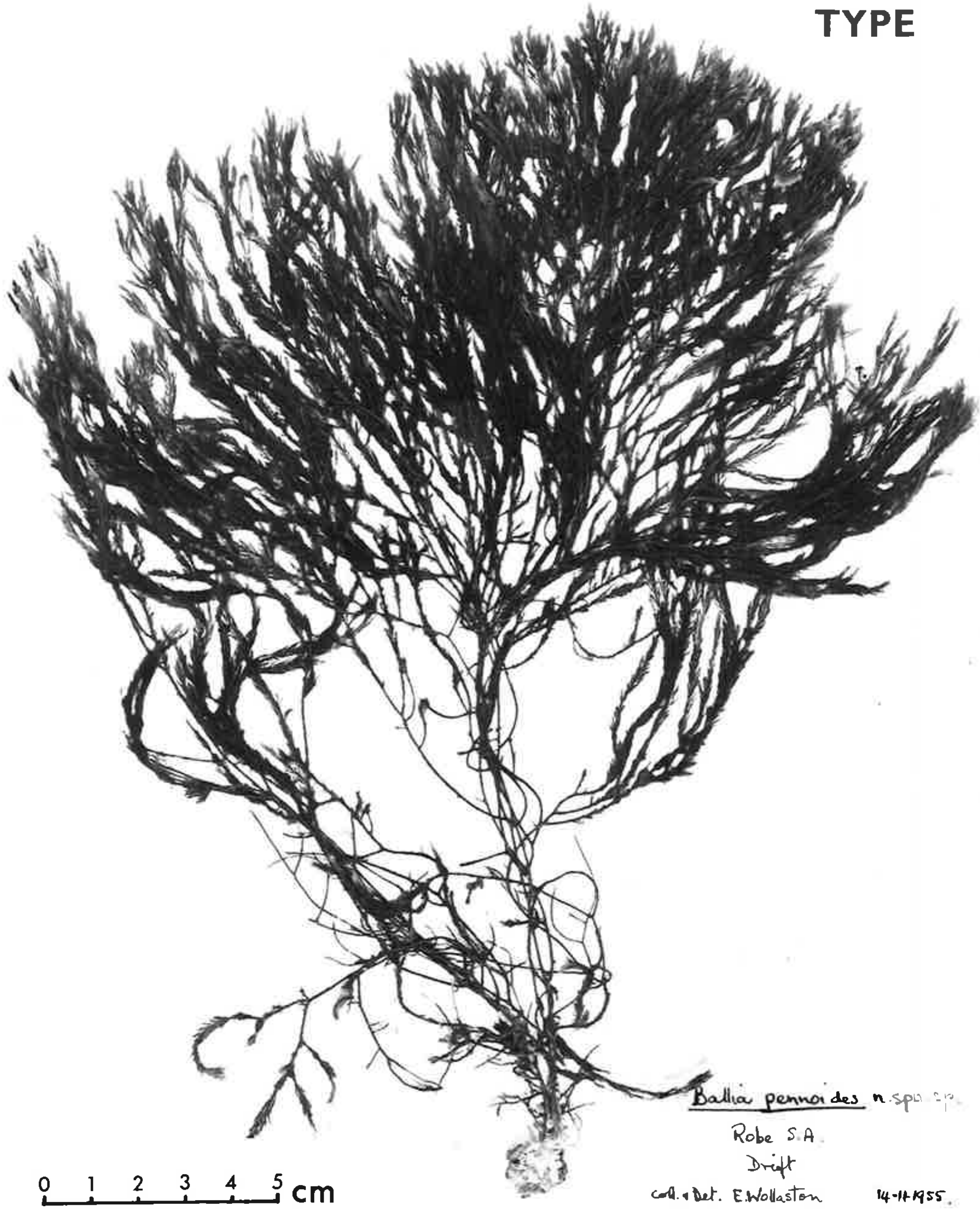
coll. E.W. 16:V-1965

PLATE 4

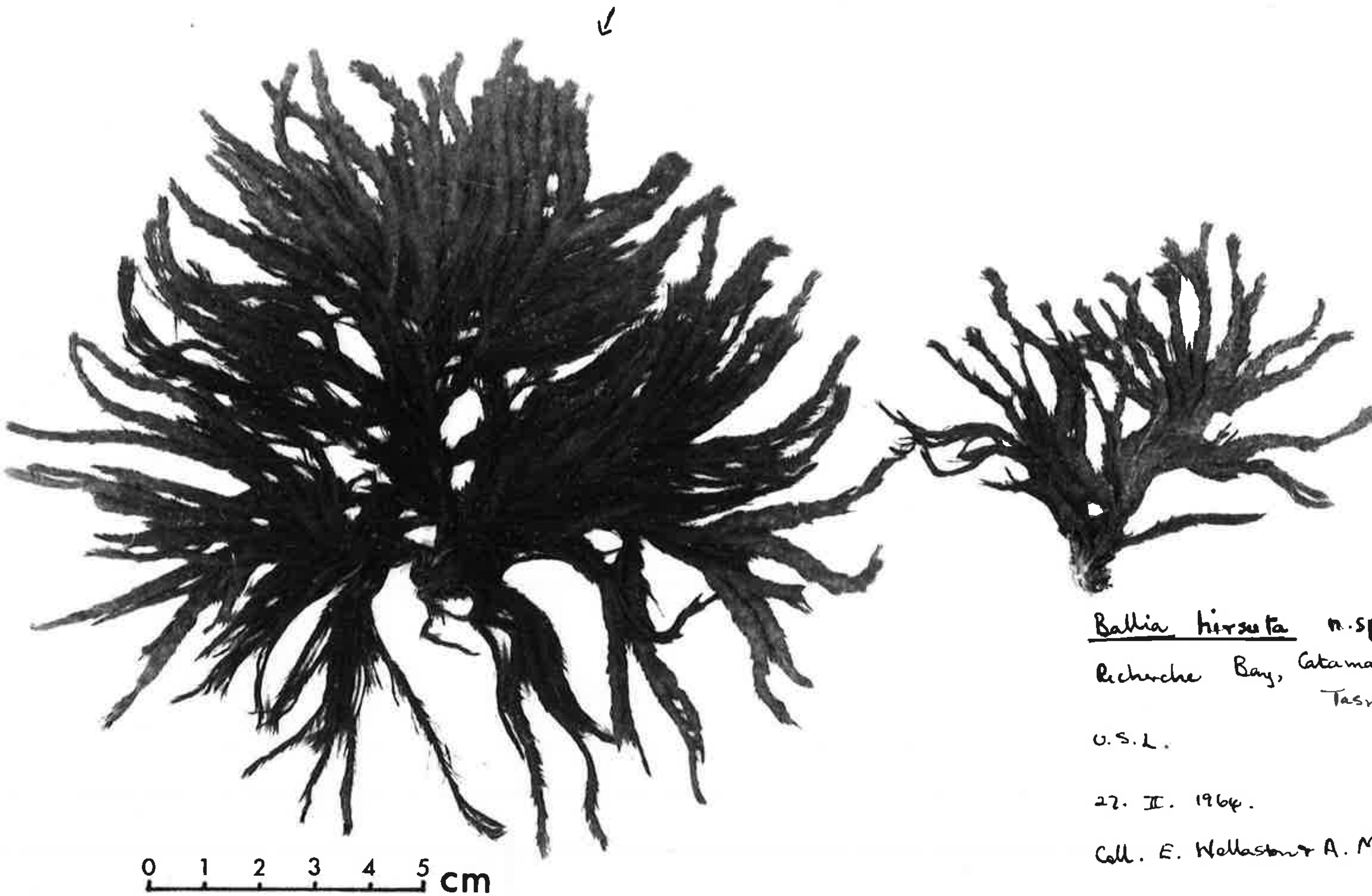
PLATE 5

A 19,999

TYPE



TYPE



Ballia hirsuta n.sp.

Recherche Bay, Catamaran, Tasmania

U.S.L.

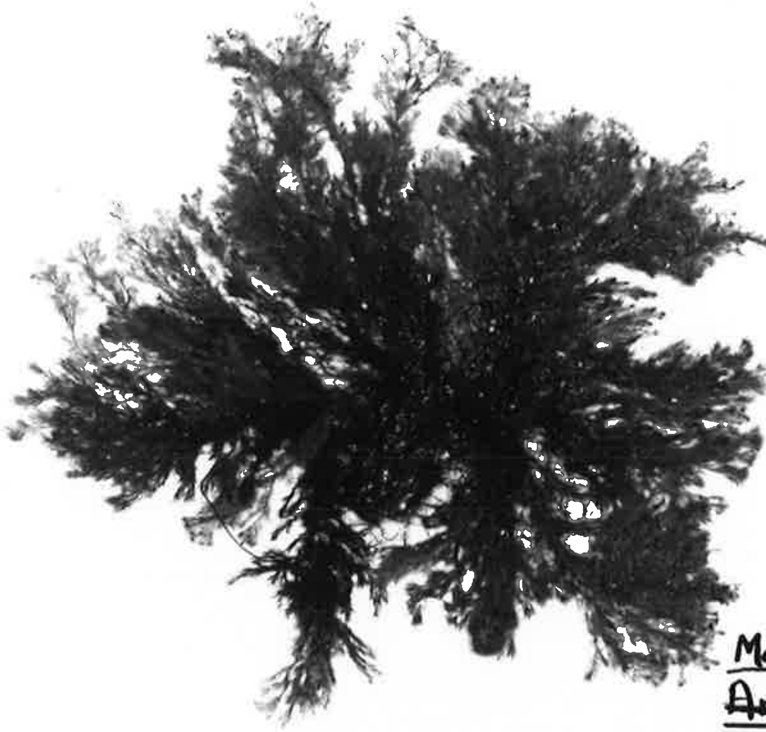
27. II. 1964.

Coll. E. Wollaston & A. Mitchell

PLATE 6

A20,161

TYPE



0 1 2 3 4 5 cm

<u>Macrothamnion secundum n.sp.</u>
~~Antithamnion~~

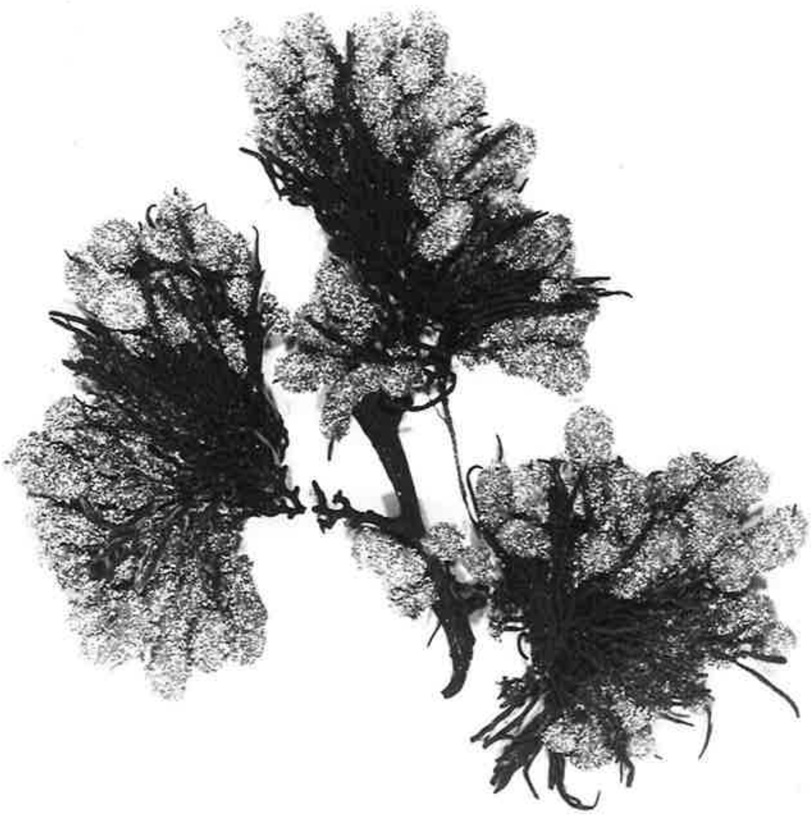
Vivonne Bay - K.I.
Lower littoral reef pools
coll. + Det. E. Wollaston 30-1-1956

PLATE 7

PLATE 8

710,935 b

TYPE



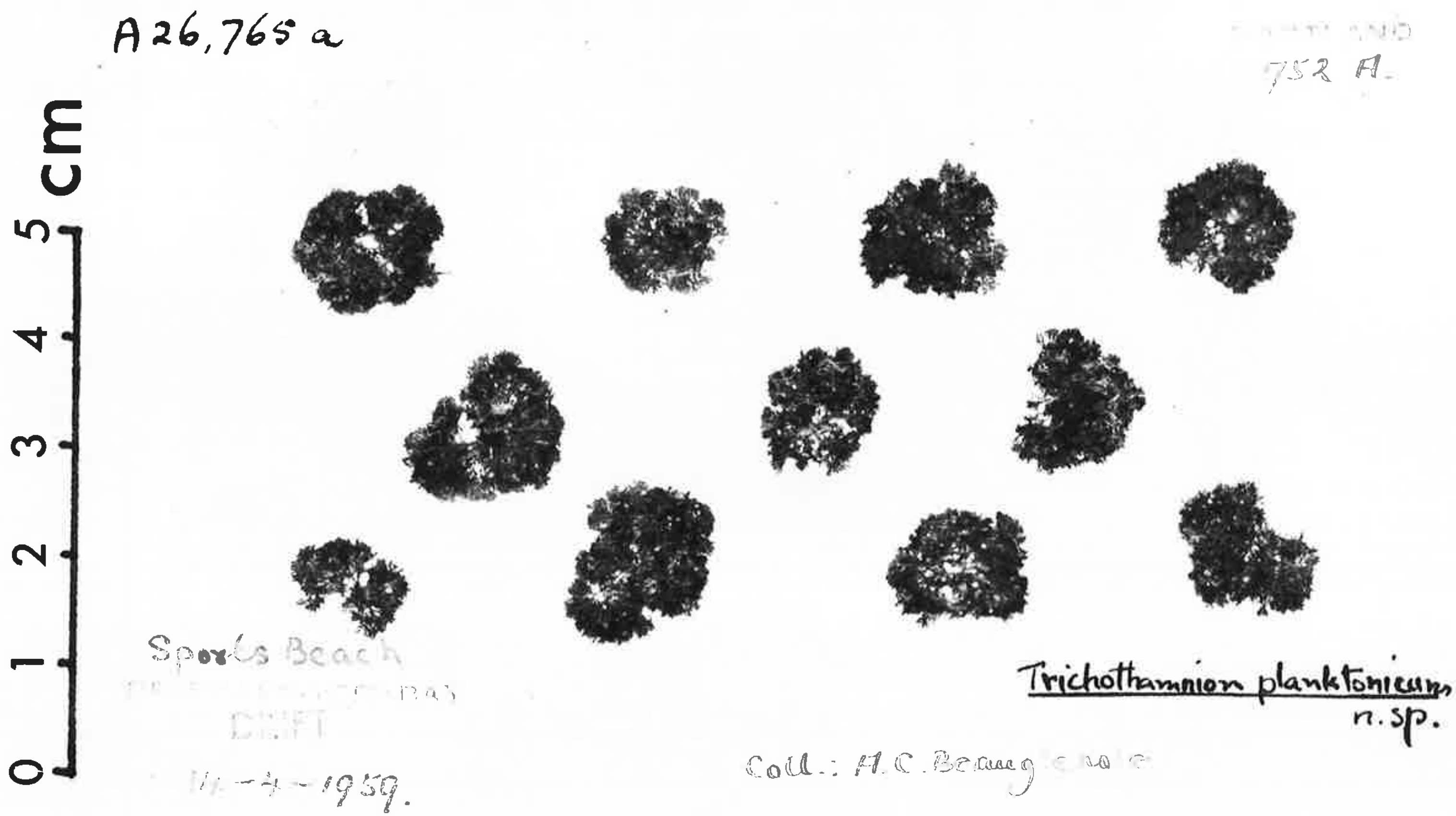
Heterothamnion episiliquosum n.sp.

Robe, S. Aus.

Drift
29/8/1949

0 1 2 3 4 5 cm

Coll.



A 26,765 a
752 A.
5 cm
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5
Sports Beach
DELFT
11-4-1959.
Coll.: H.C. Beaug
Trichothamnion planktonicum
n. sp.

PLATE 9