STUDIES ON WRANGELIEAE, SPHONDYLOTHAMNIEAE AND SPERMOTHAMNIEAE (CERAMIACEAE, RHODOPHYTA)

by

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Cystocarps of *Lejolisia aegagropila* A33,190

DECLARATION

This is to certify that the material contained in this thesis is the work of the author except where otherwise acknowledged and has not been accepted for the award of any other degree or diploma.

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ABBREVIATIONS USED IN DIAGRAMS AND FIGURES

1,2,3,4	cells of carpogonial branch
a	apical cell
abn.f.b	abnormal fertile branchlet
a.gr	apical group
aux	auxiliary cell
aux_1, aux_2	auxiliary $cell_1$, auxiliary $cell_2$
ax	axial cell
b	basal cell
ca	carposporangium
c.b	carpogonial branch
c.b.i	carpogonial branch initial
chr	chromosome
con	connecting cell
cyst	cystocarp
er.ax	erect axis
er.wh.b	erect whorl-branchlet
f.ax	fertile axial cell
f.c.b	fused carpogonial branch
fe.b	female branchlet or branch
f.p	fertile pericentral cell
fu	fusion cell
g	gonimoblast
g.i	gonimoblast initial
gl	gonimolobe
gl_1, gl_2	$gonimolobe_1$, $gonimolobe_2$
gl_1i, gl_2i	$gonimolobe_1$ initial, $gonimolobe_2$ initial
h	hair
ha	hapteron
hy	hypogenous cell
inv.b	involucral branch
n	nucleus
nl	nucleolus

o.cort.b	outer cortical branchlet
p	pericentral cell
per	pericarp
pot.ind.b	potentially indeterminate branch
pr.ax	prostrate axis
pr.wh.b	prostrate whorl-branchlet
pro.i	procarp initial
pro.sys	procarp system
pt.c	pit connection
2^{o}pt.c	secondary pit connection
r	rhodoplast
red.wh.b	reduced whorl-branchlet
rh	rhizoid
rh.i	rhizoid initial
rh.i.r	rhizoid initial residual cell
sa	subapical cell
shy	subhypogenous cell
sm	spermatium
sp	spermatangium
sp.b	spermatangial branchlet
spg	sporangium
sp.h	spermantangial head
sp.r.	spore residual cell
sp.m	spermatangial mother cell
st.gr	sterile group
stk	stalk cell
st.p	sterile pericentral cell
st.p.gr	sterile pericentral cell group
su	supporting cell
su.st	sterile cell on the supporting cell
su.st.gr	sterile group on the supporting cell
t.b	tetrasporangial branchlet
tr	trichogyne
vac	vacuole
v.b	villose branch
v.wh.b	villose whorl-branchlet
veg.wh.b	vegetative whorl-branchlet
wh.b	whorl-branchlet
wh.b.b	basal cell of whorl-branchlet
wh.b.i	whorl-branchlet initial

I. SUMMARY

While twenty four species from southern Australia have been previously placed in *Wrangelia* C.Agardh, only five of these rightly belong to this genus. A sixth southern Australian species, *Wrangelia australis* (J.Ag.) comb. nov. is transferred from *Bracebridgea* J.Ag. Of thirteen species of *Wrangelia* described from extra-Australian regions, six are studied and their systematic position confirmed.

Seven of the remaining southern Australian species of *Wrangelia* are segregated into four new genera, *Mazoyera*, *Shepleya*, *Wollastoniella* and *Drewiana*, and one into *Involucrana* Baldock and Womersley. These genera, probably with *Vickersia* Karsakoff and *Diplothamnion* Joly and Yamaguishi, are closely related to *Sphondylothamnion* Naegeli and are included in the tribe Sphondylothamnieae Feldmann-Mazoyer. Two new species of this tribe are described from southern Australia. *Mazoyera lyallii* (Harvey) comb. nov. from New Zealand is also transferred from *Wrangelia* and *Shepleya australe* (J.Ag.) comb. nov. transferred from *Antithamnion*. The remaining eleven species from southern Australia previously placed in *Wrangelia* have been reduced to synonomy or transferred to other genera not in the tribes studied.

The following six genera, including four new species, are included in the tribe Spermothamnieae Schmitz: *Spermothamnion*

Areschoug, *Tiffaniella* Doty and Menez, *Ptilothamnion* Thuret, *Lejolisia* Bornet, *Lomathamnion* gen. nov. and *Interthamnion* gen. nov.

The tribe Wrangelieae is similar to primitive Ceramiaceae in forming procarps successively near the apices of potentially indeterminate branches. However, the structure of the cystocarp, in which the gonimoblast is intermingled with sterile whorl-branchlets of the fertile axis, is relatively specialised.

The tribes Sphondylothamnieae and Spermothamnieae are closely related, the procarps being restricted to the subapical cell of the fertile axis which may be either a potentially indeterminate or a determinate branch. The Sphondylothamnieae is distinguished by the presence of an inner involucrum around the gonimoblast, formed by division of the sterile cells associated with the procarp, and by the presence of whorl-branchlets on axial cells of indeterminate branches. In the Spermothamnieae there is no inner involucrum (except in *Lejolisia*) and distinct whorl-branchlets are absent from erect axes. These two groups are probably very highly advanced in the Ceramiaceae and not very closely related to the Wrangelieae.

Culture studies using two species were undertaken to clarify stages in germination of spores. In both *Wrangelia plumosa* and *Lejolisia aegagropila*, the first division of the spore is approximately parallel to the substrate. In *L. aegagropila* prostrate axes are produced secondarily by horizontal growth of erect axes.

Nuclear studies show that the vegetative cells of the Wrangelieae are uninucleate, while those of the Sphondylothamnieae and Spermothamnieae are multinucleate.

II. INTRODUCTION

The marine algal flora of southern Australia is recognised as particularly rich, both in number of species and endemism. This is well illustrated in the genus Wrangelia in which twenty four species have been described from southern Australia, although the type species, Wrangelia penicillata (C.Ag.) C.Ag., occurs in the Mediterranean and subtropical Atlantic and Pacific Oceans. However, superficial observations on the branching patterns and cell sizes of the commoner species of Wrangelia suggested that this assemblage was heterogeneous.

Various authors have previously doubted that all the species were correctly placed in Wrangelia. For example, in several cases Harvey placed species in Wrangelia only provisionally until the structures of the "fruit" became better known. Bornet and Thuret (1880, p.184) also remarked that species such as Wrangelia halurus, in which the spores were naked instead of being accompanied by "paraphyses" should probably be placed in the genus Sphondylothamnion Naegeli (1861, p.380). This suggestion was supported by De Toni (1903, p.1258) and later by Kylin (1928b,p.1) in his detailed study of W. penicillata.

The present study was undertaken to clarify the systematic positions of species referred to Wrangelia and their relationships to genera such as Sphondylothamnion. The study was extended to include the little known southern Australian species of the tribe Spermothamnieae the members of which are closely related to Sphondylothamnion.

Supplementary culture and nuclear studies were also undertaken to further elucidate the relationships between these taxa.

The geographical distribution of each southern Australian species studied occurs within the range from Pt. Denison, W. Aust. to Pt. Jackson, N.S.W., including the coasts of Kangaroo Is., S. Aust. and Tasmania. Although some species appear to be restricted to the slightly colder waters from about Robe, S. Aust. to Pt. Phillip, Vic. and Tasmania, distribution patterns have not been analysed in detail since records are mostly too few and from scattered localities.

III. HISTORICAL BACKGROUND

C.Agardh (1828, p.136) created the genus *Wrangelia* in honour of Baron Wrangel, a Swedish naturalist, for the species which he had previously described as *Griffithsia penicillata* (1824, p.143). *Wrangelia* was classified by earlier authors (J.Agardh 1841, p.37; 1842, p.66, Decaisne 1842, p.358, Kuetzing 1843, p.376; 1845, p.288; 1849, p.664) with genera such as *Griffithsia* and *Ceramium* which are now also placed in the same family. However, in the meantime *Wrangelia* has been associated with many widely separated taxa in the Rhodophyta. The longstanding doubts about the systematic position of *Wrangelia* were mainly due to its similarity in vegetative features to genera ~~now~~ in the Ceramiaceae, ~~and~~ but its atypical cystocarp structure in which fertile gonimoblast filaments are intermingled with sterile filaments.

Because of their similar cystocarp structure, J.Agardh (1851, p.X; 1863, p.701) grouped *Wrangelia* with the genera *Naccaria* and *Atractophora* in a separate order "Wrangelieae", and this classification was accepted by Harvey (1853, p.8 - as "Wrangeliaceae").

Naegeli (1861, p.297) however based his classification on both vegetative and reproductive features and reverted to the older groupings, placing *Wrangelia* in the Ceramiaceae with other genera, including *Herpothamnion* (equivalent in part to *Spermothamnion* Areschoug), *Lejolisia* and *Sphondylothamnion*.

Other genera also associated with *Wrangelia* by other authors were *Monospora* and *Bornetia* (J.Agardh 1876, p.607), and *Chantransia* (Hauck 1885, p.39).

The distinctive structure of the cystocarp of *Wrangelia* was again used by Schmitz (1883, p.228; 1889, p.439) in placing *Wrangelia*, *Naccaria* and *Atractophora* with *Gelidium* as a tribe, the Wrangelieae, in the Gelidiaceae. *Gelidium* also has a creeping gonimoblast which intermingles with sterile branchlets on the fertile axis (Fan 1961).

Oltmanns (1904, p.716) removed *Wrangelia*, *Naccaria* and *Atractophora* in a separate family, the Wrangeliaceae (c.f. J.Agardh 1851), to the Gigartinales but later (1922, p.252) replaced *Wrangelia* in the Gelidiaceae.

The present systematic position of *Wrangelia* was clarified by Kylin (1928b) who made a detailed study of postfertilization events in *W. penicillata*, showing that the auxiliary cell is formed from the supporting cell after fertilization, whereas in *Naccaria* and *Atractophora* the supporting cell acts as the auxiliary cell. *Wrangelia* was therefore placed in the Ceramiaceae and thus finally returned to its oldest systematic position.

The Wrangelieae is now considered a monogeneric tribe in the Ceramiaceae, distinguished by its uninucleate cells, five whorl-branchlets per whorl, position of procarps near the apices of indeterminate branches and distinctive cystocarp structure (Feldmann-Mazoyer, 1940, p.238, Kylin 1956, p.382). The present study supports this classification.

The tribe Spermothamnieae described by Schmitz (1889, p.449) was one of fifteen tribes into which he divided the Ceramiaceae and contained Lejolisia, Sphondylothamnion, Spermothamnion and Ptilothamnion. This classification was followed by Schmitz and Hauptfleisch (1897, p.483) and De Toni (1903, p.1253 - including Trailliella with a query; 1924, p.450). However Feldmann-Mazoyer split Schmitz's Spermothamnieae into three tribes, retaining only Spermothamnion in the Spermothamnieae and creating the Lejolisieae for Lejolisia and Ptilothamnion. The Spermothamnieae was characterised by multinucleate cells, procarps on the subapical cells of the fertile axes and two auxiliary cells per procarp, while the Lejolisieae differed by having only one or two nuclei per cell and one auxiliary cell per procarp. Sphondylothamnion was segregated to a new tribe, the Sphondylothamnieae, which also contained Vickersia and Bornetia. Although similar to the Spermothamnieae, this tribe differed in having a large fusion cell in the cystocarp.

Kylin (1956) did not recognise Feldmann-Mazoyer's new tribes and included these six genera within the Spermothamnion group* using the production of terminal carposporangia as a unifying feature. However Baldock and Womersley (1968, p.197) have shown that Bornetia differs considerably from Spermothamnion and probably represents another tribe within the family.

Phylogenetic tendencies within the Ceramiaceae have been

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* Kylin's groups are taxa equivalent to the tribes of other authors.

discussed by Feldmann-Mazoyer (1940, p.243), Kylin (1930, p.76; 1956, p.367) and Hommersand (1963, p.330). Feldmann-Mazoyer indicated affinities within the family without dividing it into any suprageneric taxa.

Using the position of procarps, Kylin grouped the genera of the Ceramiaceae into two developmental lines (Entwicklungsreihen); the first line was represented by *Crouania, Antithamnion, Wrangelia* and *Ceramium,* in which the carpogonial branches occur on the basal cells of short shoots ("whorl-branchlets" in this study), and the second line represented by *Callithamnion, Spermothamnion, Griffithsia* and *Ptilota,* in which the carpogonial branches occur on special pericentral cells (homologous to the basal cells of the whorl-branchlets in the first group) in the upper parts of shoots.

Hommersand dismissed Kylin's developmental lines as polyphyletic and he divided the Ceramiaceae into two subfamilies: the Crouanioideae (including the Wrangelieae) and the Ceramioideae (including the Spermothamnieae, together with *Tiffaniella* Doty and Menez), separated mainly on procarp structure rather than position (see Table 11, p.285). Wollaston (1968, p.399) rejected these subfamilies on the basis of evidence from the tribes Crouanioideae, Antithamnieae, and Heterothamnieae. Further evidence which does not support Hommersand's groupings is given in the present study.

IV. MATERIALS AND METHODS

1. Morphological Studies

Collections were made from rocky reefs at low tide and from material cast up in drift. Field collections were initially preserved in 4% formaldehyde in seawater and later transferred for preservation into a 70% alcohol - 5% glycerine mixture. Where liquid preserved material was not available for study, dried herbarium specimens were softened by soaking in dilute detergent.

Material for examination was stained in 1% aniline blue, washed, acidified in 1N hydrochloric acid and mounted for permanent preservation as microscope slides in 50-80% Karo syrup with phenol. Occasionally, softened herbarium material was mounted directly in a mixture of 20% Karo, aniline blue and hydrochloric acid (20:1:1). This method is satisfactory for quick mounts.

Most drawings were made using a camera lucida.

Measurements - cell dimensions quoted include the walls of the cells as unavoidable plasmolysis of the cells during processing caused internal dimensions to vary greatly.

Certain cells of the thallus were chosen as representative of the range of cell size occurring in the species. Such are the median cells of the whorl-branchlets, which are those occurring approximately half-way between the apex and the base of the whorl-branchlets.

Herbaria quoted - Abbreviations are taken from Lanjouw & Stafleu (1964). Types have been examined unless otherwise indicated.

2. Culture and Nuclear Studies

Methods are given for these sections on p.257 and p.270 respectively.

V. FEATURES USED IN CLASSIFICATION AND THEIR TERMINOLOGY

Reproductive features, particularly the development of the procarp and carposporophyte, are used in this study to separate the higher levels of taxa such as tribes and genera, while vegetative features are used mainly in separating species. Often vegetative features can be correlated with differences in reproduction.

Where possible, terminology used is that of previous authors in this field, but where this has not been possible an explanation of the differences is included.

A. VEGETATIVE FEATURES

1. Branching

The thalli consist of systems of prostrate and/or erect axes. An axis is defined as the leading row of cells in any branch system. This includes both indeterminate and determinate branches (see below). The term "branch" includes both the axis and its determinate laterals.

Genera with both prostrate and erect axes, such as those of the Sphondylothamnieae and Spermothamnieae, would appear to be heterotrichous. This is apparently contradictory to the statement of Fritsch (1945, p. 445) that the heterotrichous habit is completely suppressed in the Ceramiales. However, studies on *Lejolisia aegagropila* (p. 264), a species with both prostrate and erect axes, have shown that the first division of the spore is approximately parallel to the substrate, thus complying with other members of the Ceramiales. The prostrate axes develop from erect axes which become secondarily prostrate. Thus these groups may by classified as secondarily heterotrichous.

(1) Indeterminate axes (or branches)

An indeterminate axis is one with an apical cell apparently capable of continued production of axial cells. Division of apical cells may be either alternately oblique (as in most species of Wrangelia) or transverse (as in Sphondylothamnieae and Spermothamnieae).

In some species, branches occur which have the structure of indeterminate branches but which are apparently not undergoing active growth. Because their structure remains typical, they are presumably capable of resuming active growth given the right conditions, and are therefore referred to as "potentially indeterminate branches". Potentially indeterminate branches are noticeable in Wrangelia princeps Harvey (p. 34) where they form a whorl associated with the whorl-branchlets on lower axial cells. Only one of these usually develops as a true indeterminate thallus branch. Wollastoniella myriophylloides (Harvey) comb. nov. is similar in having potentially indeterminate branches between whorl-branchlets on each axial cell. If damage occurs to the growing apex, or reproductive structures develop, one of these potentially indeterminate branches will overtake growth, replacing the main axis. Such branches have been referred to by Halos (1966, p.64) as "brachycladomes", adapted from the terminology of Chadefaud (1960, p.114). Although equivalent in meaning to "potentially indeterminate branches", the term is not used in the present work because Chadefaud's system of terminology is not accepted, for the reasons outlined by Wollaston (1968, p.221). Other authors have used the terms "dwarf shoots" (Hommersand 1963) or "determinate branches" (Wollaston 1968). Although these branches may be temporarily limited in growth, the lack of differentiation of the apical cells, the similarity in structure to actual indeterminate branches and their ability to resume growth under certain conditions warrants the use of a more explicit term.

(2) Determinate axes (or branches)

A determinate axis is one where the apical cell is apparently incapable of continued production of further axial cells. At maturity the determinate branch has a consistent and characteristic morphology, and in this account the term "branchlet" is used generally for this structure. "Whorl-branchlets" are determinate branches which occur in whorls at the distal ends of axial cells in the Wrangelieae and Sphondylothamnieae, and this term is used following Wollaston (1968). Many species have whorl-branchlets which are highly differentiated. However, in a few species of Sphondylothamnieae (e.g. Involucrana meredithiana) the whorl-branchlets are not easily distinguishable from indeterminate branches.

Whorl-branchlets are absent in the Spermothamieae.

(3) Orders of Branching

A primary axis is the first formed from the germinating spore and a primary branch contains an axis of the second order. In the Sphondylothamnieae only the erect system is considered in quoting the order of branching for comparison with other groups.

(4) Origin, arrangement and type of branching

(a) Indeterminate branches may be borne in three positions:

(i) on the basal cells of whorl-branchlets (Wrangelieae),

(ii) in the positions of whorl-branchlets directly on axial cells (most Sphondylothamnieae), or

(iii) in addition to whorl-branchlets on axial cells (*Wollastoniella*).

In most species studied, the main thallus branching is distichous or subdistichous. This is usually the result of the indeterminate branches being produced in association with the first-formed whorl-branchlets on each axial cell, the initials of which are usually cut off alternately on successive axial cells.

(b) Whorl-branchlets

The order of formation and number of whorl-branchlets in a whorl are usually, but not always, characteristic of the species. The basic number in the Wrangelieae is 5 per axial cell, although some species (e.g. *Wrangelia tenuis* Noda) show a reduction to 4 or 3 per whorl. Others show the development of dorsiventrality and thereby the flattening of the thallus (e.g. *Wrangelia nobilis* and *Wrangelia australis*). In the Sphondylothamnieae the order of formation is mostly in opposite pairs, the successive whorls often being arranged orthostichously although this may be obscured by twisting of the axis.

First formed whorl-branchlets on each axial cell may be initiated alternately on opposite sides of the indeterminate axis, spirally, or more rarely unilaterally. The last type can occasionally be seen in lateral branches in *Wrangelia* where the whorl-branchlets are formed abaxially. This was described by Chadefaud (1960, p.128) as an unusual "zig-zag" scorpioid pattern of whorl-branchlet initiation in *Wrangelia penicillata*.

Whorl-branchlets are all monopodially branched. They may be pinnate or unilaterally branched but are often subdi- or trichotomously branched due to development of the laterals of the whorl-branchlet to an almost equal extent to its main axis. Where there is exactly equal development of laterals, the terms "pseudodi- or trichotomous" are used.

Maturation of whorl-branchlets may be acropetal or basipetal. In the latter case, the laterals of the lowest axial cell of the whorl-branchlet are the last to develop.

2. Polarity of Axes and Cells

In many cases it is necessary to differentiate between the opposite ends of axes or cells. The distal end of an axis or cell is the one remote from the point of origin of the axis or cell, or nearer the apical end of the axis or cell. Conversely, the proximal end is the one nearest to the point of origin of the axis or cell. Terms such as "upper" and "lower", while useful in referring to the gross morphology of the plant, are confusing when applied to prostrate or descending axes (e.g. rhizoids).

3. Cortication

Cortication occurs in species with relatively large thalli and is composed of descending rhizoids which originate from either the basal cells of whorl-branchlets or from the proximal ends of axial cells or both. The cortex may be pseudoparenchymatous in cross section due to the walls of the rhizoidal cells becoming confluent with the walls of the axial cells (Wrangelieae). In most species of Sphondylothamnieae with cortication, the rhizoidal cell walls are free from the wall of the axis and the cortication is spongy. Attachment of the rhizoids to the axis may occur by means of small digitate haptera or by secondary pit connections between adjacent rhizoids and lower branchlets; these may serve to strengthen the axis. The position of the haptera (if present) on the cells of the rhizoids - whether on the proximal or distal ends -

is often of taxonomic significance.

In W. nobilis and W. australis, the primary rhizoidal cells produce outwardly a layer of short assimilatory branchlets of a form characteristic of the species. These remain after the normal whorl-branchlets have been lost.

4. Attachment

In species with prostrate axes, primary attachment occurs by haptera and further rhizoids from erect axes increase anchorage as the plant grows larger (Sphondylothamnieae). In species with only erect axes (Wrangelieae), attachment of the sporeling occurs by means of an elongate rhizoid, and further rhizoids from the erect axes in older plants extend downwards over the substrate.

5. Hairs

Unicellular hairs are rare in the groups studied. They have been reported by Rosenvinge (1911, p.210, figs. 8,9) in Spermothamnion turneri* where the apical cell of an erect axis becomes narrow and elongate. Multicellular hair-branches occur more commonly, formed from extensions of the ultimate parts of normal erect axes (as in Lejolisia aegagropila) or by the cells of complete whorl-branchlets or potentially indeterminate branches becoming hair-like. These are referred to as "villose whorl-branchlets" or "villose branches". The term "trichoblast" has been applied to structures comparable to

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* Syn. Spermothamnion repens (Dillwyn) Rosenvinge.

villose whorl-branchlets in the Griffithsieae by Feldmann-Mazoyer (1940, p.148) and others, but it is avoided in the present work because of its association with special branchlets in the Rhodomelaceae, where they are not obviously derived from structures comparable with whorl-branchlets.

6. Nuclei and Rhodoplasts

Vegetative cells of the Wrangelieae are uninucleate, but those of the Sphondylothamnieae and Spermothamnieae contain (1-)10-4,000 nuclei. This forms a useful taxonomic feature at the tribe level.

Rhodoplasts in all three groups are numerous per cell and discoid to elongate or lobed (Fig. 1D, rhodoplasts of a mature whorl-branchlet cell in *Wrangelia princeps*). When elongate, they are usually oriented parallel with the long axis of the cell. Sometimes several smaller rhodoplasts lie adjacent in a row, suggesting segmentation of an elongate plastid.

B. REPRODUCTIVE FEATURES

1. Meiosporangia

Meiosporangia may be in the form of tetrahedral tetrasporangia or polysporangia with 8 - 64 angular spores.

In some tetrasporangia, the four nuclei are formed first, followed by simultaneous wall division as in normal tetrahedral division, but the final orientation of the spores is such that the sporangium appears cruciately divided. In others, although the four nuclei are formed first, the wall divisions occur in two successive stages as in cruciate division but the final orientation of the walls is tetrahedral ("oblique" in Wollaston 1968).

2. Spermatangia

The spermatangia are formed in compact, ovoid or elongate heads. The fertile axes are of 2 - 6 short cells which each produce 3-4(-6) pericentral cells. These may act directly as spermatangial mother cells, each budding off outwardly 2-3 spermatangia and also, laterally, further spermatangial mother cells which contribute to the compactness of the head. Occasionally the pericentral cells do not produce spermatangia directly but only spermatangial mother cells. The lowest fertile axial cell is usually the longest, and because the pericentral cells are produced from its distal end it often appears as a short stalk.

Spermatangial heads may be sessile or stalked, naked or involucrate. They are usually situated on the lower cells of whorl-branchlets which may or may not be modified.

Spermatangial heads are relatively unimportant as taxonomic features.

3. Procarp and Carposporophyte

(1) Position of procarps

This is one of the most important features used in separation of the tribes of the Ceramiaceae. In the groups studied, two types occur:

(a) *Wrangelieae* - the procarps occur on successive axial cells near the apices of indeterminate branches, one or two per axial cell. In different species, the supporting cell may or may not bear a terminal sterile cell. The presence or absence of this cell has been used by Hommersand (1963, p.330) as one feature to separate two subfamilies in the Ceramiaceae (see p.285).

(b) *Sphondylothamnieae and Spermothamnieae* - the procarps are always restricted to the subapical cell of the fertile axis which may be determinate or potentially indeterminate.

The terms "apical", "subapical" and "hypogenous" are applied to the last three cells of the fertile axis following Baldock and Womersley (1968, p.211). The terms "apical", "central" and "basal" were used respectively for these cells by Gordon and Womersley (1966) following Drew (1934, p.560) in her study of *Spermothamnion turneri*, but are replaced here since the "basal" cell is seldom the true basal cell of the fertile axis. The term "subhypogenous" is applied to the cell below the hypogenous cell. The apical and subapical cells are always smaller and more densely protoplasmic than the lower cells of the fertile axis. The hypogenous and subhypogenous cells may also be relatively small and densely protoplasmic, and if so they do not usually bear any laterals. The sizes of these cells relative to the subapical cell, and the presence or absence and number of laterals on the hypogenous cell are important features in separating genera.

The subapical cell bears one or two other pericentral cells besides the supporting cell, and these are designated fertile or sterile depending on whether a second auxiliary cell (besides the one from the supporting cell) is produced after fertilization. The supporting cell always bears a terminal sterile cell.

The smaller cells of the fertile axis and the procarp and pericentral cells on the subapical cell are always enclosed within a common gelatinous sheath or wall, and the whole structure is referred to as the "procarp system".

(2) Development of the Carposporophyte

(a) Wrangelieae

The supporting cell of the fertilized procarp produces an auxiliary cell on the opposite side to that on which the carpogonial branch is borne, and the diploid nucleus is transferred to it through the nearer of the two small discoid connecting cells which are cut off, one on each side of the carpogonium. The trichogyne is lost and the cells of the carpogonial branch fuse somewhat, but the fused branch, together with the unfertilized carpogonial branches from the same fertile axis, eventually degenerate. The auxiliary cell divides to produce a single gonimoblast initial which divides repeatedly and subtrichotomously. The gonimoblast filaments creep over the still short axial cells and between the lower cells of the sterile whorl-branchlets of the fertile axis; these were about 1-2 cells long at fertilization leaving the procarps exposed but by now have developed considerably giving a compact spherical mass of modified whorl-branchlets. The sterile cell on the supporting cell, if present, divides similarly.

After one or two subtrichotomous divisions, the terminal cells of the gonimoblast become carposporangia, while the subterminal cells divide further and continue the growth of the gonimoblast in a sympodial manner. The lower gonimoblast cells fuse gradually with each other, with lower cells of the sterile whorl-branchlets and with 2-3 fertile axial cells, giving a large fusion cell with many ramifying processes.

The spherical mass of intermingled sterile and fertile tissue is surrounded by an outer involucrum of whorl-branchlets from lower axial cells of the fertile axis.

This description agrees essentially with that of Kylin (1928b) for the type species, Wrangelia penicillata. Segawa (1950, p.235) described the procarp and gonimoblast development for a previously unknown species of *Wrangelia* from Japan, in which a sterile cell is absent from the supporting cell as in several southern Australian species.

(b) Sphondylothamnieae and Spermothamnieae

Within these two groups there is much greater variation in gonimoblast development than in the Wrangelieae. Fusion of cells of the carpogonial branch and production of connecting cells occur as in the Wrangelieae. There may be one auxiliary cell per procarp produced from the supporting cell, or two, the second one produced from the fertile pericentral cell which is adjacent to the carpogonium. In the latter case, both connecting cells transfer the diploid nuclei, one to each auxiliary cell. The presence or absence of a second auxiliary cell is considered an important feature in separating genera.

The auxiliary cells may divide~~d~~ directly, giving up to 5 gonimoblast initial cells each of which gives rise to a separate gonimolobe. The gonimolobe initials may become multinucleate (*Mazoyera*) and produce many 1-2 celled filaments with the terminal cells becoming lachrimiform carposporangia, or remain uninucleate (*Ptilothamnion schmitzii*) giving successive separate gonimolobes of many tightly packed cells, all of which simultaneously become angular carposporangia. The daughter cells of uninucleate gonimoblast initials from one auxiliary cell may remain together as a single gonimolobe (*Wollastoniella*, *Involucrana*, *Sphondylothamnion*, *Drewiana*, *Spermothamnion*, *Tiffaniella*, *Lomathamnion* and *Interthamnion*). The auxiliary cell(s) may also produce only one apical functional gonimoblast initial (*Sheplyea* and *Lejolisia*), although the two basal lobes of the somewhat pyramidal auxiliary cell may be cut off early in development but do not divide further. The growth of the gonimoblast in *Lejolisia* is sympodial.

In all genera except *Lomathamnion* and *Interthamnion* extensive fusions occur, involving the lower gonimoblast cells (only these in *Drewiana* and *Lejolisia*) and the subapical cell (*Mazoyera*, *Involucrana* and *Ptilothamnion*) and the hypogenous cell (*Shepleya*, *Wollastoniella*, *Spermothamnion* and *Tiffaniella*).

The Sphondylothamnieae is particularly characterised by the post-fertilization division of the sterile cells associated with the procarp - the apical cell, the sterile pericentral cell(s) and sterile cell on the supporting cell. These form 2-4 inner involucral groups around the carposporophyte. The division of these cells, in *Lejolisia aegagropila* giving a pericarp enclosed within a single gelatinous sheath and in *Interthamnion* giving 3 groups of 2-5 cells, is not considered to align these genera with the Sphondylothamnieae. They are more probably special developments in the Spermothamnieae since these genera lack whorl-branchlets.

The term "cystocarp" is used generally in the Wrangelieae to refer to the spherical head of intermingled gonimoblast and sterile filaments, in the Sphondylothamnieae to refer to the carposporophyte with enclosing inner involucrum, and in *Lejolisia* to refer to the carposporophyte with surrounding pericarp.

VI. CRITERIA ACCEPTED FOR PHYLOGENETIC COMPARISONS

It is often possible to detect certain tendencies in the morphology and reproduction of the subunits of any given taxon but it is not easy to determine the direction of these tendencies. In the absence of information about the real ancestors of a group (or fossil data) the criteria accepted in suggesting the direction of evolution must be recognised as partly arbitrary. There are many examples in the literature where reverse evolutionary lines have been proposed for a particular taxon depending on the criteria accepted by each author.

It is not necessary that all the primitive features are possessed by one group and all the advanced features by another. Because of the generally independent nature of inheritance of genetic traits, it is possible for one group to be at the same time primitive in some features and advanced in others. Therefore it is often more profitable to discuss these features separately.

The general criteria listed below are adapted from concepts developed both from the morphology of Angiosperms and other groups in the red algae, where in general unspecialised structures are considered more primitive than specialised structures.

VEGETATIVE FEATURES

(1) Determinate branches are taken as more specialised than indeterminate branches since determination involves differentiation of constituent cells. Thus indeterminate branches are taken as the

more primitive.

(2) Lateral branches which are whorled and spirally arranged are taken to be more primitive than those arranged in an orthostichous or distichous manner.

(3) Whorls containing a large number of laterals are taken to be more primitive than those containing a small number.

(4) Whorls with all members equally developed are taken to be more primitive than those containing unequal members. This has involved differentiation of some members of the whorl and, depending on positions, may lead to dorsiventrality.

(5) Indeterminate branches originating from axial cells are taken to be more primitive than those originating from the basal cells of whorl-branchlets. The latter condition probably represents a lateral of the whorl-branchlet which has become secondarily indeterminate, whereas the former probably shows a retention of the original indeterminate nature of the lateral branch.

(6) Cortical rhizoids originating from the proximal ends of axial cells are taken to be more primitive than those originating from the basal cells of whorl-branchlets, as the latter condition represents a restriction of the rhizoids to the lateral branches. Spongy rhizoidal cortication is taken to be more primitive than pseudoparenchymatous rhizoidal cortication, where the walls of the rhizoidal cells have become confluent with or attached to the wall

of the axial cell. The spongy cortication is usually accompanied by the presence of specialised haptera or secondary pit connections.

The presence or absence of cortication is usually a reflection of the size of the plant and cannot be taken as primitive or advanced.

REPRODUCTIVE FEATURES

(1) Reproductive structures which are not restricted in position are generally taken as more primitive than those which are restricted to certain parts of the plant. However, the occurrence of procarps on both determinate and indeterminate branches may be an advance over their occurrence on only indeterminate branches, as the latter structures are probably more primitive.

(2) A decrease in the proportion of fertile cells to sterile cells probably represents an evolutionary advance. This may be seen in the number of procarps occurring on one fertile axis, the number of auxiliary cells per procarp, or the proportion of carposporophyte cells which become carposporangia.

In comparing this proportion between different taxa it is important to compare the same structural units in each case - for example, a fertile axis of a given number of cells in length. It is possible that two widely separated genera have both achieved the same degree of efficiency in quite different ways. In *Wrangelia*, for example, several procarps are produced along the one fertile axis, presumably giving a greater chance that fertilization will occur in one of them. In *Wollastoniella myriophylloides* only one procarp is produced per fertile axis but up to 5 fertile axes are produced in close proximity, thus achieving the same result as in *Wrangelia*.

VII. DESCRIPTIONS OF TAXA

KEY to TRIBES of CERAMIACEAE STUDIED

1. Procarps formed successively on axial cells near apices of potentially indeterminate axes; carposporophyte intermingled with modified whorl-branchlets of fertile axis; whorl-branchlets five, rarely fewer, per axial cell; indeterminate branches originating from basal cells of whorl-branchlets ... ... TRIBE 1. WRANGELIEAE

1. Procarps confined to the subapical cell of the fertile axis; carposporophyte naked or surrounded by involucral branchlets; whorl-branchlets present or absent; indeterminate branches originating from axial cells of main axes 2

    2. Carposporophyte surrounded by special, free, inner involucral branchlets formed after fertilization by division of sterile cells associated with the procarp; whorl-branchlets present, 2-5 on each axial cell; rhizoidal cortication present or absent .. .. TRIBE 2. SPHONDYLOTHAMNIEAE

    2. Carposporophyte naked or surrounded by free involucral branchlets from lower axial cells; sterile cells associated with the procarp generally not dividing after fertilization, or if dividing, then the resultant branchlets not free but enclosed within a common gelatinous sheath; whorl-branchlets absent; rhizoidal cortication absent ... ... TRIBE 3. SPERMOTHAMNIEAE

1. TRIBE WRANGELIEAE Schmitz

The monogeneric tribe Wrangelieae is here distinguished from the other tribes in the Ceramiaceae by the following combination of characteristics:

(1) thallus with erect axes only; apical cells of indeterminate branches small (about 10µ diameter), generally dividing by alternately oblique divisions; five, rarely fewer, whorl-branchlets per axial cell; potentially indeterminate branches borne on basal cells of whorl-branchlets; cortication, when present, of descending rhizoids from basal cells of whorl-branchlets; cells uninucleate,

(2) tetrahedral tetrasporangia formed on lower cells of whorl-branchlets,

(3) spermatangial heads formed in compact spherical heads, stalked on lower cells of whorl-branchlets,

(4) procarps borne on successive axial cells near the apices of potentially indeterminate branches; supporting cell of carpogonial branch with or without a terminal sterile cell; auxiliary cell one per procarp, producing a subtrichotomously branched gonimoblast which intermingles with the modified sterile whorl-branchlets of the fertile axis; large fusion cell formed from lower gonimoblast cells, fertile axial cell, and lower cells of the sterile whorl-branchlets.

KEY to SOUTHERN AUSTRALIAN SPECIES of WRANGELIA

1. Ends of thallus branches flattened due to stronger development of lateral whorl-branchlets; whorl-branchlets alternately pinnate or subdichotomously branched; cortical rhizoidal cells producing an outer layer of branchlets 2

1. Ends of thallus branches terete; whorl-branchlets subdichotomously to unilaterally branched; cortical rhizoidal cells not producing an outer layer of branchlets 3

    2. First and second formed whorl-branchlets of each whorl formed on opposite sides of the axis, strongly developed and reaching 3 mm long, other whorl-branchlets shorter, terminal cells acute; outer cortical branchlets terminating in acute cells ... ... *W. nobilis*

    2. First and second formed whorl-branchlets of each whorl both formed on the same side of the axis, alternating on successive axial cells, villose, reaching 4 mm long, other whorl-branchlets much shorter, terminal cells mucronate; outer cortical branchlets terminating in large spherical cells ... ... *W. australis*

3. Terminal cells of whorl-branchlets mucronate, 1-2 times longer than wide . ... <u>W. velutina</u>

3. Terminal cells of whorl-branchlets not mucronate, usually more than twice as long as wide 4

    4. Thallus (2-)5-10(-25) cm high; whorl-branchlets subdichotomously to unilaterally branched 5-8 times, ultimate branchlets of 2-4(-6) cells; each tetrasporangium surrounded by 2-4 curved involucral branchlets of small cells . ... <u>W. plumosa</u>

    4. Thallus 15-30(-60) cm high; whorl-branchlets subdichotomously branched 2-3 times near the base, ultimate branchlets of 9-10 cells; tetrasporangia not surrounded by special small-celled involucral branchlets 5

5. Median cells of whorl-branchlets 35-45u diam., 3-5 times longer than wide, terminal parts of whorl-branchlets obtuse. (rare - only sterile specimens known) .. .. <u>W. abietina</u>

5. Median cells of whorl-branchlets 25-30µ diam., 5-7 times longer than wide, terminal parts of whorl-branchlets tapering markedly ... ... <u>W. princeps</u>

WRANGELIA PRINCEPS Harvey 1862: pl. 234; *Alg. Aust. Exs. no. 257E; 1863: synop. no. 322. J.Agardh 1876: 624. Bornet and Thuret 1880: 184. De Toni 1897: 136. Lucas 1909: 23; 1929b: 48. Lucas and Perrin 1947: 143. May 1965: 365. Okamura 1932: 133. Reinbold 1899: 44. Sonder 1880: 29. Tate 1882: 21. Tisdall 1898: 511. Wilson 1892: 170. Womersley 1950: 181.

TYPE LOCALITY - Pt. Phillip Heads, Vic. (Harvey).

LECTOTYPE - Herb. Harvey, TCD (Alg. Aust. Exs. no. 257E - not seen). An isotype is present in N.S.W. and has been examined.

DISTRIBUTION - The species has a disjunct distribution, having been collected near Fremantle and Cape Naturaliste, W. Aust., the southern coast of Kangaroo Is. and Stinky Bay, S. Aust., and Pt. Phillip Bay, Vic.

The species has only been found as drift, often epiphytic on Codium spp. or Sargassum sp.

The material used for detailed investigation was collected from Seal Bay (ADU, A30,841, Gordon, 29.x.1966), and Stanley Beach, Kangaroo Island (ADU, A20,089, Womersley, 7.ii.1956).

VEGETATIVE STRUCTURE. (Fig. 1A-D, Plate 1).

The thallus is generally 15-30 cm high but may reach 60 cm (Harvey 1862), and is alternately pinnately branched with 3-4 orders of branching (Plate 1).

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* Although this is not a reference, it is included here for convenience.

Apical cells (about 8µ diam.) of indeterminate branches give rise by alternately oblique divisions (Fig. 1A) to axial cells which enlarge gradually, at first becoming spherical, then cylindrical, and when mature reaching about 900µ diam. and 3 mm long near the base of the plant. Each axial cell bears five whorl-branchlets, the initials of which are cut off obliquely from the upper end of the axial cell, usually in alternating sequence (Fig. 10H), but occasionally the positions of the third and fourth whorl-branchlets are reversed (Fig. 10I). First formed whorl-branchlets on each axial cell are produced on alternate sides of the axis. Mature whorl-branchlets reach 2 mm long, and are at first subdichotomously branched 2-3 times at the base,with the ultimate branchlets simple, of 9-10 cells and tapering (Fig. 1B). In older parts, further laterals are produced from the basal cell. Adjacent whorls overlap only in younger parts.

Median cells of whorl-branchlets are 25-30µ diam. and 5-7 times longer than wide. Basal cells in older parts of the plant become embedded in the walls of the cells of the main axes, and are covered with cortical rhizoids from above (see below).

Potentially indeterminate lateral branches are initiated from the upper sides of the basal cells of whorl-branchlets (Fig. 1C), eventually one from each whorl-branchlet. Usually only one per axial cell (that on the first-formed whorl-branchlet) develops into a true thallus branch, the others remaining short and not exceeding the length of the whorl-branchlets.

Descending rhizoids are initiated from the basal cells of whorl-branchlets (Fig. 1C) below about the 5th-11th axial cells, and are embedded in the walls of the main axial cells. Each basal cell eventually produces 3-4(-6) rhizoids which grow over the rhizoids produced by the lower whorl-branchlets for a distance of 2-3 axial cells. The thick pseudoparenchymatous cortex so formed increases the diameter of the main axis in lower parts of the thallus to 1-8 mm. The inner rhizoidal cells reach about 80µ diam., and the outer rhizoids about 6µ diam.

REPRODUCTION

Tetrasporangia (Fig. 2A)

The tetrasporangia reach 100µ diam. and arise terminally from the lower 1-3 cells of the whorl-branchlets, mostly on ecorticate or slightly corticate lateral branches. There is no apparent modification of the whorl-branchlets into special involucral filaments as occurs in other species of *Wrangelia*.

Spermatangial heads (Fig. 2B-E)

The spermatangial heads are spherical and reach about 60µ diam. They are terminal on stalk cells (Fig. 2D, E) which are borne on the lower 1-2 cells of the whorl-branchlets, or directly on the axes of ecorticate or slightly corticate lateral branches. Five curved involucral branchlets arise from each stalk cell, the abaxial one produced first, and subsequent ones in alternating sequence (Fig. 2E).

The two fertile axial cells of the spermatangial head divide obliquely, each producing about 4 pericentral cells (Fig. 2B, C). Each of these cells further divides obliquely giving (1-)2 vertical and lateral chains of small cells, which together with the pericentral cells become elongate in a radial direction and act as the spermatangial mother cells. Each one buds off 2-3 spermatangia, about 3µ diam. (Fig. 2D). The spermatia are about one quarter the length of the spermatangia and appear to consist mainly of nuclear material.

Procarp and Carposporophyte (Figs. 2F,G, 3A-C)

Any potentially indeterminate axis may become fertile at the apex. Procarps arise successively from about the third to the sixth axial cells, one per axial cell. A maximum of four have been observed on one fertile axis. The supporting cell corresponds to the basal cell of the first-formed whorl-branchlet on each axial cell, and bears a terminal sterile cell and a lateral four-celled carpogonial branch (Fig. 2F). The first cell of the carpogonial branch is cut off towards the distal end of the supporting cell, the second cell cut off in a terminal position, the third cell laterally, and the carpogonium adaxially by an oblique division.

One or two cells of the carpogonial branch may be binucleate before fertilization. The sterile whorl-branchlets in the fertile region of the axis are only about 1-2 cells long before fertilization, leaving the procarps exposed.

After fertilization, the trichogyne is lost and two small discoid connecting cells (Fig. 2G) are cut off laterally from the carpogonium, and occasionally similar cells are produced abaxially from the other cells of the carpogonial branch. An elongate auxiliary cell is produced from the supporting cell on the opposite side to the carpogonial branch and fuses with the nearer of the connecting cells. The auxiliary cell cuts off a gonimoblast initial cell in an adaxial direction, and this cell then produces (2-)3 further cells which again divide subtrichotomously. Of the three daughter cells the first (and sometimes the second-formed) becomes a carposporangium, while the second and third-formed divide subtrichotomously again and similarly form further carposporangia, repeating the process in a sympodial manner (Fig. 3A,B).

The gonimoblast filaments creep irregularly over the cells of the fertile axis which remains relatively short. The sterile whorl-branchlets develop considerably after fertilization, forming a compact spherical mass with cells much smaller (about 8µ diam. x 40µ long) than those of the vegetative whorl-branchlets. The sterile cell on the supporting cell divides similarly (Fig. 3A, su. st. gr). The apex of the fertile axis may continue to divide a short time after fertilization, but soon the apical cell becomes elongate and ceases to divide (Fig. 3A). The cells of the old carpogonial branch generally fuse and together with the unfertilized carpogonial branches from the same axis are eventually lost. Gonimoblast development has been observed from one only fertilized procarp per axis.

As gonimoblast development proceeds, the lower cells fuse gradually and the resultant fusion cell encloses 2-3 axial cells. In the mature cystocarp (Fig. 3C) tear-shaped carposporangia, about 50µ diam. x 100µ long, escape from between the modified sterile whorl-branchlets. One or two cells of the fertile axis directly below the fusion cell are usually very densely protoplasmic, with widened pit connections. Unmodified whorl-branchlets from lower axial cells loosely surround the fertile region (Fig. 3C).

DISCUSSION

W. princeps is very similar to the type species, *W. penicillata* (p. 72). In the original description of *W. princeps*, Harvey noted that these species differed mainly in size, with *W. plumosa* forming an intermediate between them. However, Boergesen (1916, p.120) reported a maximum height of 20 cm for *W. penicillata*, thus showing a slight overlap in size range. *W. penicillata* is distinguished from *W. princeps* by the greater diameter of the median cells of the whorl-branchlets (30-50µ in contrast to up to 30µ for *W. princeps*) and the denser branching of whorl-branchlets (4-8 subdichotomous divisions in contrast to 2-3 in _W. princeps_). The tetrasporangia of _W. penicillata_ are protected abaxially by 1-2 curved involucral filaments each of 2-3 relatively small cells, but similar filaments are absent in _W. princeps_.

The sexual structures of the two species are essentially identical. The presence of a sterile cell on the supporting cell does not occur in any other southern Australian species of _Wrangelia_, and has not been reported for extra-Australian species other than _W. penicillata_.

WRANGELIA PLUMOSA Harvey 1844: 450; Alg. Aust. Exs. no. 256; 1860: 308; 1963; synop. no. 323. J.Agardh 1863: 706; 1876: 624. De Toni 1897: 136. Guiler 1952: 99. Hooker and Harvey 1847: 410. Kuetzing 1849: 664. Lucas 1909: 23; 1929a: 16. Lucas and Perrin 1947: 143, fig. 16. May 1965: 365. Okamura 1932: 133. Saenger 1967: 170. Sonder 1880: 29. Tisdall 1898: 511. Wilson 1892: 170. Womersley 1950: 181.

Wrangelia gunniana J.Agardh 1876: 617. De Toni 1897: 128. Guiler 1952: 99. Lucas 1909: 22; 1929a: 16. May 1965: 365. Okamura 1932: 133. Sonder 1880: 28.

Wrangelia penicillata sensu Harvey 1854: 545; 1863: synop. no. 324; Alg. Aust. Exs. no. 257. Lucas 1909: 23. May 1965: 365. Okamura 1932: 133. Sonder 1880: 29.

TYPE LOCALITY - Georgetown, Tas. (Gunn).

LECTOTYPE - Herb. Harvey, TCD (no. 1315 of Gunn). Not seen.

DISTRIBUTION - Widely distributed, from Rottnest Is., W. Aust. to Pt. Stephens, N.S.W., including Tas.

Common on rough to moderately rough reefs, usually growing directly on rock in the lower littoral and upper sublittoral zones, occasionally on jetty piles and buoys, or epiphytic on other algae, e.g. *Sargassum*. Also dredged from 2-6 m on the channel edge in American River Inlet, Kangaroo Is., S. Aust. (ADU, A30,823, Gordon, 31.x.1966).

Sexual and tetrasporangial plants usually occur together in the same population.

Material used for detailed investigation was obtained from the lower littoral on jetty piles at Vivonne Bay, Kangaroo Is. (ADU, A30,825, Bailey, 31.x.1966, tetrasporangial), from the lower littoral outer reef, Robe, S.Aust. (ADU, A27,894, Gordon, 18.v.1964, sexual and tetrasporangial) and from the upper sublittoral pools, Pt. Roadnight, Vic. (ADU, A29,569, Mitchell, 26.viii.1965, sterile).

VEGETATIVE STRUCTURE (Fig. 4A,B, Plate 2A,B).

The mature thallus is (2-)5-10(-25) cm high and is alternately pinnately branched with 3(-4) orders of branching, the main fronds tapering to the apices (Plate 2A). Specimens occurring in calm regions are usually more openly and irregularly branched with longer main axes (Plate 2B) than those growing under conditions of very rough wave action. The colour of plants from different populations varies from a very deep purplish red to light yellow at higher light intensities.

The holdfast is small (2-8 mm diam.), discoid and composed of intertwining rhizoids which grow downwards from the main axis. One to five axes may develop from the one holdfast, probably originating from indeterminate laterals produced at the sporeling stage.

The structure of the apices of indeterminate branches (Fig. 4A) is similar to that of W. princeps (p. 35). Axial cells reach 400-500µ diam. and 1.5-2.5 mm long near the base of the plant. The first and second of the five whorl-branchlets per axial cell are adjacent, the third opposite the second, the fourth opposite the first, and the fifth between the third and fourth, or rarely between the first and third or second and fourth (Fig. 10H,J,G). The primary, secondary and tertiary laterals of the young whorl-branchlet are produced unilaterally, but later by elongation of the younger cells, the whorl-branchlet appears subdichotomously branched 5-8 times

(Fig. 4B). The whorl-branchlets gradually taper towards the apices, with the ultimate branchlets of 2-4(-6) cells. In lower parts of the plant the basal cells of the whorl-branchlets produce further laterals which are reflexed and curve downwards over the cortex. Mature whorl-branchlets reach 2 mm long, and generally overlapping of whorls only occurs near the apices of indeterminate branches.

Median cells of whorl-branchlets are 40-70µ diam. and ($3\frac{1}{2}$-)5-7 times longer than wide. Terminal cells are 12-20µ diam. and $1\frac{1}{2}$-2(-6) times longer than wide.

Indeterminate branches are produced as in *W. princeps*, from the basal cells of first-formed whorl-branchlets, with usually only one per whorl. Rhizoids are produced as in *W. princeps*, and the pseudoparenchymatous cortex increases the diameter of the main axes to about 2 mm in lower parts of the thallus.

REPRODUCTION

Tetrasporangia (Fig. 4C,D,E)

The tetrasporangia reach 100µ diam. and are borne terminally on small cells of modified lateral branchlets arising from lower cells of the whorl-branchlets (Fig. 4C) which occur mostly on short, ecorticate potentially indeterminate branches of the third and fourth orders. Each sporangium is surrounded by 2-5 curved involucral branchlets of small cells about 20µ diam. and 55µ long

(Fig. 4E) arising from the stalk cell. Repeated production of further sporangial stalk cells from the primary ones gives a compact cluster of branchlets. Usually one whorl-branchlet of the five in each fertile whorl has a vegetative portion unmodified for reproduction (Fig. 4C), and in the others this portion is rudimentary or absent (Fig. 4D).

Spermatangial heads (Figs. 4F,G, 5A)

The spermatangial heads reach about 110µ diam. and are terminal on stalk cells which are borne on the lower 1-2 cells of whorl-branchlets on ecorticate or slightly corticate lateral branches, generally of the third and fourth orders. One to three stalk cells (Fig. 4F) may be borne on the one cell. As in the tetrasporangial plant, usually only one whorl-branchlet per whorl is completely unmodified (Fig. 4F, veg.wh.b), and one other partly modified for reproduction. In the remaining whorl-branchlets the vegetative parts are reduced to downwardly projecting curved filaments (Fig. 4F, red.wh.b). Each spermatangial head has 4(-5) branched involucral filaments (Fig.4F,G).

The spermatangial head develops by oblique divisions of two fertile axial cells, each producing about 5 pericentral cells. Later, 1-3 further pericentral cells may be cut off from at least the basal cell of the fertile axis. The pericentral cells divide both terminally and laterally, the outer cells becoming wedge-shaped and elongate. These act as spermatangial mother cells, each budding off 3 elongate spermatangia.(Fig. 5A). The pericentral cells themselves may also produce spermatangia when close to the surface of the head.

Procarp and Carposporophyte (Fig. 5B-D)

The apex of any potentially indeterminate branch may become fertile. Up to 7 procarps arise alternately or unilaterally from the second to sixth axial cells (Fig. 5B). Only one is formed per axial cell. No terminal sterile cell occurs on the supporting cell as in *W. princeps*. The first and second cells of the carpogonial branch are cut off by slightly oblique divisions, and the third cell is cut off laterally, alternately clockwise and anticlockwise in procarps on successive axial cells (Fig. 5B). The carpogonium is cut off in the direction of the apex of the fertile axis. Thus the second and third cells of the carpogonial branch generally appear superimposed.

After fertilization, production of the auxiliary cell, loss of the trichogyne, production of connecting cells (Fig. 5C) and gonimoblast development proceeds as in *W. princeps*. Usually one auxiliary cell (rarely to three - one from each of three fertilized procarps) is produced per fertile axis. The median cells of the mature modified sterile whorl-branchlets have basal adaxial lobes [Fig. 5D (i), (ii)], which are not present in *W. princeps*.

DISCUSSION

W. plumosa and W. princeps are superficially similar but may be differentiated on features of cell size, branching of whorl-branchlets and tetrasporangia (Table 1).

TABLE 1.- Comparison of W. plumosa and W. princeps

	W. plumosa	W. princeps
Diam. median cells of whorl-branchlets	40-70µ	25-30µ
Branching of whorl-branchlets	unilateral to subdichotomous 5-8 times	alternate to subdichotomous 2-3 times
Ultimate branchlets of whorl-branchlets	2-4(-6) cells	9-10 cells
Involucral branchlets of sporangia	2-5 filaments of small cells	no modified involucral branchlets
Habitat	lower littoral (-upper sublittoral)	deep water

WRANGELIA VELUTINA (Sonder) Harvey 1854: 546; Alg. Aust. Exs. no. 265. 1858: pl. 46; 1863: synop. no. 329. J.Agardh 1876: 617; 1879: 193, pl. 32, fig. 1,2. Bornet and Thuret 1880: 184. De Toni 1897: 128. Guiler 1952: 99. Levring 1946: 224. Lucas 1909: 22; 1929b: 48. Lucas and Perrin 1947: 136, fig. 9. May 1965: 365. Okamura 1930-31: 116; 1932: 133. Reinbold 1898: 40. Sonder 1880: 28. Tate 1882: 21. Tisdall 1898: 511. Weber van Bosse 1921: 222. Wilson 1892: 170. Womersley 1950: 181; 1959: 568.

Dasya velutina Sonder 1845: 53; 1846: 179. J.Agardh 1863: 1226. Harvey 1847: 63, pl. 23.

Phlebothamnion velutinum (Sonder) Kuetzing 1849: 659.

Haliacantha incrustans J.Agardh 1899: 112, pl. 1, fig.2 a-f. De Toni 1903: 1438; 1924: 151. Kylin 1956: 382. Lucas 1909: 52. Lucas and Perrin 1947: 365. May 1965: 370. Okamura 1932: 130.

TYPE LOCALITY - South western coast of Australia (Preiss).

TYPE - MEL 15,237 (Preiss no. 2578).

DISTRIBUTION - From Rottnest Is., W. Aust. along the southern coast to Flinders, Vic., and Tas. (The Tas. record of Levring gives no exact locality.) Okamura records this species from Kotosho, Japan, but he only had sterile fragments. The record of Weber van Bosse (1921: 222) from the Malay Archipelago is also doubtful as only sterile specimens were collected, and although they were compared with Harvey's no. 265 (not the type), this species may be confused vegetatively with other species (see Discussion).

Material used for detailed investigation was collected from Wedge Is. (ADU, A27,325, Baldock, 29.xii.1963), Sleaford Bay, Eyre Pen. (ADU, A32,169, Robinson, 12.v.1968) and Pt. Elliot (ADU, A27,500, Gordon, 21.iii.1964).

VEGETATIVE STRUCTURE (Fig. 6A-C, Pl. 3A,B)

Plants cast up from deeper water are usually 10-16 cm high and irregularly branched, with laterals of the second and third orders distichous and diverging widely, alternate or secund and very unequal in length (Harvey 1858, pl. 46). Reef plants (Pl. 3A) are usually smaller (4-7 cm high) and more closely branched than the plants from deeper water (Pl. 3B), with ultimate branches often regularly alternate from each axial cell and equal in length, especially on fertile plants. The main axes are terete and often denuded of whorl-branchlets in the lower parts. The hold-fast is discoid, composed of intertwining rhizoids which continue down from the main axis. A "prostrate stem" as reported by Harvey (1858) has not been observed.

The development of the apex of an indeterminate branch (Fig. 6A) is similar to that of W. princeps, and the axial cells reach about 250µ diam. and 500µ long near the base of the plant.

The first-formed initials of the five whorl-branchlets on each axial cell are often produced unilaterally (Fig. 6A). The first three whorl-branchlets are cut off in sequence around the axial cell, followed by the fourth opposite the second. and the fifth between the third and fourth (Fig. 10I). The laterals borne from cells of the upper parts of whorl-branchlets are initiated and mature first, while the laterals in lower parts mature later (Fig. 6B). Mature whorl-branchlets reach 1.5 mm long and are pseudodichotomously branched 7-8 times, with ultimate parts 2-4 cells long and terminated by smaller mucronate cells. In lower parts of the plant further laterals may be produced from the basal cells of the whorl-branchlets. These consist of narrower cells, and are curved and reflexed over the cortex. Adjacent whorls always overlap forming a net-like covering over the axis.

Median cells of whorl-branchlets are 55-90µ diam. and 2-4 times longer than wide, but those occurring in plants from deeper water tend to be somewhat shorter and thicker than those of reef plants. Terminal mucronate cells are about 14µ diam. and 1-2 times longer than wide.

Indeterminate branches originate from basal cells of whorl-branchlets. In reef plants there is usually one per whorl, alternating on opposite sides of the axis, but in plants from deeper water they are produced irregularly.

The rhizoidal cortex (Fig. 6C) is produced as in W. princeps, with some of the inner rhizoids winding spirally around the axial cells. The diameter of the corticated axis in lower parts is about 1.5 mm.

REPRODUCTION

Tetrasporangia (Fig. 6D)

The tetrasporangia reach 90µ diam. and are borne in positions similar to those of W. plumosa. Each sporangium is surrounded by 1-2 small-celled involucral branchlets arising from the stalk cell of the tetrasporangium.

Spermatangial heads (Fig. 6E, (i), (ii))

Spermatangial heads are about 125µ diam. and are terminal on stalk cells which are borne on cells of small modified lower laterals of whorl-branchlets (Fig. 6E). As in W. plumosa, an axial cell of a fertile branch may bear completely or partly modified fertile whorl-branchlets, as well as completely vegetative whorl-branchlets.

The development of the spermatangial heads is the same as for W. plumosa.

Procarp and Carposporophyte (Fig. 6F)

Fertile axes are similar in position and structure to those of W. plumosa, with one or two procarps per axial cell and without a sterile cell on the supporting cell. In contrast to W. plumosa, it is the carpogonium (instead of the third cell of the carpogonial branch) which is cut off in a lateral direction, alternately clockwise and anticlockwise in successive procarps. Thus the carpogonium and the third cell appear superimposed in each procarp (Fig. 6F). Some of the distal cells of the sterile whorl-branchlets of the fertile axis become elongate and slightly hair-like in early stages.

Immediate post-fertilization stages, including the production of an auxiliary cell and connecting cells, the development of gonimoblast and carposporangia, and continued development of the sterile whorl-branchlets of the fertile axis are the same as in W. plumosa and W. princeps. The median cells of the sterile whorl-branchlets are not, however, basally lobed as in W. plumosa. The axial cells immediately below the fusion cell become swollen and the pit connections between them enlarge considerably.

One plant collected at Sleaford Bay, Eyre Pen., S. Aust. (A32,169) bore tetrasporangia on the whorl-branchlets on the lower axial cells of a female axis with a terminal cystocarp.

DISCUSSION

Herbarium specimens of W. velutina are often confused with Dasya velutina. Brooke's specimens (in LD) from Israelite Bay, W. Aust. were placed by J.Agardh under Dasya velutina Sonder. A fragment of one of these specimens differs considerably from Sonder's specimen (MEL 15,237) in having a polysiphonous main axis corticated with rhizoids between the pericentrals and the main axial cell. The pseudolaterals are 3-4 times pseudodichotomously branched near the base with ultimate branchlets 7-8 cells long, in contrast to the 7-8 pseudodichotomies and 2-4 ultimate branchlet cells in the whorl-branchlets of W. velutina. However, in J.Agardh's description of Dasya velutina (1863, p.1226), he refers to Sonder's original description and to Harvey's description (1847, p.63) although he had not seen Harvey's specimens. Thus it is likely that his description does not refer to Brooke's collection which was possibly determined later than 1863.

Other species of Dasyaceae from southern Australia are superficially very similar to W. velutina but may be quickly distinguished by the nature of the dichotomies of the whorl-branchlets which are closely appressed near their bases giving an inverse Y-shaped intersection, whereas those of W. velutina are not so appressed giving an inverse V-shaped intersection.

J.Agardh reported that his Haliacantha incrustans (= W. velutina) was calcified, giving effervescence with acid. Kylin (1956, p.382), after examining Agardh's specimens, concluded that this was due to small shell fragments trapped between the whorl-branchlets and most often found in drift specimens of the species. Some plants recently collected from rock platforms subjected to rough wave action have a white opaque substance in the outer cells of the whorl-branchlets. This gives no immediate effervescence with acid but disappears after soaking in acid for several weeks. It is doubtful that this is the phenomenon to which J.Agardh referred.

WRANGELIA NOBILIS Hooker and Harvey 1847: 411; Alg. Aust. Exs. no. 269. J.Agardh 1863: 709; 1876: 622. De Toni 1897: 133. Guiler 1952: 99. Harvey 1860: 308; 1863: synop. no. 325. Kuetzing 1849: 665. Lucas 1909: 23; 1929a: 16. Lucas and Perrin 1847: 141, fig. 14. May 1965: 366. Okamura 1932: 133. Sonder 1852: 691; 1880: 29. Tisdall1898: 511. Wilson 1892: 170.

Wrangelia jeannerettii Hooker and Harvey 1847: 411. J.Agardh 1863: 709; 1876: 624. De Toni 1897: 129. Guiler 1952: 99. Harvey 1860: 308; 1863: synop. no. 328.

Kuetzing 1849: 665. Lucas 1909: 23; 1929a: 16. May 1965: 366. Okamura 1932: 133. Sonder 1880: 29.

Wrangelia comosa Hooker and Harvey 1847: 411.

J.Agardh 1863: 710. Kuetzing 1849: 664; 1962: 13, pl. 41, fig. a-d.

Wrangelia dasyclada Harvey ex Kuetzing 1849: 664.

J.Agardh 1863: 710; 1876: 625. Kuetzing 1862: 13, pl. 41. fig. e-f.

Wrangelia clavigera Harvey 1863: pl. 287, synop. no. 326;

Alg. Aust. Exs. no. 268. J.Agardh 1876: 621; 1894a: 138, pl. 2, fig. 8-11. Bornet and Thuret 1880: 184. De Toni 1897: 132; 1924: 149. Lucas 1909 : 23; 1929b: 48. Lucas and Perrin 1947: 140, fig. 13. May 1965: 366. Mazza 1919: 1302. Okamura 1932: 133. Reinbold 1897: 46. Sonder 1880: 29. Tate 1882: 21. Tisdall 1898: 511. Wilson 1892: 170. Womersley 1950: 180.

Wrangelia ballioides J.Agardh 1876: 621. De Toni 1897: 132.

Guiler 1952: 99. Lucas 1909: 23; 1929a: 16. Lucas and Perrin 1947: 141, fig. 15. May 1965: 366. Okamura 1932: 133. Sonder 1880: 29. Tisdall 1898: 511. Wilson 1892: 170.

Griffithsia radiciformis Hooker and Harvey 1847: 411.

TYPE LOCALITY - Georgetown, Tas. (Gunn).

TYPE - Herb. Hooker, K (now at BM - Gunn no. 1324)

DISTRIBUTION - From Pt. Lincoln and the southern islands of Spencer's Gulf, along the southern coast of Kangaroo Is., S. Aust. to Portsea, Vic., and the northern and eastern coasts of Tasmania.

Material used for detailed investigation was collected from Pt. Elliot (ADU, A28,004, Womersley, 21.vi.1964, tetrasporangial), Cape Thomas, Guichen Bay, S. Aust. (ADU, A24,383, Womersley, 24.viii.1960, tetrasporangial), Portland Bay, Vic. (ADU, A21,622, C.Beuglehole, 22.vi.1952), Robe, (ADU, A27,900, Gordon, 18.v.1964, male), Stinky Bay (ADU, A27,885, Wollaston, 19.v.1964, female), Victor Harbour (ADU, A29,523, Womersley, 19.ix.1965, sterile), from Pennington Bay, Kangaroo Is., S.Aust. (ADU, A2,845, Womersley, 15.i.1946, sterile), and from Low Head, Tas. (ADU, A16,415, Perrin, 8.x.1950, sterile).

VEGETATIVE STRUCTURE (Fig. 7A-D, Plate 4A,B)

Plants from deeper water (Pl. 4A) are generally 15-35 cm high, while those growing in the upper sublittoral zone ("W. clavigera Harv." Pl. 4B) are 10-20 cm high and usually more robust than the former. The branching is distichous and irregularly alternate, to about 4 orders, with the lateral branches widely spreading, unequal in length and often clavate due to denuding at their proximal ends (Harvey 1863, pl. 287). The ultimate branches are flattened (see below). The discoid holdfast is composed of intertwining rhizoids which continue down from the main axis.

Apical structure of indeterminate branches (Fig. 7A) is similar to that in other species of *Wrangelia*. Axial cells reach about 380µ diam. and 880µ long in the central part of the plant. The initials of first-formed whorl-branchlets on each axial cell are cut off alternately from successive axial cells. The second-formed whorl-branchlet is cut off opposite the first, the third between the first and second, the fourth opposite the third, and the fifth between the second and third (Fig. 10K). Thus the third and fifth whorl-branchlets always occur on the same side of the axis giving a dosiventral arrangement. The first and second whorl-branchlets ("lateral whorl-branchlets") develop to a much greater extent than the others, thus producing a flattened thallus. The difference in length is greater in deep water forms (Fig. 7B) than those in shallow water forms (Fig. 7C), giving a greater flattening of the thallus in the former. Mature lateral whorl-branchlets reach 3 mm long; they are alternately pinnately branched and taper gradually to the terminal cells which are acute, but not mucronate as in *W. velutina*. Adjacent whorls of whorl-branchlets overlap.

Median cells of lateral whorl-branchlets in the deeper water form are 55-80µ diam. and 3-5(-10) times longer than wide, but in the shallow water form are 60-90µ diam. and only (1-)2-3 times longer than wide. Descending rhizoids, initiated from basal cells of whorl-branchlets (Fig. 7B,C) form a pseudoparenchymatous cortex over the axis (Fig. 7D). Rhizoids on the surface of the cortex produce outwardly a thick mat of short branchlets which are simple or 1-2 times furcate, about 200µ long and composed of cells about 25µ diam. and 30µ long. The diameter of the cortex is thus increased to about 2mm. In lower parts of the thallus the axes become denuded of whorl-branchlets leaving the outer layer of cortical branchlets exposed.

REPRODUCTION

Tetrasporangia (Fig. 8A, Plate 5A)

The tetrasporangia reach 100µ diam. and are terminal on cells of small modified laterals on the basal cells of whorl-branchlets (Fig. 8A) which occur on short potentially indeterminate branches 1-1.5 mm long. These short branches are obvious in winter when the main axes have become denuded of whorl-branchlets. The sporangial stalk cells may bear further stalk cells or curved, small-celled involucral branchlets. Near the apices of the tetrasporangial branches, the vegetative parts of the sporangial whorl-branchlets are considerably reduced or absent.

Spermatangial heads (Fig. 8B)

The spherical spermatangial heads, about 100μ diam., are borne in positions similar to the tetrasporangia. The small cells of the modified laterals bearing the spermatangial heads are comparatively longer than corresponding cells in the tetrasporophyte. Two or three small-celled involucral branchlets arise from the stalk cell of each spermatangial head. Near the bases of the short spermatangial branches, the modified laterals bearing the spermatangial heads are borne alternately on the first-formed whorl-branchlets on successive axial cells, but near the apices of these branches they occur on all whorl-branclets, the vegetative parts being reduced or absent as in the sporophyte.

The development of the spermatangial heads is the same as that of W. plumosa.

Procarp and Carposporophyte (Fig. 8C,D)

The structure of the fertile axis is similar to that of W. velutina but usually two procarps per axial cell occur. The supporting cell does not bear a terminal sterile cell. The carpogonium is cut off in a lateral direction, alternately clockwise and anticlockwise on successive axial cells (Fig. 8C) in this species, while in W. princeps and W. plumosa the third cell of the carpogonial branch is cut off laterally. In both procarps occurring on one axial cell, both carpogonia are cut off in the same radial direction, The distal cells of the sterile whorl-branchlets of the fertile axis may become hair-like as in *W. velutina*.

Post fertilization stages are similar to those in *W. plumosa* and *W. velutina* (Fig. 8D - auxiliary cell cut off from supporting cell, connecting cells and other small cells cut off from cells of the carpogonial branch). Cells of the sterile whorl-branchlets involved in the cystocarp are similar to those in *W. velutina* and not basally lobed as in *W. plumosa*.

DISCUSSION

Type fragments of *W. jeannerettii* and *W. dasyclada* (ex TCD and L respectively) have been examined and are similar in cell proportions to the commoner forms ("*W. clavigera*") of *W. nobilis* (see Table 2). An isotype specimen of *W. ballioides* (MEL 15381) shows no differences from the type of *W. nobilis*.

The name *Wrangelia comosa* was first published by Hooker and Harvey (1847, p.411) with *Callithamnion comosum* Harvey (1844, p.451) as a synonym. Later Kuetzing (1862, p.13, pl. 41) rejected the above synonym and applied Harvey's mscr. name *Warrenia comosa* to the original *C. comosum*. De Toni (1903, p.1368) followed Kuetzing and pointed out the difference in the tetrasporangial structures of the two species (*Warrenia* - cruciate, *Wrangelia* - tetrahedral). Kuetzing's illustration of *Wrangelia comosa* shows secondary branchlets arising from the cortical rhizoids as is typical of W. nobilis. Cell dimensions are similar to those of W. jeannerettii (Table 2).

TABLE 2.- Cell dimensions and frequencies of species synonomous with Wrangelia nobilis (median cells of whorl-branchlets)

	Diameter	Proportions	Frequency of Species
W. jeannerettii	75µ	1-2 times	rare
W. comosa	75µ	1-2 times	rare
W. clavigera	60-90µ	(1-)2-3 times	common
W. nobilis	55-80µ	3-5(-10) times	fairly common
W. ballioides	50µ	8-9 times	
W. dasyclada			rare

W. jeannerettii and W. dasyclada probably represent the extremes of distribution in cell sizes and proportions, the largest number of plants falling in the range represented by W. clavigera and W. nobilis. However, as there is almost continuous variation in these dimensions, the above "species" are reduced to synonomy.

WRANGELIA AUSTRALIS (J.Agardh) comb. nov.

Bracebridgea australis J.Agardh 1894a: 103, pl. 2 , fig. 1-3; 1899: 114. De Toni 1903: 1438; 1924: 504. Kylin 1956: 395, fig. 308C. Lucas 1909: 52. Lucas and Perrin 1947: 365. May 1965: 369. Okamura 1932: 130.

TYPE LOCALITY - Pt. Elliot, S. Aust. (Hussey, no. 190).

TYPE - Herb. Agardh, LD (35,852).

DISTRIBUTION - From Eucla, W. Aust., and the southern coast of Kangaroo Is. to Kingston, S. Aust.

Plants occur in deep water and have been collected to a depth of 10 m in St. Vincent Gulf, S. Aust. (ADU, A33,175, Shepherd, 2.ii.1969).

Collections studied in detail are from Pennington Bay, (ADU, A20,120, Womersley, 11.ii.1956, tetrasporangial), and Stanley Beach, Kangaroo Is. (ADU, 20,081, Womersley, 7.ii.1956, male, ADU, A20,910, Womersley, 6.ii.1957), St. Vincent Gulf (ADU, A33,175, female) and Seal Bay, Kangaroo Is., S. Aust. (ADU, A32,174, Womersley, 22.xi.1968, sterile).

VEGETATIVE STRUCTURE (Fig. 9A-D, 10A-C, Plate 5B)

The thallus reaches about 22 cm high, and is richly branched in one plane to about four orders, with the main branches irregularly spaced and ultimate branches regularly alternate (see below).

Apical division (Fig. 9A) is similar to other species of Wrangelia, and axial cells reach 250µ diam. and 500µ long near the base of the plant when mature. Each axial cell bears five whorl-branchlets, the initials of which are cut off in alternating sequence (Figs. 9A,B and 10H). First-formed whorl-branchlets on successive axial cells are produced in a zig-zag manner on one side of the axis, and the second-formed whorl-branchlets are produced alternately clockwise and anticlockwise on successive axial cells, thus coming to lie on alternate sides of the axis (Fig. 9B). The third, fourth and fifth-formed whorl-branchlets are similar in form to those of W. velutina, being pseudodichotomously branched 5-6 times, with the median cells 50-65µ diam. and 1½-2 times longer than wide The terminal cells are small (about 12µ diam.) and mucronate (Fig. 9C). The first and second-formed whorl-branchlets become villose (Fig. 9D) reaching about 4 mm long, and are alternately pinnately branched. The laterals near the apices are elongate and flexuous with cells 15-25µ diam. and 8-11 times longer than wide, while the laterals near the base resemble normal whorl-branchlets with short cells and mucronate tips.

Potentially indeterminate branches are produced from the basal cells of the second-formed whorl-branchlets on successive axial cells (Fig. 9A,B) and are therefore arranged on alternate sides of the main axis in one plane (Fig. 10A). The first-formed whorl-branchlets on each axial cell of these potentially indeterminate branches are abaxial and also become villose.

Descending rhizoids are initiated from the basal cells of whorl-branchlets about 15-20 axial cells below the apex. About 10 further axial cells below this, initials of the outer cortex are produced from the rhizoidal cells and develop into short branchlets 2-3 times subdichotomously branched, with spherical terminal cells about 45µ diam. (Fig. 10B,C). The thick cortex so formed remains after the plant has become denuded of whorl-branchlets. The diameter of the axis with cortication may reach 5 mm near the base of the plant.

REPRODUCTION

Tetrasporangia (Fig. 10D)

Tetrasporangia reach 140µ diam. and are formed terminally on 1-3 celled stalks borne laterally on the lower one to two cells of the whorl-branchlets. Stalk cells are about 25µ diam. and 30µ long, each usually bearing a short curved involucral branchlet partly encircling the tetrasporangium.

Spermatangial heads (Fig. 10E)

The spermatangial heads reach 140µ diam., which is greater than other species of Wrangelia. They are borne on 1-2 celled stalks which occur in place of laterals of about the second to fifth axial cells of the whorl-branchlets (either normal or villose), near the upper ecorticate or slightly corticated parts of indeterminate branches. The stalk cell bears 2(-3) reduced involucral filaments which are 1(-4) cells long, rarely once branched.

The development and structure of the spermatangial head is similar to that of W. plumosa (p. 44).

Procarp and Carposporophyte (Fig. 10F)

The structure and position of the fertile axis is similar to that of W. velutina and W. nobilis. The first three cells of each carpogonial branch are cut off by slightly oblique divisions, while the carpogonium is cut off laterally. Two abnormal 5-celled carpogonial branches (Fig. 10F), both on the same axial cell, were observed.

Immediate post-fertilization details were not followed, but the structure of the cystocarp is the same as other species of Wrangelia.

DISCUSSION

J.Agardh (1894a, p.103) first placed the genus Bracebridgea with Codium and Anadyomene in the siphonaceous green algae, based on a bleached and denuded specimen. Later, however, he recognised the similarities of this species to genera such as Wrangelia and

Spyridia, now placed in the Ceramiaceae, and transferred *Bracebridgea* to the Florideae.

Although this species is unique in its vegetative structure, the development of the reproductive organs is typical of *Wrangelia*. The differences from the type, *W. penicillata*, are of the same order as those between *W. nobilis* and the type. Thus *Bracebridgea* does not merit retention as a separate genus.

WRANGELIA ABIETINA Harvey 1854: 546; 1863: synop. no. 327.
J.Agardh 1876: 621. De Toni 1897: 131. Lucas 1909: 23. May 1965: 366. Sonder 1880: 29.

TYPE LOCALITY - Garden Is., W. Aust. (Harvey).

LECTOTYPE - Herb. Harvey, TCD (Alg. Aust. Exs. no. 267).

DISTRIBUTION - Known only from the type collection.

VEGETATIVE STRUCTURE

The lectotype specimen is about 15 cm high, alternately pinnately branched with 2-3 orders of branching, and is similar in many features to *W. princeps* of which it may be a form. It differs however in the structure of the whorl-branchlets which in *W. abietina* are inwardly curved with obtuse terminal cells, the median cells 35-45µ diam. and 3-5 times longer than wide, while in

W. princeps they are lax and tapered, with median cells 25-35µ diam. and 5-7 times longer than wide.

REPRODUCTION - Unknown.

DISCUSSION

At present it seems best to keep *W. abietina* separate from *W. princeps* until further material referable to *W. abietina* is collected.

SOUTHERN AUSTRALIAN SPECIES OF WRANGELIA NOW REFERRED TO OTHER GENERA*

1. *WRANGELIA AGARDHIANA* Harvey 1854: 545.

    Correct name: *Ptilocladia agardhiana* (Harvey) Wollaston 1968: 261.

2. *WRANGELIA INCURVA* J.Agardh ex Wilson 1892: 170 (nomen nudum).

This name was first published in lists (Wilson 1892, p.170, Tisdall 1898, p.511) without valid specific description, and no specimen under this name has been found in Herb. J.Agardh, Lund. According ~~the~~ to May (1965, p.365), Lucas, in notes on specimens, suggests that the specimens may be of *Antithamnion mucronatum* (J.Ag.) De Toni, now *Macrothamnion pellucidum* (Harvey) Wollaston. However, examination of specimens from MEL and NSW, collected and determined by J.B. Wilson, has shown that this species is neither a *Wrangelia* nor *M. pellucidum*, and therefore determination of the correct systematic position must await further work.

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* *Wrangelia galeae* Sonder 1880: 105 (nomen nudum) - Material with this name has not been seen, and the name has not been published since Sonder's list. If material exists, it may or may not belong to *Wrangelia*.

3. WRANGELIA SETIGERA Harvey 1860: 309, pl. 191A; 1863: synop. no. 330. J.Agardh 1876: 622; 1879: pl. 32, fig. 3. De Toni 1897: 133; 1924: 149. Guiler 1952: 99. Lucas 1909: 23; 1929a: 16. May 1965: 365. Mazza 1919: 1307. Okamura 1932: 133. Sonder 1880: 29. Tisdall 1898: 511. Wilson 1892: 170.

Harvey based this species on his previously described Spyridia filamentosa β verticillata Harvey (1844, p.449). This was later elevated to a separate species of Spyridia, S. tasmanica, by Kuetzing (1862, p.14, pl. 42, c-d). Kuezting's figures clearly show small cells at the nodes of the monosiphonous filaments, which is typical of Spyridia. Material from Missionary Bay, Bruny Is., Tas. (ADU, A10,182a, Womersley, 15.i.1949) has been checked and identified by Womersley with Harvey's type specimen of W. setigera. This material is also Spyridia. Thus Spyridia setigera (Harvey) comb. nov. is the correct name for this species.

4. WRANGELIA SQUARRULOSA Harvey 1855: 236; Alg. Aust. Exs. no. 266. J.Agardh 1877-8: 27; 1892: 52.

Correct name: Ptilota hannafordi Harvey 1862, pl. 221.

Although this species was originally described from New Zealand, Harvey later put it into synonymy with P. hannafordi in Phycologica Australica as no. 266 in the Alg. Aust. Exs. set. However, J.Agardh (1876, p.81) comments that Harvey's original description of

W. squarrulosa from N.Z. does not agree with his description of *P. hannafordi*, and hence J.Agardh places this species in synonomy with *Callithamnion? confusum* J.Agardh (1876, p.25).

5. *WRANGELIA TENELLA* Harvey 1854: 546; Alg. Aust. Exs. no. 270; 1863: synop. no. 339. J.Agardh 1876: 618. De Toni 1897: 129; 1924: 149. Lucas 1909: 23. May 1965: 366. Mazza 1919: 1300. Sonder 1880: 28.

Correct name: *Trithamnion tenellum* (Harvey) Wollaston 1968: 389.

EXTRA-AUSTRALIAN SPECIES of WRANGELIA

Thirteen species of Wrangelia have been described from areas other than southern Australia, and material of six of these have been available for study (* below - Table 3).

TABLE 3.- Extra-Australian species of Wrangelia

Species	Area of type locality
* W. penicillata	Mediterranean Sea
* W. argus	Canary Is.
W. bicuspidata	Caribbean Sea
* W. purpurifera	Cape of Good Hope
* W. tanegana	Japan
W. tagoi	"
* W. tenuis	"
* W. japonica	"
W. hainanensis	China
W. tayloriana	"
W. anastomosans	Carolline Is.
W. sceptrifera	Arabian coast, Indian Ocean
W. pylaisaei	Newfoundland

From the published descriptions and diagrams in the literature it is possible to deduce that all but one species, W. pylaisaei (Mont.) J.Agardh, probably belong to the genus Wrangelia as defined in the present work.

WRANGELIA PENICILLATA (C.Ag.) C.Agardh 1828: 138. J.Agardh 1841: 38; 1863: 708; 1876: 623. Almodovar 1964a: 144; 1965: 11. Almodovar and Blomquist 1961: 91. Boergesen 1916: 120, figs. 131, 132; 1927: 94; 1945: 18. Bornet and Thuret 1880: 183, pl. 48. Burkholder, P.R. and L.M., and Almodovar 1960: 153. Chadefaud 1960: 128, fig. 87. Chapman 1963: 167, fig. 172. Collins and Hervey 1917: 103. Dawson 1957: 119. Derbes and Solier 1856: 71, pl. 18, figs. 6-8. De Toni 1897: 135; 1924: 150. Diaz-Piferrer 1964a: 366. Edelstein 1964: 200, fig. 4, A-D. J. Feldmann 1937: 276; 1942: 311. Feldmann-Mazoyer 1940: 131, 173, figs. 21C, 22, 42, 43, 63w, 64; 1941: 70, 73, 75. Fritsch 1945: 457, 685, 712, figs. 152A,B,F, 271A-E, 289I,J. Godward 1966: 196. Harvey 1853: 143, pl. 34B, 1-9. Hauck 1885: 51, fig. 15. Howe 1920: 559. Joly, Ugadim, Oliveira and Cordeiro 1967: 177. Kuetzing 1845: 288; 1849: 664; 1862: 13, pl. 40a-e. Kylin 1928b: 1, figs. 1-3; 1937: 107; 1956: 382. Lucas 1931: 53. Magne 1964: 544, pl. 12, figs. 386-393. Maze and Schramm 1870-77: 231. Mazza 1906: 44. Nasr 1940: 197. Naegeli 1861: 382. Neal 1930: 66, fig. 17e. Noda 1964: 19, fig. 4; 1967: 29. Okamura 1932: 133.

Oltmanns 1904: 718, fig. 360; 1922: figs. 472, 605. Petersen 1918: 13. Schmidt 1957: 717. Schmitz 1883: 228; 1889:439. Schmitz and Hauptfleisch 1897: 345, fig. 209F. Schussnig and Yahoda 1927: 245, pl. 5, fig. 19a,b, fig. 20a. Sonder 1871: 21. Taylor 1925: 130; 1928: 144, pl. 20, figs. 11, 12, 19, pl. 32, figs. 1,7; 1950: 136; 1960: 503, pl. 66, figs. 5, 6, pl. 74, fig. 5; 1964: 7. Zerlang 1889: 373, fig. 1-6..

BASIONYM - Griffithsia penicillata C.Agardh 1824: 143.

For synonomy see J.Agardh 1863, p.708.

TYPE LOCALITY - On the coast of Italy.

TYPE — Probably in Herb. Agardh, LD. Not seen.

REPORTED DISTRIBUTION - Mediterranean Sea, Atlantic coasts of Europe, Mauritius, Malay Archipelago, north-west coast of Japan, Cape Yorke Pen., Aust., Marshall Is., Hawaii, Caribbean Sea Is., south Florida, Bermuda.

This species has been described and illustrated by many earlier authors particularly Boergesen (1916), Bornet and Thuret (1880), Feldmann-Mazoyer (1940), Kylin (1928), Naegeli (1861) and Zerlang (1889).

Examination of specimens in ADU (A30,379, Roscoff, France, Delépine, Sept. 1964) confirmed the observations of the above authors.

VEGETATIVE STRUCTURE

The thallus is 5-11(-20) cm high and regularly to irregularly pinnately branched. Apical cells of indeterminate branches divide by alternately oblique divisions, and five whorl-branchlets per axial cell are cut off in alternating sequence from the upper ends of axial cells (Kylin 1928b, fig.1A). Chadefaud (1960, fig. 87.2) illustrates a "scorpoiod" form of development for this species, in which the first-formed whorl-branchlets are initiated from one side of the axis. His diagram possibly represents the apex of a lateral branch where the first-formed whorl-branchlets are sometimes produced abaxially. The apex of of a main axis is usually symmetrical. Mature whorl-branchlets are 4-8 times subdichotomously branched and taper slightly toward the apex. Median cells are 30-50µ diam. and 4-10 times longer than wide.

Potentially indeterminate branches are initiated from the basal cells of first-formed whorl-branchlets on each axial cell (Feldmann-Mazoyer 1940, fig. 42, Kylin 1928b, fig.1B, Oltmanns 1922, fig. 472). Descending rhizoids, forming the cortex in lower parts of the thallus, are also produced from the basal cells of whorl-branchlets (Kylin 1928b,fig. 1B, C).

REPRODUCTION

Tetrasporangia

Tetrasporangia reach 75µ diam. (Boergesen 1916, p.121) and are formed terminally on cells of small-celled laterals of whorl-branchlets. The first stalk cell produces 1-2 further stalk cells or 1-2 curved involucral filaments (Kyling 1928b, fig. 3A-D).

Spermatangial heads

Spherical spermatangial heads reaching 75µ diam. are borne terminally on stalk cells which occur on the lower cells of whorl-branchlets. Each stalk cell bears about 3 curved involucral branchlets (Boergesen 1916, fig. 132). The internal structure of the spermatangial head is similar to that of W. plumosa (p. 44).

Procarp and Carposporophyte

Procarps occur near the apices of potentially indeterminate branches as in W. princeps. The supporting cell bears a terminal sterile cell and lateral carpogonial branch in which both the third and fourth cells are cut off by lateral divisions (Kyling 1928b, fig. 2, A-E). The production of the auxiliary cell, development of gonimoblast and carposporangia, development of sterile whorl-branchlets on the fertile axis and production of fusion cell (Bornet and Thuret 1880, pl. 48) also occur as in W. princeps. A detailed description of the above features is given by Kylin (1928b, pp4-6).

WRANGELIA ARGUS (Montagne) Montagne 1856: 444. Almodovar 1962: 277; 1964a: 144; 1964b: 45; 1965: 11. Almodovar and Blomquist 1959: 167. Almodovar and Pagan 1967: 111. Boergesen 1916: 116, figs. 125-6; 1927: 93; 1945: 18; 1952: 59. Burkholder P.R. and L.M., and Almodovar 1960: 153. Chapman 1963: 164, fig. 170. Collins 1901: 252. Dawson 1954: 444, fig. 54g; 1956: 56; 1957: 119; 1960: 50; 1961: 442. 1962b: 185, fig. 39; 1962c: 387. De Toni 1924: 150. Dickinson and Foote 1951: 137. Howe 1920: 559. Joly 1964: 14; 1965: 199, pl. 30, fig. 425, pl.35, fig. 469-471. Joly and Cordiero 1962: 225, pl.3. Lawson 1957: 855. Okamura 1932: 133. Olesen, Maretzki and Almodovar 1964: 226. Taylor 1925: 130; 1928: 144, pl. 20, fig. 13, pl. 22, fig. 6, pl. 32, fig. 4; 1964: 7; 1929: 623. 1936: 200. 1942: 120; 1960: 502, pl. 66, figs. 7,8. Vickers 1905: 61. Vroman 1968: 56.

non Boergesen 1937: 338. Hirose 1957: 101, pl. I, fig. E; 1958: 268. Ho 1962: 99. Kang 1956: 11. Okamura 1934: 46, pl. 324. Segawa 1956: 102, pl. 61, no. 484. Segawa and Kamura 1960: 56. Weber van Bosse 1921: 220.

These latter descriptions probably refer to Wrangelia tayloriana Tseng (p. 87).

BASIONYM - Griffithsia argus Montagne in Webb and Berthelot 1840: 176, pl. 8, fig. 4 (reference not seen).

For synonomy, see Boergesen 1916, p.116.

TYPE LOCALITY - ?

TYPE - Probably PC. Not seen.

DISTRIBUTION - Tropical and subtropical coasts - Pacific and Atlantic Panama, Mexico, Florida, Venezuela, Caribbean Is., Bahamas, Canary Is., Ghana, Mauritius, Vietnam, Marshall Is.

Material studied in detail was collected from St. Eustatius Is., Netherlands Antilles (ADU, A29,575, Vroman, 21.v.1958, female).

VEGETATIVE STRUCTURE

Plants are small and tufted, reaching only about 2 cm high.

Apical segmentation, production of whorl-branchlets and origin of indeterminate branches are typical of the genus Wrangelia. A diagram of Boergesen (1916, fig. 126) suggests that there are only two whorl-branchlets produced per axial cell, whereas in fact 4(-5) occur. The first three produced on each axial cell are 3-4 times subdichotomously branched with ultimate branchlets of 2-3 cells. The terminal cells are acute, and the median cells 35-50µ diam. and 4-6 times longer than wide. The fourth-formed whorl-branchlet is usually very much reduced, with smaller cells and about one quarter the length of the older ones on the same axial cell. From its basal cell are produced 3-4 small-celled branchlets which curve around the main axis both above and below the node but do not form a continuous cortex (Boergesen 1916, fig. 125).

REPRODUCTION

Tetrasporangia (Boergesen 1916, p.117, fig. 126) and spermatangial heads (Boergesen 1952, p.59) are similar to those of W. penicillata.

Stages in procarp and carposporophyte development are typical of the genus. The supporting cell of the carpogonial branch does not bear a terminal sterile cell.

WRANGELIA BICUSPIDATA Boergesen 1916: 118. Almodovar 1964a: 144; 1964b: 46; 1965: 11. Almodovar and Blomquist 1961: 90. Burkholder, P.R. and L.M., and Almodovar 1960 : 153. Chapman 1963: 164, fig. 171. Dawson 1962a: 77. De Toni 1924: 151. Diaz-Piferrer 1964a: 366; 1964b: 535. Howe 1920: 559. Okamura 1932: 133. Taylor 1925: 130: 1928: 144, figs 14, 20, pl. 32, fig. 2; 1960: 503, pl. 66, figs. 9, 10; 1964: 7. Taylor and Arndt 1929: 658.

non Weber van Bosse 1921: 220 (see Tseng 1942: 264).

TYPE LOCALITY - Saint Jan Is., Danish West Indies.

TYPE - Probably in C. Not seen.

DISTRIBUTION - Islands of the Caribbean Sea, south Florida, Bahamas, Bermuda.

This species is separated from W. argus by its larger size (to 7 cm) and the two, almost equal mucronate cells at the tips of each whorl-branchlet. In habit it is typical of the genus but as the only reproductive structures reported are tetrasporangia (Taylor 1928, p.144), confirmation of its systematic position must await discovery of sexual structures.

A drawing given by Chapman (1963, fig. 171a) is probably of W. argus, as the typical bicuspid tips of W. bicuspidata are not shown.

WRANGELIA PURPURIFERA ~~Harvey mscr. ex~~ J.Agardh 1863: 707; 1876; 623. Barton 1893: 173. De Toni 1897: 134; 1924: 149. Isaac 1949: 134, 140 (?). Okamura 1932: 133.

Callithamnion purpuriferum Harvey 1838: 403 (nomen nudum).

non Wrangelia purpurifera sensu Yendo 1917: 203.

Phlebothamnion purpuriferum Kuetzing 1849; 656; 1862: 3, pl. 7, c-e.

Callithamnion purpuriferum sensu J. Agardh 1851: 59; 1876: 36. Westbrook 1927: 161.

Aristothamnion purpuriferum J. Agardh 1892: 45.

Pleonosporium purpuriferum De Toni 1903: 1307.

TYPE LOCALITY - Muysenberg, Cape of Good Hope (Harvey).

TYPE - LD? Not seen.

DISTRIBUTION - False Bay, South Africa.

Material studied in detail was collected from Muysenberg, the type locality (ADU, A30,844, Papenfuss, 23.ix.1936), Strandfontein (ADU, A30,845, Papenfuss, 1935, A30,846, Papenfuss, 10.x.1937, A30,847, Papenfuss, 14.ii.1937), and St. James, False Bay, South Africa (ADU, A31,430, Simons 11.v.1967).

At St. James, the plants grow in the upper sublittoral to lower littoral zones on a rocky platform.

VEGETATIVE STRUCTURE

The apical segmentation, production of whorl-branchlets, origin of indeterminate branches and rhizoidal cortication are typical of Wrangelia. The total number of whorl-branchlets (5 per axial cell) may not be reached until about 20 cells below the apex of indeterminate branches, and often considerable differences occur in the extent of development of whorl-branchlets in any one whorl. Some may be relatively long and 2-3 times subdichotomously branched, while others are shorter and simple or once-branched. Median cells of the well developed whorl-branchlets are 60-100µ diam. and 2½-4 times longer than wide, while the ultimate branchlets are of 4-5 cells and taper to an acute terminal cell about 30µ diam.

REPRODUCTION

Tetrasporangia and spermatangial heads are borne in positions similar to those of the type species.

Stages in procarp and carposporophyte development are also typical of the genus, and the supporting cell of the carpogonial branch lacks a terminal sterile cell.

DISCUSSION

Herbarium specimens from TCD (Herb. Harvey) include specimens from Muysenberg, the type locality, although none ~~are~~ is labelled as the type. One specimen, labelled "*Callithamnion purpuriferum*, curious metamorphosis of the ultimate ramuli. C.B.S. 1836" (not Harvey's handwriting) has only one whorl-branchlet per axial cell and does not agree with specimens labelled *W. purpurifera* in Harvey's handwriting on the same sheet.

The name *Callithamnion purpuriferum* was first published by Harvey (1838, p.403) as an example of the genus *Callithamnion*, but was not described and is thus a nomen nudum. Kuetzing (1849, p.656) based his name *Phlebothamnion purpuriferum* on this species. However he did not examine Harvey's specimens. but a dried specimen from Table Bay, determined and set to him by Pappe. Later, J. Agardh (1851, p.59) in his description of *Callithamnion purpuriferum*, also based on specimens of Pappe, excluded Harvey's C. purpuriferum.

Yendo (1917, p.203) described W. purpurifera from Japan, but his specimens were later included by Tseng (1942, p.269) in his Wrangelia tayloriana and by Noda (1964, p.18) in his Wrangelia japonica (see p.85). His specimens were almost certainly of a different species from Harvey's W. purpurifera.

WRANGELIA TANEGANA Harvey 1859b: 331. J.Agardh 1876: 625.
Dawson 1959: 17. De Toni 1897: 137. Segawa and
Kamura 1960: 56.

TYPE LOCALITY - Tanegashima, Japan.

TYPE - Herb. Harvey, TCD

DISTRIBUTION - Known only from the type collection.

On the type sheet in TCD, labelled by Harvey, are two specimens. The left hand one belongs to the Dasyaceae. The right hand specimen and a small piece on mica are probably what Harvey described as W. tanegana.

In the type description Harvey suggested that this specimen may belong to Callithamnion or Halurus, as the "fruit" was unknown. Examination of the type specimen, however, reveals the presence of very young tetrasporangia and a vegetative structure typical of the genus Wrangelia.

The whole specimen is only about 3.5 cm long and is possibly part of a larger plant.

The whorl-branchlets are 2-4 times subdichotomously branched, with ultimate branchlets of about 5 cells, tapering abruptly to a small mucronate terminal cell. Median cells are 120-140µ diam. and 1 - 1½ times longer than wide. Main axes are corticated in lower parts.

Tetrasporangia are borne terminally on small-celled laterals from the lower cells of the whorl-branchlets.

The short cells of the whorl-branchlets separate this species quite distinctly from other Japanese species of Wrangelia.

WRANGELIA TAGOI (Okamura) Okamura and Segawa 1936 (not seen).

Noda 1964: 15. Segawa 1956: 102, pl. 61, no. 483.

Segawa and Yoshida 1961: 18.

Dasyphila tagoi Okamura 1912: 132 (Japanese p. no. 135), pl.88.

TYPE LOCALITY - Wagu, Province Shima, Japan (Tago).

TYPE - Probably Imp. Fish.Inst., Tokyo (see Koster 1957, p.52). Not seen.

DISTRIBUTION - Amakusa, Japan.

The description and illustrations given by Okamura indicate that this species is probably correctly placed in Wrangelia, although fertile structures were not described.

WRANGELIA TENUIS Noda 1960: 3 (nomen nudum); 1964: 21, figs. 5,6; 1967: 30.

TYPE LOCALITY - Ogi, Sado Is., Japan Sea.

TYPE - Probably Niigata University, Japan. Not seen.

DISTRIBUTION - Known only from the type locality.

A sterile specimen (ADU, A31,416, Noda, 27.xi.1959) was kindly provided for examination by Dr. Noda and appears to be a distinct species of *Wrangelia*.

The structure of the apices of indeterminate branches and formation of whorl-branchlets are typical of the genus *Wrangelia*. Four whorl-branchlets occur on each axial cell (in contrast to five in most other species). The first-formed one is about 4 times branched either unilaterally or subdichotomously. Median cells are 45-80µ diam. and 4-10 times longer than wide, the basal cells approximately cubical. The other two or three whorl-branchlets of each whorl are considerably reduced in size and form, simple or once branched and only a few cells long, with the median cells about 16µ diam. and 2½ times longer than wide. Noda describes the larger whorl-branchlets as being only 1-2 times dichotomously branched, possibly due to loss of outer laterals in specimens examined.

Noda's drawings of reproductive structures, although lacking in detail, also suggest that the species belongs to the genus *Wrangelia*.

WRANGELIA JAPONICA Noda 1964: 17, figs. 1,2; 1966: 73; 1967: 28.
Kang 1966: 92.

TYPE LOCALITY - Tassha, Sado Is., Japan Sea (Noda, 22.viii.1954).

TYPE - Probably Niigata University, Japan. Not seen.

DISTRIBUTION - Sado Is., western coast of Honshu, Japan, and the eastern and southern coasts of Korea.

Herbarium material (ADU, A31,412, Sado Is., Noda, 11.vii.1956; A31,413, Hakata Bay, Tsuyazaki, 9.ii.1956; A31,414, Hakata Bay, Tsuyazaki, 15.ii.1957) was kindly supplied by Dr. Noda for study, but unfortunately lacked fertile plants.

The structure of the plant is typical of Wrangelia. The whorl-branchlets are 5-6 times subdichotomously branched with median cells 40-50µ diam. and 3-5 times longer than wide. The terminal cells are acute, about 15µ diam. and 2½ times longer than wide. Noda describes the "verticillate ramuli" as only 1-2 times dichotomous and obtuse at the apices. His figures indicate, however, that the terminal parts of the whorl-branchlets had been lost so that they appeared obtuse and less branched.

Noda aligns this species both with the plant described by Yendo (1917, p.203) as Wrangelia purpurifera, and the specimens from the coasts of Japan referred to as Wrangelia argus by other Japanese phycologists. The same comparison was made by Tseng (1942, p.267) in describing his species Wrangelia tayloriana from Amoy, China. The present observations agree well with Tseng's description, and thus it is highly likely that *W. tayloriana* Tseng and *W. japonica* Noda are synonymous.

WRANGELIA HAINANENSIS Tseng 1942: 261. Dawson 1962a: 77.

Wrangelia bicuspidata sensu Weber van Bosse 1921: 220, *non* Boergesen 1916: 118.

TYPE LOCALITY - Near Sama, Hainan, China (Tseng, 23.iv.1934).

TYPE - Herb. Tseng (no. 883). Not seen.

DISTRIBUTION - China, Malay Archipelago.

This species is probably correctly placed in *Wrangelia* and is very similar to *W. bicuspidata* Boergesen. The thallus is larger (to 12 cm) and has unequal bicuspid tips to the whorl-branchlets, in contrast to the equal or nearly equal tips in *W. bicuspidata*.

The only fertile structures described by Tseng are tetrasporangia and these also agree with those of the genus *Wrangelia*.

WRANGELIA TAYLORIANA Tseng 1942: 264. Dawson 1962a: 77.

Wrangelia argus sensu Boergesen 1937: 338. Hirose 1957: 101; 1958: 268. Ho 1962: 99. Kang 1956: 11. Okamura 1936: pl. 484 (not seen). Segawa 1956: 102, pl. 61, no. 484. Weber van Bosse 1921: 220.

non Montagne 1856: 444.

Wrangelia purpurifera sensu Yendo 1917: 203.

non Harvey ex. J.Agardh 1863: 707.

TYPE LOCALITY - Amoy, east coast of China (Tseng 195 , May 1932).

TYPE - Herb. Tseng. Isotype in Herb. Univ. Michigan. Not seen.

DISTRIBUTION - Amoy, Stevens Is., east coast of China (Japan Sea? India? Malay Archipelago? - see below).

Tseng describes this species as closely related to the West Indian *Wrangelia argus* (Mont.) Mont. and concisely lists the main differences. *W. tayloriana* reaches a larger size (to 5 cm) and is more heavily corticated than *W. argus* (to 2 cm and only lightly corticated at the nodes). The tetrasporangia are larger (75µ diam., *W. argus* 60µ), and the involucral branchlets around the sporangia are 2-3 celled, 15-20µ diam., simple and loosely applied, whereas those of *W. argus* are 3-5 celled, 10-15µ diam., subdichotomous and closely applied to the sporangia.

Specimens of *W. argus* from the Solomon Is. (Womersley and Bailey 1970) agree reasonably well with the description of Boergesen (1916, p.116), but in height (to 3 cm), axis width, heavier lower cortication and 2-3 celled, simple tetrasporangial involucral filaments, they approach *W. tayloriana*.

Tseng aligns his species with the *W. argus* described from the Malay Archipelago by Weber van Bosse (1921, p.220), from India by Boergesen (1937, p.338) and from Japan by Okamura (1934, p.46). *W. purpurifera* sensu Yendo (1917, p.203) from Japan is also included by Tseng as probably synonomous. Noda (1964, p.18) also ~~describes~~ treats these species as synonyms of *W. japonica* and it is likely therefore that *W. tayloriana* and *W. japonica* are conspecific.

WRANGELIA ANASTOMOSANS Yamada 1944: 41, pl. 7, fig. 2.
Dawson 1957: 119, fig. 25d; 1962a: 77.

TYPE LOCALITY - Atoll of Ant, 20 m south-west from the Island of Ponape, east Carolline Is., Micronesia.

TYPE - Probably SAP. Not seen.

DISTRIBUTION - Carolline Is., Marshall Is.

Yamada noted that this species is very close to *W. plumosa*, differing mainly in having branches which adhere to one another and to other algae. This is probably an environmental effect and may not be an important specific difference.

W. anastomosans is almost certainly a true species of *Wrangelia*.

WRANGELIA SCEPTRIFERA J.Agardh 1894b:75. Newton 1953: 398.

TYPE LOCALITY - South-east Arabian shores, Indian Ocean (W.Hunt?)

TYPE - K? Not seen.

The description of this species is the only published record of 33 species of algae collected by W. Hunt during Theodore Bent's Expedition in the "Hydramaut", of 1893-4 (Newton 1953, p.398).

Agardh placed this species provisionally in Wrangelia until reproductive features were better known. His description of the 2-3 mucronate cells terminating the whorl-branchlets is suggestive of W. bicuspidata or W. hainanensis. Tseng (1942, p.264) aligned his W. hainanensis with the record of W. bicuspidata from the Malay Archipelago, and so it is possible that W. sceptrifera is an earlier name for W. hainanensis.

WRANGELIA ? PYLAISAEI (Montagne) J.Agardh 1863: 705. De Toni
1897: 137. Montagne 1856: 447.

Callithamnion pylaisaei Montagne 1837: 351.
Harvey 1853: 239, pl. 36, 1-4. Kuetzing 1861:
29, pl. 90, f-h.

This species from Newfoundland almost certainly does not belong to the genus Wrangelia. The figures of Harvey show opposite whorl-branchlets, themselves oppositely and distichously branched, with cruciate tetraspores on lower cells. Such features are not characteristic of Wrangelia.

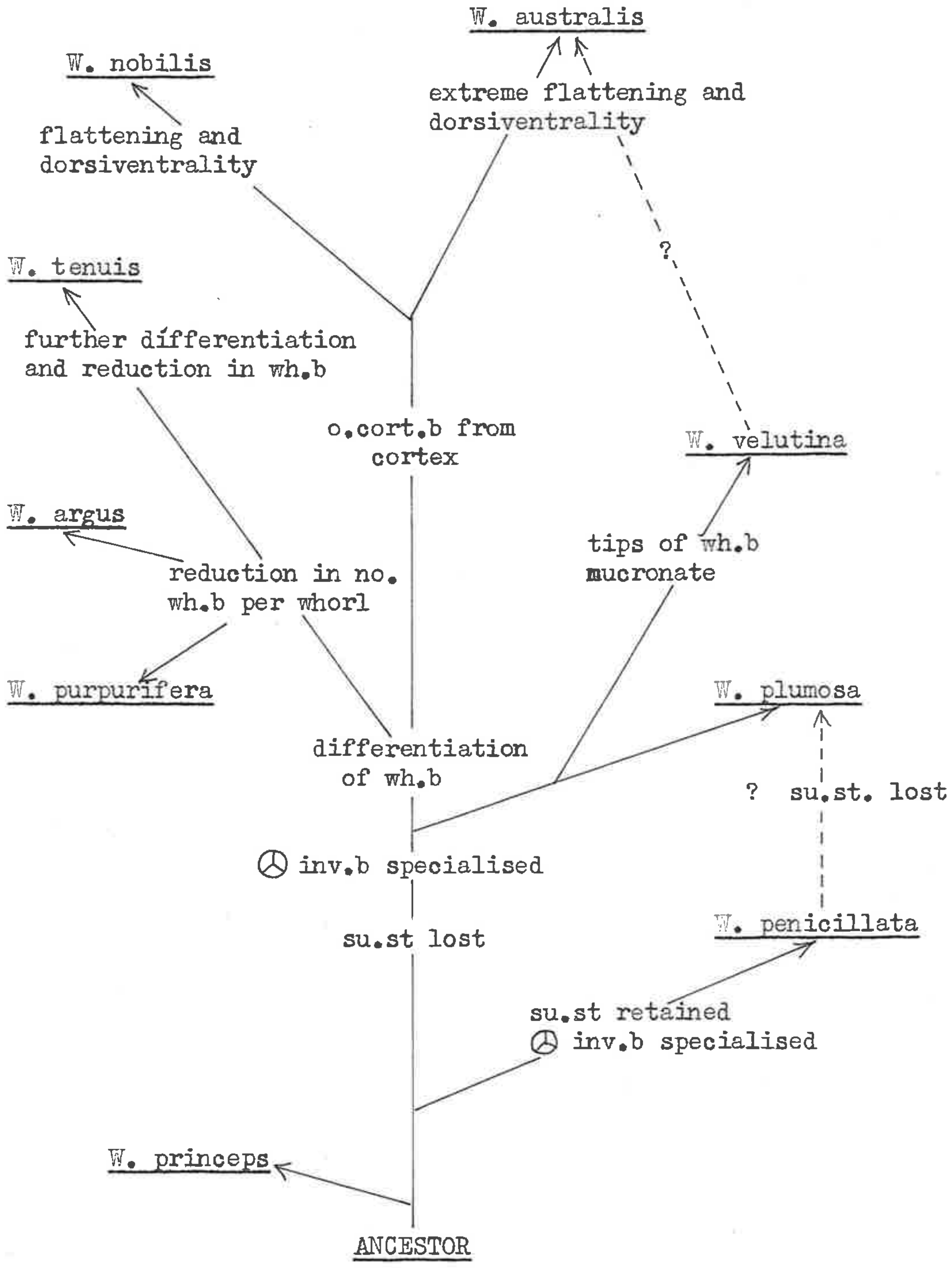
DISCUSSION ON WRANGELIEAE

In both vegetative and reproductive features, the least specialised species of *Wrangelia* is probably *W. princeps*, in which the tetrasporangia are borne on virtually unmodified cells of whorl-branchlets without specialised involcural filaments. *W. penicillata* probably arose from a *W. princeps*-like ancestor by modification of laterals of whorl-branchlets into special small-celled involucral filaments around the tetrasporangia. In female plants a sterile cell on the supporting cell was retained - *W. princeps* and *W. penicillata* are the only two species of *Wrangelia* known to possess this feature.

W. plumosa is similar to *W. penicillata* in most features, but lacks a sterile cell on the supporting cell. Loss of this cell may have occurred before or after the specialisation of the tetrasporangial involucral branchlets (Diag. 1).

W. velutina probably arose from the *W. plumosa* line of evolution by specialization of the form of the whorl-branchlets, the terminal cells becoming mucronate. Another evolutionary line may also have arisen by differentiation of the members of a whorl of whorl-branchlets. This tendency could have led in one direction to *W. purpurifera* and *W. argus* where the fifth whorl-branchlet per axial cell is reduced or absent, and finally to *W. tenuis* where only 3(-4) whorl-branchlets are developed on each

DIAGRAM 1.- Possible mode of evolution of species of *Wrangelia*



axial cell, the third and fourth whorl-branchlets being extremely reduced.

A further line may have been initiated through the production of secondary lateral branchlets from the outer cortical rhizoids. In *W. nobilis* the terminal cells of these secondary branchlets have remained similar to those of the whorl-branchlets, and in *W. australis* they have developed swollen spherical terminal cells. Both these species have flattened ultimate branches. This characteristic is due to the development of longer first and second whorl-branchlets, on opposite sides of the axis in *W. nobilis*, and on the same side in *W. australis* but alternate on successive axial cells. *W. nobilis* is dorsiventral because of the formation of the third and fifth whorl-branchlets on each axial cell always on the one face of the axis. However, the dorsiventrality of *W. australis* is due to the second-formed whorl-branchlet of each whorl always being formed on one face of the axis.

It is also possible that *W. australis* may have arisen directly from an ancestor very similar to *W. velutina*. The normal whorl-branchlets of the two species are very similar. In this case, the production of secondary laterals from the cortex and flattening of the branches would have occurred independently from the line which produced *W. nobilis*.

The presence or absence of a sterile cell on the supporting cell of the carpogonial branch has been used, with other features, by Hommersand (1963, p.330) to separate two subfamilies, the Ceramioideae and the Crouanioideae, in the Ceramiaceae (see Table 11). The present studies show, however, that there are no other consistent differences which can be correlated with this feature in the Wrangelia group of species and so even the separation of two genera within the group on one feature alone is not justified. Future studies may bring to light other characteristics which could be correlated with this difference and used as a basis for separation of two genera. In such a case, the genus Bracebridgea would have to be resurrected to include species lacking a sterile cell on the supporting cell.

2. TRIBE SPHONDYLOTHAMNIEAE Feldmann-Mazoyer 1940: 240.

The genera to be included in the Sphondylothamnieae have the following features in common:

(1) prostrate and erect axes (erect axes absent in *Shepleya australe*), apical cells of indeterminate branches dividing transversely; whorls of whorl-branchlets formed on the distal ends of axial cells of indeterminate branches which are usually easily distinguishable from whorl-branchlets (except *S. australe* and *Involucrana meredithiana*); indeterminate branches formed directly on axial cells; multinucleate cells,

(2) spermatangia formed in compact heads,

(3) procarp on the subapical cell of the fertile axis, enclosed in a gelatinous sheath common with associated sterile cells (procarp system); one or two auxiliary cells per procarp; carposporangia formed from terminal cells of the gonimoblast; fusion cell involving the lower gonimoblast cells, and at least the subapical cell of the fertile axis (except *Drewiana*),

(4) post-fertilization division of sterile cells associated with the procarp to produce an inner involucrum surrounded by an outer involucrum of branchlets from the lower cells of the fertile axis.

TYPE GENUS - *Sphondylothamnion* Naegeli 1861: 380.

KEY to GENERA of SPHONDYLOTHAMNIEAE

1. Female axis three cells long, subapical cell with two pericentral cells; meiosporangia 180-220µ diam., each with about 32 spores; corticating rhizoids anastomosing by secondary pit connections. .. Involucrana

1. Female axis more than three cells long, subapical cell with three pericentral cells; meiosporangia not exceeding 160µ diam., each producing four or rarely eight spores; corticating rhizoids when present not anastomosing by secondary pit connections (except Drewiana) 2

    2. Haptera with digitate disc absent 3
    2. Haptera with digitate disc present, occurring on corticating rhizoids, cells of holdfast, and prostrate axes 4

3. Auxiliary cells two per procarp, fusion cell bilobed, hypogenous cell producing four lateral branchlets surrounding gonimoblast; tetrasporangia about 100µ diam.; whorl-branchlets subdichotomously branched 2-3 times, terminal cells obtuse (Europe). .. Sphondylothamnion (S. multifidum)

3. Auxiliary cells one per procarp, fusion cell more or less spherical, hypogenous cell without lateral branchlets; tetrasporangia not exceeding 60µ diam.; whorl-branchlets pinnate to subdi- trichotomously branched 5-8 times, terminal cells acute.. .. Drewiana (D. nitella)

4. Tetrasporangia borne directly on cells of main indeterminate axes and on cells of whorl-branchlets; whorl-branchlets in opposite decussate pairs on each axial cell (South America) ... ... .Diplothamnion (D. tetrastichum)

4. Tetrasporangia always borne on cells of whorl-branchlets; whorl-branchlets two or more per axial cell, distichously or orthostichously arranged, or not in longitudinal rows 5

 5. Tetrasporangia and spermatangial heads sessile, borne in large numbers (to 50 or more) on basal cells of whorl-branchlets (Europe). . . Vickersia

 5. Tetrasporangia and spermatangial heads sessile or stalked, borne singly (rarely in twos) on cells of whorl-branchlets 6

6. Indeterminate branches formed in addition to whorl-branchlets on axial cells, up to eight laterals per axial cell; terminal cells of whorl-branchlets short and mucronate; corticating rhizoids when present produced from lower parts of axial cells and from basal cells of lateral branches ... . Wollastoniella

6. Indeterminate branches formed in positions of whorl-branchlets on axial cells, up to four (rarely to five) laterals per axial cell; terminal cells of whorl-branchlets elongate and obtuse or tapering; corticating rhizoids when present produced only from basal cells of whorl-branchlets 7

7. Hypogenous cell bearing a single, curved adaxial branchlet; auxiliary cell one per procarp, producing up to five free gonimolobes of carposporangia, fusion cell not involving hypogenous cell; whorl-branchlets generally radial on main axes (rarely distichous when two per axial cell) ... ... Mazoyera

7. Hypogenous cell without lateral branchlets; auxiliary cells two per procarp, carposporangia produced from a bilobed fusion cell which involves the hypogenous cell; whorl-branchlets distichous (when two per axial cell), or orthostichous (when four per axial cell) .. .. Shepleya

(1) *SPHONDYLOTHAMNION* Naegeli 1861: 380.

SPHONDYLOTHAMNION MULTIFIDUM (Hudson) Naegeli 1861: 380.

Batters 1902: 83. Boergesen 1930: 11. Boergesen and Jonsson 1905: V. Bornet and Thuret 1880: 181, pl.47. Chadefaud 1960: 128, fig. 86,1. de Virville 1936: 748; 1938: 25; 1962: 26, 35; 1963: 16. de Virville and Belval 1938: 55. De Toni 1903: 1258. Dickinson 1963: 190, fig. 76. Dixon 1959: 69; 1961: 77; 1963a: 219. J.Feldmann 1937: 275; 1943a: 63; 1943b:155; 1954a: 39; 1954b: 53; 1954c: 100. Feldmann-Mazoyer 1940: 46, 203, 384, figs. 12, 21b, 150; 1941: 67, 71. Funk 1927: 461. Ginsburg-Ardré 1963: 38. Gordon and Womersley 1966: 23. Hauk 1885: 49, fig. 14. Kain 1960: 625. Knight and Parke 1931: 93. Kylin 1956: 388. Mazza 1910: 446. Miranda 1931: 189. Park 1953: 512. Parke and Dixon 1964: 509; 1968: 792. Preda 1908: 165, fig. 53. Sauvageau 1897: 18, 54.

Conferva multifida Hudson 1778: 596 (not seen).

Griffithsia multifida (Huds.) C.Agardh 1817: XXVIII; 1824: 143; 1828: 133.

Wrangelia multifida (Huds.) J.Agardh 1841: 38; 1842: 79; 1863: 705; 1876: 618. Harvey 1846: pl. 27; 1849: 170, pl. 23. Le Jolis 1880: 109.

Callithamnion multifidum (Huds.) Kuetzing 1849: 651; 1861: 29, Pl. 91.

TYPE LOCALITY - England?

TYPE - BM? (see Dixon 1963b, p.265). Not seen.

DISTRIBUTION - West coast of Britain to southern Scotland, English Channel, west coast of Portugal, Canary Is., western Mediterranean Sea.

The type species, *S. multifidum*, of this monotypic genus was investigated recently by Gordon and Womersley (1966, p.23 - see Appendix) who showed that it differs from other known genera of the Ceramiaceae by the post-fertilization development of the sterile cells associated with the procarp, producing inner involucral branchlets which surround the gonimoblast (Fig. 11J). A similar development was subsequently reported in *Involucrana meredithiana* (J.Ag.) Baldock and Womersley (1968, p.211), and has also been found in certain species of *Wrangelia* studied in the present work, now to be referred to new genera.

The other main features of *S. multifidum* are:

(1) prostrate and erect ecorticate axes; whorl-branchlets 2-4 per axial cell, subdi- or trichotomously branched once or twice, ultimate branchlets of 8-9 cells (Fig. 11A) with obtuse terminal cells; indeterminate branches formed in positions of whorl-branchlets,

(2) tetrahedral tetrasporangia, sessile on lower cells of whorl-branchlets (Fig. 11B, C, D).

(3) spherical spermatangial heads (Fig. 11E) in positions similar to tetrasporangia,

(4) procarps formed at apices of either potentially indeterminate branches (Fig. 11F) or whorl-branchlets (Fig. 11G); subapical cell of fertile axis with 3 pericentral cells (Fig. 11H); two auxiliary cells per procarp (Fig. 11I); only one gonimoblast initial per auxiliary cell (Fig. 11I); fusion cell involving subapical cell; hypogenous cell bearing outer involucral filaments (Gordon and Womersley, fig. 17).

G. Feldmann (1950, p.311) reported a second species, *Sphondylothamnion thouarsii* (Mont.) Feldmann which she transferred from *Antithamnion*. This was based on a dried specimen of Lindauer (no. 223), which is probably *Mazoyera lyallii* (Harvey) comb. nov. (see p.113).

(2) MAZOYERA gen. nov.

Thallus axibus prostratis et erectis, axes principales aut prostrati aut erecti, ramificatio sparsa et irregularis ad alternatim subdisticha. Cellulae apicales 45-50μ diam. Ramuli-verticillati 2-4(-5) in cellula quaque axiali, oppositi aut verticillati, pinnatim ad subdichotome ramosi, cellulae medianae 35-140μ diam. Rami indeterminati in positione ramulorum-verticillatorum exorientes. Corticatio rhizoidorum absens aut praesens, rhizoidea a cellulis basalibus ramulorum-verticillatorum descendentia, a hapteris adhaerentia.

Sporangia tetrahaedralia in cellulis inferioribus ramulorum-verticillatorum exorientia.

Capitula spermatangiorum sphaerica ad oblonga, in cellulis ramulorum-verticillatorum exorientia.

Procarpia subapicalia in ramulis brevibus lateralibus, cellulae ultimae duae parvae, cellula subapicalis cellulas duas steriles et cellulam supportantem cum ramo carpogoniali laterali et cellula sterili terminali ferens; cellula hypogena ramulum adaxialem curvum involucralem ferens; cellula prima gonimoloba a extremo quoque cellulae unae auxiliaris elongatae exorientes. Carposporangia a cellula quaque filamentorum multorum 1-2 cellularium quorum in cellulis gonimolobis 3-6 sphaericis exorientium facta. Cellulae steriles cum procarpio consociatae ramulos 3-4 interiores involucrales cellularum parvarum elongatarum efferentes.

Thallus with prostrate and erect axes; main axes either prostrate or erect, branching sparse and irregular to alternately subdistichous. Apical cells 45-50µ diam. Whorl-branchlets 2-4(-5) per axial cell, opposite or whorled, pinnately to subdichotomously branched; median cells 35-140µ diam. Indeterminate branches formed in positions of whorl-branchlets. Rhizoidal cortication, when present, of descending rhizoids from basal cells of whorl-branchlets, adhering by haptera.

Sporangia tetrahedral, borne on lower cells of whorl-branchlets.

Spermatangial heads spherical to oblong, borne on cells of whorl-branchlets.

Procarps subapical on short lateral branchlets with the last two cells small, the subapical cell bearing two sterile pericentral cells and a supporting cell which bears a lateral carpogonial branch and a terminal sterile cell; hypogenous cell bearing an adaxial, curved involucral branchlet. Auxiliary cell elongate, producing a primary gonimolobe cell from each end. Carposporangia developed from each cell of many 1-2 celled filaments borne on 3-6 spherical gonimolobe cells. Sterile cells associated with procarp produce 3-4 inner involucral branchlets of small elongate cells.

The genus is named in honour of Madame Feldmann-Mazoyer, who has contributed significantly to our knowledge of the Ceramiaceae, particularly from the Mediterranean region.

TYPE SPECIES - *Mazoyera protensa* (Harvey) comb. nov.

BASIONYM - *Wrangelia protensa* Harvey 1860: 308.

The most important reproductive features which separate *Mazoyera* from the other genera of the Sphondylothamnieae are:

(1) the single, multicellular, adaxial involucral branchlet on the elongate hypogenous cell, in contrast to the single celled, later multicelled one in *Involucrana*, the 3-5 post-fertilization laterals of *Sphondylothamnion*, and the absence of laterals on the hypogenous cell in the other genera,

(2) the single auxiliary cell per procarp, in contrast to 2 per procarp in *Sphondylothamnion* and *Shepleya*, and

(3) the successive development of multinucleate gonimolobe cells, the first two of which are produced laterally from the auxiliary cell. The early divisions of the auxiliary cell in the other genera produce short chains of small, uninucleate gonimoblast cells.

KEY to SPECIES of MAZOYERA

1. Thallus with main axes prostrate, producing erect branchlets 1-5 mm high; axial cells to 1 mm long; rhizoidal cortication absent; thallus epiphytic on *Cystophora* spp. . ... *M. repens*

1. Thallus with main axes erect, 4-30 cm high; axial cells to 4 mm long; rhizoidal cortication present or absent; thallus epiphytic on algae or marine angiosperms 2

    2. Whorl-branchlets 4-5 per axial cell, subdi- or tri-chotomously branched, curved inwardly, with adjacent whorls regularly imbricating along erect axis .. .. *M. halura*

    2. Whorl-branchlets (1-)2-4(-5) per axial cell, generally pinnately or pectinately branched, not markedly inwardly curved, with adjacent whorls imbricating only near apices of erect axes 3

3. Whorl-branchlets lax, widely spreading, tapering markedly, median cells 35-40μ diam., 5-6½ times longer than wide; tetrasporangia borne on small stalk cells on lower cells of whorl-branchlets, 1-2 per cell . ... *M. protensa*

3. Whorl-branchlets rigid, fastigiate to widely spreading, not tapering markedly, median cells 60-90μ diam., 2-4 times longer than wide; tetrasporangia sessile on most cells of whorl-branchlets, 1-4 per cell, often arising from middle of cell (New Zealand) . ... .. *M. lyallii*

MAZOYERA PROTENSA (Harvey) comb. nov.

Wrangelia protensa Harvey 1860: 308; Alg. Aust. Exs. no. 263; 1863: synop. no. 333. J.Agardh 1876: 619. De Toni 1897: 130. Guiler 1952: 99. Lucas 1909: 23; 1929a: 16. Lucas and Perrin 1947: 137, fig. 10. May 1965: 366. Okamura 1932: 133. Sonder 1880: 28. Tisdall 1898: 511. Wilson 1892: 170. Womersley 1950: 181; 1966: 152.

TYPE LOCALITY - Pt. Phillip, Vic. (Harvey).

TYPE - Herb. Harvey, TCD (Alg. Aust. Exs. no. 263F). Isotypes MEL, 15,268, ADU, A8,303. The TCD specimen is labelled "original". Apparently Harvey considered Pt. Phillip as the original locality, although the species was first described in Flora Tasmaniae. Gunn's specimens are also in TCD. Holotype not seen.

DISTRIBUTION - From Kangaroo Is. and the south-east coast of Yorke Pen., S. Aust., to Pt. Phillip, Vic., and Tasmania.

The species is known to a depth of 13 m in Pt. Phillip Bay (ADU, A23,170, MacPherson, 29.vi.1958), and in the upper sublittoral zone (3-6 m) at American River Inlet, Kangaroo Is. (ADU, A26,849, Womersley, 22.viii.1963). It is often found as drift.

The material used for detailed investigation was collected as drift at Saunders Beach, American River Inlet, Kangaroo Is. (ADU, A26,719, Womersley, 25.viii.1963, and A30,730, Womersley, 29.ix.1964).

VEGETATIVE STRUCTURE (Fig. 12A-C, Plate 6A)

The thallus is 4-30 cm long, the branching irregularly alternate and subdistichous (Fig. 12A, Plate 6A) with three orders of branching. The main erect axes arise from prostrate branched axes which are attached to the substrate by digitate haptera. Cortical rhizoids strengthen attachment by extending downwards over the substrate and becoming intertwined, forming a holdfast up to 3 mm diam.

Apical cells (about 45µ diam.) of indeterminate branches give rise by transverse divisions to axial cells (Fig. 12B) which enlarge gradually to about 1 mm diam. and 3 mm long at the base of larger plants. Each axial cell bears 3-4(-5) whorl-branchlets, with the second produced opposite the first, and the third and fourth opposite each other, between the first and second. The first-formed whorl-branchlets of each whorl are produced spirally. Mature whorl-branchlets are widely divergent, lax and pinnately or subdichotomously branched, markedly tapering. Adjacent whorls do not usually imbricate except near the apex and in well developed sterile plants. Basal cells of whorl-branchlets are about 75µ diam. and 2-3 times longer than wide. Median cells are 35-40µ diam. and 5-6½ times longer than wide.

Indeterminate branches are borne in the positions of whorl-branchlets, one or two on any one axial cell. Descending branched rhizoids are initiated from the basal cells of whorl-branchlets in lower parts of the thallus and twist irregularly around axial cells, adhering to them by haptera borne on the distal ends of the rhizoidal cells (Fig. 12C). Elongate hair cells, reaching 3 mm long are occasionally produced from the middle parts of axial cells.

REPRODUCTION

Tetrasporangia (Fig. 12D).

The tetrasporangia reach 75µ diam. and are formed terminally on small stalk cells borne on the lower cells of whorl-branchlets. They are often displaced to a lateral position by the production of further branchlets or stalk cells from the primary stalk cell (Fig. 12D).

Spermatangial heads - unknown.

Procarp and Carposporophyte (Figs. 13A-H, 14A-D)

The fertile axis is 6-7 cells long and is formed in the position of a young whorl-branchlet. The apical and subapical cells of the fertile axis are small and densely protoplasmic, while the hypogenous cell is elongate (Fig. 13A, B). The subapical cell bears three pericentral cells. The abaxial pericentral and one lateral pericentral are sterile (Fig. 13C-F), while the other lateral pericentral is the supporting cell and bears both a terminal sterile cell and a lateral, curved carpogonial branch. The short trichogyne has a characteristic bulge. The cells of the carpogonial branch appear uninucleate before fertilization. The hypogenous cell bears at its distal end an adaxial, 2-celled involucral filament which is curved in the same plane as the carpogonial branch (Fig. 13F). Occasionally one of the "sterile" pericentral cells produces a second carpogonial branch and terminal sterile cell (Fig. 13G). In the two such cases observed, both procarps had been fertilized and had produced auxiliary cells.

After fertilization the trichogyne is lost and the cells of the carpogonial branch begin to fuse, although the first cell may remain distinct longer than the others. The third cell may become binucleate (Fig. 13H).

A curved elongate auxiliary cell is cut off from the supporting cell opposite the attachment of the carpogonial branch (Fig. 13H). At about this time the apical cell, sterile pericentral cells and sterile cell on the supporting cell become multinucleate and begin to divide (see below).

The fusing cells of the carpogonial branch eventually form a lobed structure. One small discoid connecting cell is then produced from each end of the original carpogonium, now considerably expanded (Fig. 14A), and the auxiliary cell fuses with the nearer of them (Fig. 14B). The fused carpogonial branch may also produce other small lateral cells of unknown function. After fusion with a connecting cell, the auxiliary cell gives rise to two small discoid cells which are gonimolobe initials, one at each end

(Fig. 14C). These become multinucleate and produce many 1-2-celled filaments, the cells of which develop successively into uninucleate, clavate carposporangia, 30-40µ diam. and 2-3 times longer than wide (Fig. 14D). Further gonimolobe initial cells are produced from the residual auxiliary cell between the first two, so that 2-5 groups of carposporangia (gonimolobes) occur in the mature carposporophyte. Segmentation of the residual auxiliary cell may occur before the production of the later gonimolobe cells.

Gradual fusion takes place between the auxiliary cell, supporting cell, subapical cell and sometimes the basal cells of the involucral branchlets to produce a lobed fusion cell.

The multinucleate apical cell, sterile pericentral cells and sterile cell on the supporting cell eventually give rise to four inner involucral branchlets, the upper cells of which are narrow and elongate, about 16µ diam. and the basal cells approximately isodiametric (Fig. 14D). These form a delicate inner involucrum around the carposporophyte. The involucral branchlet on the hypogenous cell elongates and branches in a similar manner to a normal whorl-branchlet. Together with whorl-branchlets on lower cells of the fertile axis this forms a loose outer involucrum around the carposporophyte. These filaments may produce further procarps at their apices, which may be fertilized and develop further, but mature carposporophytes have not been found in these positions.

MAZOYERA HALURA (Harvey) comb. nov.

Wrangelia halurus Harvey 1854: 546; Alg. Aust. Exs. no. 262; 1859a: pl. 70; 1863: synop. no. 331. J.Agardh 1876: 619. Bornet and Thuret 1880: 184. De Toni 1897: 130; 1924: 149. Lucas 1909: 23. Lucas and Perrin 1947: 138. May 1965: 366. Mazza 1919: 1301. Okamura 1932: 133. Sonder 1880: 29. Tate 1882: 21. Tisdall 1898: 511. Wilson 1892: 170. Womersley 1950: 181.

TYPE LOCALITY - Fremantle, W. Aust., on Cymodocea (Harvey).

TYPE - Herb. Harvey, TCD (travelling set no. 127). Not seen.

DISTRIBUTION - From Rottnest Is., W. Aust., along the southern coast to Western Port, Vic., and Northern Tas.

In Herb. Agardh, Lund, J.Agardh uses a manuscript name W. confluens for this species. According to May (1965, p.365) this name was published in a list without description, but she gives no reference to the publication of this list.

The species is most commonly found as drift, often attached to the stems of Cymodocea antarctica (Labill.) Endl. or Acrocarpia paniculata (Turn.) Areschoug. It has also been collected from the sublittoral fringe at Pennington Bay, Kangaroo Is., growing on Wrangelia nobilis Harvey (ADU, A31,449, Gordon, 17.xi.1967).

The material used for detailed investigation was collected from Pt. Phillip, Vic. (MEL, 15,359, male), Pt. Elliot, S. Aust.

(ADU, A28,003, Gordon, 21.vi.1964, female), near Eucla, W. Aust. (ADU, A19,301, Womersley, 3.ii.1954, sporangial), Phillip Is., Vic. (ADU, A27,489, Norris, 20.i.1963, sporangial), Stinky Bay, S. Aust. (ADU, A27,887, Gordon, 19.v.1964), and Aldinga Beach, S. Aust., (ADU, A30,629, Gordon, 29.vii.1966).

VEGETATIVE STRUCTURE (Fig. 15A, B, Plate 6B)

The thallus reaches 15 cm long and is sparsely and irregularly branched (Fig. 15A, Plate 6B). The main erect axes arise from prostrate axes which are attached to the substrate by haptera (Fig. 15B) similar to those in Mazoyera protensa. Corticating rhizoids occur rarely near the base of the thallus.

Apical cells (about 50µ diam.) of indeterminate branches give rise by transverse divisions to axial cells which enlarge gradually to about 1 mm diam. and 3 mm long at the base of larger plants. Each axial cell bears 4-5 whorl-branchlets, the first formed of which are produced spirally. Mature whorl-branchlets are subdi- or trichotomously branched or occasionally subquadrichotomously branched at the base and are incurved. Adjacent whorls imbricate regularly along the whole axis allowing sand grains and other small particles to become trapped between them. The terminal cells of the whorl-branchlets are obtuse, 30-40µ diam. and not tapering markedly. The median cells are 50-60µ diam. and 3½-5 times longer than wide.

Indeterminate branches are borne in the positions of whorl-branchlets, one or two on any one axial cell.

REPRODUCTION

Tetrasporangia (Fig. 15C)

The tetrasporangia reach 60μ diam. and are formed terminally or laterally on small stalk cells borne on lower cells of the whorl-branchlets. Each stalk cell may produce 1-3 sporangia (Fig. 15C).

Spermatangial heads (Fig. 15D, E)

Almost spherical spermatangial heads, about 70μ diam., are produced terminally on short stalk cells borne adaxially on the cells of the whorl-branchlets (Fig. 15D). Two fertile axial cells (Fig. 15E) each give rise to a whorl of pericentral cells which each produce 1-3 spermatangial mother cells. These each produce 2-3 spermatangia.

Procarp and Carposporophyte (Fig. 16A-F)

The structure and development of the procarp is essentially similar to that of *M. protensa*. The fertile material available of *M. halura* was not in as good condition as that of *M. protensa* and so some stages were not observed. Figs. 16A and 13F illustrate the mature procarp systems of the two species and show the similarities. The one illustrated of *M. halura* is a mirror image of that of *M. protensa*, but this is not a constant difference.

The adaxial curved involucral filament on the hypogenous cell is similar to that in *M. protensa*, and the production of the auxiliary cell (Fig. 16B), fusion of the cells of the carpogonial branch (Fig. 16C), post-fertilization division of the sterile cells associated with the procarp (Fig. 16D, E), production of gonimolobes (Fig. 16F), carposporangia (30-40μ diam.) and fusion cell occur as in M. protensa. M. halura does not develop a very expanded end in the fused carpogonial branch, and does not produce secondary procarps at the apices of the outer involucral filaments as found in M. protensa.

MAZOYERA LYALLII (Harvey) comb. nov.

Wrangelia lyallii Harvey 1855: 236. J.Agardh 1876: 618; 1877-8: 27. De Toni 1897: 129. Laing 1902: 306; 1927: 148; 1939: 142. Naylor 1954: 660. Okamura 1932: 133.

TYPE LOCALITY - Ruapuke Is., Foveaux Strait, New Zealand (Lyall, Jan. 1851).

TYPE - Herb. Harvey, TCD. The main specimen is tetrasporangial, and there is also a small cystocarpic specimen in an envelope labelled "conceptacular fruit".

DISTRIBUTION - From Akaroa on the eastern coast of the South Is. of New Zealand to Preservation Harbour on the Southern Coast, Ruapuke and Stewart Islands.

The material used for detailed investigation was collected as drift from Ringa Ringa, Stewart Is. (ADU, A29,774, Womersley, 4.i.1966, female and sporangial), Akaroa (ADU A28,114, Womersley, 9.ix.1964, sporangial) and dredged from 4-6 m at Portobello (ADU, A21,354, Womersley, 4.ii.1958, sporangial). The species has also been collected from the sublittoral zone on the jetty piles at Portobello (ADU, A11,407, Womersley, 5.iii.1949).

VEGETATIVE STRUCTURE (Fig. 17A-C, Plate 7A).

The thallus is 10-20 cm long and is sparsely to richly branched (Plate 7A). The species exhibits several intergrading forms. In one form, the branching is alternate and subdistichous with up to three equally spaced whorl-branchlets per axial cell (Fig. 17A), the whorl-branchlets themselves regularly to irregularly pinnate, tending to pectinate in the male plant. In others the branching is regularly opposite and distichous, with two opposite whorl-branchlets per axial cell. In these forms the whorl-branchlets are mostly pinnate and distichous, and whorl-branchlets and indeterminate branches are less distinct.

The main erect axes arise from prostrate, branched axes which are attached to the substrate by haptera (Fig. 17B) similar to the previous species. Intertwining of the prostrate axes and the cortical rhizoids from the lower parts strengthen attachment. Apical cells are about 50µ diam., somewhat larger than the preceding species; axial cells also reach a greater length, to 4 mm near the base of the plant. Adjacent whorls of whorl-branchlets do not usually overlap except near the apex. Median cells of whorl-branchlets are 60-90μ diam. and 2-4 times longer than wide, the shorter cells occurring more frequently in the male plant. The terminal parts of the whorl-branchlets do not taper markedly. In lower parts of the main axes, the basal cells of the whorl-branchlets and lateral branches each produce several descending rhizoids which form a loose cortication, the rhizoids adhering to the axis by haptera (Fig. 17C).

REPRODUCTION

Tetrasporangia (Fig. 17D, E)

The tetrasporangia reach 70μ diam. and are sessile on the adaxial sides of cells of the whorl-branchlets. One to four tetrasporangia may be produced per cell.

Spermatangial heads (Fig. 18A-E)

The spermatangial heads are spherical to slightly ovoid, 50-60μ diam. and 1-1½ times longer than wide. They are sessile on the adaxial sides and distal ends of cells of the whorl-branchlets (Fig. 18A). Two to three fertile axial cells each produce a whorl of 3-4 spermatangial mother cells (Fig. 18B-D) which each give rise to about 2 terminal spermatangia, and further lateral spermatangial mother cells (Fig. 18E).

Procarp and Carposporophyte (Figs. 18F-H, 19A-D)

The structure and development of the procarp ~~is~~ essentially are similar to that of M. protensa and M. halura. The fertile axis (Fig. 18F) is (4-)6-7(-8) cells long. The presence of an adaxial curved involucral filament on the hypogenous cell (Fig. 18G) conforms to the type species. The production of the auxiliary cell (Fig. 18H), the fusion of the cells of the carpogonial branch, post-fertilization division of the sterile cells associated with the procarp (Fig. 19A, B), the production of two lateral gonimolobe initials with subsequent segmentation of the auxiliary cell and production of gonimolobes (Fig. 19C, D), carposporangia and fusion cell are similar to parallel stages in M. protensa. M. lyallii and M. halura are similar in producing a fused carpogonial branch which lacks an expanded end as found in M. protensa. Only remnants of connecting cells were observed for M. lyallii and this species does not produce secondary procarps at the apices of the outer involucral filaments as does M. protensa.

DISCUSSION

G. Feldmann (1950, p.311) identified the specimen distributed by V.W. Lindauer (no. 223) under the name Antithamnion plumula (Ellis) Thuret with Callithamnion thouarsii Montagne from Valparaiso, Chile. She transferred this species to Sphondylothamnion because of the multinucleate cells, mode of plasmolysis of the axial cells and the opposite distichous branching (similar to that in f.*disticha* Feldmann-Mazoyer (1940, p.386) of *Sphondylothamnion multifidum*).

A specimen also labelled *Antithamnion plumula* (Ellis) Thuret from Timaru, from Herb. V.W. Lindauer, no. 6,841 (ADU, A3,920, 27.xii.1945, female) has been examined and identified with *Mazoyera lyallii*. It is therefore probable that Mme. Feldmann's specimen of Lindauer's was also *M. lyallii* and thus *Sphondylothamnion thouarsii* is conspecific with this species. In this case, the distribution of this species would extend across the Pacific to Chile. If this synonymy is confirmed, this species would have to be named *Mazoyera thouarsii* (Montagne) comb. nov. as this specific epithet was published first.

After examining Montagne's type specimen of *C. thouarsii* in Museum National d'Histoire Naturelle, Paris, Dixon (1963a,p.222) confirmed the similarity of this material to the distichous form of *S. multifidum* and suggested that Montagne's specimen was probably not worthy of specific status. However he did not mention the presence or absence of reproductive structures. The vegetative structure of sterile distichous forms of *M. lyallii* are extremely similar to corresponding forms in *S. multifidum*, although the reproductive structures of the two species are quite different. Thus it will be necessary to wait until fertile specimens of *C. thouarsii* are collected before definite synonymies can be drawn.

MAZOYERA REPENS sp. nov.

TYPE LOCALITY - Kingston, Lacepede Bay, S. Aust., epiphytic on Cystophora platylobium (J.Agardh) Mertens (Womersley, 19.viii.1966).

TYPE - ADU, A30,665.

DISTRIBUTION - Isolated records from Elliston, Daly Head, and the south coast of Kangaroo Is. to Kingston, S. Aust.

The species is epiphytic on Cystophora platylobium and Cystophora siliquosa J.Agardh.

The type collection was used for detailed investigation.

DIAGNOSIS

Thallus pusillus in Cystophora spp. epiphyticus; rami principales prostrati, a hapteris adhaerentes. Ramuli-verticillati 3 in cellula quaque axiali, unus erectus et validus, saepe ad 4 mm alt., alii parviores in latere quoque prostrati; cellulae medianae 60-140μ diam., $2\frac{1}{2}$-4 longiores quam latiores.

Sporangia tetrahaedralia ad 190μ diam., in cellulis inferioribus ramulorum tertiariorum et quaterniariorum posita.

Capitula spermatangiorum ovoidea, circa 60x90μ, terminalia in cellulis ramulorum-verticillatorum posita.

Procarpia subapicalia in ramulis-verticillatis erectis posita. Structura carposporophyti eadem atque geno.

VEGETATIVE STRUCTURE (Fig. 20A, B, Plate 7B)

The thallus is small and epiphytic with the main axes prostrate, growing along the edge of receptacles and over the vesicles of the host (Fig. 20A, Plate 7B); erect branchlets reach 4 mm high.

Apical cells (about 50µ diam.) of indeterminate branches give rise by transverse divisions to axial cells (Fig. 20B) which reach about 200µ diam. and 2-3 times longer than wide. Each axial cell bears 3(-5) whorl-branchlets, 1(-2) of which is erect and strongly developed to 4 mm long, while the others are prostrate and usually smaller, one on each side of the larger erect whorl-branchlet. The erect whorl-branchlets tend to branch pectinately, with the tertiary laterals being produced on the adaxial side. Median cells of the erect whorl-branchlets are 60-140µ diam. and $2\frac{1}{2}$-4 times longer than wide. Lateral branches of indeterminate growth are produced in the positions of prostrate whorl-branchlets. The distinction between whorl-branchlets and indeterminate branches is not clear, the erect whorl-branchlets often possessing a distinct central axis and apical cell but being limited in growth.

Haptera, 20-50µ long, are produced mostly in pairs from the proximal ends of the cells of the prostrate axis. and occasionally from the lower cells of the prostrate whorl-branchlets (Fig. 20B). Many axial cells produce 1-3 small additional branchlets and haptera between the regular whorl-branchlets and haptera.

REPRODUCTION

Tetrasporangia (Fig. 20B, C)

The tetrasporangia reach about 100µ diam. and are sessile or stalked on the lower cells of the laterals of the erect whorl-branchlets, 1-2 tetrasporangia per cell.

Spermatangial heads (Fig. 20D, E)

The spermatangial heads are ovoid, about 60µ diam. and $1\frac{1}{2}$ times longer than wide. They occur terminally on short laterals in the upper parts of the erect whorl-branchlets. There are 3(-4) fertile axial cells each producing 4 pericentral cells, each of which cuts off 2-4 terminal spermantangia and further lateral spermatangial mother cells.

Procarp and Carposporophyte (Figs. 21A-D, 22A-C)

The fertile axis develops in the position of an erect whorl-branchlet and is (4-)6-9(-14) cells long. The structure and development of the procarp is essentially similar to that of the other species of Mazoyera.

Fig. 21A and B illustrate early stages of procarp development. The presence of an adaxial, curved involucral filament on the hypogenous cell (Fig. 21C) conforms to the type species. The production of the auxiliary cell, connecting cells (Fig. 21D), two lateral gonimolobe initials (Fig. 22A) and further gonimolobes between the first two (Fig. 22B), carposporangia (Fig. 22C) and fusion cell occur as in *M. protensa*. The cells of the carpogonial branch may fuse (Fig. 21D) or remain separate and gradually disintegrate (Fig. 22A). Only the apical cell, sterile cell on the supporting cell and one sterile pericentral cell divide after fertilization to produce in total 3 inner involucral filaments (Fig. 22B). The other sterile pericentral cell (Fig. 22A, B) remains undivided. In the other species of *Mazoyera*, all four sterile cells divide after fertilization.

DISCUSSION ON MAZOYERA

Evolution of the species of *Mazoyera* has probably occurred along two main lines (Diagram 2):

(1) one in which the main axes are prostrate and the tetrasporangia and spermatangial heads either sessile or stalked, leading to *M. repens*, and

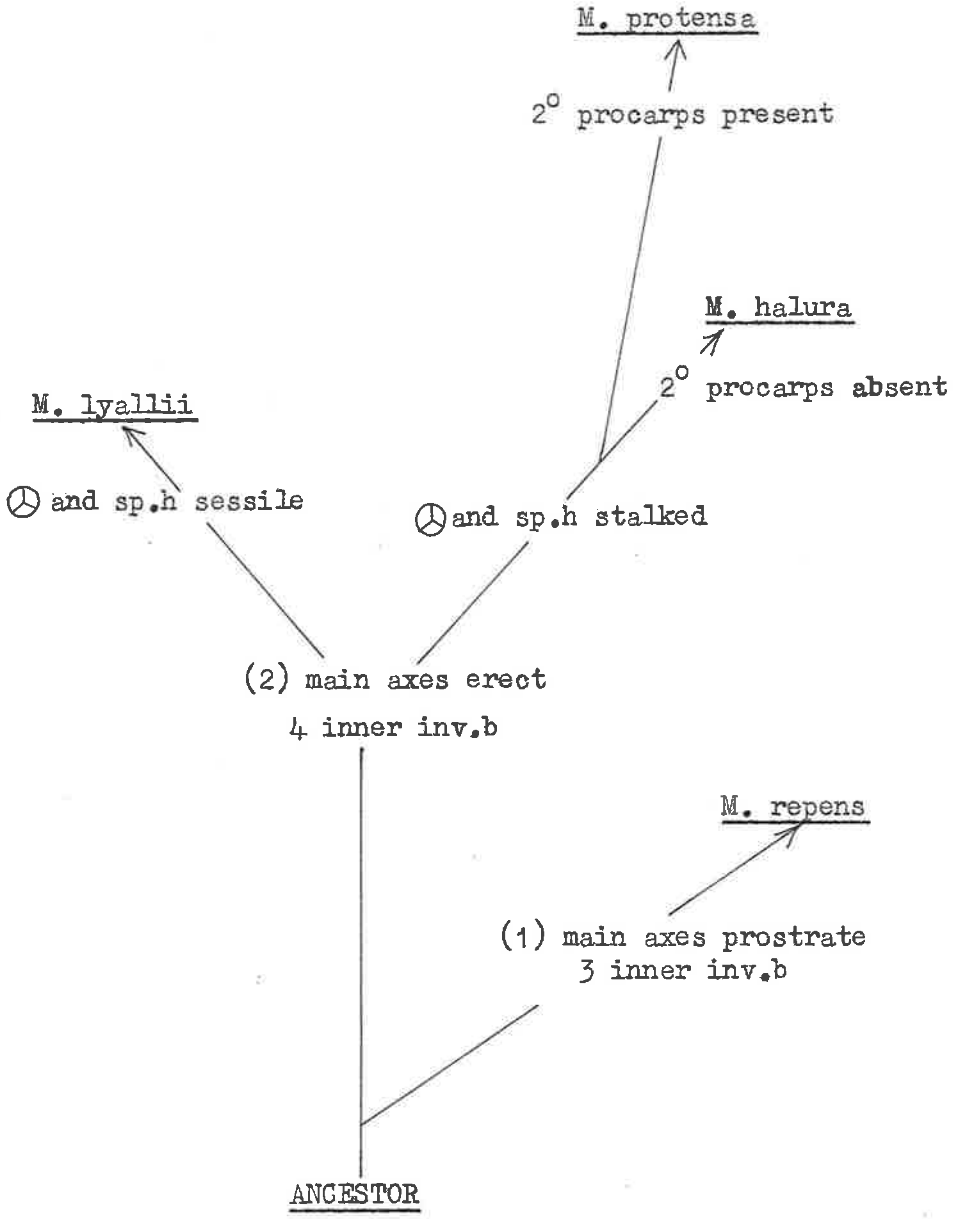
(2) one in which the main axes are erect. This line probably branched early, giving rise to a species in which the tetrasporangia and spermatangial heads are sessile (*M. lyallii*), and another line with species having only stalked tetrasporangia and spermatangial heads (*M. halura* and *M. protensa*). *M. protensa* is possibly a little more advanced than *M. halura* in the ability for outer involucral filaments of the carposporophyte to develop secondary procarps at their apices. In *M. halura* the outer

involucral filaments of the carposporophyte never produce secondary procarps.

Correlated with the development of main axes which are prostrate is the production of only three inner involucral groups around the carposporophyte, in contrast to the four produced in species with main axes erect. This is probably a derived condition resulting from the loss of the ability of one sterile pericentral cell to divide after fertilization.

The four species of *Mazoyera* form a well defined unit, the structure and development of the procarp and carposporophyte being almost identical in each species.

DIAGRAM 2.- Possible mode of evolution of species of *Mazoyera*



(3) SHEPLEYA gen. nov.

Thallus axibus prostratis et erectis vel axibus prostratis solis, ramificatio irregularis alterna subdisticha ad disticha. Cellulae apicales 60 - 220µ diam. Ramuli-verticillati 2-4(-5) in cellula quaque axiali, orthostichi paribus oppositis, plerumque ramosi adaxialiter, cellulae medianae 55 - 580µ diam. Rami indeterminati in positione ramulorum-verticillatorum exorientes. Corticatio rhizoidorum absens aut praesens, rhizoidea a cellulis basalibus ramulorum-verticillatorum descendentia, a hapteris adhaerentia.

Sporangia tetrahaedralia, adaxialia in ramulis lateralibus ramulorum-verticillatorum.

Capitula-spermatangiorum sphaerica ad oblonga, in positionibus similibus sporangiis exorientia.

Procarpia subapicalia in ramulis brevibus lateralibus, cellulae ultimae tres parvae, cellula subapicalis cellulam sterilem pericentralem, fertilem pericentralem, et cellulam supportantem cum ramo carpogoniali laterali et cellula sterili terminali ferens. Cellula hypogena ramos laterales numquam ferens; cellulae duae auxiliares gonimoblastem efferentes, cellula-fusionis bifurcata cellulam hypogenam involvens. Cellulae steriles cum procarpio consociatae ramulos 2-3 interiores involucrales cellularum parvarum elongatum efferentes.

Thallus with prostrate and erect axes or with prostrate axes only, branching irregularly alternate and subdistichous to distichous. Apical cells 60 - 220µ diam. Whorl-branchlets 2-4(-5) per axial cell, orthostichous in opposite pairs, mostly adaxially branched; median cells 55 - 580µ diam. Indeterminate branches formed in positions of whorl-branchlets. Rhizoidal cortication when present of descending rhizoids from basal cells of whorl-branchlets, adhering by haptera.

Sporangia tetrahedral, adaxial on laterals of whorl-branchlets.

Spermatangial heads spherical to oblong, borne in positions similar to sporangia.

Procarps subapical on short lateral branchlets, the last three cells smaller, the subapical cell bearing a sterile pericentral cell, a fertile pericentral cell and a supporting cell which bears a lateral carpogonial branch and a terminal sterile cell. The hypogenous cell bears no laterals. Two auxiliary cells each produce gonimoblast. Fusion-cell two-armed, involving the hypogenous cell. Sterile cells associated with the procarp produce 3-4 inner involucral branchlets of small elongate cells.

The genus is named in honour of E. Ann Shepley (Mrs. F.J. Mitchell) who has contributed significantly to our knowledge of southern Australian algae.

TYPE SPECIES - *Shepleya wattsii* (Harvey) comb. nov.

BASIONYM - *Wrangelia wattsii* Harvey 1862: pl.233.

The most important reproductive features which separate *Shepleya* from the other genera of the Sphondylothamnieae are:

(1) the relatively small hypogenous cell bearing no laterals, in contrast to the hypogenous cell with one lateral branch in *Mazoyera*, the 3-5 post-fertilization laterals in *Sphondylothamnion* and the single-celled (later multicelled) lateral in *Involucrana*. In *Wollastoniella* and *Drewiana* the hypogenous cells also bear no laterals. However, in *Wollastoniella* the subhypogenous cell is also small and lacks laterals, while in *Drewiana* the hypogenous cell is relatively elongate,

(2) the two auxiliary cells per procarp, separating *Shepleya* from all other genera except *Sphondylothamnion*, and

(3) the bifurcate fusion cell involving the hypogenous cell - *Sphondylothamnion* also produces a bilobed fusion cell but it does not involve the hypogenous cell.

KEY to SPECIES of SHEPLEYA

1. Thallus to about 25 cm high with both erect and prostrate axes; rhizoidal cortication of axes present; 3 inner involucral groups around carposporophyte 2

1. Thallus to about 4 cm high, creeping and epiphytic, prostrate axes with or without erect axes; rhizoidal cortication of axes absent; 2 inner involucral groups around carposporophyte 3

   2. Whorl-branchlets 2 per axial cell, distichous, with median cells 200-300µ diam. and 2-3 times longer than wide; reproductive structures formed on small-celled, highly modified laterals adaxial on the whorl-branchlets .. .. <u>S. wattsii</u> .

   2. Whorl-branchlets 4 per axial cell, orthostichous, with median cells 130-150µ diam. and 3-5 times longer than wide; reproductive structures formed on small-celled laterals of the whorl-branchlets which are not highly modified ... ... <u>S. verticillata</u>

3. Thallus prostrate and distichously branched, without erect axes; usually epiphytic on <u>Pterocladia lucida</u>; whorl-branchlets 2 per axial cell, often not distinct from indeterminate branches, with median cells 55-85µ diam. .. .. <u>S. australe</u>

3. Thallus creeping with prostrate and erect axes, epiphytic on <u>Callophycus oppositifolia</u>, whorl-branchlets (2-)4(-5) per axial cell, claviform, simple or once branched, distinct from indeterminate branches, with median cells 340-580µ diam. ... ... <u>S. claviformis</u>

SHEPLEYA WATTSII (Harvey) comb. nov.

Wrangelia wattsii Harvey 1862: pl.233; 1863: synop. no. 335. J. Agardh 1876:620. De Toni 1897: 131; 1924: 149. Lucas 1909 : 23; 1929b: 48. Lucas and Perrin 1947: 138, fig. 12. May 1965: 366. Mazza 1906: 43. Okamura 1932: 133. Reinbold 1898: 40. Sonder 1880: 29. Tate 1882: 21. Tisdall 1898: 511. Womersley 1950: 181.

TYPE LOCALITY - Warrnambool. Vic. (Watts).

TYPE - Herb. Harvey, TCD (Watts no. 85). Not seen.

DISTRIBUTION - West Bay, Kangaroo Is. (a single record), and from Adelaide, S. Aust. to Pt. Phillip Bay, Vic. and Southport, Tas. (also a single record).

The species grows in the sublittoral zone, often epiphytic on *Phacelocarpus* and has been collected from depths of 6-13 m from Robe (ADU, A31,422, Baldock, 15.v.1967), and Nora Creina Bay (ADU, A26,496, Mitchell, 26.v.1963). It is commonly found as drift.

The material used for detailed investigation was collected as drift at Stinky Bay near Nora Creina, S. Aust. (ADU, A21,262, Womersley, 19.viii.1957), and Robe, S. Aust. (ADU, A31,422 , and A27,904, Gordon, 18.v.1964).

VEGETATIVE STRUCTURE (Fig. 23A-C, Plate 8A)

The thallus reaches about 25 cm long with many subdistichous spreading branches of almost equal length, arising alternately or irregularly from every second to fifth axial cell of the main axes (Plate 8A). Branching occurs to the third and fourth orders, with the main axes sometimes furcate. The main erect axes arise from prostrate axes which are attached to the substrate by haptera. Rhizoids which corticate the axes near the base of the plant continue downwards over the substrate and intertwine to form a thick holdfast.

Apical cells (about 220µ diam.) of indeterminate branches give rise by transverse divisions to axial cells which enlarge gradually to about 0.3 mm diam. and 1.5 mm long near the base of the plant. Each axial cell bears 2(-3) whorl-branchlets in opposite distichous pairs (Fig. 23A, B - these illustrate the difference between unplasmolysed living and plasmolysed fixed material). The first-formed whorl-branchlets usually alternate in pairs (Fig. 23A). Mature whorl-branchlets are spreading and slightly incurved at their apices, only slight tapering. The lower 1-4(-7) cells bear adaxial, rarely abaxial, usually simple laterals, with up to 4 on the basal cell and fewer on upper cells. These laterals project above and below the plane of thallus branching, obscuring its distichous nature. Median cells of whorl-branchlets are 200-300µ diam. and 2-3 times longer than wide.

Indeterminate branches are borne in the positions of whorl-branchlets on axial cells. Descending, sparingly branched rhizoids are initiated from the basal (sometimes the lower two) cells of whorl-branchlets below about the 15th axial cell of each axis. They twist irregularly about the axis and adhere by haptera produced from the proximal ends of their constituent cells (Fig. 23C). The cortex formed from these rhizoids increases the diameter of the main axes in lower parts to about 5 mm.

REPRODUCTION

Tetrasporangia (Fig. 23D, Plate 8B)

The tetrasporangia reach about 150μ diam. and are sessile on the adaxial sides and distal ends of cells of small curved subdi- or trichotomous laterals, which are adaxial (occasionally abaxial or terminal) on the cells of the whorl-branchlets (Fig. 23D). The cells of these small fertile laterals are about 50μ diam. and 2-2½ times longer than wide, i.e. about one fifth of the diameter of vegetative whorl-branchlet cells.

Spermatangial heads (Fig. 23E-G)

The spermatangial heads are spherical, to 105μ diam., and are borne in positions similar to the tetrasporangia and also terminally on the small fertile laterals (Fig. 23E). The cells of these laterals are about 85μ diam. and 1½-2 times longer than wide. Each of the two to three fertile axial cells (Fig. 23F) produces a whorl of 3 or 4 pericentral cells. These act as spermatangial mother cells and also produce lateral chains of further spermatangial mother cells (Fig. 23G). These are flask-shaped and bud off 2-3 spermatangia.

Procarp and Carposporophyte (Figs. 24A-G, 25A-E)

The small fertile axes (Fig. 24A) are borne in positions similar to their counterparts in the sporangial and spermatangial thalli. They are usually more distinctly monopodial with 1-4 laterals arising from most of the fertile axial cells. Each fertile axis is about 4-6(-8) cells long. The cells of the fertile branchlets are about 90µ diam. and 1½-3 times longer than wide. The apical, sub-apical and hypogenous cells (Fig. 24B) are relatively short, about 25µ in length at fertilization. The subapical cell bears three pericentral cells. The adaxial one is sterile (Fig. 24C, D), while the other two form respectively the supporting cell, bearing a terminal sterile cell and a lateral curved carpogonial branch, and the fertile pericentral cell which is always adjacent to the carpogonium. The hypogenous cell produces no laterals. The cell below the hypogenous cell (the subhypogenous cell) bears three involucral branchlets at this stage.

After fertilization and loss of the trichogyne, the cells of the carpogonial branch begin to fuse by means of outgrowths from adjacent cells, often embedding pit discs or excluding them from the fused mass (Fig. 24E, G). One small discoid connecting cell is produced from each side of the original carpogonium. The supporting cell and fertile pericentral cell then segment obliquely near their bases to produce two pyriform auxiliary cells (Fig. 24F).

The apical cell, sterile pericentral cell and sterile cell on the supporting cell begin to divide (Fig. 24G) and eventually form three inner involucral groups surrounding the gonimoblast. Each auxiliary cell divides into three cells, the lower two cells produced from the basal lobes remaining undivided, while the upper cell divides to form a cluster of small uninucleate primary gonimoblast cells. The fused carpogonial branch gradually degenerates until only the wall remains. The lower gonimoblast cells, auxiliary cells, supporting cell, fertile pericentral cell, subapical cell and hypogenous cell fuse extensively to form a large densely staining, two-armed fusion-cell (Fig. 25A) reaching 200µ long. Carposporangia develop from the end cells of the lateral gonimoblast branchlets. The carposporangia are at first approximately isodiametric and highly vacuolate, but later they become clavate and densely staining, about 40µ diam. and 150µ long (Fig. 25B-D).

The three inner involucral groups are about three times subtrichotomously branched and protect the young carposporophyte. The distal one or two cells of the involucral branchlets become elongate, about 35µ diam. and $3\frac{1}{2}$-5 times longer than wide. These cells do not contain rhodoplasts. and clearly show structures which are probably nuclei, about 7 per cell. The lower cells of the inner involucral branchlets remain approximately isodiametric (Fig. 25E). The subhypogenous cell bears usually six outer involucral branchlets which surround the inner involucrum.

Up to twelve carposporophytes may occur on one whorl-branchlet but usually only one, rarely two, develop on each small fertile branchlet.

ABNORMAL REPRODUCTION (Fig. 25F, G)

Plants have been collected from Robe (ADU, A2085a,b, Macklin, Dec. 1925; A16,154a-d, Feb. 1928, and A27,904c, Gordon, 18.v.1964) and Pt. Elliot, S. Aust. (ADU, A31,384, Parsons, 15.i.1968) which show development of sporangia, carposporophytes and spermatangial heads on the same thallus. The small fertile branchlets are not restricted to a few cells in length as normally, but they are profusely branched and grow irregularly in all directions along the whorl-branchlets and main axes. They adhere by haptera (simulating rhizoids) and produce tufts of reproductive organs. (Fig. 25F - young sporangial tuft). Both sporangial and female branchlets have been seen arising from the one whorl-branchlet cell. Spermatangial heads and procarps can occur on the same abnormal branchlet (Fig. 25G), but more often a single abnormal tuft is either male, female, or sporangial.

In each case the reproductive structures appear normal except for their slightly smaller size. The average diameter of the gonimoblast, together with the inner involucrum is about 350μ compared with 400μ for that of the normal plants, and the average diameter of the tetrasporangia is 100 μ compared with a normal 150μ.

Abnormal small fertile branchlets have been observed on both sporangial and spermatangial plants which are otherwise normal. The physiological or genetic reason for this abnormal reproduction is unknown.

SHEPLEYA VERTICILLATA nom. nov.

Wrangelia verticillata sensu Harvey 1963: synop. no. 332.

J.Agardh 1876:619. De Toni 1897: 130. Guiler 1952: 99. Lucas 1909: 23; 1929b: 48. Lucas and Perrin 1947: 138, fig. 11. May 1965: 366. Okamura 1932: 133. Reinbold 1898: 40. Sonder 1880: 29. Tisdall 1898: 511. Wilson 1892: 170. Womersley 1950: 181.

non *Wrangelia verticillata* Kuetzing 1849: 664 (see below).

TYPE LOCALITY - Western Port, Vic.

TYPE - Herb. Harvey, TCD (Alg. Aust. Exs. no. 260).

DISTRIBUTION - From West Bay, Kangaroo Is. and Royston Heads, Yorke Peninsula, S. Aust., to Western Pt., Vic. and the northern coast of Tasmania.

The species has been found growing in a shaded pool on a rough reef near Robe, S. Aust. (ADU, A29,650, Womersley, 7.xi.1965), and to a depth of 12 m near Royston Hd., S. Aust. (ADU, A26,574, Shepherd, 14.iv.1963), but is usually found as drift. It is not common.

The material investigated in detail was collected as drift at Stinky Bay, Nora Creina, S. Aust. (ADU, A27,886, Baldock, 19.v.1964, tetrasporangial), from about 16 m depth at Guichen Bay, S. Aust. (ADU, A10,984, Womersley, 1.ix.1949, male) and from Pt. Phillip Heads, Vic. (MEL 15,325, Wilson, 1.ii.1893, female - only known specimen). A specimen showing abnormal reproductive development was collected at Stinky Bay (ADU, A31,420, Gordon, 15.v.1967).

The specific epithet of Wrangelia verticillata Harvey is invalidated by the earlier use of the name by Kuetzing (1849, p.664). Kuetzing's specimen was later examined by J.Agardh (1863, p.708) and put into synonomy with Wrangelia penicillata (C.Agardh) C.Ag. However, as Harvey's species is here transferred to the genus Shepleya, the name "verticillata" can be used.

DIAGNOSIS

Thallus axibus prostratis et erectis, axes erecti ad 30 cm alt. Ramificatio axium erectorum irregulariter alternata, subdisticha et patens. Ramuli-verticillati 4 in cellula quaque axiali, orthostichi, incurvi parum, cellulis terminalibus obtusis, angustatis parum. Cellulae medianae ramulorum-verticillatorum 130 - 150μ diam., 3 - 5 longiores quam latiores. Rhizoidea corticalia a cellulis basalibus ramulorum-verticillatorum descendentia per haptera adhaerentia.

Tetrasporangia tetrahaedralia, ad ~~80~~ 160μ diam., in cellulis inferioribus ramulorum-verticillatorum posita.

Capitula spermatangiorum sphaerica, ad 80μ diam., in positionibus similibus sporangiis posita.

Procarpia subterminalia in ramulis brevibus. Structura carposporophyti eadem atque geno.

VEGETATIVE STRUCTURE (Fig. 26A, B, Plate 9A)

The thallus reaches 30 cm high and is superficially similar to S. wattsii but more slender (Plate 9A). The branching is irregularly alternate, subdistichous, sparse to moderately dense, spreading and to about the fourth order. Several main erect axes often become intertwined and are held together near the base by rhizoidal filaments which may increase the diameter of the stem to about 8 mm. Erect axes are produced from the distal ends of cells of the prostrate axes which are attached to the substrate by haptera (Fig. 26A).

Apical cells (about 160µ diam.) of indeterminate branches give rise by transverse divisions to axial cells (Fig. 26B) which reached about 570µ diam. and 2.5 mm long near the base of the plant. Each axial cell bears 4 whorl-branchlets and these are produced orthostichously in opposite pairs, the second opposite the first, and the third and fourth between the first two. The third whorl-branchlet is initiated from the fourth to seventh axial cells below the apex and the fourth whorl-branchlet up to 5 axial cells below this. Young erect axes often show only the first pair of whorl-branchlets on each axial cell (Fig. 26A). Mature whorl-branchlets are slightly incurved and usually three times branched, the first division quaternate, the second ternate and the third binate, the laterals tending to be adaxial. Terminal cells are obtuse and taper slightly. Median cells are 130-150µ diam. and 3-5 times longer than wide.

Indeterminate branches are borne in the positions of whorl-branchlets on axial cells. Descending, sparingly branched rhizoids are initiated from the basal cell or occasionally the lower two cells of the whorl-branchlets below about the 20th axial cell. The rhizoids adhere to the axis by haptera produced from the proximal ends of their cells, and twist irregularly producing a loose cortex. Upper rhizoidal cells may produce small branchlets of whorl-branchlet form outwardly.

REPRODUCTION

Tetrasporangia (Fig. 26C, D)

The tetrasporangia reach about 160µ diam. and are borne on the distal ends and adaxial sides of whorl-branchlet cells which are somewhat smaller than vegetative cells, about 85µ diam. and 2-3 times longer than wide.

Spermatangial heads (Fig. 26E, F)

The spermatangial heads are spherical to slightly ovoid and about 80µ diam. They are borne in positions similar to the tetrasporangia, but they are usually nearer the apices of the whorl-branchlets which bear them (Fig. 26E). There are usually 3 fertile axial cells (Fig. 26F), each producing a whorl of 4 pericentral cells. These cut off terminal spermatangial mother cells, which each produce 1-2 spermatangia and further lateral spermatangial mother cells.

Procarp and Carposporophyte (Fig. 26G)

A 74-year old herbarium specimen was the only normal female plant available for study and hence many details of the development of the carposporophyte could not be followed. However, it appears to be essentially the same as that of *Shepleya wattsii*. Study of the procarp in the abnormal thallus supports this. The subhypogenous cell in *S. verticillata* bears only one lateral at fertilization (Fig. 26G) in contrast to the three in *S. wattsii* (Fig. 24D).

The fertile axes are usually 4-7 cells long. They occur in the positions of whorl-branchlets, or are laterals of the whorl-branchlets. One fertile lateral may bear up to 4 procarps. The cells of the fertile axes are about 100µ diam. and $2\frac{1}{2}$-3 times longer than wide - i.e. about equal in size to the sporangium-bearing cells, and slightly smaller than the vegetative cells of the whorl-branchlets. There is a much greater difference between the sizes of the vegetative cells of the whorl-branchlets and those of the small fertile branchlets in *S. wattsii* than in *S. verticillata*.

The young carposporophyte of *S. verticillata* has a large central bilobed fusion cell, apparently involving the hypogenous cell. Mature carposporangia were not seen. The carposporophyte is surrounded by the typical inner involucrum of small-celled filaments and an outer involucrum of 4 branchlets from the subhypogenous cell.

ABNORMAL REPRODUCTION

On one thallus (A31,420), filaments bearing sporangial, male and female reproductive structures arose from cells of the normal whorl-branchlets. They grew irregularly up and down the main axes, producing small, dense tufts at irregular intervals and adhering by haptera. The cells of these filaments are similar in size to the cells bearing reproductive organs in the normal thallus. The reproductive organs are normal in their mode of development. Two auxiliary cells per procarp are produced, one from the supporting cell and the other from the fertile pericentral cell.

Usually the sporangial, male and female tufts are separated, but in one case female and sporangial filaments were intertwined although they were not apparently connected directly by pit connections.

This type of abnormal development appears to be similar to that found in *S. wattsii*.

SHEPLEYA AUSTRALE (J.Agardh) comb. nov.

Callithamnion australe J.Agardh 1841: 42; 1851: 26; 1876: 21; 1885: 2. Kuetzing 1849: 649. Sonder 1880: 10.

Antithamnion australe (J.Ag.) De Toni 1903: 1407. Lucas 1909: 51. Okamura 1932: 129.

TYPE LOCALITY - Pt. Phillip, Vic., on Pterocladia lucida (R. Brown) J.Ag.

TYPE - Herb. Agardh, Lund (no. 17,960) - not seen. Probable isotype in MEL, 10,269.

DISTRIBUTION - Isolated occurrences from Garden Is., W. Aust. to Pt. Lonsdale, Vic.

The species is usually epiphytic on Pterocladia lucida which is found in the sublittoral zone to a depth of about 9 m. There is one record of the species epiphytic on Zonaria crenata J.Ag. from Daly Hd., Yorke Peninsula, S. Aust. (ADU, A31,270, Gordon, 26.iii.1967).

The material used in this investigation was collected under reef ledges from Garden Is., W. Aust. (ADU, A31,007, Chittleborough, 21.ix.1966).

VEGETATIVE STRUCTURE (Fig. 27A)

The thallus is prostrate, with the main axes creeping along the flat sides of the host thallus. Several axes may grow side by side on the wider lower parts of the thallus of the host, but there is usually only one main axis on the narrower upper parts. Lateral branching usually coincides with the branching of the host (see below) and is either opposite or alternate.

Apical cells (about 60µ diam.) give rise by transverse divisions to axial cells which enlarge gradually to about 185µ diam. and 500µ long. Whorl-branchlets are produced in opposite distichous pairs, in the same plane as the host thallus (Fig. 27A) and are not clearly distinct from indeterminate branches. They grow actively as indeterminate branches where they coincide with a lateral branch of the host, or where there is room on broader parts. They usually extend a short way (0.4-2 mm) over the host thallus edge where they may become fertile. Each whorl-branchlet is oppositely and distichously branched in the plane of the host thallus, with the adaxial laterals usually more strongly developed and ultimate cells obtuse. The basal cell of each whorl-branchlet usually produces adaxially a third lateral which is simple or once branched. Median cells of whorl-branchlets (when they appear determinate) are 55-85µ diam. and 2-4 times longer than wide.

Haptera are produced in opposite pairs from the proximal ends of axial cells (Fig. 27A).

REPRODUCTION

Tetrasporophyte (Fig. 27B)

The tetrasporangia are about 90µ diam. and are produced terminally (but displaced laterally) or laterally on the outer cells of the whorl-branchlets where the latter are free at the host thallus edge. The terminal cells of the whorl-branchlets are slightly curved around the sporangia.

Spermatangial heads (Fig. 27C)

The spermatangial heads are spherical to slightly ovoid and about 80µ diam. They are borne in positions similar to those of the tetrasporangia. Two to three fertile axial cells each produce a whorl of 4 pericentral cells, each of which cuts off 1-3 terminal spermatangia and lateral chains of further spermatangial mother cells (Fig. 27C).

Procarp and Carposporophyte (Figs. 27D-H, 28A-D)

The structure and development of the procarp is essentially similar to that of S. wattsii (Figs. 27F and 24D - the mature procarp systems of the two species). The sterile pericentral cell in S. australe is adaxial and is the first-formed (Fig. 27D) while the supporting and fertile pericentral cells are lateral, and the second and third-formed respectively (Fig. 27E, F). Any branch apex may become fertile, particularly if free from the host thallus (e.g. at the edge). The fertile axis may be 4-12 cells long.

Fusion of the cells of the carpogonial branch and production of connecting cells (Fig. 27G), the production of the two auxiliary cells (Fig. 28A, B), gonimoblast development (Fig. 28C), and production of the two-armed fusion cell and carposporangia (Fig. 28D) occur as in *S. wattsii*. The auxiliary cells are wider at their apices than at their bases. and do not cut off small cells at the base during early gonimoblast development as in *S. wattsii*. Only the apical cell and sterile pericentral cell divide after fertilization to produce a total of two inner involucral groups (Fig. 28B), while the sterile cell on the supporting cell remains undivided. *S. wattsii* produces 3 inner involucral groups per carposporophyte.

SHEPLEYA CLAVIFORMIS sp. nov.

TYPE LOCALITY - Garden Is., W. Aust., epiphytic on *Callophycus oppositifolia* (C.Agardh) C.Ag., under reef ledges, Chittleborough, 21.ix.1966.

TYPE - ADU, A31,008.

DISTRIBUTION - The only records are from the type locality, and as drift from Pt. Denison, W. Aust. (ADU, A32,179, Gordon, 8.xi.1968).

DIAGNOSIS

Thallus pusillus, in Callophycus oppositifolia (C.Ag.) C.Ag. epiphyticus, axes erecti ad 4 cm alt. ab axibus prostratis repentibus ad substratum per haptera adhaerentes orientes; axes erecti non ramosi vel ramosi parce. Ramuli-verticillati (2-3)4(-5) in cellula quaque axiali, claviformes, simplices vel semel divisi; cellulae medianae 340-580µ diam., 2-3 longiores quam latiores.

Sporangia tetrahaedralia ad 140µ diam., in ramulis parvis-cellularibus curvis adaxialibus in cellulis inferioribus ramulorum-verticillatorum positis, per cellulas superiores protecta.

Capitula spermatangiorum sphaerica, 130µ diam., in positionibus similibus sporangiis posita.

Procarpia subterminalia in ramis brevibus lateralibus, structura carposporophyti eadem atque geno.

VEGETATIVE STRUCTURE (Fig. 29A, B, Plate 9B)

The thallus is small, to 4 cm high and epiphytic on Callophycus oppositifolia, the erect axes arising from prostrate sparingly branched axes which creep over the host branches and may continue past their apices as erect axes (Plate 9B).

Apical cells (about 160µ diam.) of indeterminate branches give rise by transverse divisions to axial cells (Fig. 29A) which reach about 500µ diam. and 1350µ long in lower parts of erect axes, The cells of the creeping axes are about 325μ diam. and $1\frac{1}{2}$-2 times longer than wide, and may bear one or two whorl-branchlets. Haptera are produced from the proximal ends of prostrate axial cells and may reach over 1 mm long (Fig. 29B). Erect axes are produced from the distal ends of the cells of the prostrate axes. Anchorage is strengthened by occasional reflexed branches borne on the lowest cells of the erect axes. These branches creep along the host in the opposite direction to the prostrate axes.

Young erect axes bear 2 distichously arranged whorl-branchlets per axial cell near the apices. A third and fourth are usually produced lower on the axis between the first two. A fifth whorl-branchlet has occasionally been observed on a sporangial axis. The basically orthostichous arrangement of the whorl-branchlet becomes obscured in older parts by twisting of the axis. Mature whorl-branchlets are either simple and 1-3 celled, or once branched (Fig. 29A), the basal cells bearing 2 or 3 cells. The median cells are narrower at the proximal ends than the distal ends giving the characteristic claviform outline. The terminal cells may be small and domed or large and claviform. Median cells are 340-580μ diam. and 3-5 times longer than wide.

Indeterminate branches occur in the positions of whorl-branchlets on axial cells.

Rhodoplasts vary considerably in shape from approximately discoid to elongate, sometimes appearing dissected (Fig. 29C).

REPRODUCTION

Tetrasporangia (Fig. 29D)

The tetrasporangia reach 140µ diam. and are produced terminally or laterally on cells of branchlets borne adaxially on lower cells of whorl-branchlets (Fig. 29D). The lower cells of the sporangium-bearing branchlets are about 55µ diam. and 1½-2 times longer than wide - i.e., much smaller than the vegetative cells. The upper cells, 150-260µ diam. and about 2 times longer than wide, are somewhat larger than the lower cells and they curve protectively over the sporangia. Only two fertile whorl-branchlets have been observed on any one axial cell, together with 2 or 3 vegetative whorl-branchlets.

Spermatangial Heads (Fig. 30A)

The spermatangial heads are spherical, reaching 150µ diam. and are borne adaxially on small-celled whorl-branchlets (Fig. 30A). The upper cells are not enlarged as in the sporangial branchlets and are often slightly narrower than the lower cells.

Each of the two fertile axial cells produces a whorl of 3 or 4 pericentral cells which act as spermatangial mother cells and produce lateral chains of further spermatangial mother cells. These each bud off 2-3 spermatangia.

Procarp and Carposporophyte (Fig. 30B-D)

The fertile axes are usually 4-6(-7) cells long and occur in the positions of whorl-branchlets. From one to three fertile axes may occur on one axial cell, together with three to one (respectively) sterile whorl-branchlets. Usually only one procarp occurs on any one fertile branch in contrast to the 1-6 found in S. wattsii.

The structure and development of the procarp system is essentially similar to that of S. wattsii (Figs. 30B and 24D - similarities at fertilization stage). The cells of the procarp system of S. claviformis are about twice the diameter of those of S. wattsii, and this conforms to the difference in diameter of the respective vegetative cells. Production of two auxiliary cells per procarp (Fig. 30C), fusion of cells of the carpogonial branch, production of connecting cells, gonimoblast (Fig. 30D) and a two-armed fusion-cell occur as in S. wattsii. Only the apical cell and sterile pericentral cell divide after fertilization to produce two inner involucral groups (Fig. 30D). The sterile cell on the supporting cell remains undivided, as in S. australe. The subhypogenous cell bears up to six outer involucral filaments as in S. wattsii.

DISCUSSION

S. claviformis shows a number of similarities with Vickersia baccata (J.Ag.) Karsakoff from the Canary Is., Azores and Mediterranean Sea (Gulf of Naples). In particular, the creeping habitat, the lack of clear differentiation between the creeping and erect axes, the presence of haptera, the large size of the vegetative cells and their shape, and the structure of the mature procarp system are similar in the two species. Boergesen (1930, p.22, fig. 8) illustrates a cystocarp of V. baccata showing the presence of involucral filaments but does not discuss their origin. These may or may not develop from the sterile cells associated with the procarp as in S. claviformis.

The whorl-branchlets of S. claviformis are either simple and 2-3 celled or branched once subdi- or trichotomously at the base, and often small cells are cut off at their apices (Fig. 29A). In contrast, the whorl-branchlets of V. baccata are single-celled (the female plant) or two-celled (the male and tetrasporangial plants), or less often three or more cells and simple.

The most important difference between the two species is in the positions of the tetrasporangia and spermatangial heads. In V. baccata (Boergesen, figs. 8b, 9a,d) these are sessile on the basal cells of the two-celled whorl-branchlets, whereas in S. claviformis they are borne on small-celled laterals of the whorl-branchlets. In V. baccata, up to 50 or more tetrasporangia, each about 60µ diam., are borne on the one sporangial mother cell, unprotected by any involucrum. In S. claviformis only one tetrasporangium, up to 140µ diam., is borne on any one sporangial mother cell and the sporangia are protected by upper cells of the laterals. Similar differences apply to the spermatangial heads, those of V. baccata reaching about 50µ diam. and those of S. claviformis up to 150µ diam. The closely parallel way in which the tetrasporangia and spermatangial heads are formed in the four species of Shepleya aligns them as a distinct group, quite different from Vickersia.

The above features suggest that S. claviformis is both specifically and generically distinct from V. baccata, but clarification of the post-fertilization development in the latter is needed for a better understanding of the relationships, and this must await discovery of more fertile material of V. baccata.

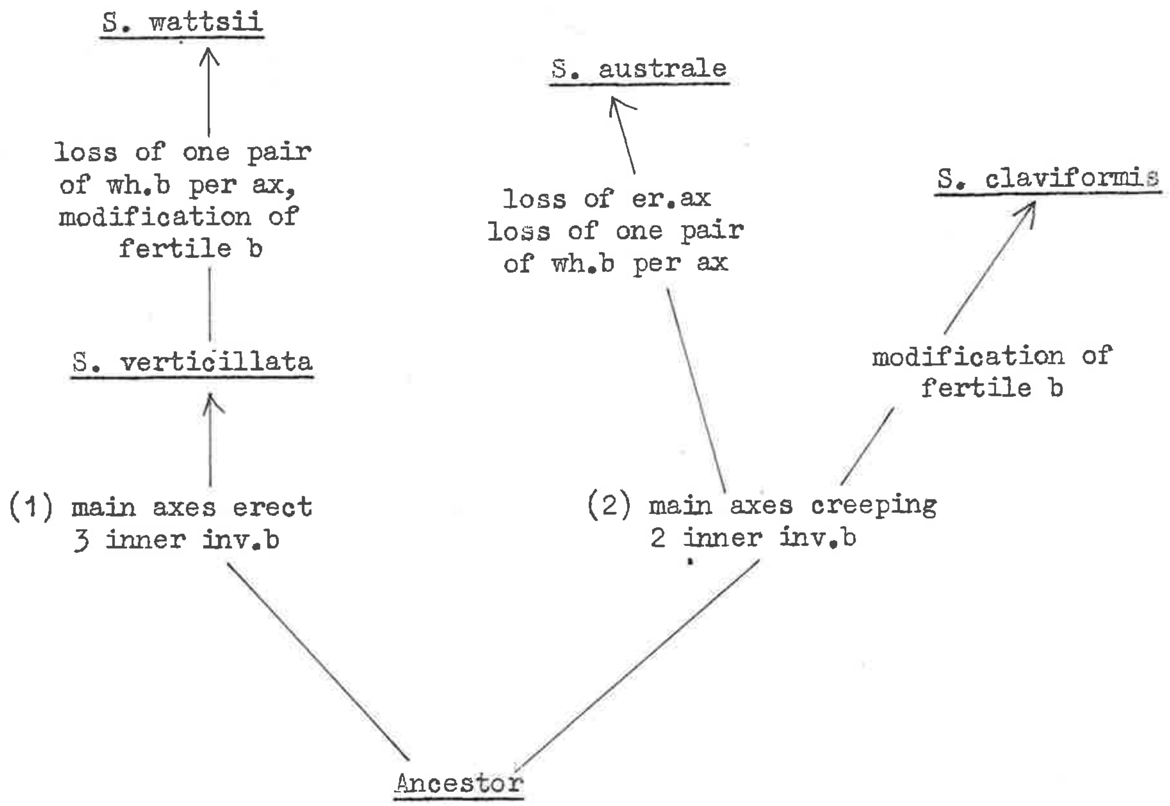
DISCUSSION on *SHEPLEYA* (Diagram 3)

It is probable that dichotomy of the *Shepleya* complex of species occurred firstly into (1) species in which the main axes were erect, and (2) species in which the main axes were creeping or prostrate.

Shepleya verticillata may represent an ancestral form of *Shepleya wattsii*. It is easy to postulate that *S. wattsii* could have arisen from a *S. verticillata*-like form by loss of one pair of whorl-branchlets per axial cell leaving the single distichous pair. This could have been accompanied by increased modification of the fertile branchlets.

The second developmental line in which the main axes are creeping probably gave rise to *Shepleya claviformis* and *Shepleya australe*. In both of these species, the sterile cell on the supporting cell has lost the ability to divide after fertilization, so that only two inner involucral groups surround the carposporophyte instead of three as in *S. verticillata* and *S. wattsii*. In *S. australe* all erect axes have been lost, and there has also been a retention of the primitive lack of differentiation between determinate branches (whorl-branchlets) and indeterminate branches. There is almost no modification of the cells which bear tetrasporangia and spermatangial heads. In contrast, in *S. claviformis*, there is complete differentiation between determinate and indeterminate laterals and the branchlets bearing tetrasporangia and spermatangial heads are much smaller than the ordinary vegetative cells of the whorl-branchlets.

DIAGRAM 3.- Possible mode of evolution of species of *Shepleya*



S. australe may have retained the primitive form of branching (with indeterminate and determinate branches not clearly differentiated) during its evolution because of its completely prostrate habit. Since the plant is only able to grow on the host, it would be advantageous to be able to grow indeterminately wherever there is space available. The species with erect branches are not so limited and so have tended to become more highly differentiated into indeterminate axes for growing and determinate axes for assimilation and reproduction.

There is a very large range in the vegetative cell size in the genus. Median cells in S. australe are 55-85µ diam., while those of S. claviformis are 300-470µ diam. However, there is a much closer agreement between the sizes of the fertile cells.

(4) WOLLASTONIELLA gen. nov.

Thallus axibus prostratis et erectis, axes principales erecti, ramificatio sparsa vel densa et irregulare ad alternatim subdisticha. Cellulae apicales 70-170µ diam. Ramuli-verticillati (3-)4 in cellula quaque axiali, in ordine circulari exorientes, pseudodichotomi ad pseudotrichotomi, basipete maturescentes, cellulae medianae 90-195µ diam., cellulae terminales breves et mucronatae. Rami indeterminati (0-)4 in cellula quaque axiali, in cellulis axialibus in additione ramulo-verticillato exorientes. Corticatio rhizoidorum absens aut praesens, rhizoidea ab extremis proximalibus cellularum axialium descendentia, a hapteris adhaerentia. Rami indeterminati potentiales in ramis villosis per elongatione cellularum constituentium mutati sint.

Sporangia tetrahaedralia, in cellulis inferioribus ramulorum-verticillatorum modificatorum. Verticillus sporangialis infra apicem ramorum brevium lateralium factus.

Capitula spermatangiorum sphaerica in cellulis ramulorum-verticillatorum villosorum exorientia.

Procarpia subapicalia in axibus brevibus lateralibus, cellulae ultimae quatuor parvae, cellula subapicalis cellulas duas steriles et cellulam supportantem cum ramo carpogoniali laterali et cellula sterili terminali ferens; cellula hypogena et subhypogena ramulos laterales nihil exorientes; cellula auxiliaris una a procarpio quoque. Cellulae steriles cum procarpio consociatae ramulos 4 interiores involucrales cellularum parvarum elongatarum exorientes.

Thallus with prostrate and erect main axes, branching sparse to dense and irregularly to alternately subdistichous. Apical cells 70-170µ diam. Whorl-branchlets (3-)4 per axial cell, formed in a circular order, each pseudodichotomously to pseudotrichotomously branched, maturing basipetally; median cells of whorl-branchlets 90-195µ diam., terminal cells short and mucronate. Indeterminate branches formed in addition to whorl-branchlets on axial cells, up to 4 per axial cell. Rhizoidal cortication, when present, of descending rhizoids from the proximal ends of axial cells, adhering by haptera.

Sporangia tetrahedral, on lower cells of modified whorl-branchlets which are situated just below the apices of short lateral branches.

Spermatangial heads spherical, borne on cells of villose whorl-branchlets.

Procarps subapical on short lateral axes of which the last four cells are smaller than the others. The subapical cell bears 2 sterile pericentral cells and a supporting cell with a lateral carpogonial branch and a terminal sterile cell; the hypogneous and subhypogenous cells do not bear any laterals. Only one auxiliary cell per procarp produces the gonimoblast.

The genus is named in honour of Dr. Elise Wollaston who has contributed significantly to our knowledge of the Ceramiaceae.

TYPE SPECIES - Wollastoniella myriophylloides (Harvey) comb. nov.
BASIONYM - Wrangelia myriophylloides Harvey 1854: 546.

The most important reproductive features which separate Wollastoniella from the other genera of the Sphondylothamnieae are:

(1) the four comparatively small cells which terminate the female axis, only the subapical cell producing pericentral cells - in all other genera at least the subhypogenous cell produces laterals, and

(2) the single auxiliary cell per procarp, in contrast to Sphondylothamnion and Shepleya with two auxiliary cells per procarp.

The main vegetative features which distinguish Wollastoniella are:

(1) the formation of potentially indeterminate branches in addition to whorl-branchlets on axial cells - in all the other genera of the Sphondylothamnieae, indeterminate branches are formed in the positions of whorl-branchlets on axial cells,

(2) the short, mucronate cells terminating the whorl-branchlets - in Drewiana the terminal cells are acute but are comparatively longer,

(3) the production of villose branches by elongation of the cells of potentially indeterminate branches,

(4) the position of haptera on the proximal ends of rhizoidal cells - in the other genera which produce haptera, they are borne on the distal ends of rhizoidal cells, and

(5) the basipetal maturation of the whorl-branchlets.

KEY to SPECIES of WOLLASTONIELLA

1. Branching of thallus and whorl-branchlets widely divergent; whorl-branchlets 4 per axial cell, each pseudotrichotomously branched 3-4 times, with median cells 160-200µ diam. and 3-5 times longer than wide; up to 4 potentially indeterminate branches per axial cell; cortication present .. .. *W. myriophylloides*

1. Branching of thallus and whorl-branchlets narrowly divergent; whorl-branchlets 3(-4) per axial cell, each branched once or twice, with median cells 90-160µ diam. and 5-7 times longer than wide; up to 2 potentially indeterminate branches per axial cell; cortication absent .. .. *W. mucronata*

WOLLASTONIELLA MYRIOPHYLLOIDES (Harvey) comb. nov.

Wrangelia myriophylloides Harvey 1854: 546; Alg. Aust. Exs. no. 259; 1862: pl. 224; 1863: synop. no. 337. J.Agardh 1876: 617. De Toni 1897: 128; 1924: 149. Lucas 1909: 22; 1929b: 48. Lucas and Perrin 1947: 136. May 1965: 365. Mazza 1906: 42. Okamura 1932: 133. Reinbold 1897: 47; 1899: 44. Sonder 1880: 28. Tate 1882: 21. Tisdall 1898: 511. Womersley 1950: 181; 1953: 38.

TYPE LOCALITY -- Rottnest Is., W. Aust.

TYPE - Herb. Harvey, TCD (travelling set no. 246). Not seen.

DISTRIBUTION - From Pt. Denison, W. Aust. to Pt. Phillip, Vic.

Moderately common as drift, often epiphytic on Cymodocea antarctica (Labill.) Aschers, Metagoniolithon charoides (Lam.) Weber van Bosse, Corallina sp. and Jania sp. Harvey mentions that the species grows "on the larger fucoids at Rottnest".

The material used for detailed investigation was collected from Elliston, Eyre Pen., S. Aust. (ADU, A31,432, Parsons, 23.viii.1967, female), D'Estrees Bay (ADU, A12,732, Womersley, 11.i.1950, A12,731, Womersley, 11.i.1950, tetrasporangial), and Pennington Bay, Kangaroo Is. (ADU, A6,619, Womersley, 4.i.1948, sporangial), Cable Hut Bay, Yorke Pen., S. Aust. (ADU. A32,167, Gordon, 23.ix.1968, male), and Kingston, S. Aust. (ADU, A30,667, Gordon, 19.viii.1966, and A27,888, Womersley, 20.v.1964).

VEGETATIVE STRUCTURE (Figs. 31A-D, 32A,B, Plate 10A)

The thallus reaches 18 cm high, with branching irregularly alternate or opposite, and generally sparse and widely spreading (Plate 10A). Up to four orders of branching occur. The erect axes arise from intertwined prostrate axes which form a thick mat over the substrate (Fig. 31A) to which they are attached by haptera.

Apical cells (about 170μ diam.) of indeterminate branches give rise by transverse divisions to axial cells (Fig. 31B) which reach 350μ diam. and 3.5 mm long in lower parts of the plant. Each axial cell bears up to 4 whorl-branchlets, which are produced in a circular sequence. They arise in alternately clockwise and anticlockwise directions on successive axial cells (Fig. 31B). The primary axis of each whorl-branchlet is 4 main cells long, the terminal cells maturing first and the laterals of lower cells being produced in a basipetal sequence (Fig. 31B). The two primary laterals on each of the second and third cells of the whorl-branchlet axis develop in a similar way to the portion of the whorl-branchlet distal to them. The two primary laterals on the basal cell of the whorl-branchlet are usually 4 main cells long, and their laterals (secondary) develop to the same extent as the portion of the primary lateral distal to them. Thus the mature whorl-branchlet appears to be three or four times trichotomously (occasionally dichotomously) branched, each arm of the branching consisting of one rigid cell divering widely from the others (Fig. 31C). The terminal cells are short and mucronate, about 35μ diam. and to 55μ long. The median cell, taken as the second cell of the primary axis of the whorl-branchlet, ranges from about 160μ diam. in slender plants to about 200μ diam. in more robust ones, and 3-5 times longer than wide. Adjacent whorls of whorl-branchlets do not overlap except at the apex and usually about 0.5 - 2.5 mm of axis is exposed between them.

Up to 4 potentially indeterminate branches may be produced in addition to whorl-branchlets on each axial cell. The potentially indeterminate branches are initiated after all the whorl-branchlets on one axial cell have been initiated. The first is formed between the first and second whorl-branchlets, the second opposite the first, between the third and fourth whorl-branchlets. The third and fourth branches (when they occur) are produced between the first and fourth, and second and third whorl-branchlets respectively (Fig. 31D). Less often the sequence is circular or alternating. The maximum of eight laterals is not often reached and various combinations of whorl-branchlets and potentially indeterminate branches may occur. The potentially indeterminate branches may develop in three ways: They may:

(1) continue to divide apically and become a main thallus branch, usually only one or occasionally two on an axial cell (Fig. 31A),

(2) become fertile, not reaching more than 9 cells in length (see reproduction), or

(3) become villose, not reaching more than 9 cells in length. In the third type of development, the cells of the axis and laterals become narrow and hair-like, about 15µ diam. (Fig. 32A), and the whorl-branchlets lack the mucronate tips. The lower cells of the branch enlarge following the basipetal pattern of maturation, and reach 50-100µ diam. and about 2 mm in length. The whole axis may reach 6 mm in length. Spermatangial heads are borne on cells of such branches (see below). Often a secondary potentially indeterminate branch may be seen on a lower axial cell of the villose branch apparently ready to continue growth (Fig. 32A). Villose branches may also occur as laterals on lower cells of potentially indeterminate branches which develop procarps.

Rhizoids which corticate the axis are produced in the lower parts of the plant from the proximal ends of axial cells and from basal cells of lateral branches. Haptera occur on the proximal ends of rhizoidal cells (Fig. 32B). Potentially indeterminate branches may also be produced from the distal ends of basal cells of rhizoids and contribute to the compactness of the whorl of laterals on the axial cell. Rhizoids increase the diameter of the erect axes to about 7 mm and extend down over the substrate and prostrate axes, thus strengthening attachment. One holdfast may consist of the bases of several erect axes held together by rhizoids.

REPRODUCTION

Tetrasporangia (Fig. 32C)

The tetrasporangia reach 160µ diam. and are slightly ovoid. Rarely sporangia of 8 spores occur, reaching 200µ diam. They are borne terminally or laterally on small cells of highly branched and modified whorl-branchlets. Usually the sporangium-bearing cell also produces 1-3 involucral branchlets, with cells about 35-55µ diam. and 1½-4 times longer than wide, either simple or branched (Fig. 32C). Whorls of whorl-branchlets bearing sporangia are produced just below the apex of short, lateral potentially indeterminate branches. The apex of such a branch may become villose, and in this case a potentially indeterminate branch from the axial cell which bears the sporangial whorl may continue growth. Thus the sporangial whorl appears to be intercalary. Potentially indeterminate branches borne on basal cells of rhizoids may produce sporangia in a similar manner.

Spermatangial heads (Fig. 32D,E)

The spermatangial heads are spherical to slightly ovoid, about 110µ diam., and are sessile and adaxial on the distal ends of cells of whorl-branchlets (Fig. 32D) borne on villose branches (see above). These branches occur in distichous opposite pairs on each axial cell of the main thallus branches and may reach about 3 mm long. They are colourless and project beyond the normal whorl of whorl-branchlets.

Two to four fertile axial cells each produce whorls of 3-4 pericentral cells which each bud off 2-3 terminal spermatangia and further lateral spermatangial mother cells (Fig. 32E).

Procarp and Carposporophyte (Figs. 33A-E, 34A,B)

The fertile axis is 5-9 cells long and is formed from a lateral potentially indeterminate branch. On the sixth or seventh cell below the apex of the main fertile axis there are up to 4 whorl-branchlets alternating with up to 4 further lateral fertile axes which are usually 5-6 celled. At this stage, the main axial cell above this whorl may bear up to 4 whorl-branchlets which act as outer involucral branchlets for the carposporophyte. The last four cells of each fertile axis are relatively small and densely protoplasmic (Fig. 33A). The subapical cell bears three pericentral cells - two abaxial pericentral cells are sterile (Fig. 33A) while the third (lateral) pericentral cell is the supporting cell and bears both a terminal sterile cell and a lateral, curved carpogonial branch. The hypogenous and subhypogenous cells bear no laterals. One exception was observed where the subhypogenous cell bore a one-celled lateral and in this case the procarp was not present. In another case, a second pericentral had produced a terminal sterile cell and lateral carpogonial branch (Fig. 33B).

After fertilization the trichogyne is lost, the cells of the carpogonial branch begin to fuse, and two small connecting cells are produced, one on each side of the original carpogonium (Fig. 33C). These are often displaced to a position above the carpogonium, possibly caused by breaking off of the trichogyne. The supporting cell enlarges and cuts off an auxiliary cell (Fig. 33D). A small nucleated protruberance from the auxiliary cell (Fig. 33D) may represent a connecting cell partially fused with the auxiliary cell. The apical cell, two sterile pericentral cells and sterile cell on the supporting cell begin to divide (Fig. 33D), and eventually form four inner involucral groups surrounding the carposporophyte. Segmentation of the auxiliary cell produces up to four small gonimoblast initials (Fig. 33E) which divide further several times, the terminal cells developing into carposporangia about 100µ diam. and 150µ long (Fig. 34A). Gradual fusion occurs between the lower gonimoblast cells, auxiliary cell, supporting cell, subapical cell and hypogenous cell to produce a large, multinucleate fusion cell about 260µ diam. (Fig. 34A,B - compare Fig. 35F for W. mucronata). The subhypogenous cell remains distinct.

The basal cells of the inner involucral filaments are almost isodiametric while the ultimate cells are elongate and narrow, about 14µ diam.

All the procarps on the one lateral branch may produce carposporophytes; up to 4 per branch have been observed.

WOLLASTONIELLA MUCRONATA (Harvey) comb. nov.

> Wrangelia mucronata Harvey 1860: 309, Pl. 191B; 1863: synop. no. 338. J.Agardh 1876: 616. De Toni 1897: 127. Guiler 1952: 99. Lucas 1909: 22; 1929a: 16. Lucas and Perrin 1947: 135. May 1965: 365. Okamura 1932: 133. Sonder 1880: 28; Tisdall 1898: 511. Wilson 1892: 170.

TYPE LOCALITY - Tasmania (Gunn).

TYPE - Herb. Harvey, TCD.

DISTRIBUTION - Isolated occurrences at Stinky Bay and Pt. MacDonnell, S. Aust., and Low Head and Currie River, Tasmania.

The species is rare and has only been collected in the drift.

The material used for detailed investigation was collected from Currie River Mouth, Tas. (MEL 15,322, Perrin, Jan. 1938, female) and Pt. MacDonnell, S. Aust. (ADU, A18,987, Womersley, 19.viii.1953, tetrasporangial).

VEGETATIVE STRUCTURE (Figs. 34C,D, 35A, Plate 10B)

The thallus is 5-11(-20) cm long, with dense branching which is irregularly alternate and fastigiate (Plate 10B). There are up to five orders of branching. Many erect axes arise from intertwined prostrate axes (Fig. 34C) which form a thick mat.

Haptera produced from the cells of the prostrate axes aid attachment.

Apical cells (about 70µ diam.) of indeterminate branches give rise to axial cells which enlarge to about 180µ diam., and to 3.5 mm long. Each axial cell bears usually 3 whorl-branchlets (occasionally 4 in fertile parts) which are fastigiate and about one third to two thirds the length of the axial cell above. Each whorl-branchlet is pseudodi-oor trichotomously branched once or twice with the second division, if present, usually pseudodichotomous. Each arm of the di- or trichotomy is one rigid cell (Figs. 34D, 35A). The terminal cells are small and mucronate, about 35µ diam. and 80µ long. Median cells, taken as the second cell from the base, are 90-160µ diam. and 5-7 times longer than wide. Maturation proceeds basipetally.

Potentially indeterminate branches are formed in addition to whorl-branchlets on axial cells and occur between the first and second formed whorl-branchlets. Occasionally the apex of a potentially indeterminate branch becomes villose, as in W. myriophylloides, with the cells of the villose whorl-branchlets about 25µ diam. and lacking mucronate tips. In this case a lateral branch borne on a lower axial cell may take over the growth of the axis (Fig. 35A). This type of growth is found particularly in the female and tetrasporangial plants, where lateral branches continue the growth of the axis which has become fertile at its apex. This form of growth may be continued several times giving an irregular sympodium.

REPRODUCTION

Tetrasporangia [Fig. 35B(i), (ii)]

The tetrahedral sporangia reach about 145µ diam. and are borne terminally or laterally on small cells of modified whorl-branchlets near the apices of potentially indeterminate axes. The sporangial whorls may appear to be intercalary at a lower point on the axis because a new lateral potentially indeterminate branch has taken over the growth of the original one. The cells of the sporangial whorl-branchlets are smaller than those of the vegetative whorl-branchlets, being about 75µ diam. and 2½-3½ times longer than wide [Fig. 35B(i)]. They usually retain their mucronate tips, which are lacking in the sporangial involucral filaments of W. myriophylloides. Rarely sporangia with 8 spores are produced [Fig. 35B(ii)].

Spermatangial heads - Unknown.

Procarp and Carposporophyte (Fig. 35C-F)

The fertile axis is 6-7 cells long and is formed from a lateral potentially indeterminate branch. On the fifth or lower cell below the apical cell another lateral fertile branch may be formed, but a whorl as in W. myriophylloides never occurs.

The structure and development of the procarp system is essentially similar to that of W. myriophylloides (Figs. 35C and 33A - comparison of the two species). The comparatively small apical, subapical, hypogenous and subhypogenous cells (the latter two lacking laterals) are similar to those of the type species. Production of the auxiliary cell (Fig. 35D), fusion of the cells of the carpogonial branch (Fig. 35E), post-fertilization division of the sterile cells associated with the procarp and production of gonimoblast proceed as in W. myriophylloides (Fig. 35F - a young gonimoblast of W. mucronata). The primary gonimoblast chain, the auxiliary cell, supporting cell and subapical cell fuse to form an elongate fusion cell. The carposporangia are produced terminally on the lateral gonimoblast chains. The irregular surfaces of the carposporangia are probably due to densely packed oil droplets. Carposporophytes available for study were very few and so microchemical tests could not be carried out. Very little fusion occurs between the subapical cell and the hypogenous cells. In each of the four inner involucral groups, the lowest division is ternate or quaternate and the second binate or ternate. Whorl-branchlets on lower axial cells, particularly the cell below the subhypogenous cell, act as a loose outer involucrum.

DISCUSSION on WOLLASTONIELLA

W. myriophylloides and *W. mucronata* form a closely related species pair, with almost identical procarp and carposporophyte structure. *W. myriophylloides* appears to be more primitive in vegetative features, having a larger number of whorl-branchlets and potentially indeterminate laterals per axial cell than *W. mucronata*. There appears also to have been a reduction in the number of di-trichotomies in each whorl-branchlet in *W. mucronata*, but this trend could as well be interpreted in the opposite direction.

However, *W. myriophylloides* has probably advanced over *W. mucronata* in reproductive features. The whorl-branchlets bearing tetrasporangia in *W. myriophylloides* are more highly modified from vegetative whorl-branchlets than those of *W. mucronata*, in which most of the involucral branchlets still retain the mucronate tips; these are lacking in the corresponding branchlets of *W. myriophylloides*. The whorls of female axes are the result of the comparatively complex vegetative branching, in which the potentially indeterminate branches are formed in whorls.

Both species have the ability to produce villose branches and for a lateral potentially indeterminate branch on a lower cell to overtake growth. Although spermatangial plants of *W. mucronata* are unknown, it is highly likely that spermatangial heads will be found to occur on the cells of villose whorl-branchlets as in *W. myriophylloides*.

It seems likely that species of *Wollastoniella* may have occurred, or may still occur, in which the main axes are prostrate or creeping, thus paralleling this type of development in *Mazoyera* and *Shepleya*.

(5) DREWIANA gen. nov.

Thallus axibus prostratis et erectis, axes principales erectis, ramificatio disticha, alternata aut opposita. Cellulae apicales circa 50µ diam. Ramuli-verticillati 4-5 in cellula quaque axiali, cellulae terminales acutatae, cellulae medianae 25-70µ diam. Rami indeterminati in positione ramulorum-verticillatorum exorientes. Rhizoides corticalia a cellulis basalibus ramulorum-verticillatorum.

Sporangia tetrahaedralia, adaxialia in cellulis inferioribus ramulorum-verticillatorum posita.

Capitula spermatangiorum incognita.

Procarpia subapicalia in ramulis brevibus lateralibus aut ramulis lateralibus ramulorum-verticillatorum, cellulae ultimae duae parvae, cellula subapicalis cellulas duas steriles et cellulam supportantem cum ramo carpogoniali laterali et cellula terminali ferens; cellula hypogena elongata, ramulos laterales numquam ferens. Cellula auxiliaris una a procarpio quoque gonimoblastum exorientes. Cellulae steriles cum procarpio consociatae 4 systemata interior involucralia efferentes.

Thallus with erect main axes arising from prostrate axes, branching distichous, alternate or opposite. Apical cells about 50µ diam. Whorl-branchlets 4-5 per axial cell, the terminal cells acute, median cells 25-70µ diam. Indeterminate branches formed in the positions of whorl-branchlets. Rhizoids of cortex arising from basal cells of whorl-branchlets.

Sporangia tetrahedral, adaxial on lower cells of whorl-branchlets.

Spermatangial heads unknown.

Procarps subapical on short lateral branchlets or on laterals of whorl-branchlets. The last two cells of the fertile axis are relatively small, the subapical cell bearing two sterile pericentral cells and a supporting cell which gives rise to a lateral carpogonial branch and a terminal sterile cell; the hypogenous cell is elongate and bears no laterals. One auxiliary cell is formed per procarp and produces the gonimoblast. Sterile cells associated with the procarp divide after fertilization to give 4 inner involucral branchlets.

The genus is named in honour of the late Dr. Kathleen Drew (Mrs. Baker) whose detailed studies on the life histories of red algae have had widespread significance. The genus is monotypic.

<u>TYPE SPECIES</u> - <u>Drewiana nitella</u> (Harvey) comb. nov.

<u>BASIONYM</u> - <u>Wrangelia nitella</u> Harvey 1854: 546.

The most important features which separate <u>Drewiana</u> from the other genera of the Sphondylothamnieae are:

(1) the elongate hypogenous cell without laterals - in *Involucrana* and *Mazoyera* the hypogenous cell bears a single curved involucral filament, in *Sphondylothamnion* 3-5 post-fertilization laterals occur, and in *Shepleya* and *Wollastoniella* this cell is relatively short,

(2) the single auxiliary cell per procarp - *Sphondylothamnion* and *Shepleya* each have two auxiliary cells per procarp, and

(3) the pre-fertilization laterals on the subhypogenous cell, separating this genus from *Wollastoniella* in which the subhypogenous cell bears no laterals.

DREWIANA NITELLA (Harvey) comb. nov.

Wrangelia nitella Harvey 1854: 546; Alg. Aust. Exs. no. 258; 1859a: pl.105; 1863: synop. no. 336. J.Agardh 1876: 616. De Toni 1897: 127. Lucas 1909: 22. Lucas and Perrin 1947: 135. May 1965: 365. Okamura 1932: 133. Sonder 1880: 28. Tisdall 1898: 511. Wilson 1892: 170.

TYPE LOCALITY - Rottnest Is., W. Aust.

TYPE - Herb. Harvey, TCD (no. 213 of travelling set). Not seen.

DISTRIBUTION - Isolated occurrences from Rottnest Is., W. Aust., to Tasmania. The species is apparently rare.

The species has been collected by dredging in Pt. Phillip Bay, Vic. (MEL 15,320, Wilson, 18.i.1890) and by diving at 15 m in St. Vincent Gulf, S. Aust. (ADU, A33,177, Shepherd, 2.ii.1969).

The material used for detailed investigation was collected from Tasmania (NSW, Archer, female), Middleton, S. Aust. (ADU, A29,688, Womersley, 14.xi.1965, tetrasporangial) and Garden Is. W. Aust (ADU, A18,252, Clifton, sterile). The Western Australian specimens are in most cases small and ecorticate, while those from Pt. Phillip Bay and Tasmania (one specimen) are larger, more robust and basally corticated.

VEGETATIVE STRUCTURE (Fig. 36A-C, Plate 11A,B)

The thallus is 5-13 cm long. In smaller specimens the free erect axes arise from prostrate, creeping axes (Fig. 36A, Plate 11A), while in larger specimens the prostrate axes are often intertwined, forming a holdfast (Plate 11B). Branching of erect axes is regularly alternate or opposite, and distichous.

Apical cells (about 50µ diam.) of indeterminate branches give rise by transverse divisions to axial cells (Fig. 36B) which gradually enlarge to about 500µ diam. and 4-6 times longer than than wide. Each axial cell bears 4-5 whorl-branchlets which are pinnately to subdichotomously branched 5-8 times. The terminal cells are acute, 18-24µ diam. and about $2\frac{1}{2}$-7 times longer than wide. Seldom are they as short as illustrated by Harvey (1859, pl.105, Figs. 3 and 4). Median cells are 25-70µ diam. and 2-6 times longer than wide, the larger cells occurring in the more robust plants. Adjacent whorls of whorl-branchlets usually overlap only near the apices of branches.

Potentially indeterminate branches occur in the positions of whorl-branchlets on axial cells and initially resemble whorl-branchlets. In the more slender creeping plants, lateral branches in the lower parts of the erect axes may produce reduced whorl-branchlets which are short and simple or only once or twice branched. The apices of these laterals become curled, and presumably act as attachment organs (Fig. 36A).

Rhizoids which corticate the axes are produced in the lower parts of the more robust plants. They arise from the basal cells of whorl-branchlets and lateral indeterminate branches, with up to six from one basal cell. The cells of these rhizoids produce irregular whorls of 3 or 4 reduced whorl-branchlets, making a more compact covering to the main axis. Laterals of rhizoids may form secondary pit connections with neighbouring cells.

REPRODUCTION

Tetrasporangia (Fig. 36B,C)

The tetrasporangia are about 55µ diam. and are borne terminally (Fig. 36C) or laterally (Fig. 36B) on the adaxial sides of lower cells of the whorl-branchlets.

Spermatangial heads - Unknown.

Procarp and Carposporophyte (Fig. 36D-G)

The fertile axis is 5-6 cells long and is formed in the position of a whorl-branchlet or a lateral of a whorl-branchlet. The apical and subapical cells are comparatively small, while the hypogenous cell is longer and about 2½ times the length of the subapical cell (Fig. 36D). The subapical cell bears three pericentral cells. The abaxial pericentral cell and one lateral pericentral cell are sterile, while the other pericentral acts as the supporting cell and bears both a terminal sterile cell and a lateral curved carpogonial branch. The hypogenous cell bears no laterals.

After fertilization and loss of the trichogyne, two small connecting cells are produced on each side of the carpogonium. The cells of the carpogonial branch then fuse (Fig. 36E) and the supporting cell cuts off an auxiliary cell by an oblique division. The apical cell, two sterile pericentral cells and the sterile cell on the supporting cell begin to divide (Fig. 36F) and eventually form 4 inner involucral groups around the carposporophyte (Fig. 36G). The inner involucral group from a sterile pericentral cell is usually only two-celled. The basal cells are almost isodiametric, while the ultimate cells are elongate and about 20µ diam. Segmentation of the auxiliary cell produces a whorl of 4-5 small gonimoblast cells which divide further to produce a small cluster (Fig. 36F). The lower ones gradually fuse with each other and with the auxiliary cell and supporting cell (Fig. 36G). The subapical cell is not involved in the fusion cell. The terminal cells form claviform carposporangia about 25µ diam.

DISCUSSION

Superficially, D. nitella resembles very closely Sphondylothamnion multifidum (See Appendix). Thalli are about equal in size, show similar branching patterns with erect axes arising from prostrate axes, similar numbers of whorl-branchlets per axial cell, potentially indeterminate branches occurring in the positions of whorl-branchlets, and both are capable of forming secondary pit connections. Both produce sporangia in similar positions and the prefertilization structure of the procarp system in each is similar.

However, many of the differences between these two species are of generic importance. S. multifidum produces two auxiliary cells per procarp whereas D. nitella has only one. The hypogenous cell in S. multifidum ("basal cell" of Gordon and Womersley 1966, p.25) is only slightly larger than the subapical cell ("central cell" of Gordon and Womersley) and after fertilization produces an outer involucral whorl of whorl-branchlets. In D. nitella, however, the hypogenous cell is at least twice the length of the subapical cell and does not produce any pre- or postfertilization laterals. In other genera of the Sphondylothamnieae these features are constant within each genus. The tetrasporangia of S. multifidum are slightly less than twice the diameter of those of D. nitella.

Vegetative differences, although individually not of generic importance, when considered together with the reproductive differences clearly indicate the generic distinctness of Drewiana. In S. multifidum, the whorl-branchlets are subdi- or trichotomously branched, incurved, with an ultimate unbranched part of 8-9 cells (Fig. 11A). In D. nitella, the whorl-branchlets are mostly pinnately to subdichotomously branched, widely spreading, with 1-3 cells in the ultimate unbranched part (Fig. 36C). The terminal cells of whorl-branchlets of S. multifidum are obtuse, but those in D. nitella are acute.

(6) *INVOLUCRANA* Baldock and Womersley

The genus *Involucrana* was proposed and described by Baldock and Womersley (1968, p.214) for the species *Bornetia meredithiana* J.Ag., which differs considerably from *Bornetia* in reproduction.

The main features which separate *Involucrana* from the other genera of the Sphondylothamnieae are:

(1) the three celled fertile axis laterally placed on a whorl-branchlet - the fertile axes in all other genera are never less than 4 cells long,

(2) the presence of two pericentral cells on the subapical cell in contrast to the three in other genera - in *Involucrana meredithiana* occasionally one or rarely two extra pericentrals arise from the subapical cell after fertilization and divide to produce one or two extra inner involucral groups,

(3) the single celled, later multicelled, abaxial lateral branchlet on the hypogenous cell at fertilization - *Mazoyera* has also a lateral on the hypogenous cell at fertilization, but it is adaxial and two-celled (later multicelled), and *Sphondylothamnion* produces 3-5 laterals on the hypogenous cell but only after fertilization,

(4) the polysporangia of up to 32 spores - other genera produce tetrasporangia, or rarely sporangia of 8 spores (*Wollastoniella*).

A further species, Involucrana crassa (Hooker f. et Harvey) comb. nov. is here added to the genus Involucrana. This species agrees with I. meredithiana in the above features and differs from it mainly in vegetative features.

KEY to SPECIES of INVOLUCRANA

1\. Thallus branching irregular, subdistichous; whorl-branchlets often indistinct from indeterminate branches, 2-3(-4) per axial cell, radial on main axes, mostly about 10 mm long, with median cells 2-4 mm long ... ... *I. meredithiana*

1\. Thallus branching strictly distichous; whorl-branchlets nearly always distinct from indeterminate branches, distichous on main axes, 2(3-4) per axial cell, mostly $2\frac{1}{2}$-4 mm long, with median cells 0.7-1.2 mm long ... ... *I. crassa*

INVOLUCRANA CRASSA (Hooker f. et Harvey) comb. nov.

Wrangelia crassa Hooker and Harvey 1847: 410. Harvey, Alg. Aust. Exs. no. 261; 1860: 308; 1863: synop. no. 334. J.Agardh 1863: 706; 1876: 620. De Toni 1897: 131. Guiler 1952: 99. Kuetzing 1849: 665. Lucas 1909: 23; 1929a: 16; 1929b: 48. Lucas and Perrin 1947: 138. May 1965: 366. Okamura 1932: 133. Sonder 1880: 29. Tate 1882: 21. Tisdall 1898: 511. Wilson 1892: 170. Womersley 1950: 181.

TYPE LOCALITY - Georgetown, Tas. (Gunn).

TYPE - K. There are no specimens labelled "Gunn" in this herbarium. It is probable that the central one on the type sheet is the type. Not seen.

DISTRIBUTION - From Elliston, S. Aust., to Pt. Phillip Bay, Vic., and the northern coast of Tasmania.

The species is moderately common in drift, often growing on the axes of Acrocarpia paniculata (Turner) Areschoug, rarely on Metagoniolithon charoides (Lamx.) W.v.Bosse, and has also been collected on the axes of Wrangelia nobilis from the sublittoral fringe at Pennington Bay, Kangaroo Is. (ADU, A2,616, Womersley, 25.i.1944). It is rarely fertile and only one plant of each reproductive phase has ever been collected.

The material used for detailed investigation was collected at 20 m from Spencers Gulf, S. Aust. (NSW, Hedley, "Endeavour", Sept. 1909), Daly Head, Yorke Pen., S. Aust. (ADU, A31,009, Gordon, 26.iii.1967, male), Nora Creina Bay, S. Aust. (ADU, A25,467, Womersley, 8.viii.1961, female), Robe, S. Aust. (ADU, A31,159, Gordon, 26.i.1967), and Stinky Bay, S. Aust. (ADU, A27,896, Gordon, 19.v.1964).

The superficial appearance of the thallus is very similar to that of *Shepleya wattsii*, particularly that of the cystocarpic plant, but *I. crassa* can usually be distinguished by the curling tips and excessive plasmolysis occurring after death or fixation, causing the walls of the cells to appear relatively thick in *I. crassa* (Fig. 37B).

VEGETATIVE STRUCTURE (Fig. 37A,B)

The thallus reaches 19 cm long and the branching is alternate and distichous, with 3-4 orders of branching. Erect axes arise from intertwined, anastomosing prostrate axes which form a thick mat at the base.

Apical cells (about 200µ diam.) give rise to axial cells (Fig. 37A,B) which reach about 800µ diam. and 1½-3 times longer than wide. Each axial cell bears usually two whorl-branchlets which are cut off in opposite distichous pairs. Occasionally a third is produced (Fig. 37A) and rarely a fourth opposite the third. First-formed whorl-branchlets alternate on each side of the axis, singly, in pairs or in threes. Mature whorl-branchlets are widely spreading, subpolychotomously branched at the base and subdi- and trichotomous above with ultimate branchlets of 1-3 cells, tapering slightly. Up to six further laterals are produced in lower parts of the plant from the central regions or the proximal ends of the basal cells of the whorl-branchlets. These project across the axial cells in the direction of the opposite whorl-branchlet thus obscuring the distichous nature of the arrangement of the whorl-branchlets. Median cells of whorl-branchlets are 200-300µ diam. and 2½-6 times longer than wide. Adjacent pairs of whorl-branchlets overlap.

Potentially indeterminate branches are formed in the positions of whorl-branchlets on axial cells. Frequently axial cells near the apices of indeterminate branches bear reduced whorl-branchlets, or occasionally none at all, thus allowing the axes to curl in a flat spiral. Rhizoids which corticate the axis are produced in the lower parts of the plant from the proximal ends of basal cells of laterals and grow irregularly downwards. These form secondary pit connections with cells of lower whorl-branchlets and neighbouring rhizoidal cells.

REPRODUCTION

Polysporangia (Fig. 37C)

The sporangia are about 200µ diam. and are polyhedrally divided with 27-30(-32?) angular spores, each about 50µ diam. with a warted outer surface. Each spore is attached at the centre of the sporangium. The sporangia are borne terminally or laterally on the lower cells of small-celled laterals borne on the lower cells of the whorl-branchlets. Each spore is surrounded by curved involucral filaments arising from the stalk cell. The cells of the filaments are about 70µ diam, and 4-8 times longer than wide.

Spermatangial Heads (Fig. 37D-F)

The spermatangial heads are ovoid, about 90µ diam. and 1½ times longer than wide. They are borne on branchlets similar to those bearing the polysporangia, but the spermatangial heads may also occur on the upper cells of these branchlets (Fig. 37D). The cells of the involucral branchlets are shorter than those in the sporangial thallus, about 2½-4 times longer than wide.

Each spermatangial head consists of three to four fertile axial cells, each of which produces a whorl of three pericentral cells (Fig. 37E). These divide transversely and obliquely to produce rows of cells (Fig. 37F), the ultimate ones of which cut off 1-2 spermatangia. The lower cells of the rows produce outwardly further spermatangial mother cells.

Procarp and Carposporphyte (Fig. 37G-I)

The fertile axis is 3 cells long and arises from the distal end and adaxial side of a subterminal cell of a whorl-branchlet. The hypogenous cell (Fig. 37G) bears adaxially an elongate cell which develops later into an outer involucral branchlet. No secondary pit connection was observed between this cell and the lower subterminal cell as in I. meredithiana.

The subapical cell (Fig. 37G) bears two pericentral cells, the sterile pericentral cell and the supporting cell, which bears a terminal sterile cell and a lateral curved carpogonial branch. As only dried material was available, details of post-fertilization development could not be followed.

The carposporophyte consists of a central lobed fusion cell about 200µ diam., with tube-like anastomosing processes extending from it (Fig. 37H). These bear small cells which enlarge into carposporangia, at firstly highly vacuolate, but later clavate and densely packed with rhodoplasts and storage bodies. Mature carposporangia are about 50µ diam. and 3 times longer than wide. The carposporophyte is surrounded by 3 inner involucral branchlets (Fig. 37I), with the lower cells isodiametric and the ultimate cells elongate, about 35µ diam. and 5½ times longer than wide. These are enclosed by outer involucral branchlets from the lower vegetative whorl-branchlet cells.

DISCUSSION

The two species I. meredithiana and I. crassa are very similar in reproductive features, but further study of liquid preserved material of *I. crassa* is necessary for confirmation of details of post-fertilization events in this species.

In vegetative features, *I. crassa* is probably more advanced with its distichous pair of whorl-branchlets per axial cell, in contrast to the radial 2-3 whorl-branchlets which are often indistinct from indeterminate branches in *I. meredithiana*. Similarly, *I. crassa* shows a restriction of the cortical rhizoids to the basal cells of laterals, whereas *I. meredithiana* shows the probably more primitive condition where the rhizoids can be produced from both the proximal ends of the axial cells and from the basal cells of laterals.

The spermatangial heads of *I. crassa* are relatively shorter than those of *I. meredithiana*, again suggesting the more advanced condition of *I. crassa*.

(7) VICKERSIA Karsakoff 1896: 285.

VICKERSIA BACCATA (J.Agardh) Karsakoff. ~~emend.~~ Boergesen 1930: 20, fig. 7-10. Feldmann, J. and G. 1940a: 461. Feldmann-Mazoyer 1940: 380, figs. 11, 45, 149; 1941: 66. Ginsburg-Ardré 1963: 380. Kylin 1956: 388, fig. 306A.

Callithamnion baccatum J.Agardh 1870: 364; 1876: 27.

Vickersia baccata (J.Agardh) Karsakoff 1896: 287, pl.3.

Vickersia canariensis Karsakoff 1896: 281. Vickers 1896: 305.

Synonomy from Feldmann-Mazoyer 1940.

TYPE LOCALITY - Azores.

TYPE - Herb. Agardh, LD? Not seen.

DISTRIBUTION - Azores, Canary Is., Sines, Portugal, western Mediterranean Sea.

The type species grows above low water mark, epiphytic on other algae or on rocks in habitats both sheltered and exposed (Boergesen 1930, p.28).

Material of V. baccata, the type species of this monotypic genus was not available for study, but it was well described and illustrated by Boergesen (1930), Feldmann-Mazoyer (1940) and Karsakoff (1896, pl. 3).

The main distinguishing features of the species are:

(1) prostrate axes attached by unicellular digitate haptera

(Boergesen, Fig. 7b), with erect axes to 3 cm high (Karsakoff, pl.3, Figs. 1-5); whorl-branchlets 1-4 per axial cell, generally consisting of one cell (female plant, Boergesen Fig. 8a), two cells (male and tetrasporangial plants, Boergesen Fig. 8b), or more rarely 4-5 celled (sterile plants, Feldmann-Mazoyer, Fig. 149) - cells are swollen, claviform, 100-400μ diam. and 1½-3 times longer than wide; indeterminate branches formed in positions of whorl-branchlets (Boergesen Fig. 7a),

(2) tetrahedral tetrasporangia, 60μ diam., sessile, to 50 or more on basal cells of 2-celled whorl-branchlets (Karsakoff pl.3, Figs. 5-7, Boergesen, Fig. 9a),

(3) spherical spermatangial heads in positions similar to tetrasporangia (Boergesen Figs. 9d, 10b,c),

(4) procarps formed at apices of indeterminate branches (Boergesen Fig. 10a); subapical cell of fertile axis with 3 pericentral cells (Boergesen Fig. 9b,c); carposporophyte (Boergesen Fig. 8a) with terminal carposporangia surrounded by an involucrum of sterile filaments.

The main distinguishing feature of *Vickersia* is the large number (to 50 or more) of sessile sporangia on the basal cell of a 2-celled whorl-branchlet. In all other genera of the tribe, only one or two (rarely to four in *Mazoyera lyallii*) sporangia are borne terminally or laterally on cells of the whorl-branchlets.

Unfortunately, no details are available of postfertilization events (Boergesen only saw one cystocarp) and so the number of auxiliary cells per procarp and the origin of the involucral branchlets around the gonimoblast are unknown. Thus the placing of this genus in the Sphondylothamnieae is open to question.

(8) DIPLOTHAMNION Joly and Yamaguishi

DIPLOTHAMNION TETRASTICHUM Joly and Yamaguishi in ~~ex~~

Joly 1965: 209, pl. 43, figs. 549-551.

TYPE LOCALITY - Sao Paulo, Brazil.

TYPE - Herb. University of Sao Paulo ? Not seen.

DISTRIBUTION - Recorded only from the type locality. The species grows epiphytically on other algae and on hydrozooids.

Unfortunately no material was available for study, but the species has been well described and illustrated by Joly 1965. The main features are:

(1) thallus with prostrate axes attached by unicellular digitate haptera, and erect axes to 1 cm high; whorl-branchlets 2 per axial cell, pseudodichotomously branched once (rarely twice), oppositely and decussately arranged (Joly 1965, Fig. 549). Terminal cells are 60-105μ diam., about 4 times longer than wide and acute at the distal ends; indeterminate branches formed in positions of whorl-branchlets,

(2) tetrahedral tetrasporangia, 60-75μ diam., borne in upper parts of the thallus, directly on axial cells (between the two whorl-branchlets) of indeterminate branches or on the distal ends of basal cells of whorl-branchlets (Joly 1965, Fig. 549),

(3) spherical spermatangial heads, about 60µ diam., sessile in positions similar to the tetrasporangia (Joly 1965, Fig. 551),

(4) procarps formed at apices of indeterminate branches (Joly 1965, Fig. 550) on the subapical cell; carposporophyte with large fusion cell surrounded by small-celled involucral filaments.

Unfortunately, Joly gives no description of exact post-fertilization stages and so the origin of the involucral filaments is unknown. However, Diplothamnion appears to agree with the other genera of the Sphondylothamnieae in main features.

Distinguishing features of the genus are:

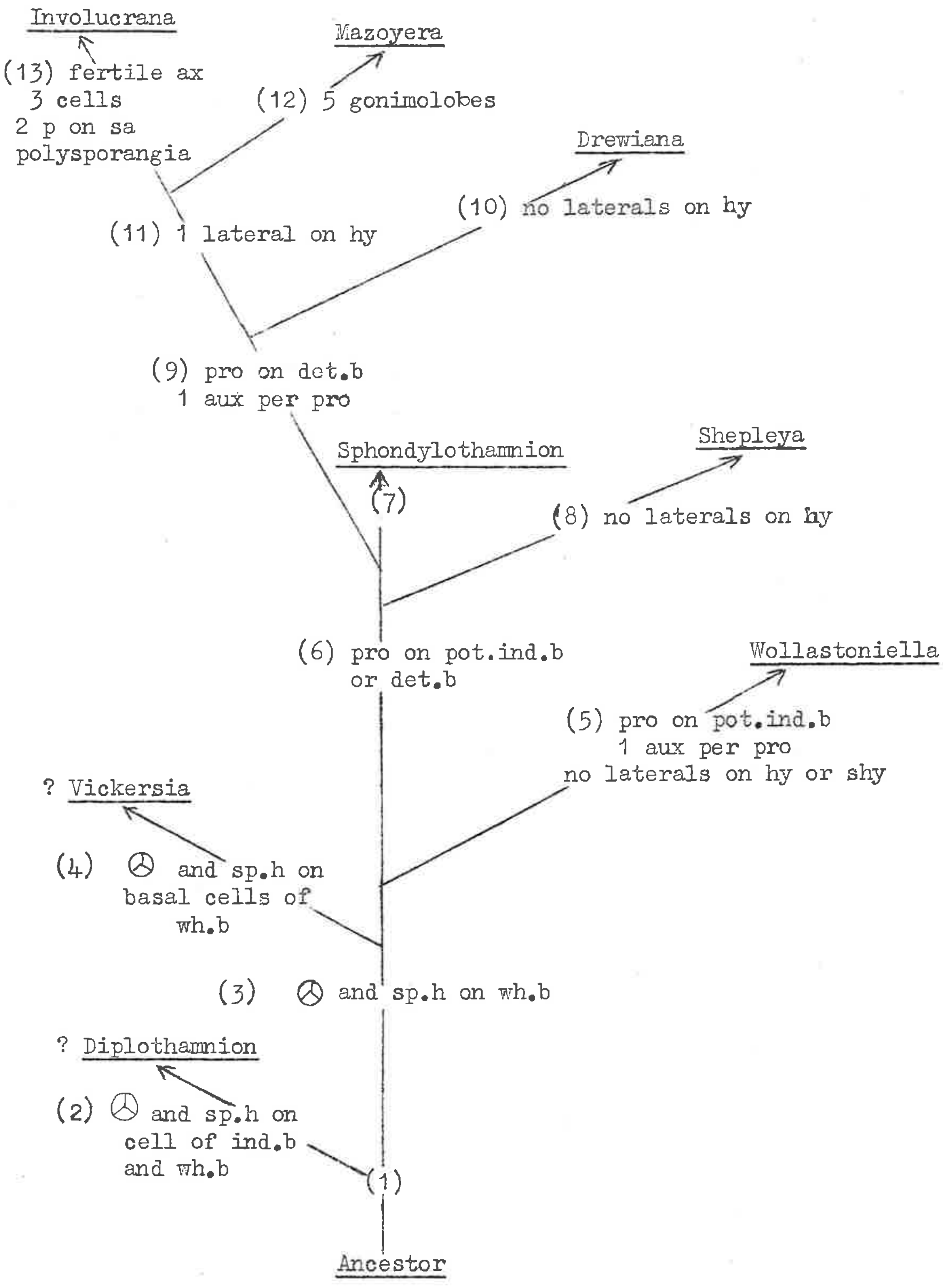
(1) the opposite decussate whorl-branchlets - in other genera of this group in which two whorl-branchlets per axial cell are formed, they are distichously arranged,

(2) the tetrasporangia and spermatangial heads which are sessile on axial cells of indeterminate branches - this feature is unique in the Sphondylothamnieae.

DISCUSSION on SPHONDYLOTHAMNIEAE

Diagram 4 illustrates the possible phylogenetic relationships between the genera of the Sphondylothamnieae, based mainly on the female reproductive structures. The ancestor of the group probably formed procarps on potentially indeterminate branches, with 3 pericentral cells on the subapical cell, two auxiliary cells per procarp, about 4 lateral branchlets on the hypogenous cell and up to 5 gonimoblast initials produced from the auxiliary cells. Wollastoniella probably arose fairly early as an offshoot (5) by loss of the second auxiliary cell per procarp, and loss of lateral branchlets from both the hypogenous and subhypogenous cells. The lines leading to Sphondylothamnion (7) and Shepleya (8) developed by production of procarps on both potentially indeterminate branches and determinate branches (whorl-branchlets). The number of gonimoblast initials produced from the auxiliary cell was reduced to one, although sometimes two additional nonfunctional cells may be produced in Shepleya. The laterals on the hypogenous cell have been lost in Shepleya and this cell now becomes incorporated into the fusion cell. A further line (9) probably developed by restriction of the procarps to whorl-branchlets and reduction of the number of auxiliary cells per procarp to one. In the Drewiana line (10), all the lateral branchlets on the hypogenous cell have been lost, whereas one has been retained in the Mazoyera (12) and

DIAGRAM 4.- Possible mode of evolution of genera of the Sphondylothamnieae.



Involucrana (13) lines. *Mazoyera* has become further distinct by development of separate multinucleate gonimolobes in the carposporophyte. In *Involucrana*, the fertile axis has become reduced to 3 cells in length and the number of pericentral cells on the subapical cell reduced to two. *Involucrana* is further distinguished by the production of polysporangia.

Vickersia and *Diplothamnion* are placed only provisionally in the group until the details of their reproduction become better known. Both genera may be closely related, *Diplothamnion* showing the primitive characteristic of bearing tetrasporangia and spermatangial heads on cells of both the indeterminate axes and the whorl-branchlets. In *Vickersia*, they are restricted to the basal cells of the whorl-branchlets but are produced in much larger numbers per cell. However, *Diplothamnion* shows a reduction in number of whorl-branchlets per axial cell (2 compared with 2-4 in *Vickersia*) and these have become stabilised in a decussate arrangement.

Many of the genera possess at the same time characteristics which are both primitive and advanced. *Wollastoniella*, for example, has procarps formed on potentially indeterminate branches, a large number of laterals (up to eight - 4 determinate and 4 potentially indeterminate) per axial cell and cortical rhizoids from the proximal ends of axial cells and laterals. These are all relatively primitive features. However, the large multinucleate cells, the highly differentiated whorl-branchlets, the complex system of villose branchlets, the high degree of specialization in the arrangement of fertile axes, and the specialized involucral filaments around the tetrasporangia all indicate a relatively advanced state.

It is probable that reduction in various characteristics, such as the loss of the second auxiliary cell per procarp, has occurred on several different occasions in the sequence.

The high speculative nature of the above evolutionary relationships must be stressed. It is probably better to consider the lines in Diagram 4 as the types of changes which have taken place rather than the directions of gene flow. For example, *Mazoyera* and *Involucrana* are probably not very closely related, as they differ considerably in vegetative structures.

The genera of the Sphondylothamnieae are quite distinct from each other in many features and it is probable that they have been evolving independently for a considerable time.

3. TRIBE SPERMOTHAMNIEAE

The genera included in the Spermothamnieae have the following features:

(1) prostrate axes attached by digitate or saccate haptera, erect axes usually less than 3(-5) cm high; multinucleate cells (except *Lejolisia mediterranea*); lack of whorl-branchlets,

(2) spermatangia formed in compact heads,

(3) procarps on the subapical cell of the fertile axis enclosed in a common gelatinous sheath (procarp system); one or two auxiliary cells per procarp; fusion cell present or absent,

(4) sterile cells associated with procarps generally remain undivided after fertilization, or if divided, (e.g. *Interthamnion* and *Lejolisia*) no inner involucrum of free filaments formed.

TYPE GENUS - *Spermothamnion* Areschoug 1847: 334.

The key to the southern Australian genera of the Spermothamnieae (p. 198) is based solely on the female reproductive structures which are used in the phylogenetic separation of the genera. However as each genus is only represented by one or two species in southern Australia, the separate keys are united into one based mainly on the vegetative and tetrasporangial features (p. 200). This second key will probably be more useful for laboratory identifications.

KEY to SOUTHERN AUSTRALIAN GENERA of SPERMOTHAMNIEAE

1. Carposporophyte with a pericarp of one layer of cells developing from the sterile cells associated with the procarp and with a common gelatinous sheath... Lejolisia

1. Carposporophyte without such a pericarp, with or without an involucrum of free filaments, not from the sterile cells associated with the procarp 2

    2. Carposporophyte without an involucrum 3

    2. Carposporophyte with an involucrum of two to four free filaments arising from the hypogenous or subhypogenous cells 4

3. Subapical cell of female axis with three pericentral cells, carposporophyte developing from two auxiliary cells; fusion cell T-shaped, involving the hypogenous cell; each carposporangium enclosed within an individual gelatinous sheath .. .. Tiffaniella

3. Subapical cell of female axis with two pericentral cells, carposporophyte developing from one auxiliary cell; fusion cell absent; carposporangia in two to four groups, each group enclosed within a separate gelatinous sheath .. .. Lomathamnion

4. Carposporophyte developing from one auxiliary cell; hypogenous cell much longer than subapical cell, producing before or after fertilization two opposite involucral filaments ... Ptilothamnion

4. Carposporophyte developing from two auxiliary cells; hypogenous cell only slightly longer than subapical cell, with or without involucral filaments 5

5. Hypogenous cell without lateral branchlets and becoming incorporated into the fusion cell; sterile cells associated with the procarp remaining undivided; involucral filaments from subhypogenous cell ... ... Spermothamnion

5. Hypogenous cell producing four branched involucral filaments, fusion cell absent; sterile cells associated with the procarp dividing after fertilization to produce three groups, each of three to five cells and enclosed within a common gelatinous sheath ... ... Interthamnion

KEY to SOUTHERN AUSTRALIAN SPECIES of SPERMOTHAMNIEAE

1. Prostrate axes creeping just below the summit of the utricles of *Codium galeatum* J.Ag, or on *Cymodocea* 2

1. Prostrate axes not in such a position, or if on *Codium* then penetrating to the base of the utricles ... 3

   2. Erect axes up to 15 mm long, subdichotomously to irregularly branched; median cells of erect axes 50-90µ diam.; up to two erect axes borne on each cell of the prostrate axes; tetrasporangia borne on cymose branchlets ... ... *Tiffaniella cymodoceae*

   2. Erect axes up to 4 mm long, simple to sparingly branched; median cells 30-40µ diam.; up to four erect axes borne on each cell of the prostrate axes; tetrasporangia borne singly on unicellular stalks .. .. *Lomathamnion epicodii*

3. Each cell of the prostrate axes producing two distichous prostrate laterals in vegetative parts, but where thallus is reproductive producing only one erect lateral per axial cell; epiphytic on *Xiphophora* ... *Spermothamnion pinnatum*

3. Each cell of the prostrate axis producing up to two erect axes 4

   4. Tetrasporangia (rarely octosporangia) terminal on stalk cells in cymose branchlets lateral on erect axes 5

   4. Tetrasporangia terminal on one to several-celled, simple stalks lateral on erect axes or sessile and lateral on erect axes 6

5\. Erect axes up to 2 mm long, median cells 20-40µ diam.; epiphytic on *Zonaria* sp. ... *Interthamnion attenuata*

5\. Erect axes up to 3 cm long, median cells 75-85µ diam.; growing on sand covered rock... *Spermothamnion cymosum*

6\. Carposporophyte surrounded by an urceolate pericarp one cell thick and embedded in a common gelatinous sheath; branching of erect axes unilateral to irregularly alternate or opposite, terminal filaments obtuse or sometimes hair-like ... ... *Lejolisia aegagropila*

6\. Carposporophyte surrounded by two free, branched involucral filaments; erect axes simple to sparingly branched, not tapering markedly 7

7\. Carposporangia produced in successive distinct gonimolobes, most cells of each gonimolobe forming carposporangia which mature simultaneously; tetrasporangia mostly terminal on one to several-celled stalks; median cells of erect axes 15-20µ diam; epiphytic on *Zonaria* spp. ... ... *Ptilothamnion schmitzii*

7\. Carposporangia not produced in obviously distinct gonimolobes, and maturing centripetally; tetrasporangia sessile; median cells of erect axes 30-60µ diam.; epiphytic on *Lenormandia* sp. ... ... *Ptilothamnion subsimplex*

(1) SPERMOTHAMNION Areschoug 1847: 334

The genus Spermothamnion was created by Areschoug for Ceramium turneri Mertens (1806, p.127, Pl.5 - not seen). He listed three forms (p.335):

α turneri, with branches generally opposite,

β roseolum (based on Callithamnion roseolum C.Agardh 1824, p.182) with branches generally alternate, and

γ repens (based on Conferva repens Dillwyn 1802, Pl.18) with branches alternate to secund. However Rosenvinge (1923-4, p.298) has pointed out that Dillwyn's specific name was published earlier than that of Mertens and so has precendence. Thus Spermothamnion repens (Dillwyn) Rosenvinge is the correct name for the type species of this genus. This species has been fully described and illustrated by the following authors: (1) Rosenvinge (1923-4, p.298, figs. 202-212) who also gives a comprehensive synonomy, (2) Kylin (1923, p.53, fig. 36; 1930, p.60, fig. 46 - as Spermothamnion roseolum (C.Agardh) Pringsheim), and (3) Drew (1934, p.549, figs. 1,2, pl. 12,13 - as Spermothamnion turneri (Mertens) Areschoug).

Spermothamnion repens has been reported from southern Australia by Harvey (1860, p.334) as Callithamnion turneri var repens. The present study indicates, however, that the species described by Harvey is different (see p.208) from the type species and must be referred to a new species, Spermothamnion pinnatum sp. nov. Spermothamnion repens is probably confined to the northern Atlantic and Mediterranean coasts. Spermothamnion cymosum (Harvey) De Toni has also been described from southern Australia, but as sexual plants are not known, its systematic position remains doubtful.

The genus Herpothamnion of Naegeli (1861, p.345) contained species from several genera, including Spermothamnion. However his type subgenus Euerpothamnion was based on Spermothamnion turneri and so the generic name Herpothamnion is a direct synonym of Spermothamnion.

The main features of Spermothamnion as understood in the present work are: (1) prostrate and erect axes, with prostrate axes attached by digitate haptera,

(2) tetrasporangia tetrahedral, terminal on short stalks mostly in small cymose branchlets lateral on the erect axes,

(3) spermatangial heads elongate, sessile or stalked on upper parts of erect axes,

(4) procarps subapical on erect axes, subapical cell with three pericentral cells, two auxiliary cells per procarp, fusion cell involving hypogenous cell,

(5) subhypogenous cell with usually four involucral branchlets.

SPERMOTHAMNION PINNATUM sp. nov.

Callithamnion turneri var. repens sensu Harvey 1860: 334; Alg. Aust. Exs. no. 521.

Spermothamnion turneri sensu Guiler 1952: 95. Lucas 1909: 48; 1929a: 28. Okamura 1932: 125.

non Spermothamnion turneri (Mertens) Areschoug 1847: 334.

TYPE LOCALITY - Southport, Tas. (Wollaston and Mitchell, 27.ii.1964), epiphytic on Xiphophora.

TYPE - ADU, A27,713.

DISTRIBUTION - From Antechamber Bay, Kangaroo Is., S. Aust. to Portland, Vic. (only two collections), and from the south-eastern coast of Tas. Epiphytic on Xiphophora chondrophylla (R. Brown ex Turner) Mont. ex Harv.

The specimens used for detailed investigation were from Southport, Tas. (ADU, A27,713), Ninepin Pt., Tas. (ADU, A21,366, Womersley, 5.iii.1958), and Antechamber Bay, Kangaroo Is., S. Aust. (ADU, A20,082, Womersley, 8.ii.1956).

DIAGNOSIS

Thallus pusillus, in Xiphophora chondrophylla epiphyticus, axibus prostratis et erectis. Axes prostrati ramos distichos oppositos prostratos, vel axes erectos ad 1.5 mm alt. efferentes. Ramificatio axium erectorum adaxialis ad subdichotoma. Cellula axium prostratorum 35-50µ diam., $2\frac{1}{2}$-4 longiores quam latiores; cellulae medianae axium erectorum 30-45µ diam., $3\frac{1}{2}$-$5\frac{1}{2}$ longiores quam latiores.

Tetrasporangia tetrahaedralia, terminalia in pedicellis brevibus lateralibus efferentia.

Capitula spermatangiorum, procarpia et carposporophyta eadem atque geno.

The species is named after the pinnate branching of the prostrate axes.

VEGETATIVE STRUCTURE (Fig. 38A-C)

The thallus is small, to 1.5 mm high, with the main prostrate axes irregularly branched and attached to the host by digitate haptera (Fig. 38A,C). Opposite prostrate laterals may be produced distichously from each axial cell (Fig. 38A), later curving slightly upwards at their tips. Rarely one or both branches may be erect from the start. When only one lateral is produced from each prostrate axial cell (Fig. 38B,C), it is always erect, reaching 1.5 mm high and usually associated with the production of reproductive organs. The prostrate laterals are pinnately to adaxially branched, the erect laterals mostly adaxially to subdichotomously branched and when mature tapering slightly.

Cell size varies considerably. When the prostrate axis produces only pairs of prostrate laterals, the cells of the axes are about 35µ diam. and $2\frac{1}{2}$-3 times longer than wide; the median cells of the prostrate laterals are about 20µ diam. and 2-$2\frac{1}{2}$ times longer than wide (Fig. 38A). When the laterals are erect, the cells of the prostrate axes are 35-50µ diam. and $2\frac{1}{2}$-4 times longer than wide; the median cells of the erect laterals are 25-55µ diam. and $3\frac{1}{2}$-$5\frac{1}{2}$ times longer than wide (Fig. 38C).

REPRODUCTION

Tetrasporangia (Fig. 38B,D)

The tetrasporangia are tetrahedrally divided, about 75µ diam., and are borne terminally on short unicellular (rarely 2-celled) stalks which occur laterally on the erect axes. On smaller-celled branches they are borne near the base (Fig. 38B), while on larger celled branches they occur in the middle parts of the axes (Fig. 38D).

Spermatangial heads (Fig. 38E,F)

The spermatangial heads are elongate, about 40µ diam., 2½-3½ times longer than wide, and sessile on the adaxial sides of erect axes in upper parts (Fig. 38E). The 4-5 fertile axial cells each produce (1-)2-3(-4) pericentral cells which in turn produce 2-3 spermatangia and further lateral chains of spermatangial mother cells (Fig. 38F).

Procarp and Carposporophyte (Fig. 39A-D)

The procarp structure (Fig. 39A) is essentially the same as that described and illustrated for Spermothamnion roseolum by Kylin (1923, p. 53, Fig. 36; 1930, p. 60, Fig. 46). This species is ~~synonymous~~ identical with the type species, S. repens (Dillwyn) Rosenvinge.

The last three cells are relatively small and densely protoplasmic. The subapical cell bears three pericentral cells – the supporting cell with a terminal sterile cell and lateral curved carpogonial branch, the fertile pericentral cell, and the sterile pericentral cell. In a few cases, the apical cell divides several times, probably in the absence of fertilization (Fig. 39B).

After fertilization, each of the two auxiliary cells cuts off 3-4 gonimoblast cells which divide further once or twice (Fig. 39C), the terminal cells becoming carposporangia. Extensive fusion occurs between the lower gonimoblast cells, the supporting and fertile pericentral cells, the subapical cell and the hypogenous cell (Fig. 39D). Four branched involucral filaments are produced from the subhypogenous cell. These filaments may produce further procarps at their apices as on the outer involucral filaments of *Mazoyera protensa*.

DISCUSSION

A large fusion cell has not been reported in the type species, *S. repens*. Kylin (1923, Fig. 36, i) showed the subapical cell, lower gonimoblast cells and the hypogenous cell to be completely distinct in *S. roseolum* (syn. *S. repens*). However, in a species of *Spermothamnion* from Trevone, Cornwall, U.K. (ADU, A28,323, Womersley, 13.viii.1964) which appears similar in vegetative structure to *S. repens* (it was not possible to confirm this identification from herbarium material in ADU), a quite definite fusion cell similar to that in *S. pinnatum* occurs. Illustrations of Janczewski (1876-7, Pl. 3, Fig. 14) of *Spermothamnion hermaphroditum* (syn. *S. repens*) also show fusion between the lower gonimoblast cells and the subapical and hypogenous cells.

In *S. pinnatum*, the carposporangia are embedded together in a common mucilaginous sheath, rather than a separate one for each carposporangium as in S. roseolum (Kylin 1923, Fig. 36, i,k). This could possibly be due to immaturity of the few carposporophytes present in the available material of S. pinnatum.

Although type material of S. repens has not been examined, data from the literature indicates that this species differs considerably from S. pinnatum (Table 6).

TABLE 6.- Vegetative differences between S. repens and S. pinnatum

Feature	S. repens	S. pinnatum
Length of erect axes	1-4 cm	1.5 mm
Branching of prostrate axes	irregular	opposite and distichous
Branching of erect axes	opposite alternate or secund	adaxial to subdichotomous

SPERMOTHAMNION CYMOSUM (Harvey) De Toni 1903: 1226. Lucas 1909: 48. Okamura 1932: 125.

Callithmanion cymosum Harvey 1854: 560; Alg. Aust. Exs. no. 524; 1863: synop. no. 707. J.Agardh 1876: 10.

TYPE LOCALITY - Middleton Bay, King George's Sound, W. Aust., on sand covered rocks (Harvey).

TYPE - Herb. Harvey, TCD (Alg. Aust. Exs. no. 524B). Not seen.

DISTRIBUTION - King George's Sound and Rottnest Is., W. Aust. (Harvey).

Sterile material from Vivonne Bay, Kangaroo Is., S. Aust. has been tentatively identified as this species, but confirmation must await discovery of fertile material.

The material studied in detail was an isotype specimen (ADU, A18,288). No sexual material has been seen and so its generic position must remain doubtful.

VEGETATIVE STRUCTURE (Pl. 12)

The thallus is densely tufted and composed of interwoven, branched prostrate axes giving rise to erect axes reaching 3 cm long. The prostrate axes bind together sand particles and are attached to the substrate by digitate haptera. The erect axes are sparingly and irregularly to subdichotomously branched.

Cells of the prostrate axis are 50-100µ diam. and 5-10 times longer than wide. Median cells of erect axes are 75-85µ diam. and 6-7 times longer than wide. Cells near the apices are 65-80µ diam.

REPRODUCTION

Sporangia (Fig. 39E)

The sporangia are divided into 4 or 8 spores and are terminal on short stalks borne laterally on the cells of the upper parts of erect axes. By successive production of further stalk cells laterally from the older ones, uni- or bilateral "cymes" are produced (Fig. 39E). Mature sporangia were not seen; the oldest present in the material were about 65μ diam.

DISCUSSION on SPERMOTHAMNION

While some 28 species are now recognised in the genus *Spermothamnion*, only two species definitely agree with the type species. These are:

(1) *Spermothamnion flabellatum* Bornet in Bornet and Thuret (1876, p. 24, pl. 8, Fig. 1-3, pl. 9), also illustrated by Hauck (1885, p. 45, Fig. 11a-c) and Feldmann-Mazoyer (1940, p.360, Figs. 137-8).

(2) *Spermothamnion johannis* Feldmann-Mazoyer (1940, p.362, Figs. 70, 139).

In both species, the cystocarps appear to agree with those of the type species. Of the remaining species, five are transferred to other genera in this study, and four more possibly belong to different genera but cannot be placed definitely until further investigated. In the remaining 17 species, sexual and in some cases tetrasporangial structures have not been described, and consequently their systematic position must remain doubtful for the present.

(2) TIFFANIELLA Doty and Menez 1960: 135, Figs. 1-14.

The genus Tiffaniella was described by Doty and Menez to include four species, Spermothamnion saccorhiza (Setchell and Gardner) Feldmann-Mazoyer, Spermothamnion codicola Yamada and Tanaka, Spermothamnion gorgoneum (Montagne) Vickers, and Spermothamnion capitatum Bornet, all epiphytic on species of Codium. The characteristics they used to separate these species from other species of Spermothamnion were:

(1) the inflated rhizoids or haptera,

(2) the absence of an involucrum around the gonimoblast, and

(3) the formation of polysporangia.

Doty and Menez (p.140) described the unfertilized procarp system and the superficial appearance of the carposporophyte of the type species, T. saccorhiza, but without detailed figures. They expressed doubt as to whether there were one or two auxiliary cells per procarp.

Material of this species from Waikiki, Hawaii, on Codium reediae Silva (ADU, A26,004, Womersley, 26.i.1962) has now been further investigated (Fig. 40A-C). Two auxiliary cells are produced per procarp and the fusion cell involves the hypogenous cell (Fig. 40C) as in Spermothamnion pinnatum sp. nov., but the carposporophyte is completely devoid of an involucrum.

The spermatangial development of Tiffaniella saccorhiza does not differ from that of Spermothamnion repens as described by Feldmann Mazoyer (1940, p.172, Fig. 63).

The genus Tiffaniella as now emended differs from Spermothamnion mainly by the absence of the involucral filaments produced from the subhypogenous cell of the female axis. The main features of Tiffaniella are:

(1) prostrate and erect axes, with the prostrate axes attached by digitate or saccate haptera and the erect axes reaching 2(-5) cm high,

(2) sporangia tetrahedral or polyhedral (8-64 spores), terminal on short stalks, mostly in small cymes lateral on the upper parts of erect axes,

(3) spermatangial heads elongate, sessile or stalked on upper parts of erect axes,

(4) procarps subapical on erect axes, subapical cell with three pericentral cells, two auxiliary cells per procarp, fusion cell involving hypogenous cell,

(5) subhypogenous cell without laterals.

TIFFANIELLA CYMODOCEAE (Boergesen) comb. nov.

Spermothamnion cymodoceae Boergesen 1952: 54, Figs. 27, 28.

TYPE LOCALITY - Riambel, Mauritius (Vaughan, no. 996, epiphytic on Cymodocea).

TYPE - Probably C. Not seen.

DISTRIBUTION - Mauritius, and Hopetoun, W. Aust. to Stanley Beach, Kangaroo Is., S. Aust. The species is epiphytic on Cymodocea and Codium spp.

Material studied in detail was isotype material (ADU, A17,892) and material from Seal Bay, Kangaroo Is. (ADU, A32,149 on Codium galeatum, Gordon, 31.x.1966).

VEGETATIVE STRUCTURE (Fig. 40D)

The erect axes of the specimens from Mauritius are much longer (to 15 mm) than the southern Australian specimens (to 7 mm). The prostrate axes creep just below the apices of the Codium utricles or on the stems of Cymodocea, and are attached by digitate haptera (Fig. 40D). One erect axis (rarely two) is borne on each prostrate axial cell; these are subdichotomously branched, with the laterals mostly adaxial and tapering slightly when mature.

Cells of the prostrate axes are 40-90μ diam. and 2-3½ times longer than wide. Median cells of the erect axes are 30-90μ diam. and 3-7½ times longer than wide. Median cells of the erect axes of the Mauritius plant are narrower (25-40μ diam.) than the

Australian plant (40-90µ diam.) but these differences are not considered important enough to separate two species.

REPRODUCTION

Tetrasporangia (Fig. 40E, Boergesen, Fig. 27b)

The tetrasporangia are about 50µ diam. and are produced terminally on short unicellular stalks, mostly in the upper parts of the erect axes. Stalk cells are borne abaxially, or on both sides of the erect axes, and further stalk cells are produced abaxially or on both sides of the first ones, these again producing terminal sporangia. This form of branching may be repeated up to four times, giving cymose branchlets. The sporangia are pushed to one side and thus appear sessile. Up to three cymose branchlets may occur on each main axial cell.

In the southern Australian material, wall formation had not occurred in the sporangia, although in some 4 nuclei were present, suggesting that meiosis had occurred.

Spermatangial heads (Figs. 40F, 41A, Boergesen, Fig. 28a)

The spermatangial heads are elongate, 30-50µ diam. and 2-3 times longer than wide. They are borne terminally on short stalks, or rarely sessile on the upper parts of the erect axes. Two or rarely three heads may occur on the one stalk (Fig. 40F). The 5-6 fertile axial cells each produce 3-4 pericentral cells, each of which cuts off up to 3 terminal spermatangia and lateral rows of further spermatangial mother cells (Fig. 41A).

Procarp and Carposporophyte (Fig. 41B-F, Boergesen, Figs. 27c,28b)

The fertile axis is usually a lateral branch 4-5(-13) cells long. The last four cells are comparatively short (Fig. 41B), while the fifth (if present) is 4-5 times longer than the hypogenous cell. The subapical cell bears three pericentral cells; the adaxial one is sterile (Fig. 41C) and one of the lateral pericentrals is fertile. The other lateral pericentral is the supporting cell which bears a terminal sterile cell and lateral carpogonial branch. Neither the hypogenous nor the subhypogenous cells bear laterals before or after fertilization. The apical cell may rarely divide once before fertilization.

The post-fertilization fusion of the cells of the carpogonial branch (Fig. 41D), formation of connecting cells, auxiliary cells and gonimoblast (Fig. 41E) occur as in Spermothamnion pinnatum. Development of carposporangia (Fig. 41E) and fusion cell also occur as in S. pinnatum, although each carposporangium is surrounded by a separate wall. The apical cell and sterile pericentral cell normally remain undivided and intact (Fig. 41E).

Both spermatangial heads and carposporophyte may occur on the one branch. Rarely a female axis, usually with an undeveloped procarp, occurs on a tetrasporangial branch.

DISCUSSION on TIFFANIELLA

The four species of Tiffaniella as recognised by Doty and Menez were first grouped together by Feldmann-Mazoyer (1942, p. 15) in the genus Spermothamnion based mainly on the presence of polysporangia. She separated the species on the number of spores occurring in each polysporangium, and the number of cells and degree of swelling of the haptera. However it is now clear that the number of spores formed per sporangium is not constant in each species, and it probably depends on the stage of sporangial development at which the count or drawing is made as to how many spores per sporangium are reported. Material of T. saccorhiza (ADU, A26,004) from Hawaii shows about 16 spores per sporangium, whereas Doty and Menez reported 32 in their material from the same locality. For T. gorgonium, Boergesen (1930, p.14, Fig. 4) shows about 16 spores per sporangium, whereas Taylor (1942, Pl. 4, Figs. 1-4) shows about 64, and material in ADU (A9660, Haiti, Bartlett, 10.v.1941) has about 32. Similarly for T. capitatum, both Bornet (1892, p.323) and Feldmann-Mazoyer (1940, p.360) report about 64 spores per sporangium, while Boergesen (1930, Fig. 3d) shows about 32. Doty and Menez assume that Boergesen's illustration is of an immature sporangium. This would lead one to suspect that the accepted differences between these four species are subspecific in nature.

Further differences are reported for the rhizoids. Those in T. saccorhiza and T. codicola are unicellular and swollen with rounded tips, those of T. capitatum unicellular with pointed tips, and those of T. gorgonium multicellular. However, material of T. saccorhiza in ADU shows that the shape of the haptera on any one filament can vary from rounded to pointed ends. T. gorgonium (ADU, A9660) shows haptera of both one and two cells. It may be possible that the shape and extent of division of these haptera depends on the species of Codium on which the epiphyte is growing, as the length and closeness of the utricles may be the determining factors in the growth of the haptera. Other vegetative differences appear to be insignificant. However, until more authentic material of these species can be examined, they are best left separate.

Tiffaniella cymodoceae differs essentially in three ways from the type species (Table 7).

TABLE 7.- Differences between species of Tiffaniella

Feature	T. saccorhiza	T. cymodoceae
Number of cells remaining small at apex of female axis	3	4
Sporangia	polysporangia	tetrasporangia
Haptera	saccate	digitate

However, the structure of the procarp and carposporophyte in the two species is identical. Although the differences shown in the table could be regarded as of generic significance (see Sphondylothamnieae tribe), the existence of other species (transferred to *Tiffaniella* below), such as *Spermothamnion snyderae* Farlow, (see Drew 1937, p.463) and *Spermothamnion phycophilum* Taylor (1945, p.263) in which characteristics from both of the above groups of species are found, tends to obscure these distinctions.

Material of *Spermothamnion snyderae* Farlow from California (ADU, A26,067, Goleta Pt., Womersley, 31.x.1962, tetrasporangial and male, and AHFH, 62,883, West Malibu, Dawson, 17.xi.1956, female) has been examined and agrees with the descriptions of the reproductive structures given by Drew. *S. snyderae* is similar to *T. saccorhiza* in having a relatively elongate subhypogenous cell (Drew 1937, Fig. 11) and polysporangia with (8-)12-16(-32) spores (Drew, Fig. 1), but the haptera are digitate. Other features, such as the development of the gonimoblast and spermatangial heads are the same in the two species.

Material of *Spermothamnion phycophilum* Taylor has also been examined (AHFH, no.219, Santa Maria Is., Galapagos Is., Taylor no.397, 30.i.1934). The structure of the procarp, development of the carposporophyte and spermatangial heads are the same as those of *T. saccorhiza*, but the cell below the sub-hypogenous cell produces two post-fertilization laterals, the sporangia are tetrahedral and the haptera are digitate.

Culture studies with *Lejolisia aegagropila* (p. 260) have shown that in free floating culture saccate haptera are produced, but under normal conditions the haptera are digitate. This work suggests also that shape of haptera is probably not a feature of generic importance and thus *S. snyderae* and *S. phycophilum* should be included in *Tiffaniella.*

Spermothamnion tamamiru Segawa (1949, p.145, Fig. 2) on *Codium mamillare* should also probably be included in *Tiffaniella.* The procarp and carposporophyte development appear typical, although Segawa gives no description of the vegetative or sporangial structures of this species.

Spermothamnion nonatoi Joly (1957, p.140, pl.16, Figs. 2-2c) from Brazil may also be a species of *Tiffaniella.* It has polysporangia borne on small-celled lateral branches on the erect axes and digitate haptera. However, sexual structures have not been described and the systematic position of this species must remain in doubt for the present.

The following species are now included in the emended genus *Tiffaniella* (Table 8).

TABLE 8.- Species of *Tiffaniella*

	Distribution
T. saccorhiza (Setchell & Gardner) Doty & Menez	Pacific and Atlantic Mexico, Hawaii, Mauritius
T. codicola (Yamada & Tanaka) Doty & Menez	Taiwan, Caribbean ~~Is~~.
T. gorgonium (Montagne) Doty & Menez	Caribbean ~~Is~~., Canary Is., Cape Verde
T. capitatum (Bornet) Doty & Menez	Mediterranean, Canary Is., Atlantic Europe
T. cymodoceae (Boergesen) comb. nov.	Mauritius, southern Australia
**T. tamamiru* (Segawa) comb. nov.	Susaki, Japan
**T. snyderae* (Farlow) comb.nov.	Pacific Mexico
**T. phycophilum* (Taylor) comb. nov.	Ecuador

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*Basionyms: *Spermothamnion tamamiru* Segawa 1949, p.145, Fig. 2.

Spermothamnion snyderae Farlow 1899, p.74 (not seen)

Spermothamnion phycophilum Taylor 1945, p.263, pl. 3, Figs. 17-21, pl. 4, Figs. 1, 2.

(3) LOMATHAMNION gen. nov.

Thallus pusillus, epiphyticus, axibus prostratis et erectis; axes prostrati per haptera digitata affixa.

Tetrasporangia tetrahaedralia vel cruciata ut videntur, terminalia in pedicellis brevibus unicellularibus lateralibus in axibus erectis efferentia.

Capitula spermatangiorum ovoidea in positionibus similaribus sporangiis.

Procarpia subterminalia in ramis brevibus lateralibus, cellulae ultimae tres parvae, cellula subapicalis cellulam unam sterilem et cellulam supportantem cum ramo carpogoniali laterali et cellula sterili terminali ferens; cellula hypogena ramos laterales numquam ferens. Cellula auxiliaris una a procarpio quoque; carposporangia pauca, in 2-4 gonimolobiis; cellula-fusionis magna absens.

Thallus small, epiphytic, with prostrate and erect axes attached to the substrate by digitate haptera.

Tetrasporangia tetrahedral or appearing cruciate, terminal on short unicellular stalks which are lateral on the erect axes.

Spermatangial heads ovoid, in positions similar to the tetrasporangia.

Procarps subterminal on short lateral branches, the last three cells comparatively small, the subapical cell bearing 2 pericentral cells of which one is sterile, and the other the supporting cell with lateral carpogonial branch and terminal sterile cell; the hypogenous cell bears no laterals. Auxiliary cell one per procarp; carposporangia few, in 2-4 gonimolobes, each gonimolobe with a common gelatinous sheath; large fusion cell absent.

The genus is so named because the thallus of the type species grows as a little fringe around the apical part of the *Codium* utricles.

TYPE SPECIES - *Lomathamnion epicodii* sp. nov.

Lomathamnion is distinct from all the other genera of the Spermothamnieae in having only two pericentral cells on the subapical cell of the fertile axis. All other genera have three. It is similar to *Tiffaniella* in lacking an involucrum around the cystocarp but differs from this genus in having only one auxiliary cell per procarp and lacking a large fusion cell in the cystocarp.

The genus is monotypic.

LOMATHAMNION EPICODII sp. nov.

TYPE LOCALITY - Seal Bay, Kangaroo Is., S. Aust., epiphytic on Codium galeatum J.Ag. (Gordon, 31.x.1966).

TYPE - ADU, A30,961.

DISTRIBUTION - Hopetoun, W. Aust. (one record only), moderately common from Wedge Is., S. Aust., to Phillip Is., Vic.

The type collection and material from Stanley Beach (ADU, A20,909, Womersley, 6.ii.1957) and Seal Beach, Kangaroo Is., S. Aust. (ADU, A28,897, Womersley, 21.i.1965) were used for detailed investigation.

DIAGNOSIS

Thallus in Codium galeatum J.Ag. epiphyticus, axes prostrati prope apices utriculorum hospitis repentes. Cellulae axium prostratorum 30-45µ diam., 1-3 longiores quam latiores. Axes erecti ad 4 mm alt., simplices vel parce ramosi, 1-4 a cellula quaque axium prostratorum efferentes. Cellulae medianae 30-40µ diam., 2-6 longiores quam latiores.

Tetrasporangia circa 50µ diam., positio atque geno.

Capitula spermatangiorum circa 55µ diam., positio atque geno.

Structura procarpii et carposporophyti atque geno.

VEGETATIVE STRUCTURE (Fig. 42A,B)

The primary axes are prostrate, creeping just below the summit of the Codium utricles and attached by digitate haptera (Fig. 42A). Erect axes reaching 4 mm high arise from the cells of the prostrate axis, 1-4 branches per cell. Erect axes are simple to sparingly and irregularly branched, tapering towards the apex when mature.

Cells of the prostrate axis are 30-45µ diam., and 1-3 times longer than wide. Median cells of the erect axis are 30-40µ diam. and 2-6 times longer than wide. Terminal cells often become hair-like.

REPRODUCTION

Tetrasporangia (Fig. 42A)

The tetrasporangia reach 50µ diam. with the spores generally cruciately arranged although tetrahedrally divided. They are borne terminally on unicellular stalks which are lateral on the erect axes, and arranged singly or in opposite pairs. One further stalk cell with terminal sporangium may be produced laterally from the distal end of the primary one.

Spermatangial heads (Fig. 42B,C)

The spermatangial heads are spherical to ovoid, to 55µ diam., and are terminal on unicellular stalks which are lateral on the lower parts of the erect axes or borne directly on the prostrate axes (Fig. 42B). The 3-4 fertile axial cells each produce 3-4 pericentral cells, each of which produces terminally 2-3 spermatangial mother cells and laterally further cells which cut off outwardly spermatangial mother cells. Each spermatangial mother cell buds off about 3 spermatangia (Fig. 42C).

Procarp and Carposporophyte (Fig. 42D-F)

The fertile axes are (3-)4(-12) cells long and lateral on the lower cells of the erect axes, or occasionally directly on the prostrate axes. The last three cells are comparatively short (Fig. 42D), while the subhypogenous cell is 2-3 times longer than the hypogenous. Rarely the subhypogenous cell bears a second fertile axis of 3 cells. The subapical cell bears two pericentral cells - a sterile one, and the supporting cell with lateral carpogonial branch and terminal sterile cell.

Two cases were seen where a sterile cell and a carpogonial branch were produced from the "sterile" pericentral cell. In one of these, a gonimoblast had been produced from one of the procarps. Rarely the apical cell or the sterile pericentral cell may divide once before fertilization, or possibly if fertilization does not occur.

After fertilization, the trichogyne is lost and the supporting cell cuts off an auxiliary cell (Fig. 42E) which then divides to produce 2-4 gonimoblast cells. These each divide obliquely, giving 3-4 further cells which either become ovoid carposporangia or cut off further cells which become carposporangia. The carposporangia from each of the gonimoblast initials are enclosed in a common gelatinous sheath, giving 2-4 gonimolobes in the mature carposporophyte (Fig. 42F). Very little fusion occurs between the cells of the procarp or the lower gonimoblast cells, although the subapical and hypogenous cells may become slightly fused. The apical cell, sterile pericentral cell and sterile cell on the supporting cell normally remain undivided.

DISCUSSION

L. epicodii may be similar to Spermothamnion yonakuniensis Yamada and Tanaka (1938, p.79, Figs. 12, 13) from Yonakuni Is., Japan, but unfortunately there is no detailed description published of the structure of the procarp system in the latter species. The similarities between the two species lie in their simple sparingly branched erect axes, the position of the tetrasporangia, spermatangial heads and procarps, the carposporophyte with a relatively small number of carposporangia, the lack of an involucrum and apparent lack of a fusion cell.

Additional information is needed before an accurate assessment of the degree of similarity of the two species can be made. Particularly useful features would be the number of pericentral cells on the subapical cell and the number of auxiliary cells per procarp.

(4) PTILOTHAMNION Thuret ex Le Jolis 1863: 118.

The genus Ptilothamnion was based on Callithamnion pluma (Dillwyn) C.Agardh (1828, p.162), and has been described* and illustrated by Bornet and Thuret (1880, p.179, pl. 46), Feldmann-Mazoyer (1940, pp.184, 372, Figs. 68, 145-147), J. Feldmann (1943a, p. 59, Figs. 53, 54) and Kylin (1928a, p.77, Fig. 50). Kylin described in detail the structure of the procarp and mature carposporophyte but did not describe the early development of the gonimoblast. Material in ADU (A5201, Cherbanay? ex Museo Botanico Hamburgensi) shows that the gonimoblast is formed by segmentation of the auxiliary cell to form 2-3 gonimoblast initials, each of which divides subdichotomously once or twice, the terminal cells becoming carposporangia.

Further studies (p. 234) on Ptilothamnion schmitzii Heydrich, in which all the gonimoblast cells form carposporangia, extend the concept of this genus. Thus the main features of Ptilothamnion are:

(1) thallus with prostrate and erect axes, prostrate axes mostly attached by digitate haptera,

(2) tetrasporangia tetrahedral, sessile or stalked on the upper parts of erect axes,

(3) spermatangial heads spherical to elongate, sessile, stalked or terminal on the erect axes,

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* Dixon (1962, p. 154) has discussed the synonmy of P. pluma, and the variation in vegetative structures which can occur in this species.

(4) procarps subapical on erect axes, subapical cell with 3 pericentral cells; hypogenous cell bearing two laterals; one auxiliary cell per procarp, giving rise to 2-5 gonimoblast initials, each of which divides subdi- or trichotomously 1-3 times, the terminal cells (or all gonimoblast cells in *P. schmitzii*) becoming carposporangia.

PTILOTHAMNION SUBSIMPLEX sp. nov.

TYPE LOCALITY - Pennington Bay, Kangaroo Is., S. Aust., epiphytic on *Lenormandia* sp. (Womersley, 30.i.1946).

TYPE - ADU, A32,150.

DISTRIBUTION - Known for certain only from the type locality.

The type material was used for detailed investigation. In this material, *P. subsimplex* grows very closely associated with *Lejolisia aegagropila*, the prostrate axes of the two species interwoven.

DIAGNOSIS

Thallus epiphyticus, axibus prostratis et erectis; axes erecti ad 2 mm alt., simplices vel parce ramosi. Cellulae axium prostratorum 25-35μ diam., 2-3½ longoires quam latiores; cellulae medianae axium erectorum 30-60μ diam., 1-3½ longiores quam latiores.

Tetrasporangia tetrahaedralia, interdum cruciata ut videntur, 65µ diam., sessilia, unilateralia in partibus superis axium erectorum efferentia.

Capitula spermatangiorum, procarpia, et carposporophyta eadem atque generitypo.

The species is named after the simple to sparingly branched erect axes in contrast to the generally pinnate branching in the type species.

VEGETATIVE STRUCTURE (Fig. 43A).

The prostrate axes are attached to the host by digitate haptera, and give rise to simple or sparingly branched erect axes reaching about 2 mm high and only slightly tapering, with obtuse terminal cells (Fig. 43A). The cells of the prostrate axes are 25-35µ diam. and 2-3½ times longer than wide. Median cells of erect axes are 30-60µ diam. and 1-3½ times longer than wide.

REPRODUCTION

Tetrasporangia (Fig. 43B).

The tetrasporangia are about 65µ diam. and sometimes appear cruciate. They are ovoid and sessile, often unilaterally placed on the upper parts of erect axes.

Spermatangial heads (Fig. 43A,C)

The spermatangial heads are spherical to ovoid, about 40µ diam., and in positions similar to the tetrasporangia but more often alternate than unilateral (Fig. 43A).

Two fertile axial cells each produce 3 pericentral cells, and each of these produces directly 2-3 spermatangia and further lateral spermatangial mother cells (Fig. 43C). The cells of the axes bearing spermatangial heads are usually slightly shorter than those of the procarpic or tetrasporic plants.

Procarp and Carposporophyte (Fig. 43D-F)

The procarps form at the apices of the erect axes or laterals. The last two cells are comparatively short (Fig. 43D), while the hypogenous cell is comparable in size to vegetative cells and bears two lateral branchlets which are 1-2 celled before fertilization. The subapical cell bears 3 pericentral cells, 2 of which are sterile while the third is the supporting cell with a terminal sterile cell and a lateral carpogonial branch. The third and fourth cells of the carpogonial branch are about twice the size of the first and second cells.

After fertilization, the trichogyne is lost, the cells of the carpogonial branch fuse (Fig. 43E), and the auxiliary cell produced from the supporting cell cuts off up to 5 uninucleate gonimoblast initials which divide subdichotomously once or twice, the terminal cells becoming carposporangia (Fig. 43F) about 35µ diam. and maturing in a centripetal direction. The whole carposporophyte is embedded in a common gelatinous sheath, and each gonimolobe resulting from the division of one gonimolobe initial develops equally and simultaneously. Only very slight fusion occurs between the auxiliary cell and supporting cells.

The pair of involucral branchlets borne on the hypogenous cell completely encircles the mature carposporophyte, and laterals from their lower cells project above and below the plane of the primary filaments.

If a procarp is not fertilized, the involucral filaments from the hypogenous cell lengthen appreciably and produce further procarps at their apices. This process may be repeated several times with successive involucral filaments if the procarps are not fertilized.

Occasionally, spermatangial heads may be produced on short laterals of the female branches or on the involucral filaments themselves.

DISCUSSION

Ptilothamnion subsimplex differs from the type species, P. pluma, mainly in having simple to irregularly branched erect axes (in contrast to the generally regularly pinnate branching in P. pluma), and in the sessile position of the tetrasporangia and spermatangial heads (generally terminal or stalked in P. pluma, although occasionally sessile).

P. subsimplex resembles closely Spermothamnion cladophorae Yamada and Tanaka (1934, p.342) which is here transferred to Ptilothamnion. The main differences occur in the cell sizes as illustrated in Table 9.

TABLE 9.- Differences between P. subsimplex and Ptilothamnion cladophorae (Yamada & Tanaka) comb. nov.

Feature	P. subsimplex	P. cladophorae
Diam. cells of prostrate axes	30μ	23μ
Diam. cells of erect axes	40μ	18μ
Diam. tetrasporangia	65μ	45μ
Diam. spermatangial heads	40μ	30μ

Yamada and Tanaka have not shown fine details of the procarp of P. cladophorae and hence the relative sizes of the cells of the carpogonial branch could not be determined. Although these two species are very similar, they are treated as distinct until authentic material of P. cladophorae can be examined.

PTILOTHAMNION SCHMITZII Heydrich 1893: 75, pl. 22, Figs 1-6. Laing 1904a: 381; 1904b: 387; 1927: 172. Okamura 1932: 125.

TYPE LOCALITY - Pt. Noarlunga, S. Aust. (Shepherd, 27.vii.1968).

NEOTYPE - ADU, A32,154 (*see below).

DISTRIBUTION - In New Zealand there are isolated records from the Bay of Islands and along the eastern coast of the northern Island to Island Bay, Wellington, epiphytic on Zonaria turneriana J.Agardh. In Australia, the species is also epiphytic on several other species of Zonaria. It occurs from Eucla, S. Aust., to Flinders, Vic. and in Tas. (north-western and south-eastern coasts - two records only). The hosts occur in the lower littoral and upper sublittoral zones, although Zonaria crenata, also a host, is generally collected as drift.

The neotype material was used for detail investigation together with material from Daly Head, Yorke Pen., S. Aust.

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* According to Koster (1957, p. 51), Heydrich's herbarium at Berlin was destroyed. The original material was from the Bay of Islands, New Zealand, epiphytic on Zonaria sinclairii Hooker et Harvey. However, Womersley (1967, p.227) discussed the type material of Z. sinclairii, supposedly also from the Bay of Islands, and indicated doubt as to the type locality of this species which may not actually occur in New Zealand. Material of P. schmitzii in ADU (A4664), epiphytic on Zonaria turneriana J.Ag. from the Bay of Islands, is sterile and so the neotype has been selected from southern Australia.

(ADU, A31,347, Gordon, 26.iii.1967, epiphytic on Zonaria crenata).

VEGETATIVE STRUCTURE (Fig. 43G-J)

This species occurs in two morphological forms, each of which grows on a different part of the host thallus. The commoner form is that originally described by Heydrich, which creeps among the stupose fibres on the stipes of Zonaria spp. The prostrate axes are densely branched and interconnected by secondary pit connections (Fig. 43G). The erect axes are short, usually only about 500µ high (rarely to 1 mm) and scarcely protruding above the host fibres. The haptera, when present, are not regularly digitate but merely widen or fork slightly where they appress against other cells (Fig. 43H). The cells of the prostrate axes are 16-26µ diam. and 2½-4 times longer than wide. Median cells of erect axes are 18-20µ diam. and ¾-2 times longer than wide. These cells are shorter than in the following form.

The second form creeps over the fronds of Z. crenata. The sparingly branched prostrate axes are attached to the host by clearly digitate haptera (Fig. 43I), and give rise to sparingly branched erect axes, scarcely tapering and reaching 2 mm high. Prostrate axial cells are 15-40µ diam. and are 1½-4½ times longer than wide. Median cells of the erect axes are 15-20µ diam. and 2½-4½ times longer than wide. Occasional forms intermediate between these two are found.

REPRODUCTION

Tetrasporangia (Fig. 43J)

The tetrahedral tetrasporangia are about 45µ diam. and are borne on one to several celled stalks, lateral on the erect axes.

Spermatangial Heads (Figs. 43G, 44A)

The spermatangial heads are spherical to ovoid, about 35µ diam., and occur terminally on the erect axes and their laterals (Fig. 43G). The internal structure (Fig. 44A) is the same as that of *P. subsimplex*. Spermatangial heads and procarps may occur on the same branch system (Fig. 43G).

Procarp and Carposporophyte (Fig. 44B-E)

The procarps (Fig. 44B) are in similar positions and of similar structure to those of *P. subsimplex*. The main differences occur in the pair of involucral branchlets on the hypogenous cell, which are not produced until after fertilization (Fig. 44C) in *P. schmitzii* (present before fertilization in *P. subsimplex*), and in the third and fourth cells of the carpogonial branch which are approximately equal in size to the first and second cells in *P. schmitzii* (much larger in *P. subsimplex*). The post-fertilization fusion of the cells of the carpogonial branch, and production and segmentation of the auxiliary cell are similar in the two species (*P. schmitzii*, Fig. 44D). However in contrast to *P. subsimplex*, all of the division products of one gonimolobe initial mature at the same time, producing a group of equal, slightly angular carposporangia about 25µ diam. (Fig. 44E). A second gonimolobe may subsequently be produced and these carposporangia also mature simultaneously. No fusion occurs between the lower gonimoblast cells or subapical cell.

The involucral filaments from the hypogenous cell branch laterally and curve around the young gonimoblast. In the form of this species which occurs on the stipes of the host, there is occasionally only one lateral branchlet produced from the hypogenous cell. The gonimoblast is pushed to one side, and the protection given normally by the second lateral is provided by the erect axis.

DISCUSSION

The successive maturation of gonimolobes occuring in P. schmitzii is seen in some of the more primitive groups of the Ceramiaceae, and appears at first to constitute an important difference from the simultaneous maturation occurring in P. pluma. However the many resemblances between the two species indicate their close affinity, and this difference must be considered as a development analogous to rather than homologous to other groups possessing it.

Other species similar to Ptilothamnion are:

(1) Spermothamnion specuncarum (Collins and Hervey) Howe - illustrated by Boergesen 1930, p. 16, Figs. 5, 6, and by Joly

1965, p.208, pl. 42, and 43, Figs 547, 548.

(2) *Lejolisia pusilla* Dawson and Neushul 1966, p.181, pl. 41(1), Fig. 8,

(3) *Lejolisia hoshawii* Dawson 1966, p. 64, Fig. 6, J-K, and

(4) *Spermothamnion barbatum* (C.Ag.) Naegeli.

Tetrasporangia of these four species are sessile and lateral on the cells of the erect axes as in some *Ptilothamnion* spp. In both *Spermothamnion* and *Lejolisia*, the tetrasporangia are typically terminal on stalks. Miranda (1932, p.281, Fig. 4) has described and illustrated the procarp of *S. barbatum*, and although his diagram is not clear, it shows a division of the hypogenous cell which is not typical of *Spermothamnion*. However, until carposporophyte structures are understood, these species must remain in their respective genera.

Fertile material of *Ptilothamnion pectinatum* (Montagne) Laing (1904b,p.388) from New Zealand has also been examined (ADU, A5,658, on *Cladophora colensoi*, Stewart Is., 27.ii.1947, Herb. Lindauer, No. 272). The procarps are formed alternately in succession along the axial cells of the fertile axis and therefore this species does not rightly belong to *Ptilothamnion*, but is possibly related to *Gymnothamnion*.

(5) INTERTHAMNION gen. nov.

Thallus pusillus, epiphyticus, axibus prostratis et erectis; axes prostrati per haptera digitata affixa.

Tetrasporangia tetrahaedralia, terminalia in ramulis brevibus lateralibus cymosis in axibus erectis efferentibus. Tetrasporangia ultima per ramulos parvos protecta.

Capitula spermatangiorum sphaerica ad ovoidea, sessilis et adaxialia in axibus erectis efferentia.

Procarpia subapicalia in axibus erectis; cellula subapicalia cellulas pericentrales tres: cellulam sterilem pericentralem, cellulam fertilem pericentralem et cellulam supportantem cum ramo carpogoniali laterali et cellula sterili terminali ferens; cellula hypogena ramulos quatuor post fecundationem efferens. Cellulae auxiliares duae a procarpio quoque, gonimolobae duae; cellulae cum procarpio consociatae greges tres cellularum 3-5 post fecundationem efferentes.

Thallus small, epiphytic, with prostrate and erect axes, prostrate axes attached by digitate haptera.

Tetrasporangia tetrahedral, terminal on short stalks in small cymose branchlets which are lateral on the erect axes. Ultimate tetrasporangia protected by small involucral branchlets.

Spermatangial heads spherical to ovoid, sessile and adaxial on the erect axes.

Procarps subapical on the erect axes; subapical cell bearing three pericentral cells: the sterile pericentral cell, fertile pericentral cell, and supporting cell with lateral carpogonial branch and terminal sterile cell; hypogenous cell producing four post fertilization involucral branchlets. Auxiliary cells two per procarp, each producing a gonimolobe; fusion cell absent. Cells associated with the procarp produce after fertilization three groups of 3-5 cells each.

The genus is so named because it shows features of both the Spermothamnieae and Sphondylothamnieae and seems to represent a connecting link between the two groups.

TYPE SPECIES - *Interthamnion attenuata* sp. nov.

Interthamnion is distinct from *Spermothamnion*, which it most closely resembles in vegetative features, in having a relatively elongate hypogenous cell which produces four post fertilization laterals and is not incorporated into a large fusion cell. In *Spermothamnion*, the hypogenous cell is relatively short, does not produce laterals and is incorporated into a fusion cell. There is no post fertilization division of the sterile cells associated with the procarp as in *Interthamnion*.

The genus is monotypic.

INTERTHAMNION ATTENUATA sp. nov.

TYPE LOCALITY - Aldinga Beach, S. Aust., epiphytic on Zonaria spiralis (J.Agardh) Papenfuss, growing in the upper sublittoral pools on the reef edge (Womersley, 11.x.1965).

TYPE - ADU, A29,616.

DISTRIBUTION - Known only from the type collection.

The type collection was used for detailed investigation.

DIAGNOSIS

Thallus in frondibus Zonariae spiralis epiphyticus. Cellulae axium prostratorum 35-60µ diam., 3-9 longiores quam latiores. Axes erecti ad 2 mm alt., unilateraliter vel alternatim vel opposite ramosi, angustati prope apices. Cellulae medianae axium erectorum 20-40µ diam., 4-6 longiores quam latiores.

Tetrasporangia ad 80µ diam., positio atque geno.

Capitula spermatangiorum ad 30µ diam., positio atque geno.

Procarpio et carposporophyti atque geno.

The species is named after the tapered erect axes.

VEGETATIVE STRUCTURE (Fig. 45A,B)

The prostrate axes are attached to the substrate by digitate haptera and give rise to erect axes, reaching 2 mm long, which are mostly unilaterally and abaxially branched (Fig. 45A), occasionally alternate or opposite, and taper considerably near their apices (Fig. 45B).

The cells of the prostrate axes are 35-60µ diam. and 3-9 times longer than wide. Median cells of erect axes are 20-40µ diam. and 4-6 times longer than wide.

REPRODUCTION

Tetrasporangia (Fig. 45B)

The tetrasporangia reach 80µ diam. and occur on small-celled branchlets lateral on the erect axes. Each sporangium is produced terminally on a stalk cell, and 1-2 further stalk cells are produced laterally from the first one, thus forming a cymose branchlet. The ultimate sporangia are surrounded by 1-2 curved involucral branchlets.

Spermatangial heads (Fig. 45C)

Spermatangial heads are spherical to ovoid, about 30µ diam. and borne in positions similar to the tetrasporangia. There are 3-4 fertile axial cells which each produce 3 pericentral cells. These divide terminally and laterally producing spermatangial mother cells which each cut off 2-3 spermatangia.

Procarp and Carposporophyte (Fig. 45D-G)

Procarps are formed on short erect axes 5-7 cells long. The last two cells are comparatively short (Fig. 45D) and the hypogenous cell is about twice as long as the subapical cell which bears 3 pericentral cells: the sterile pericentral, fertile pericentral, and supporting cell with terminal sterile cell and lateral carpogonial branch. The hypogenous cell bears four cells at fertilization and these later produce involucral filaments surrounding the carposporophyte.

Fusion of cells of the carpogonial branch and production of connecting cells is typical of the tribe. The supporting cell and fertile pericentral cell each produce an auxiliary cell (Fig. 45E). The basal and apical lobes are cut off as gonimoblast initial cells but only the apical one develops further, dividing subdi- or trichotomously once or twice, the terminal cells becoming carposporangia (Fig. 45F,G). Mature carposporangia are lachrimiform, about 35µ diam.

The apical cell, sterile pericentral cell and sterile cell on the supporting cell divide after fertilization to produce three small groups each of 3-5 cells (Fig. 45F). Each group has a common gelatinous sheath. Only slight fusion occurs between the auxiliary, supporting and fertile pericentral cells and the subapical cell.

DISCUSSION on INTERTHAMNION

While *Interthamnion* is a typical member of the Spermothamnieae in most of its vegetative and reproductive structures, the regular post fertilization division of the sterile cells associated with the procarp is similar to divisions occurring in cystocarp development in the Sphondylothamnieae tribe. However, these divisions do not result in a true inner involucrum as in the Sphondylothamnieae. Thus although *Interthamnion* may be intermediate in features between the two tribes, it is more likely that the division of these sterile cells has occurred independently in each tribe.

(6) *LEJOLISIA* Bornet 1859: 80, pl. 1,2

The genus *Lejolisia* was described by Bornet as being closely related to *Callithamnion* in its vegetative and tetrasporangial structures while at the same time possessing a characteristic cystocarp with a pericarp similar to the "ceramidium" found in *Polysiphonia*. The structure of the procarp and post fertilization events was later described in greater detail by Bornet and Thuret (1867, p.148, pl. 12, Fig. 15, 16). They showed that the procarp is very like that of *Spermothamnion*, and that the pericarp of *Lejolisia* should be considered homologous with the involucral branchlets which surround the cystocarp in *Wrangelia*, although enclosed within a common gelatinous sheath.

L. mediterranea, the type species of *Lejolisia*, was later investigated by J. and G. Feldmann (1940b, p.308, Figs. A-C) and Feldmann-Mazoyer (1940, p.183, 377, Figs. 10, 67, 77, 78, 148). Their descriptions of the cystocarp development do not agree with the earlier one of Bornet and Thuret (see discussion).

Fertile material of *L. mediterranea* has not been available for study and because of the lack of agreement in descriptions of this species, the generic concept of *Lejolisia* as recognised here is based mainly on the southern Australian species, *Lejolisia aegagropila* (J.Agardh) J.Agardh. The main features are:

(1) thallus epiphytic, with prostrate and erect axes, prostrate axes attached to substrate by unicellular digitate haptera,

(2) tetrasporangia tetrahedral, terminal on short stalks borne on the erect axes,

(3) spermatangial heads spherical to elongate, in positions similar to the tetrasporangia,

(4) procarps subapical on erect axes and laterals; subapical cell with 3 pericentral cells, and one auxiliary cell per procarp; sterile cells associated with the procarp (apical cell, two sterile pericentral cells and sterile cell on the supporting cell) divide after fertilization to produce a pericarp one cell thick surrounding the carposporophyte, the filaments embedded in a common gelatinous sheath; auxiliary cell dividing terminally to produce one functional gonimoblast initial and laterally to produce two nonfunctional gonimoblast cells; carposporangia produced sympodially; stellate fusion cell formed from residual gonimoblast cells.

LEJOLISIA AEGAGROPILA (J.Agardh) J.Agardh 1892: 126, pl. 2, Fig. 1-8. De Toni 1903: 1255; 1924: 454. Kylin 1956: 388. Lucas 1909: 47. Lucas and Perrin 1947: 324. Mazza 1925: 1689. Okamura 1932: 125.

Callithamnion aegagropila J.Agardh 1876: 11. Sonder 1880: 11. Tate 1882: 16.

TYPE LOCALITY - "New Holland".

TYPE - Herb. Agardh. Lund (No. 35,288). Not seen.

DISTRIBUTION - From Pt. Denison to Pt. D'Entrecasteaux, W. Aust. (isolated records); moderately common from Venus Bay, S. Aust., including Kangaroo Is., to Pt. Roadnight, Vic.

The species is epiphytic on several species of algae, mostly Lenormandia sp. or on the stems of Cymodocea antarctica, and is collected mainly as drift, but occasionally in rock pools.

Material used for detailed investigation was collected as drift from Venus Bay, epiphytic on Cymodocea (ADU, A19,502, Womersley, 12.ii.1954), Pt. Elliot, S. Aust. on Lenormandia (ADU, A31,428, Womersley, 12.vi.1967, A18,689, Womersley, 23.v.1953), and Kingston, S. Aust. (ADU, A32,161, Woelkerling, 9.ix.1968).

VEGETATIVE STRUCTURE (Fig. 46A-D, Plate 12C)

The prostrate axes are irregularly branched, attached by digitate haptera, and give rise to erect axes reaching 1.5 cm high, with up to two erect axes per prostrate axial cell. The erect axes are usually adaxially branched, occasionally alternate or opposite, with branching often denser in the upper parts of the thallus (Fig. 46A). The ultimate branchlets usually taper slightly but occasionally are obtuse or hair-like (Fig. 46B).

Cell size varies considerably in plants growing on different hosts, but as there are no obvious discontinuities in the range, these forms are included within the one species (Fig. 46C - larger celled form, Fig. 46D - smaller celled form). Cells of the prostrate axes are 70-110μ diam. and $2\frac{1}{2}$-$4\frac{1}{2}$ times longer than wide. Median cells of erect axes are (25-)65-80(-105)μ diam. and 2-5 times longer than wide. Cells of the hair-like parts are 18μ diam. and up to 15 times longer than wide.

REPRODUCTION

Tetrasporangia (Fig. 46E)

The tetrasporangia reach about 80μ diam. and are terminal on short unicellular stalks. One to three stalk cells may occur laterally on the one erect axial cell. Rarely tetrasporangia are found on branches bearing both male and female reproductive structures.

Spermatangial heads (Fig. 46F,G)

Spermatangial heads are spherical to slightly ovoid, about 45μ diam., and terminal on short branchlets on the erect axes (Fig. 46F). Three fertile axial cells each produce 2-3 pericentral cells, which each cut off 2-3 terminal spermatangia and further lateral spermatangial mother cells (Fig. 46G).

Procarp and Carposporophyte (Fig. 47A-F)

Procarp systems are formed terminally on the erect axes and laterals. The last 3 cells of the fertile axis are comparatively short (Fig. 47A), while the fourth (subhypogenous) is 2-4 times longer than the hypogenous cell. The subapical cell bears two sterile pericentral cells and the supporting cell with terminal sterile cell and lateral carpogonial branch.

After fertilization and production of connecting cells by the carpogonium, the supporting cell divides obliquely near the base to produce a triangular (pyramidal?) shaped auxiliary cell (Fig. 47B). The auxiliary cell divides terminally producing a functional gonimoblast initial (Fig. 47C), and laterally giving two small cells which do not divide further but degenerate. The apical cell, sterile pericentral cells and sterile cell on the supporting cell divide (Fig. 47C) and eventually form the characteristic pericarp around the gonimoblast (see below). The hypogenous cell does not produce any laterals.

The gonimoblast initial divides obliquely three or four times producing cells which initiate the gonimolobe arms. Each of these cells cuts off three cells by oblique divisions, the first two becoming carposporangia (Fig. 47D) and the third repeating this process by three more divisions. In this way, a lateral gonimoblast cell continues the spore production and growth of the gonimoblast, giving sympodial development. Mature, ovoid carposporangia (50x 60µ) are extruded through the ostiole (see below). The gonimoblast residual cells fuse successively forming a multinucleate fusion cell with 6-9 radiating arms (Fig. 47E). On the upper sides of each arm are two rows of pit connections (Fig. 47F) which remain after the carposporangia have been released. The fusion cell arms curve outwards and upwards as they elongate.

During the production of the carposporophyte, the pericarp is produced by division of the sterile cells associated with the procarp. The four branches are subdichotomously branched once or twice, their cells lobed and containing 2-5 nuclei. The whole pericarp is completely enclosed in one gelatinous sheath common to the carposporophyte (Fig. 47E). The 7-9 terminal cells of the pericarp are elongate to triangular and surround the ostiole, being twisted outwards in a clockwise direction when viewed from above.

The mature cystocarp is urceolate, reaching about 200µ diam.

DISCUSSION

The main vegetative differences between *L. aegagropila* and the type species, *L. mediterranea*, is in the thallus size, the erect axes of *L. aegagropila* reaching about 15 mm high, while those of the type reach only about 1 mm. The vegetative cells of *L. aegagropila* are 3-4 times the diameter of those of *L. mediterranea* and similarly the tetrasporangia and spermatangial heads are about twice the diameter of those of the type. Feldmann-Mazoyer (1940, p.376) reported that the cells of *L. mediterranea* are uninucleate, whereas those of *L. aegagropila* are multinucleate (Plate 14D).

There is some disagreement in the descriptions of the development of the pericarp of *L. mediterranea*. Feldmann-Mazoyer (1940, p.199, Figs. 77,78) states that the filaments constituting the pericarp originate from the axial cell below the fertile "central cell" (i.e., from the hypogenous cell which is comparatively longer in *L. mediterranea*). Her figure (1940, Fig. 77) shows clearly that the sterile pericentral cells and apical cell (although it has divided once) do not contribute to the pericarp. However, Bornet and Thuret (1867, p.148) state that the apical cell and the three "peripheral cells" divide after fertilization to produce the pericarp, as in *L. aegagropila*. The mature carposporophyte of *L. mediterranea* appears to be much simpler than that of *L. aegagropila*. According to Feldmann-Mazoyer there is only one "sterile cell" between the 4-6 large carposporangia and the gonimoblast initial. This constrasts markedly with the large fusion cell with radiating arms and continued production of carposporangia in *L. aegagropila*. Thus the systematic position of *L. aegagropila* cannot be confirmed until detailed examination of the type species has been made.

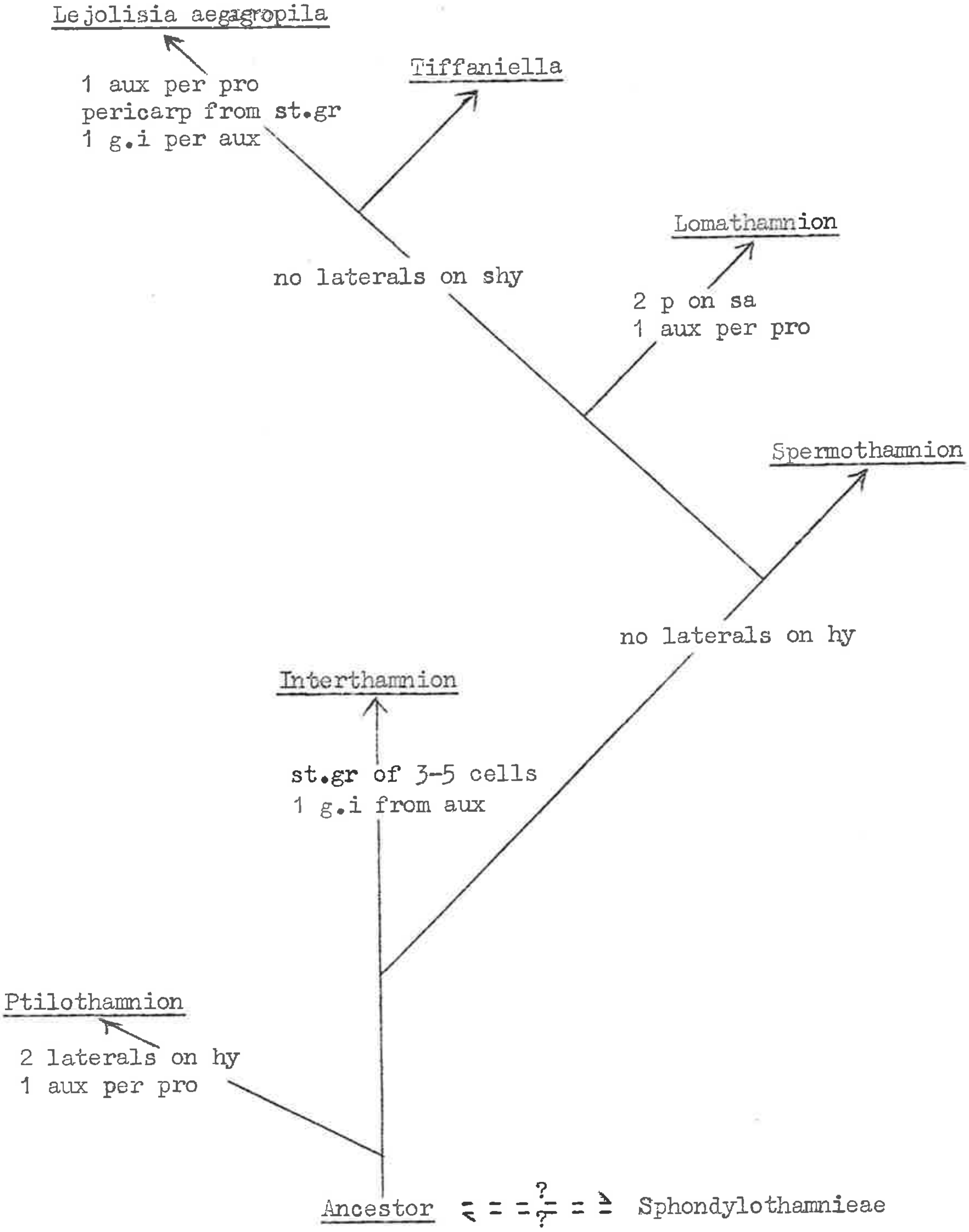
Other species which have been ascribed to *Lejolisia* are *L. columbiana* Taylor (1945, p.265, pl. 4, Figs. 3-10), *L. pusilla*

Dawson and Neushul (1966, p.181), and *L. hoshawii* Dawson (1966, p. 64). Taylor's species agrees in main characteristics with those here accepted for the genus *Lejolisia*, but no details are given for procarp or pericarp development. Material of the type specimen from Gorgona Is., Colombia (AHFH, no. 7019, Taylor, 12.ii.1934) has been examined but female plants were not found. *L. pusilla* and *L. hoshawii* have been described from tetrasporangial material only and thus must await further investigation to confirm their generic identity. The sessile tetrasporangia in both species seem to ally them more closely with *Ptilothamnion*.

DISCUSSION on SPERMOTHAMNIEAE

A possible sequence of evolutionary development for the female reproductive structures of genera of the Spermothamnieae is illustrated in Diag. 5. It is likely that the prefertilization structure of the procarp of the ancestor of the group was similar to that of the ancestor of the Sphondylothamnieae, and many of the subsequent developments which have occurred in the two groups are parallel. *Interthamnion* probably differs from the ancestor mainly in the post-fertilization division of the sterile cells associated with the procarp. In other respects, for example the retention of the lateral involucral filaments on the hypogenous cell and two auxiliary cells per procarp, and the production of only one gonimoblast initial per procarp, *Interthamnion* occupies a similar position in the evolution of the group to that of *Sphondylothamnion* in the Sphondylothamnieae. Similarly, *Spermothamnion* has evolved by loss of all laterals from the hypogenous cell in a comparable way to the development of *Shepleya* In *Tiffaniella*, the process has been carried further and all laterals lost from the subhypogenous cell. *Lomathamnion* may have developed from the *Tiffaniella* line by the loss of the third pericentral cell on the subapical cell with the corresponding loss of the second auxiliary cell per procarp, in a similar way to *Involucrana* which has only two pericentral cells on each subapical cell. *Lejolisia* probably arose by loss of the

DIAGRAM 5.- Possible mode of evolution of the Spermothamnieae



second auxiliary cell per procarp and development of the specialised pericarp from the sterile cells associated with the procarp. In the *Ptilothamnion* line, two of the laterals on the hypogenous cell have been retained and there has been no development of a large fusion cell as in *Spermothamnion* and *Tiffaniella*. Fusion cells may have been secondarily lost in *Lomathamnion* and *Lejolisia*.

Feldmann-Mazoyer (1940, p.240) included *Lejolisia mediterranea* and *Ptilothamnion* in a new tribe, the Lejolisieae, because of the elongate hypogenous cell and the small number of nuclei occurring in the vegetative cells. However, the present study on *Lejolisia aegagropila* and southern Australian species of *Ptilothamnion* indicates that the differences between these genera and other genera in the Spermothamnieae are of the same order as the differences between the genera of the Sphondylothamnieae. Thus, there is insufficient justification for separating these genera into a different tribe.

Two further genera, *Pleonosporium* and *Compsothamnion* may be found to possess features characteristic of the *Spermothamnieae*. These genera have not however been studied in southern Australia and are not included in this discussion.

VIII. CULTURE STUDIES

INTRODUCTION

Culture studies were carried out as a supplement to the main taxonomic work. In the limited time available, only species which could be obtained readily in the living condition from nearby coastal areas were used. Of the six species attempted (Wrangelia plumosa, Mazoyera protensa, Mazoyera halura, Shepleya wattsii, Involucrana crassa, and Lejolisia aegagropila) only W. plumosa and L. aegagropila provided spores which germinated to produce multicellular stages.

The aims then were:

(1) to observe and compare stages in germination of spores of the two species, and

(2) to establish the life cycles in culture.

Herbarium specimens of the plants from which spores were cultured are:

W. plumosa - ADU, A30,930, Aldinga Reef, Gordon, 15.xi.1966, A31,065, Aldinga Reef, Woelkerling, 11.xii.1966, and A32,171, Christies Beach, Womersley, 14.x.1968.

L. aegagropila - ADU, A32,170, West Beach, drift, epiphytic on Cymodocea antarctica, Gordon, 4.x.1968.

METHODS

1. Culture Media

Germination of spores of W. plumosa was first attempted using enriched seawater media as used by Drew (1952, p.40), von Stosch (1964, p.143), and Provasoli (see Tatewaki 1966, p.62). No significant differences were observed between these three media. For later experiments, that of Provasoli (Table 8) was used.

Germanium dioxide (1 ppm - 1 ml of stock solution, of 1 mg/l, to each litre of enriched seawater) was added to suppress diatom growth (Lewin 1966, p.1).

Axenic cultures were not necessary for early stages in spore germination for both species, and for growth of the sporelings to maturity in L. aegagropila. However continued growth of sporelings of W. plumosa may require further elimination of contaminants than was possible in the time available.

Whole plants of W. plumosa as collected from the reef were placed in a system of circulating seawater but these plants died due to contaminating growth. Plants of L. aegagropila were removed from the host, and sexual and sporangial material separated. Plants in still cultures grew equally as well as those which were aerated and were less contaminated.

TABLE 8. Provasoli's ES enrichment medium

Stock Solutions		Amount of Stock Added	Total Amount of Each Component
Na_2glycerophosphate	5g/100ml	10 ml	500 mg
$NaNO_3$	35g/100ml	10 ml	3.5 g
Vitamin B_{12}	1mg/100ml	10 ml	100 µg
Thiamine	50mg/100ml	10 ml	5 mg
Biotin	0.5mg/100ml	10 ml	50 µg
*Tris Buffer (Sigma Co.)	5g/100ml	100 ml	5 g
**Fe (as EDTA 1:1 molar)		250 ml	25 mg Fe
+PII Trace metals		250 ml	
Distilled water		600 ml	

* Tris HCl 4.05g
Tris base 0.95g
pH = 7.65 at 23°C

** Fe-EDTA
$Fe(NH_4)_2(SO_4)_2.6H_2O$ 351mg
Na_2EDTA 330mg
in 500ml distilled water

+ TABLE 9. PII Metal mix

Salt	Amount	Amount of metal per ml.	
H_3BO_3	0.57g	B	0.2mg
$FeCl_3.6H_2O$	24.5mg	Fe	0.01mg
$MnSO_4.4H_2O$	82.0mg	Mn	0.04mg
$ZnSO_4.7H_2O$	11.0mg	Zn	0.005mg
$CoSO_4.7H_2O$	2.4mg	Co	0.001mg
Na_2EDTA	500mg	Na_2EDTA	1 mg
Distilled water	500ml		

20ml of ES enrichment medium was added to each litre of filtered seawater.

2. Germination of spores

Small pieces of spore bearing filaments were placed in culture solution contained in small petri dishes (4 cm diam.). Cystocarps of W. plumosa were cut open to allow carpospores to escape freely in the absence of water movement, which would possibly help them to escape in the natural environment. When sufficient spores had dropped the filaments were removed. Attachment of spores to the glass usually occurred within about 3 days after which the culture solution was changed. Sporelings were selected subsequently for camera lucida drawings and photography. When sporelings had reached about 2 mm long, individual plants were removed carefully and placed separately in further small petri dishes containing culture solution. Most of these plants became attached again within about 5 days after which the lower half of the petri dish was placed in a larger glass culture vessel containing about 500 ml of culture solution.

Cultures were kept in constant temperature rooms at 14°C or 16°C, under Phillips fluorescent lights at 50 - 100 lumens per sq.ft. or 250 lumens per sq.ft. (shade or light - see below) and daylengths of 10 - 16 hrs. Light intensities were measured with a G.P. Photometer made by Evans Electroselenium Ltd., Potter St., Harlow, Essex, England.

Contaminating algae were mainly a small filamentous Phaeophyte and a red coloured Cyanophyte. The Phaeophyte was easily removed with a very small camel hair brush but the Cyanophyte was very difficult to eliminate. Mature plants of L. aegagropila were subcultured by breaking off small branch systems and placing in fresh solution in small flasks stoppered with cotton wool. These plants grew well without becoming attached to the glass.

Culture solutions were changed every 7 - 14 days.

3. Conditions of cultures

Sporelings of W. plumosa cultured under a relatively high light intensity at first grew more quickly than those cultured under low light intensity. But within about 2 weeks, the shaded plants appeared healthier and were more highly pigmented, although with shorter whorl-branchlets than the sporelings in the high light intensity. The latter were then placed in a lower light intensity and the apices rapidly became more highly pigmented. However, these plants had to be discarded later because of bacterial infection. The shaded sporelings lived for about 5 months, reaching about 1 cm long, but these too later became infected by a sudden bloom of bacteria. Treatment with penicillin at 3000 units/ml (Fries 1963, p.696) and cleaning of filaments with a small camel hair brush was of no avail. No reproductive structures were formed in this time.

RESULTS

1. Wrangelia plumosa - stages in germination of spores

(1) Tetraspores (Figs. 48A-K, 49A, Pl. 13A-C)

The spore becomes rounded and then elongates slightly in a vertical direction, becoming attached to the substrate (glass) after about 24 hrs.

The first division is transverse and usually unequal, the distal spore residual cell larger than the proximal rhizoidal initial cell (Fig. 48B) which remains attached. The rhizoidal initial elongates and cuts off a narrow primary rhizoid, the diameter being approximately one third that of the rhizoidal initial residual cell (Fig. 48C,D). The next division, usually also unequal, occurs in the spore residual cell, producing a smaller apical cell, often slightly to one side (Fig. 48D). The first whorl-branchlet initial may then be produced laterally from the distal end of the spore residual cell (Fig. 48E,F, Pl. 13A).

Axial cells at this stage are almost cubical, but after several apical divisions they elongate and become cylindrical, about 2½ times longer than wide (Figs. 48G-K, 49A). As the erect part of the sporeling grows from an oblique to a vertical position, the first formed whorl-branchlet on each axial cell tends to be produced unilaterally on the side of the axis nearest the substrate (Fig. 48I, Pl. 13B). Once the vertical position is attained, however, the first-formed whorl-branchlets are produced in a clockwise spiral looking down from the apex, and then as the thallus matures further they are produced alternately on opposite sides of the axis. The spore residual cell usually produces only one whorl-branchlet which is simple or once branched, consisting of 3-4 cells.

The primary rhizoid continues to divide apically, often reaching several times the length of the erect part and also branching laterally. Occasionally the primary rhizoid produces a small, multicellular discoid holdfast, and further rhizoids may be produced from the proximal ends of axial cells (Pl. 13B). The cells of the rhizoids are devoid of rhodoplasts. The rhizoidal gelatinous sheath is mucilaginous.

A lateral determinate branch may grow at an early stage from one of the lower axial cells (Pl. 13C), rather than from the basal cell of a whorl-branchlet as in mature plants. This may account for the way in which several main axes appear to arise from the one holdfast in mature plants.

(2) Carpospores

Stages in germination were found to be essentially the same as in the tetraspore germling.

In neither the tetrasporelings nor the carposporelings was reproductive maturity obtained.

2. Lejolisia aegagropila

When put into culture, plants from the field bore tetrasporangia and cystocarps only sparsely. After about 7 weeks, tetrasporangia were produced profusely, but further cystocarps did not develop. Tetraspores were released, but only a small percentage (about 10% as compared with about 95% in W. plumosa) survived and germinated. Carpospores were not released from the cystocarps which eventually disintegrated.

Stages in germination of tetraspores (Fig. 49B-F)

The spore becomes rounded and then produces a small protrusion (Fig. 49B) which becomes attached to the substrate and is cut off as a primary rhizoid (Fig. 49C). The spore residual cell then divides transversely producing a distal cell, which on continued division gives rise to a horizontal or oblique axis which is free from the substrate (Fig. 49D,E). Further free filaments are then produced from the spore residual cell and its immediate daughter cells, while the rhizoid continues to elongate (Fig. 49F). The free axes later begin to branch unilaterally in their characteristic manner. Cells of the horizontal axes may produce unicellular rhizoids (haptera - Pl. 14B) at irregular intervals, but the terminal digitate discs occurring on the prostrate filaments of plants collected in the field have not been observed in culture.

Sporelings produced sexual structures, both male and female on the same plants (Pl. 14A), after about 5 weeks. Vessels containing these plants were shaken at irregular intervals and about 3 weeks later post-fertilization stages were observed. However, only one mature cystocarp was produced and carposporangia obtained from it failed to survive.

Some sexual sporelings about 7 weeks old produced tetrasporangial initials (Pl. 14B), only a few of which divided tetrahedrally, the others disintegrating or remaining undivided.

DISCUSSION

1. Germination of spores

Kylin (1917, p.3) distinguished three types of spore germination:

I. der Keimschlauchtypus (the germ tube type),
II. der Haftscheibentypus (the attachment-disc type), and
III. der aufrechte Typus (the upright type).

These three types were later correlated with classifications of other authors by Boillot (1961, p.687).

The germination of spores of both *Wrangelia plumosa* and *Lejolisia aegagropila* are of Kylin's third type where the first division of the spore is parallel to the substrate. This type has been observed for other members of the Ceramiaceae, e.g., *Antithamnion plumula*, *Griffithsia corallina*, and *Ceramium rubrum* (Kylin 1917, p.15-19) and also seems typical of the Ceramiales (Fritsch 1945, p.517).

The horizontal axes of *L. aegagropila* develop from primarily erect axes which have become secondarily prostrate. Thus although Fritsch's statement (1945, p.445) that the heterotrichous habit is completely suppressed in the Ceramiales remains correct when applied to primary heterotrichy, it must be recognised that secondary heterotrichy occurs in this order.

2. Growth of plants in culture~~s~~ - (1) *Wrangelia plumosa*

Observations in the field suggest that this species grows to reproductive maturity in less than a year. Sterile plants to 9 cm high have been collected from the upper sublittoral zone on a buoy in American River Inlet, Kangaroo Is., S. Aust. (ADU, A4,126a, Womersley, 6.ix.1946). These buoys are cleaned annually. This hence gives some estimation of the possible growth rate. It is possible that plants growing in a relatively more stable environment, such as the channel at American River Inlet at about 4 m depth, may take several years to reach their larger sizes (to about 20 cm). Thus the growth rate of sporelings in culture is probably low.

Environmental conditions such as light intensity and composition, temperature, salinity, nutrient status, water movement and daylength may have been suboptimal, but as *W. plumosa* can tolerate such large fluctuations of these factors while growing in the lower littoral zone, and also grow well in the relatively stable environment of the sublittoral, the low growth rate in culture can not be easily explained in these terms. Bacterial infection which was probably the cause of the death of the sporelings, may have been a factor in retarding growth.

(2) Lejolisia aegagropila

In contrast to W. plumosa, sporelings of this species grew to reproductive maturity within 5 weeks, and although contamination with other algae was high, the plants appeared healthy, and typical in vegetative and reproductive features to plants collected in the field.

IX. NUCLEAR STUDIES

INTRODUCTION

Morphological studies of species of the genus Wrangelia as previously known, using the aniline blue staining procedure, appeared to indicate that both uninucleate and multinucleate species occur. In order to clarify this situation, specific nuclear stains following special fixation were used with a limited number of species previously included in Wrangelia, representing both the Wrangelieae and Sphondylothamnieae tribes. Lejolisia aegagropila and Lomathmnion epicodii were also examined as representatives of the Spermothamnieae.

The only species of Wrangelia which has been investigated cytologically is the type, W. penicillata. Schussnig and Yahoda (1927, p.245) reported that during the division of the young sporangium nucleus, 8 "chromophilous granules" (chromosomes) are formed from the nucleus. This has since been discredited by Westbrook (1935, p.577) who considered that their results showed fragmentation of the nucleolus (see W. plumosa below). Magne (1964, p.545, pl. 12, Figs. 386-389) studied the meiotic division of the sporangium initial and reported a haploid number of 28 chromosomes; he also failed to observe the stages described by Schussnig and Yahoda.

No attempt was made to obtain details of nuclear divisions or chromosome numbers, this being beyond the scope of this thesis.

The following species were investigated:

A. Uninucleate species

(1) Wrangelia plumosa - ADU, A31,387, Chinaman's Hat Is. Bay, Yorke Pen., S. Aust., Gordon, 17.i.1968.

(2) Wrangelia velutina - ADU, A32,156, Elliston, Eyre Pen., S. Aust., Gordon, 16.v.1968.

B. Multinucleate species

(1) Mazoyera halura - ADU, A32,143, Stinky Bay, S. Aust., Gordon, 9.ii.1968.

(2) Shepleya wattsii - ADU, A32,145, Stinky Bay, S. Aust., Gordon, 9.ii.1968.

(3) Shepleya verticillata - ADU, A32,146, Stinky Bay, S. Aust., Gordon, 9.ii.1968.

(4) Wollastoniella myriophylloides - ADU, A32,167, Cable Hut Bay, Yorke Pen., S. Aust., Gordon, 23.ix.1968.

(5) Involucrana crassa - ADU, A32,142, Stinky Bay, S. Aust., Gordon, 9.ii.1968.

(6) Lomathamnion epicodii - ADU, A32,168, Pondalowie Bay, Yorke Pen., S. Aust., Gordon, 22.ix.1968.

(7) Lejolisia aegagropila - ADU, A32,170, West Beach, S. Aust., Gordon, 4.x.1968.

METHODS

A. Fixation

Samples were fixed for approximately 24 hours in each of the following four fixatives, and then transferred to and stored in 70% ethyl alcohol.

(1) Alcohol - formalin (Drew 1934, p.551)

70% ethyl alcohol : 40% formaldehyde
100 ml : 6 ml

(2) Formalin - acetic acid - alcohol (Westbrook 1935, p.565)

40% formalin : glacial acetic acid : 50% ethyl alcohol
6.5 ml : 2.5 ml : 100 ml

(3) Modified Karpachenko (Papenfuss 1946, p.422)

Solution A	Solution B
chromic acid - 1 g	40% formaldehyde - 40 ml
glacial acetic acid - 5 ml	seawater - 35 ml
sea water - 65 ml	

(4) Alcohol - Acetic acid

95% ethyl alochol : glacial acetic acid
3 ml : 1 ml

B. Staining

(1) Iron alum - acetocarmine (Godward 1948, p.203)

The sample was rinsed in tap-water, mordanted in 2% ferric ammonium sulphate for 10 - 15 mins., washed rapidly in water and transferred to 0.5% acetocarmine on a slide. The sample was then dissected, heated gently and squashed under a coverslip which was then ringed with nailpolish. This gave a temporary mount which lasted for several weeks.

(2) Alcoholic iron haemotoxylin (Johansen 1951, p.363)

The sample was mordanted for about 5 hours in a mixture of approximately equal volumes of absolute alcohol and 2% ferric ammonium sulphate, washed rapidly in water and then stained for about 24 hours in 0.1% alcoholic haematoxylin. The sample was then differentiated for about 1 hour in the mordanting solution, taken through an alcohol - xylol series and mounted in XAM. This method was only used for *Shepleya wattsii* and *Involucrana crassa* as nuclei were not detectable in the two species using the acetocarmine method.

Numbers of nuclei in large multinucleate cells were calculated by multiplying the density (number of nuclei per unit area of the cell periphery - calculated from random quadrat counts) by the surface area of the cell.

Nuclear volumes were calculated from the formula:

$$\text{Volume} = \frac{4}{3}\pi r_2^2 r_1$$

where r_1 = larger radius of ellipsoid

r_2 = smaller radius of ellipsoid.

RESULTS

In general, formalin - acetic - alcohol was found to be the best fixative, both for prevention of plasmolysis of the cells and for staining of the nucleus by acetocarmine. Alcohol- formalin also gave reasonably good results. No clear mitotic or meiotic figures were seen.

A. Uninucleate species

(1) Wrangelia plumosa (Fig. 50A-B, Plate 13D)

The nuclei of the small dividing cells of the whorl-branchlets (Fig. 50A) are spherical, about 6µ diam. and suspended in the centre of the cell. Each nucleus contains a single nucleolus of uniform appearance, about 1µ diam. Small darkly staining bodies in the extra-nucleolar area may be chromosomes in various stages of contraction. Progressive vacuolation causes the nucleus to be pushed to the wall of the cell and in mature cells it becomes flattened (Fig. 50B - part of a median cell of a whorl-branchlet at the same magnification as Fig. 50A). The nucleus occurs in the peripheral cytoplasmic layer just below the layer of rhodoplasts. It is usually approximately lenticular in shape, 20-30μ diam. and 10μ thick. The irregular shape of the nucleus illustrated may be due to incorrect fixation. The volume is about 12 times that of the nuclei of young dividing cells.

The nucleolus occurs in a fragmented state, the fragments being 3-6μ diam. and often joined by narrow strips. Fragmentation of the nucleolus has been observed in the nuclei of other algae, e.g. in the cells of the cystocarp of Bonnemaisonia asparagoides, forming 4-8 closely associated granules (Kylin 1916, p.550) and in the resting stage of sporangium formation in Ceramium flabelligerum (Westbrook 1935, p.571, Figs. 78, 79). The extra-nucleolar area is granular.

(2) Wrangelia velutina (Fig. 50C)

The nuclei of the vegetative cells of this species are very similar to those of W. plumosa. There is a similar increase in the volume of the nucleus with increase in volume of the cell. With increase in vacuolation, there is the characteristic flattening of the nucleus against the wall. In contrast to W. plumosa, the nucleolus does not fragment in mature cells but remains a single body, often becoming elongate.

In the short cells of the fertile axis of the female gametophyte during early gonimoblast formation (Fig. 50C), the nuclei are particularly large. They are irregularly lenticular and densely staining, reaching 25 x 40μ in face view and about 25μ thick. The elongated nucleolus appears to contain several small vacuoles which are possibly concerned with secretion (de Robertis, Nowinski and Saez, 1965, p.311). The enlarged pit discs also stain very densely with acetocarmine. The fusion cell formed from the lower gonimoblast cells of the carposporophyte is clearly multinucleate.

B. Multinucleate species

(1) Mazoyera halura (Fig. 50D, E)

All the vegetative cells of this species are multinucleate. The apical cells of indeterminate axes contain 10 - 12 nuclei. The number increases in lower axial cells, the largest near the base of the plant containing over 4,000 nuclei. They occur in the peripheral cytoplasmic layer inside the rhodoplast layer in young cells, but amongst the rhodoplasts in older cells. Apical cells of whorl-branchlets contain 4 - 10 nuclei and median cells 20 - 30 (Fig. 50D - part of the surface layer of a whorl-branchlet median cell). Nucleoli were not observed. The nuclei are ellipsoid, about 4μ diam. and 2μ thick, i.e., similar in size to the rhodoplasts. The nuclei are fairly evenly spaced around the surface of the cell, being approximately 35µ apart.

Reproductive cells such as the tetrasporangial initials (Fig. 50E), tetrasporangia, cells of the carpogonial branch, supporting cells, carposporangia and all cells of the spermatangial head are uninucleate. The nucleus (about 8µ diam.) is about twice the diameter of nuclei in vegetative cells and contains a prominent nucleolus about 2µ diam. The gonimolobe cells of the carposoporophyte are multinucleate.

Although staining with aniline blue of material fixed in formalin-seawater showed no visible nuclei in M. halura, nuclei were clearly observed in vegetative cells of Mazoyera protensa after this treatment (Fig. 13F).

(2) Shepleya verticillata

The nuclei of all vegetative cells occur in the peripheral cytoplasmic layer. The density of nuclei is greatest in the apical cell of an indeterminate branch, about 5 per 1000μ^2, and decreases to a minimum of about 1 per 1000μ^2 with increase in size of the axial cell (Table 10).

TABLE 10. Nuclei in axial cells of *Shepleya verticillata*

Cell	Cell Dimensions (to nearest 5µ)		Density of nuclei (No. per $1000\mu^2$)	No. of Nuclei in cell (approx.)
	Diam.	Length		
Apical	115	170	5.0	420
2nd axial cell	150	230	2.5	370
3rd axial cell	170	300	2.3	475
4th axial cell	185	310	1.7	400
17th axial cell	575	1525	1.0	3270

The figures for the first four axial cells were obtained from a single axis.

The density of nuclei in a cell increases where a cytoplasmic division is about to occur, e.g. at the distal end of an axial cell which is initiating whorl-branchlets. The number of nuclei in median cells of whorl-branchlets is 150-200. The lower numbers of nuclei occurring in the axial cells immediately below the apex (Table 9) may be due to the production of whorl-branchlet initials, where there is probably a migration of nuclei into the distal protruberances. At first nuclear divisions are probably not sufficient to maintain the original number in the axial cell. A similar situation occurs in other multinucleate species in which nuclei can be readily detected, but comparative numerical data were not obtained in all cases.

The nuclei of S. verticillata are lenticular and granular in appearance, about 6µ diam. and 2.5µ thick in apical cells, but about 4µ diam. in older cells. Each nucleus contains one nucleolus about 1µ diam. In larger axial cells, occasional randomly placed larger nuclei of 6-9µ diam. were observed, suggesting that nuclear division in these cells is probably not synchronous.

As in Mazoyera, sporangial initials, tetrasporangia, cells of the carpogonial branch, carposporangia and all cells of the spermatangial heads are uninucleate.

(3) *Shepleya wattsii*

Nuclei were most successfully stained using alcoholic haemotoxylin in young cells. Older cells contain relatively large (20 - 200μ diam.) angular storage (?) bodies which are often grouped and take up the stain tending to obscure the nuclei. The nuclei of vegetative cells are about 5μ diam. and are similar in distribution to those of *S. verticillata*.

(4) *Wollastoniella myriophylloides*

As in the preceding species, the density of nuclei is greatest in the apical cells of indeterminate branches and decreases as the cells mature. In the larger axial cells, the density is greater at each end of the cell (about 5 nuclei per $1000\mu^2$) than in the middle of the cell (about 2 nuclei per $1000\mu^2$), This is presumably associated with the production of laterals (whorl-branchlets and rhizoids) near each end.

The mucronate cells terminating the whorl-branchlets each contain 2 - 3 nuclei (about 5μ diam.) and the median cells about 16 nuclei (about 7μ diam.). The cells of the villose branches which often develop from indeterminate laterals and which also bear spermatangial heads each contain 6 - 12 nuclei which are sparsely distributed.

As in *Mazoyera* and *Shepleya*, sporangial initials, tetrasporangia, cells of the carpogonial branch, carposporangia and all cells of the spermatangial head are uninucleate.

(5) Involucrana crassa

This species was best fixed in alcohol-formalin, although even with this fixative slight plasmolysis occurred. Structures could not be detected which were clearly recognisable as nuclei with either stain used. Spherical granular bodies 5 - 9µ diam., but not selectively stained, were observed suspended in the cytoplasm within the layer of rhodoplasts.

(6) Lejolisia aegagropila (Plate 14D)

Nuclei of vegetative cells were readily stained only in the apical cells, each of which contains 10 - 14 nuclei, about 6µ diam. As in the preceding genera, fertile and sterile cells of the procarp system are uninucleate before fertilization. The cells of the pericarp produced from the sterile cells associated with the procarp system each contain 2-5 nuclei. The hypogenous and subhypogenous cells are both multinucleate.

(7) Lomathamnion epicodii

The nuclear situation is virtually the same as in the corresponding cells of Lejolisia aegagropila.

DISCUSSION

The possession of multinucleate cells by Mazoyera, Shepleya, Wollastoniella (Sphondylothamnieae), and Lejolisia and Lomathamnion (Spermothamnieae) in contrast to the uninucleate cells of Wrangelia (Wrangelieae) supports the separation of the tribes on morphological grounds.

The large numbers of nuclei (over 4,000) occurring in the lower axial cells of some of the multinucleate genera are of the same order as those occurring in the large vesiculate cells of Griffithsia spp. as estimated by Lewis (1909, p.643) for G. globulifera (as G. bornetiana). The apical cells of Shepleya verticillata with over 400 nuclei exceed those of G. globulifera with only 12-50(-75) nuclei (Lewis p.644).

The nuclei of young cells of multinucleate species, especially those undergoing cytoplasmic division are generally slightly larger than those of older cells. Nuclei in apical cells are about 6µ diam. and those in large axial cells about 3-5µ diam. This was also reported by Lewis for G. globulifera where the nuclei of young cells are about 4µ diam. and those of older cells about 3µ diam.

In the uninucleate species examined, the size of the nucleus in small dividing cells is always smaller than in older larger cells. In Wrangelia plumosa there is about a 12-fold increase in the volume of the nucleus from the young dividing cells of the whorl-branchlets to the mature median cells, but there is an increase of about 160 in the volume of the cells. Thus there is not a linear relationship between nuclear and cell volumes, but there may well be a closer relationship between the volumes of nucleus and cytoplasm. In large cells, the function which is served by large numbers of comparatively small nuclei in multinucleate genera is performed by one comparatively large nucleus in uninucleate genera.

X. GENERAL DISCUSSION ON AFFINITIES OF TRIBES STUDIED

A. Classification of Tribes and Subfamilies

Tribes - The Wrangelieae is unique in the Ceramiaceae in the development of the cystocarp which involves the whole terminal portion of the fertile branch. The intermingling of the fertile and sterile filaments is the result of the axial cells of the fertile axis remaining relatively short and the rapid development of the sterile whorl-branchlets after fertilization. The developing gonimoblast filaments are thus forced to grow along the axis and between the sterile filaments. This feature alone is of sufficient importance to separate this group of species as a tribe distinct from other tribes where there is no comparable intermingling of fertile and sterile tissue.

The Sphondylothamnieae and Spermothamnieae are closely related to each other, but as this study shows are only distantly related to the Wrangelieae. They differ markedly in the restriction of the procarps to the subapical cell of the fertile axis in contrast to their successive development near the apex of the fertile axis in the Wrangelieae. However the Sphondylothamnieae is quite distinct from the Spermothamnieae in the development of the inner involucrum of free filaments from the sterile cells associated with the procarp. A comparable structure is not found in any of the other groups with subterminal procarps. The post fertilization stimulation of division of the homologous cells (the sterile cell on the supporting cell, other whorl-branchlets on the fertile axial cells and the main axial cells) also occurs in the Wrangelieae. However there is no intermingling of fertile and sterile filaments in the Sphondylothamnieae where the involucrum is completely external to the gonimoblast.

In the three following cases, some division of these sterile cells does occur, but not to the same extent as in the Sphondylothamnieae:

(1) In Compsothamnion thuyoides (Smith) Schmitz (Compsothamnieae) studied by Westbrook (1930, p.353), the apical cell of the fertile axis continues segmentation after fertilization to produce a short filament. The sterile cells occurring on both the sterile and fertile pericentral cells each divide once, and from the lower of the two cells so formed rhizoidal protruberances are produced which fuse by secondary pit connections with branchlets lower on the fertile axis (Westbrook, Fig. 8).

(2) In Interthamnion (Spermothamnieae) these cells divide a few times, but again, no comparable involucrum is formed.

(3) The pericarp of Lejolisia aegagropila (Spermothamnieae) originates from the same cells but it is embedded in a single gelatinous wall. The inner involucral filaments of the Sphondylothamnieae are free.

Another important feature separating the Sphondylothamnieae from the Spermothamnieae is the possession of distinct whorl-branchlets on axial cells of erect axes. The erect axes of the Spermothamnieae are mostly unbranched to subdichotomously, unilaterally or pinnately branched and do not reach the relatively greater lengths of the erect axes of the Sphondylothamnieae.

Subfamilies - The subfamilies Crouanioideae (including the Wrangelieae) and Ceramioideae (including Kylin's Spermothamnieae) of Hommersand (1966, p.330) were separated on the characteristics shown in Table 11 (p.285).

Although the Wrangelieae was placed in a different subfamily from the Sphondylothamnieae and Spermothamnieae, seemingly reflecting the relatively important differences between them, the features used by Hommersand are shown to be invalid by the following examples:

1. In several cases in the Sphondylothamnieae both spiral and orthostichous arrangement of whorl-branchlets occurs within the one species. In both Sphondylothamnion multifidum and Mazoyera lyallii a form occurs in which the first formed whorl-branchlets are formed spirally (i.e. not orthostichously), with the members of alternating whorls sometimes but not always superimposed. In other forms of these species, only two whorl-branchlets are formed per axial cell and these are distichously arranged. Both conditions also occur within one genus; the whorl-branchlets of Mazoyera repens are always orthostichous whereas those of Mazoyera halura are never orthostichous.

TABLE 11.- Differences between the Crouanioideae and Ceramioideae

FEATURE	CROUANIOIDEAE	CERAMIOIDEAE
1. Arrangement of whorl-branchlets	not orthostichous, but superimposed on alternate axial cells	orthostichous
2. Sterile cell on supporting cell	absent	present
3. Carpogonial branch initial	enlarges between divisions	does not enlarge between divisions
carpogonial branch	recurved	in a straight line
4. Connecting cell	remains as a process with own nucleus after fusion with auxiliary cell	fuses completely with auxiliary cell

2. In the genus *Wrangelia* within the tribe Wrangelieae, there are both species with a sterile cell on the supporting cell (*W. penicillata*) and species without such a cell (*W. plumosa*). This difference could be regarded as important enough to separate these species into two genera (see p. 93) but certainly not into separate tribes or subfamilies.

3. Although details of carpogonial branch formation have not been followed closely in all species in the present study, in representative cases from the three tribes the carpogonial branch initial enlarges between divisions and always produces a curved or hooked carpogonial branch. In no cases are the cells in a straight line.

4. In the Wrangelieae the connecting cell is occasionally discernable as either a process (usually without a nucleus) or empty cell wall attached to the auxiliary cell (*W. princeps* - Fig. 3B, *W. plumosa* - Fig. 5C), but in most cases fusion appears to be complete. In the Sphondylothamnieae and Spermothamnieae a similar situation occurs. In several cases (*Shepleya claviformis* - Fig. 30C, *Tiffaniella cymodoceae* - Fig. 40B, and *Ptilothamnion schmitzii* - Fig. 44C) protruberances from the auxiliary cell, which were probably remains of a connecting cell, were observed. In *Wollastoniella myriophylloides* (Fig. 33D) this process was nucleated. However in most cases in these two tribes the connecting cell is not discernable after fusion. Wollaston (1968, p.399) pointed out

that it probably depends on the stage of fusion at which the material was fixed as to whether the connecting cell can be seen attached to the auxiliary cell. Thus both situations occur in both of Hommersand's subfamilies.

On the other hand, Kylin's two developmental lines, based on the positions of the procarps, seem to reflect more fundamental differences in the reproductive structures of these plants and therefore are probably more truly phylogenetic. The Wrangelieae with procarps formed successively on the fertile axis falls into the first developmental line, whereas the Sphondylothamnieae and Spermothamnieae with subterminal procarps are placed in the second developmental line.

Detailed studies on other tribes of the Ceramiaceae will help to clarify the importance of Kylin's developmental lines.

B. Evolutionary Relationships

Relationships within each tribe and genus studied have been discussed under the separate sections. Here, more general relationships of the tribes are discussed.

1. Wrangelieae

The Wrangelieae has very definite affinities with the more primitive tribes of the Ceramiaceae, despite the highly specialised mode of development of the gonimoblast. The production of procarps in succession near the apices of potentially indeterminate branches is very similar to that found in the Crouanieae and Antithamnieae studied by Wollaston (1968). The procarps of species of *Wrangelia* lacking a sterile cell on the supporting cell are similar to those of the Crouanieae. Those with a sterile cell probably represent the more primitive condition, and may have evolved by reduction from a normal whorl-branchlet as occurs in the Antithamnieae where the supporting cell is the basal cell of an unmodified whorl-branchlet. In the Ceramieae, studied by Hommersand (1963), the sterile group on the supporting cell is represented by 2 - 3 cells. This is an intermediate condition.

The Wrangelieae also resembles the Grouanieae, Antithamnieae and Heterothamnieae in forming only one gonimoblast initial from each auxiliary cell, the residual cell being referred to as the "foot cell" in these tribes.

The tendency of some species of *Wrangelia*, e.g. *W. nobilis*, to form two carpogonial branches on each axial cell of the fertile axis is seen in some species of Antithamnieae (e.g. *Platythamnion nodiferum* (J.Ag.) Wollaston 1968, p.303).

There are also many vegetative similarities between these tribes, particularly the Crouanieae. For example, the relatively small apical cell surrounded by young whorl-branchlets, the formation of whorl-branchlets of a definite form, the origin of indeterminate branches from the basal cells of whorl-branchlets (although branches from axial cells also occur in the Crouanieae), the production of cortical rhizoids from the basal cells of whorl-branchlets, and in some genera, e.g. Ptilocladia (Crouanieae) and W. nobilis, the growth of further laterals outwards from the rhizoids, are features which indicate affinities.

The Wrangelieae resembles the Heterothamnieae in having only erect axes which are attached to the substrate by downwardly projecting rhizoids, in contrast to a tribe such as the Antithamnieae, in which prostrate creeping axes give rise to erect axes.

However, despite the similarities of the Wrangelieae to these more primitive tribes, there are a number of features which ally this tribe with those more advanced in the family. The alternately oblique manner of division of the apical cell occurring in the Wrangelieae is seen in Rhodocallis in the Dasyphilae, and Euptilota in the Ptilotae. Another relatively advanced feature occurring in at least two species of Wrangelia (W. nobilis and W. australis) is dorsiventrality, due to the asymmetric production of whorl-branchlets in a bilateral thallus (primary dorsiventrality, Hommersand, 1963, p.304). Dorsiventrality occurring in other tribes of the Ceramiaceae is mainly of the secondary type, which is the result of prostrate axes producing erect axes on one side and often haptera on the other.

The compact spermatangial heads in the Wrangelieae resemble those occurring in advanced tribes such as the Sphondylothamnieae.

In the Crouanieae, the spermatangia are the final cells of ordinary whorl-branchlets, while in the Antithamnieae they are more highly modified, but still relatively loose and branch-like compared with the constituent branchlets in the spermatangial heads of the Wrangelieae. Specialised involucral branchlets borne on the stalk cell of the spermatangial head of the Wrangelieae also show an advance over the above tribes. The production of terminal carposporangia and development of a large central fusion cell are features mostly seen in advanced Ceramiaceae.

Thus the Wrangelieae exhibits features which are both primitive and advanced. The tribe probably arose fairly early in the evolution of the family and retained a number of primitive features, while it became specialised in others, and certain developments occurred which paralleled other more advanced tribes.

2. Sphondylothamnieae

With respect to reproductive structures, the Sphondylothamnieae is probably one of the most highly evolved groups in the Ceramiaceae, although some vegetative features may be considered as relatively primitive.

The procarps have become restrictied to the subapical cell of the fertile axis, which is in many species a determinate branch - either a whorl-branchlet axis or a lateral of a whorl-branchlet. This contrasts markedly with the more primitive tribes where the procarps are produced in succession along a potentially indeterminate axis. The number of procarps per fertile axial cell has become reduced to one, although in Sphondylothamnion and Shepleya the presence of a second auxiliary cell produced from a pericentral cell other than the supporting cell probably represents a vestige of a second procarp. An occasional second carpogonial branch borne on one of the usually sterile pericentral cells in Mazoyera protensa suggests that this may be a primitive condition. The development of several gonimoblast initials from the auxiliary cell may represent an advance over the single one found in lower tribes. It is also possible that reduction may have occurred in those genera only producing one.

The restriction of carposporangium formation to the terminal cells of the gonimoblast and the formation of a large fusion cell incorporating one or two cells of the fertile axis, as in the Wrangelieae, are highly advanced features.

The most distinctive feature is the formation of the inner involucrum from the sterile cells associated with the procarp. This development parallels the production of the pericarpic filaments surrounding the gonimoblast in the Dasyaceae, Delesseriaceae and Rhodomelaceae. These filaments are similar in origin and are formed by division of the sterile pericentrals occurring on the fertile axial cells together with those from the axial cells adjacent to the fertile axial cell.

Vegetatively, most genera of the Sphondylothamnieae have retained the relatively primitive characteristics of free whorls of whorl-branchlets. There has been no vegetative reduction comparable to that occurring in Ceramium and Spyridia, where the whorl-branchlets have become condensed to a ring of "basal cells" at the proximal end of each axial cell. The cortical rhizoids of the Sphondylothamnieae are still relatively free from each other and none of the genera show any tendency towards the production of a pseudoparenchymatous cortex. Instead, the rhizoids adhere to the walls of the axial cells by digitate haptera.

A vegetative feature which is probably relatively advanced is that of multinucleate cells. In Wollastoniella, lower axial cells contain over 4,000 nuclei.

Heterotrichy is another feature which probably indicates evolutionary advance. Spore germination studies have shown that the basic habit of the Ceramiaceae is an erect one and that prostrate axes are secondarily derived. The heterotrichous condition has arisen a number of times in the Ceramiaceae, also occurring in the Antithamnieae and Heterothamnieae tribes.

3. Spermothamnieae

In reproduction, the Spermothamnieae is most closely related to the Sphondylothamnieae, many of the developments in the two tribes being parallel (see discussion on Spermothamnieae, p.253).

It is probable that the common ancestor of the two groups gave rise to the Sphondylothamnieae line by retention of the primitive whorls of whorl-branchlets and the development of the specialised inner involucrum. The Spermothamnieae line probably arose by reduction of the plants to small epiphytic forms, the system of whorl-branchlets being lost and the sterile cells failing to divide after fertilization, except in Interthamnion and Lejolisia aegagropila in which the development has probably occurred independently.

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FIGURES 1 - 50.

FIGURE 1

Wrangelia princeps Harvey

A.	A30,841	Apex of indeterminate branch showing alternately oblique segmentation of the apical cell and order of formation of whorl-branchlets.
B.	"	Mature whorl-branchlet.
D.	"	Cell of mature whorl-branchlet showing nucleus and lobed rhodoplast.
C.	A20,089	Part of a thallus branch showing origin of an indeterminate branch and rhizoids.

FIGURE 1

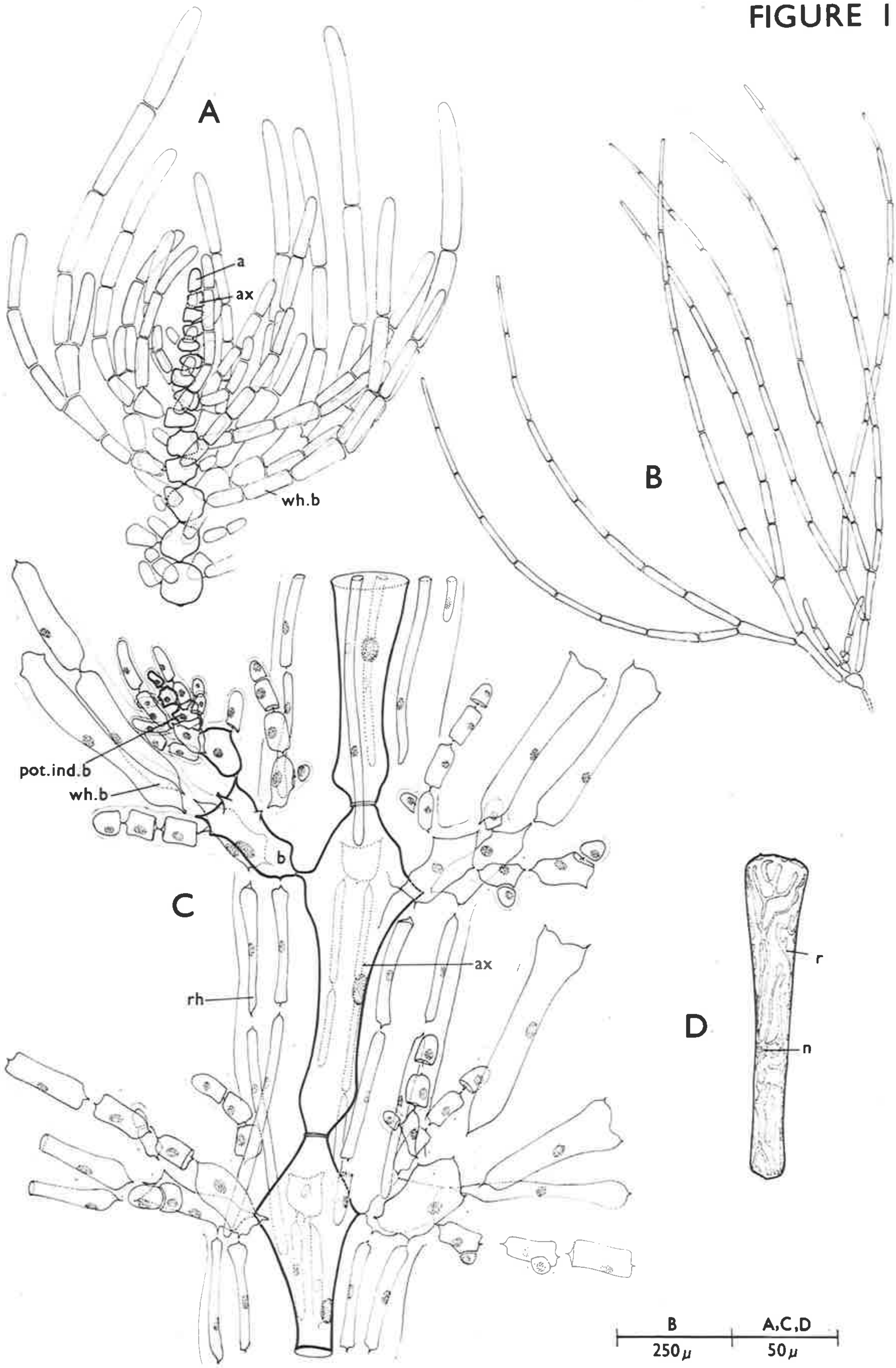

FIGURE 2

Wrangelia princeps Harvey

A.	A20,089	Apex of sporangial branch.
B, C	"	Stages in development of spermatangial head.
D.	"	Longitudinal section of mature spermatangial head with stalk cell and involucral branchlets.
E.	"	Stalk cell and involucral branchlets of spermatangial head.
F.	"	Young fertile axis showing mature and immature procarps.
G.	"	Fertile axis with fertilized procarp showing production of auxiliary cell, connecting cells and division of sterile cell on the supporting cell.

FIGURE 2

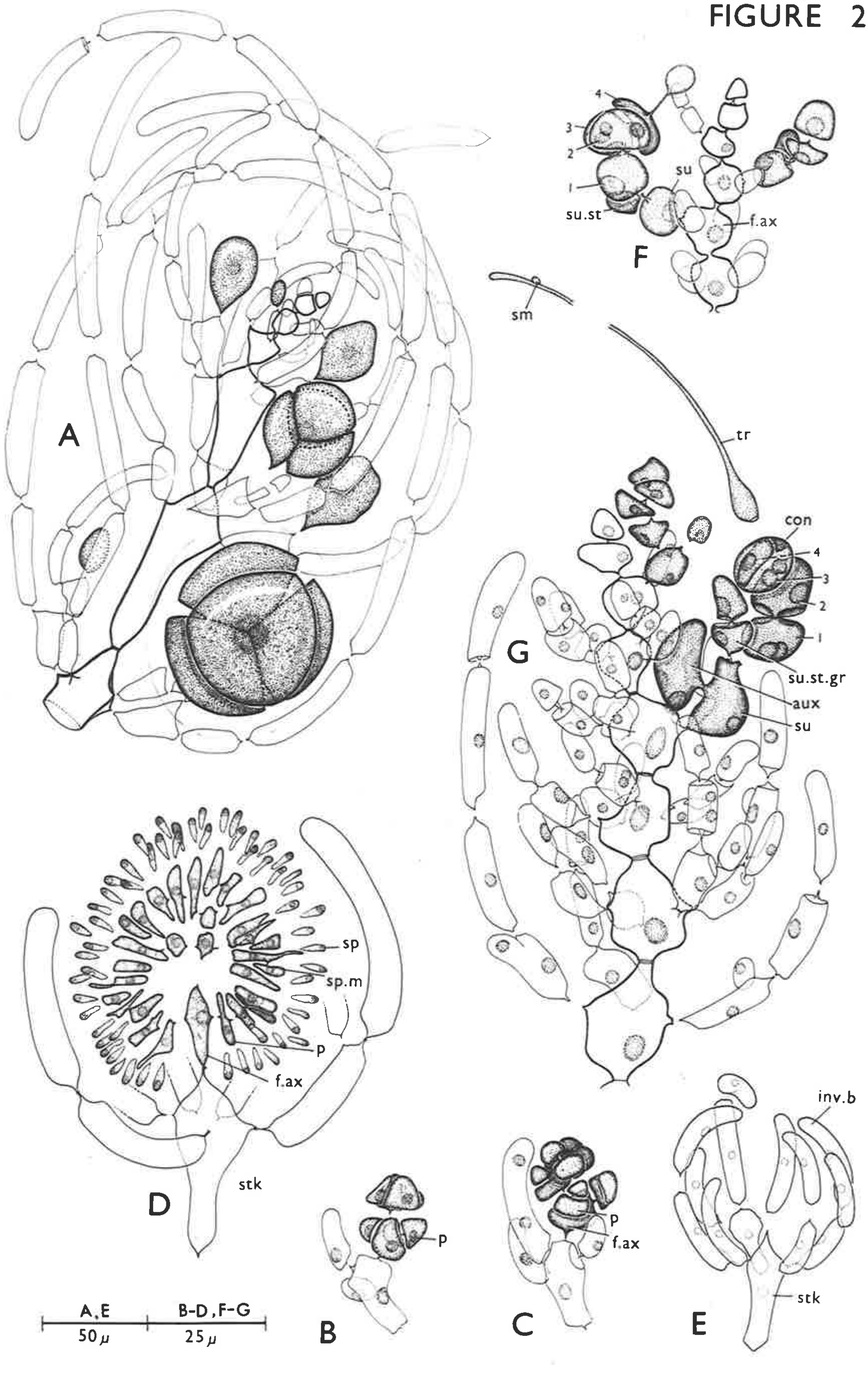
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FIGURE 3

Wrangelia princeps Harvey

A.	A20,089	Fertile axis showing development of gonimoblast and sterile whorl-branchlets.
B.	"	Further development of gonimoblast and carposporangia.
C.	"	Longitudinal section of mature cystocarp with outer involucral filaments.

FIGURE 3

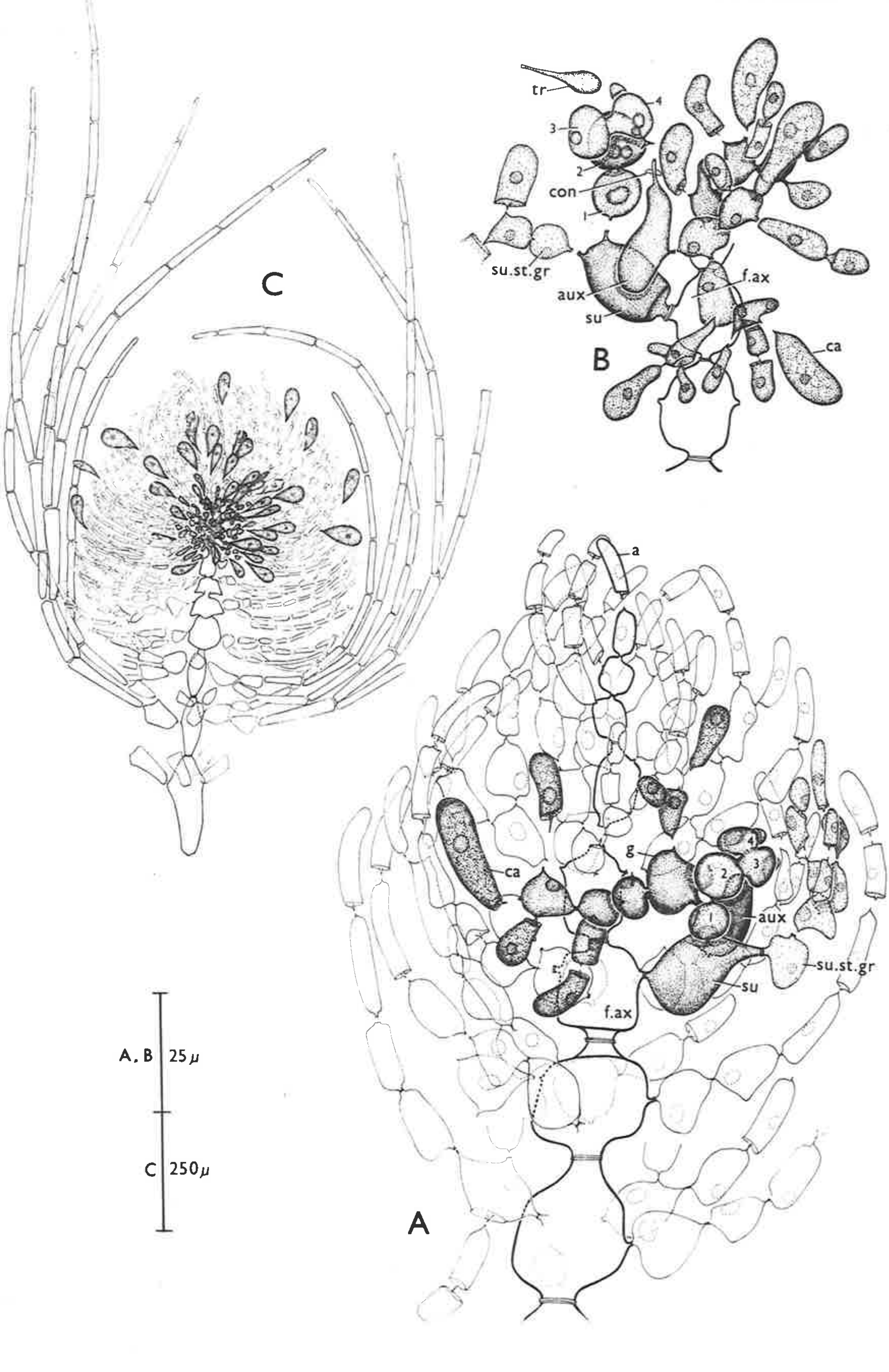

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FIGURE 4

Wrangelia plumosa Harvey

A.	A27,894	Apex of indeterminate branch showing alternately oblique segmentation of apical cell and production of whorl-branchlets.
B.	A30,825	Mature whorl-branchlet.
C.	A27,894	Sporangial whorl-branchlet with vegetative portion.
D.	"	Sporangial whorl-branchlet completely modified, lacking vegetative portion.
E.	"	Tetrasporangium, stalk cell and involucral branchlets.
F.	"	Part of a male branch with whorl-branchlets bearing spermatangial heads
G.	"	Stalk cell and involucral branchlets of spermatangial head.

FIGURE 4

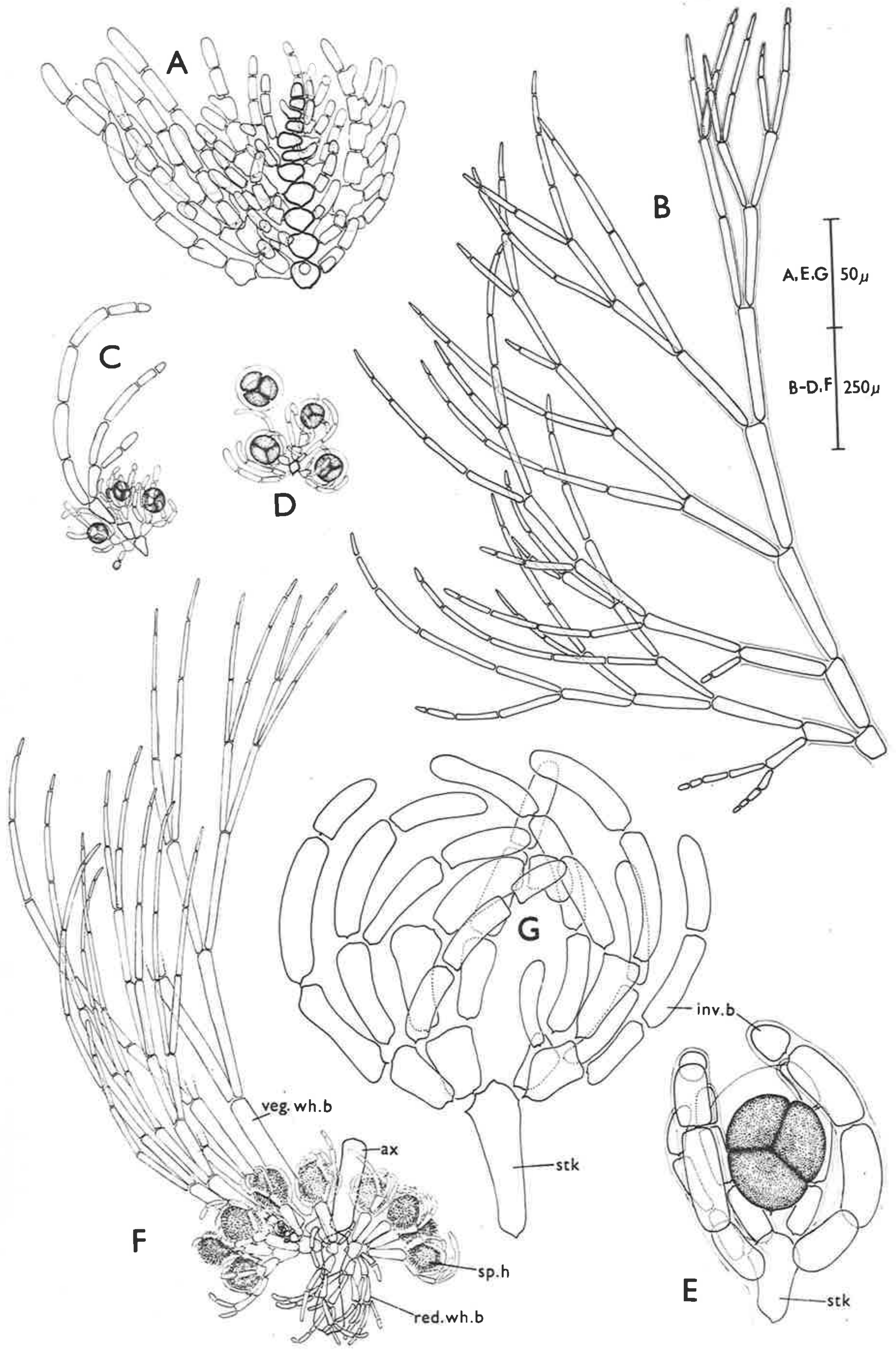
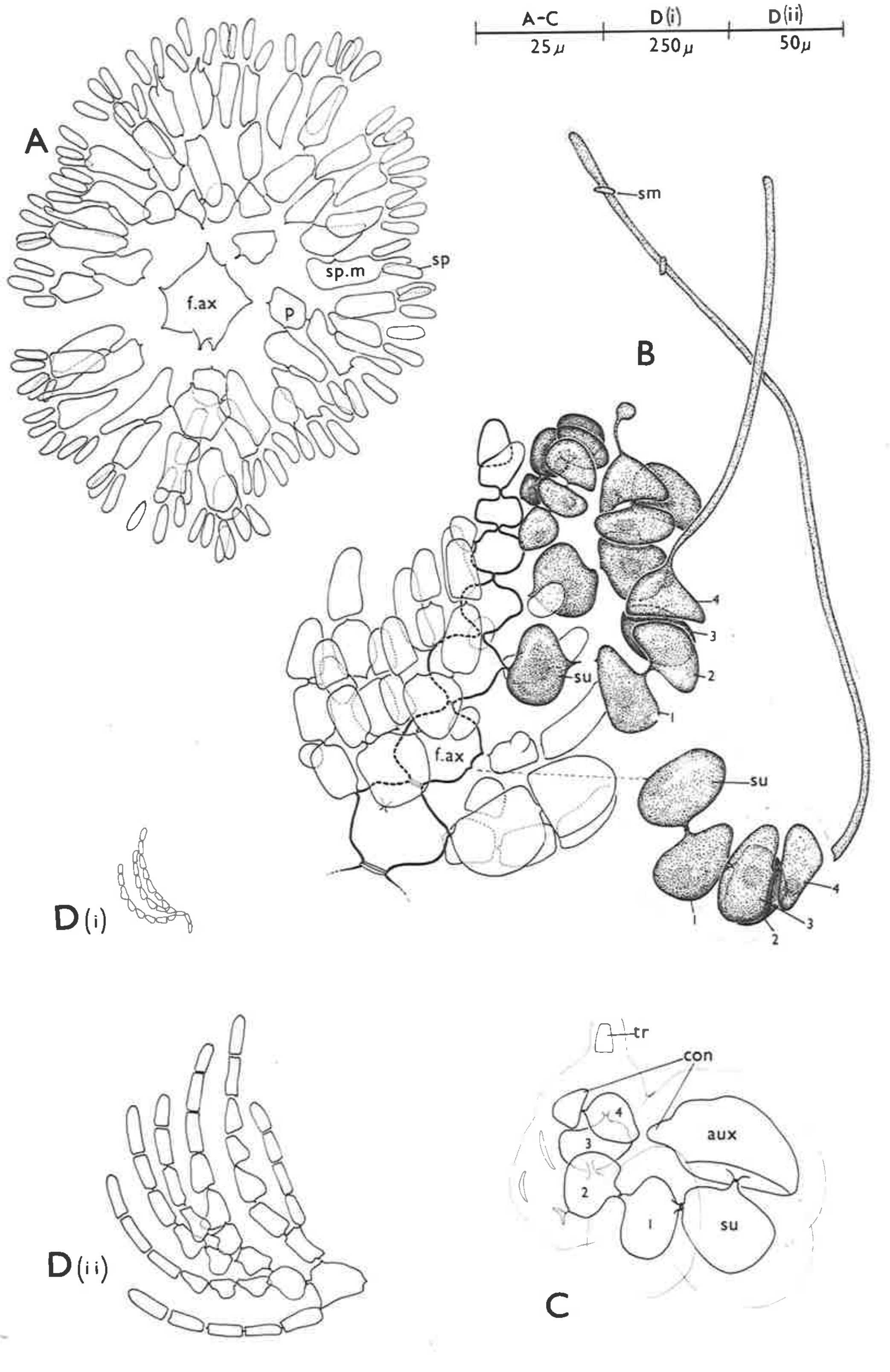


FIGURE 5

Wrangelia plumosa Harvey

A.	A27,894	Transverse section of spermatangial head.
B.	"	Fertile axis with procarps - lowest procarp has become detached.
C.	"	Detached procarp with auxiliary cell and connecting cells.
D(i)	"	Sterile whorl-branchlet of cystocarp showing cells with basal lobes.
D(ii)	"	Same as D(i) at a higher magnification.

FIGURE 5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D(ii)
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FIGURE 6

Wrangelia velutina (Sonder) Harvey

A.	A27,500	Apex of indeterminate branch showing order of formation of whorl-branchlets.
B.	A27,325	Whorl-branchlet.
C.	"	Transverse section of main axis near base of plant showing rhizoidal cortication.
D.	"	Sporangial whorl-branchlet lacking vegetative part.
E(i)	"	Whorl-branchlet bearing immature spermatangial heads.
E(ii)	"	Mature spermatangial head, stalk cell and involucral branchlets.
F.	"	Fertile axis bearing procarps.

FIGURE 6

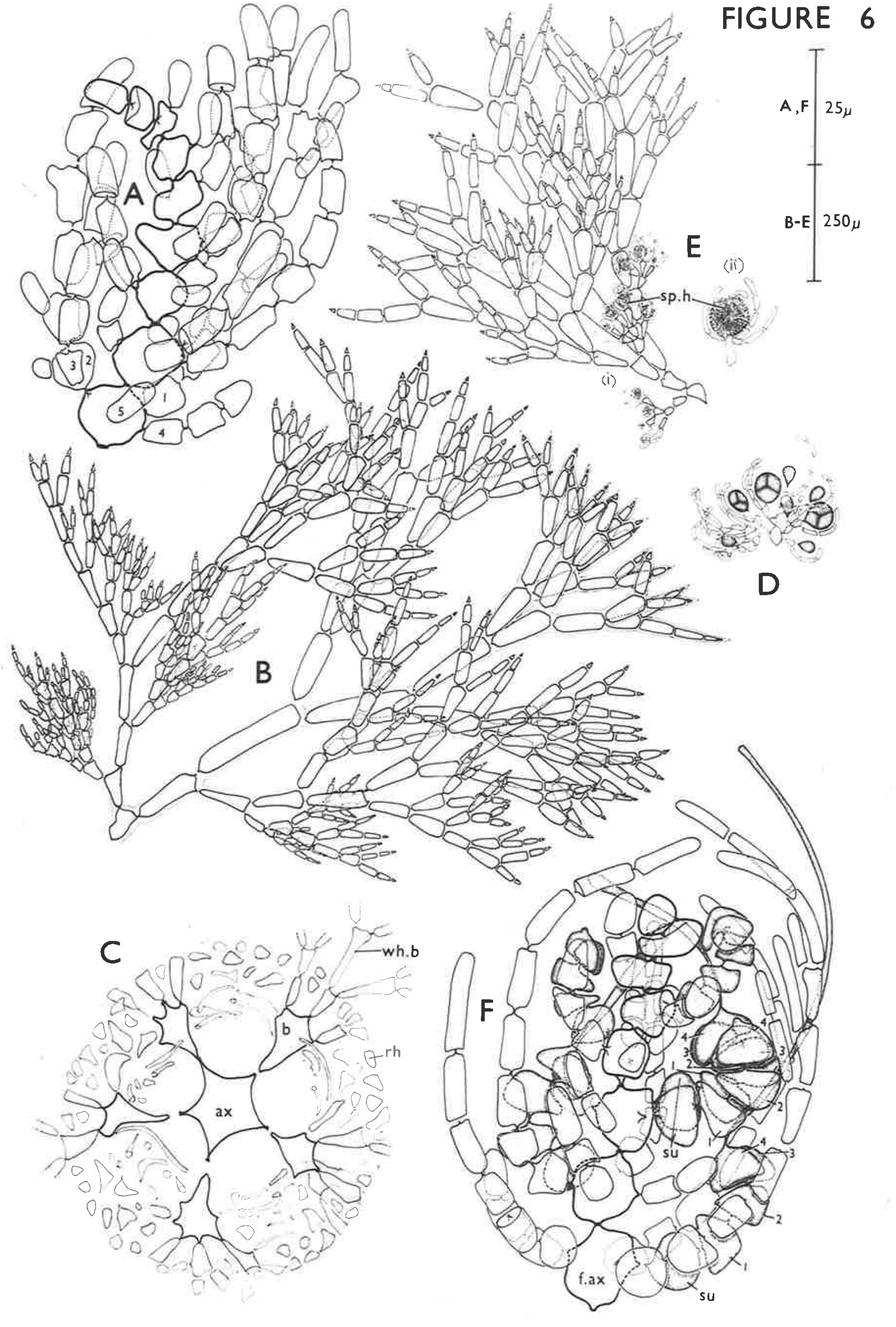
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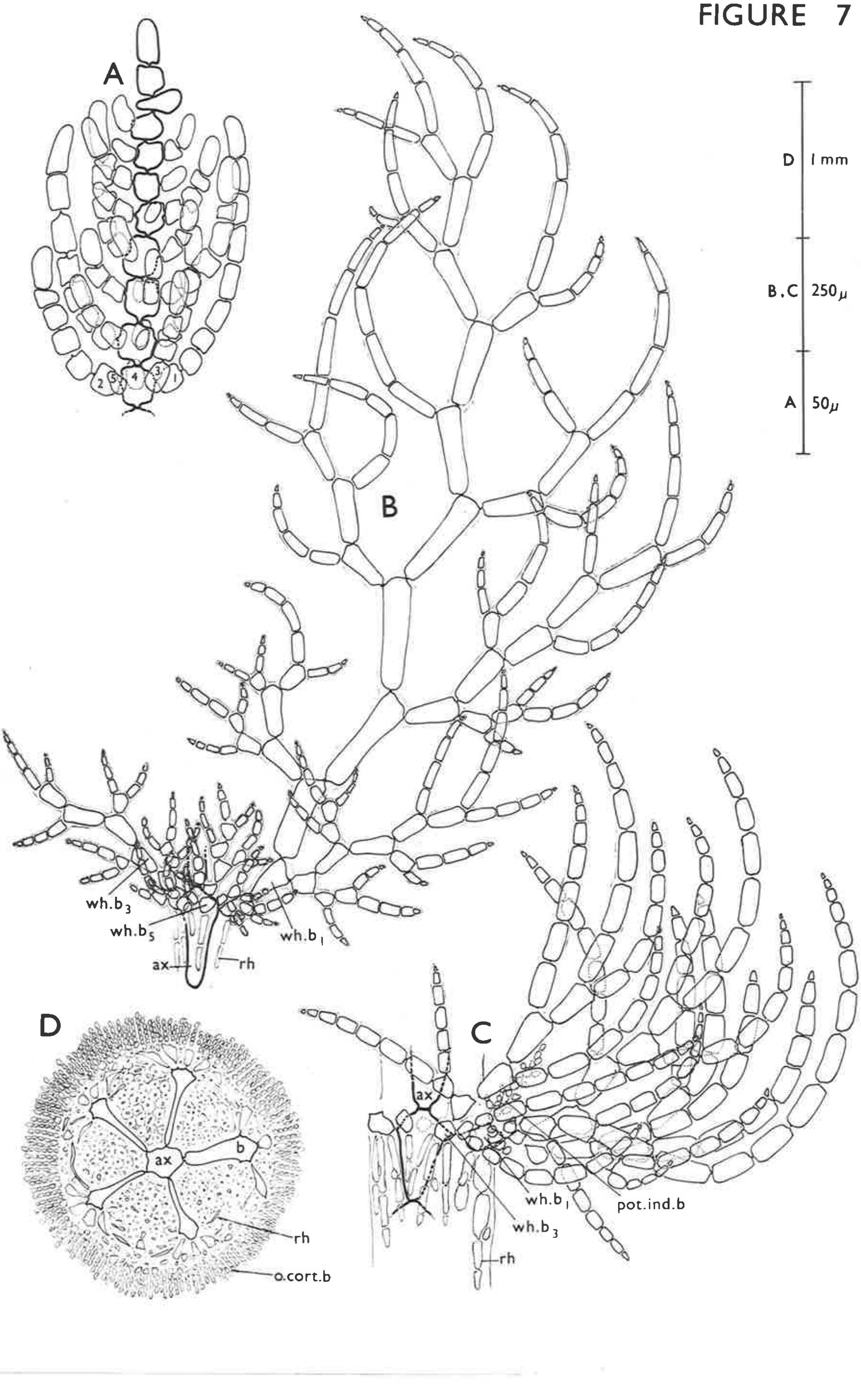
FIGURE 7

Wrangelia nobilis Hooker and Harvey

A.	A16,415	Apex of indeterminate branch showing order of formation of whorl-branchlets.
B.	A29,523	Mature whorl-branchlets of deeper water form.
C.	A2,845	Mature whorl-branchlets of shallow water form. Indeterminate branch borne on the basal cell of first whorl-branchlet.
D.	A21,622	Transverse section of main axis near base of plant showing cortication and outer cortical branchlets.

FIGURE 7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B.C 250μ
A 50μ

FIGURE 8

Wrangelia nobilis Hooker and Harvey

A.	A24,383	Transverse section of sporangial branch.
B.	A27,900	Whorl-branchlet bearing spermatangial heads.
C.	A27,885	Fertile axis with procarps.
D.	"	Procarp with connecting cells and auxiliary cell.

FIGURE 8

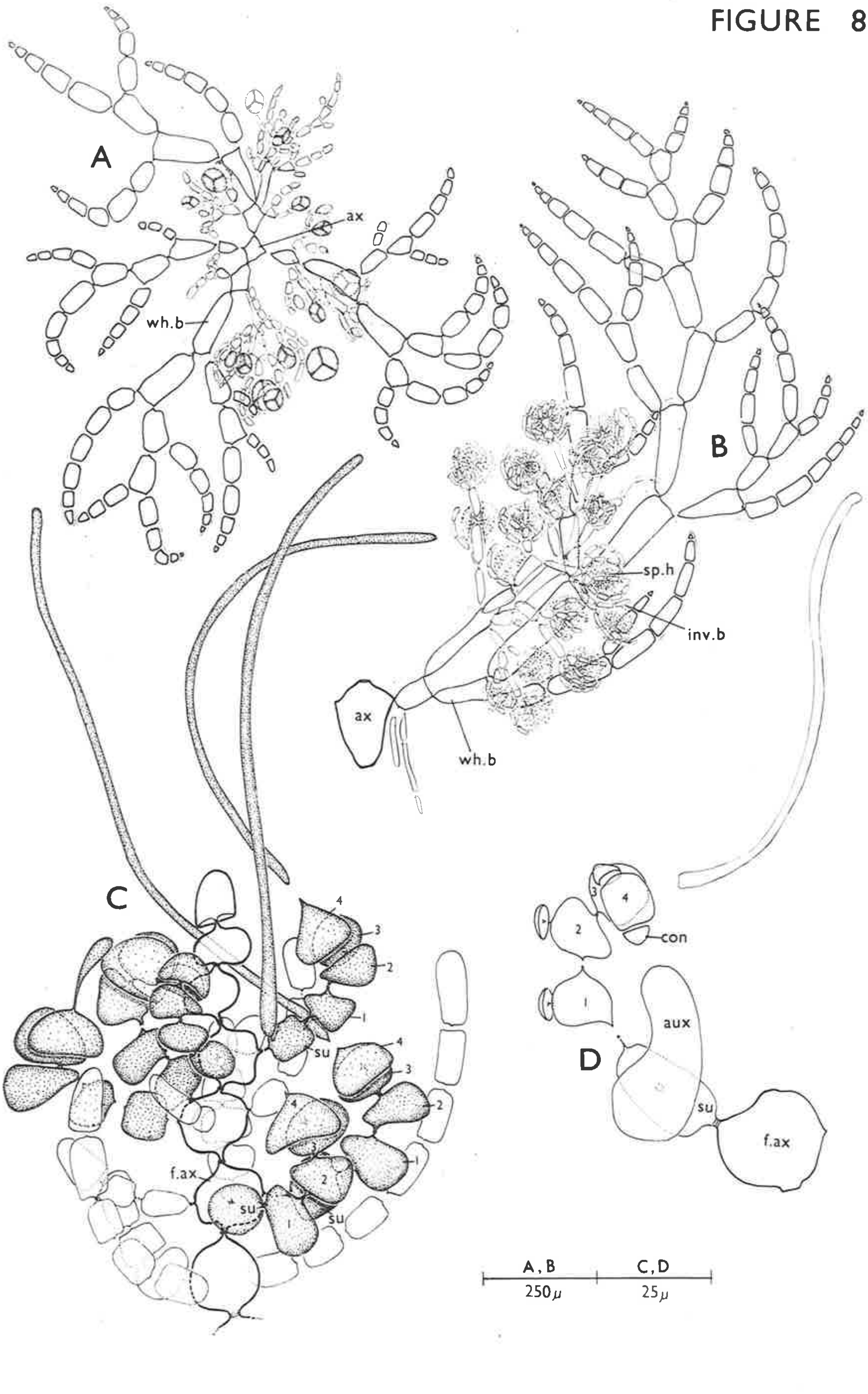
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FIGURE 9

Wrangelia australis (J.Ag.) comb. nov.

A.	A32,174	Apex of indeterminate branch showing order of formation of whorl-branchlets and potentially indeterminate branches.
B.	"	Simplified diagram of lowest two axial cells of A with axial cells of whorl-branchlets.
D.	"	Villose whorl-branchlet.
C.	"	Normal whorl-branchlet.

FIGURE 9

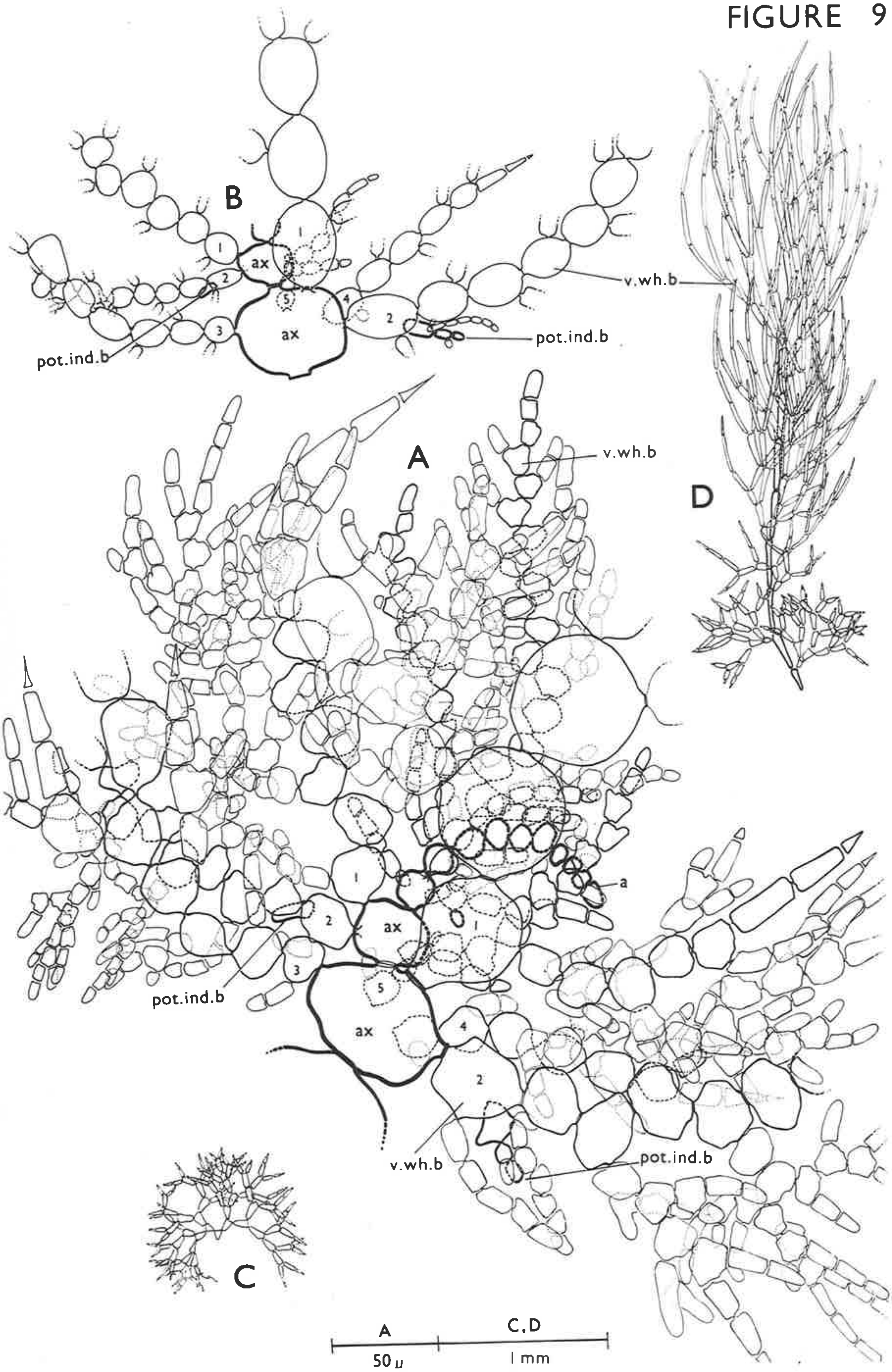
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FIGURE 10

Wrangelia australis (J.Ag.) comb. nov.

A.		Diagram of part of indeterminate axis bearing alternate potentially indeterminate branches on the second-formed whorl-branchlet on each axial cell.
B.	A20,910	Part of rhizoidal cortication showing position of outer cortical branchlets.
C.	"	Transverse section of a main axis showing cortication.
D.	A20,120	Whorl-branchlet bearing tetrasporangia.
E.	A20,081	Longitudinal section of spermatangial head, stalk cell and involucral branchlets.
F.	A33,175	Fertile axis bearing procarps. One axial cell bears two 5-celled carpogonial branches.
G - K.		Orders of formation of whorl-branchlets in *Wrangelia*:
G.		(*W. plumosa*).
H.		*W. penicillata*, *W. princeps*, *W. australis* *W. plumosa*.
I.		*W. velutina*. J. (*W. plumosa*).
K.		*W. nobilis*.

FIGURE 10

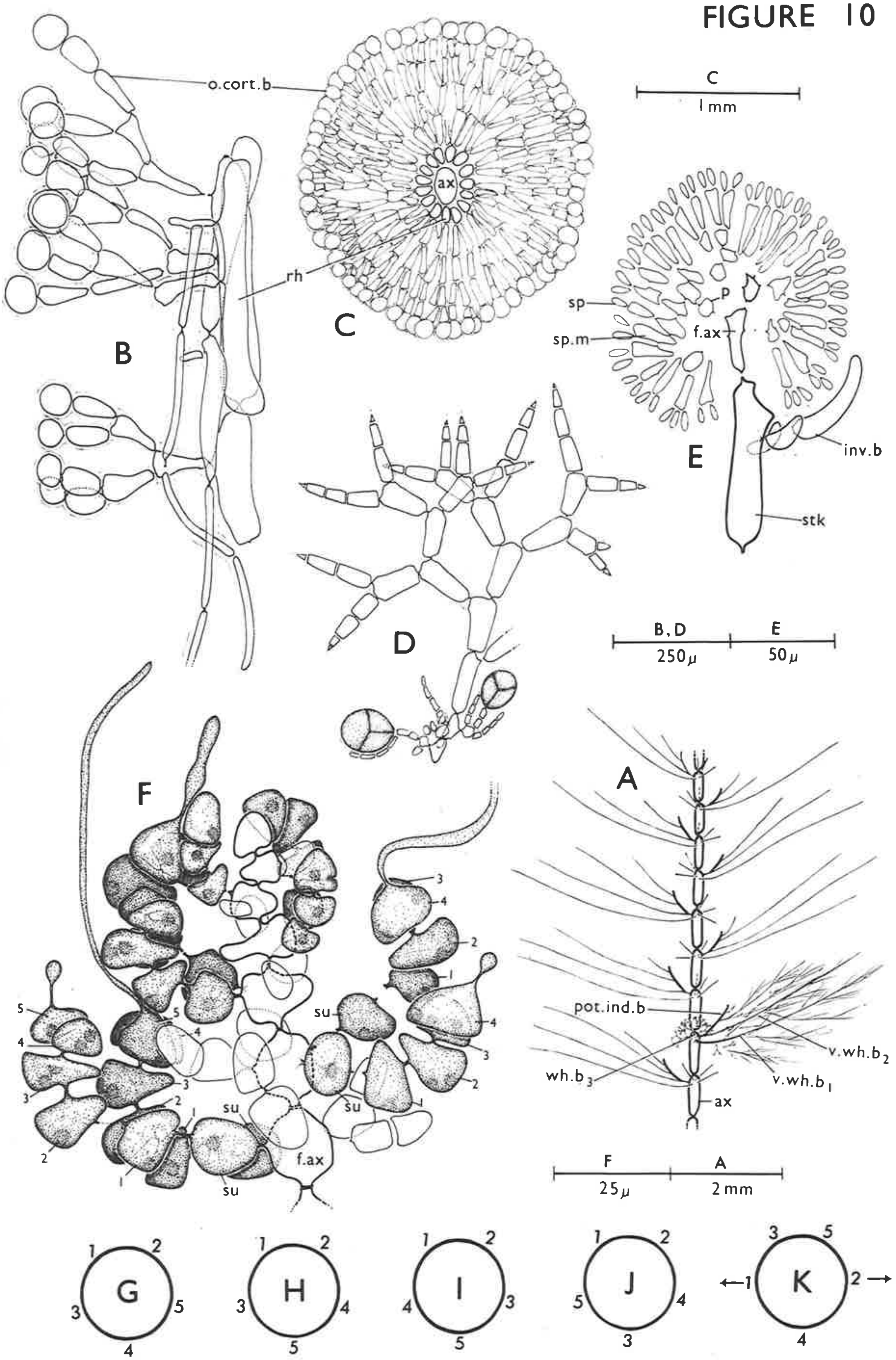
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FIGURE 11

Sphondylothamnion multifidum (Hudson) Naegeli

A.	A28,313	Whorl-branchlet.
B.	"	Apex of indeterminate branch showing production of whorl-branchlets and tetrasporangia.
C.	"	Tetrasporangium with one wall formed.
D.	"	Tetrasporangium with all walls formed.
E.	"	Longitudinal section of spermatangial head.
F.	"	Procarps formed on potentially indeterminate axes.
G.	"	Procarp formed on whorl-branchlet.
H.	"	Young procarp system.
I.	"	Post fertilization stage showing fused carpogonial branch and two auxiliary cells.
J.	"	Inner involucral branchlet from cystocarp.

FIGURE 11

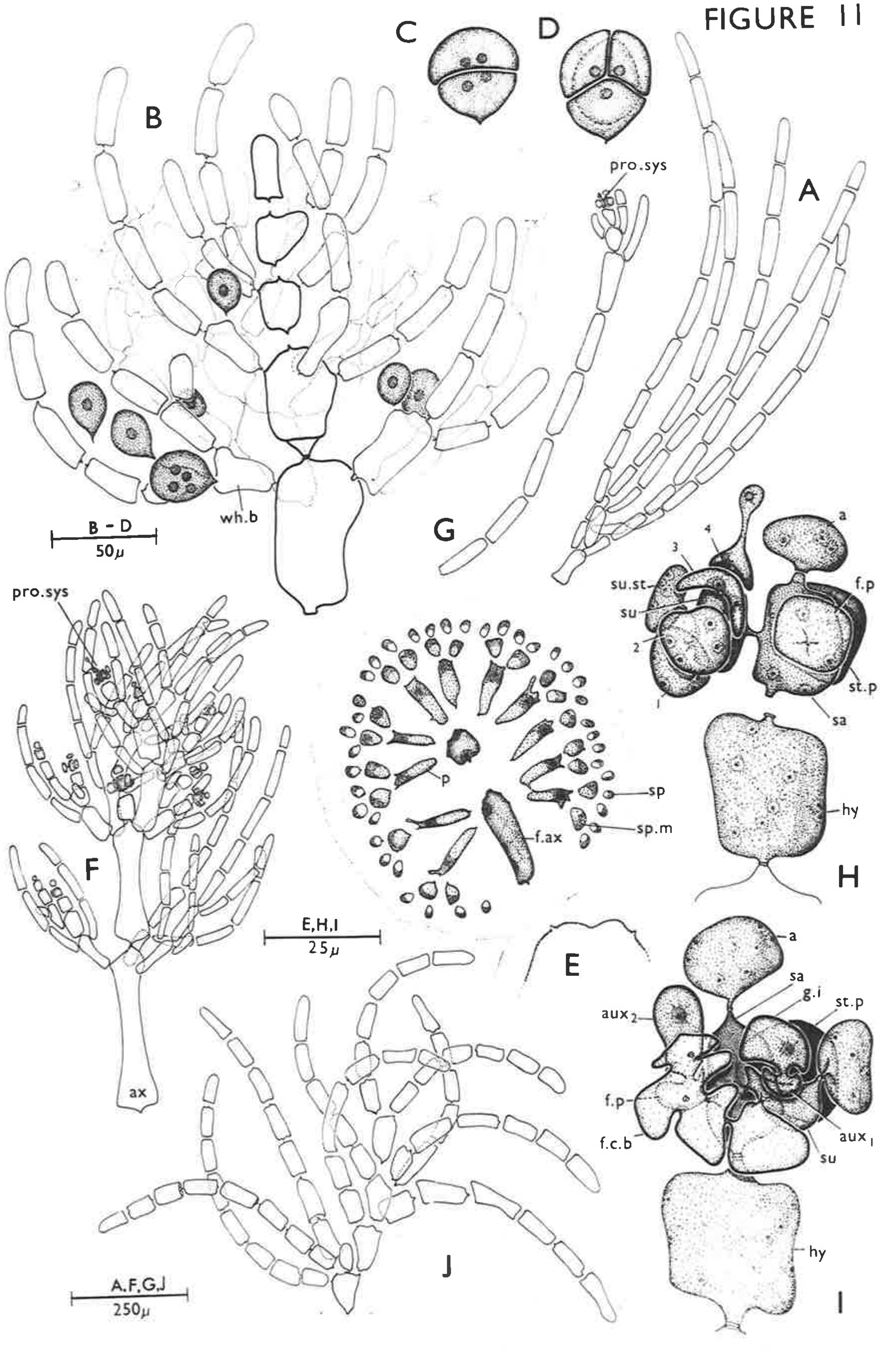
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FIGURE 12

Mazoyera protensa (Harvey) comb. nov.

A.	A26,719	Habit of plant showing non imbricating whorls of whorl-branchlets.
B.	"	Apex of indeterminate branch showing transverse division of the apical cell and production of whorl-branchlets.
C.	A30,730	Part of a main axis showing cortical rhizoids formed from the basal cells of whorl-branchlets and haptera from distal ends of rhizoidal cells.
D.	A26,719	Whorl-branchlet bearing tetrasporangia.

FIGURE 12

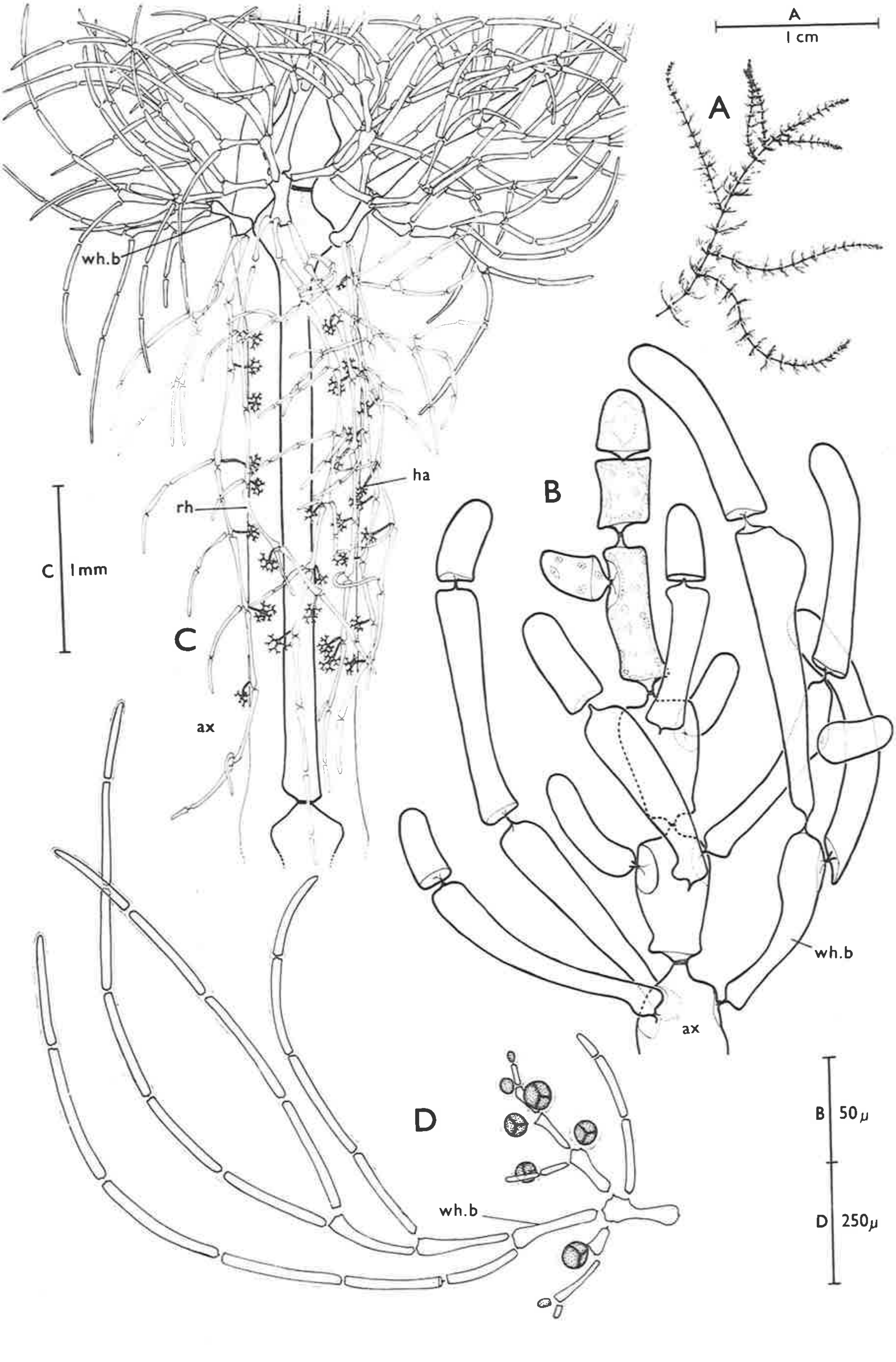


FIGURE 13

Mazoyera protensa (Harvey) comb. nov.

A.	A26,719	Terminal part of whorl-branchlet showing densely protoplasmic procarp system initial and multinucleate vegetative cells.
B - F.	"	Stages in formation of mature procarp system.
B.	"	Procarp system initial has divided to produce apical and subapical cells.
C.	"	Subapical cell with three pericentral cells.
D.	"	First cell of carpogonial branch produced.
E.	"	Second cell of carpogonial branch produced.
F.	"	Mature procarp system with fully formed carpogonial branch.
G.	"	Two procarps produced on one subapical cell (post fertilization).
H.	"	Post fertilization stage showing auxiliary cell, fusion of cells of carpogonial branch and division of sterile cells associated with the procarp.

FIGURE 13

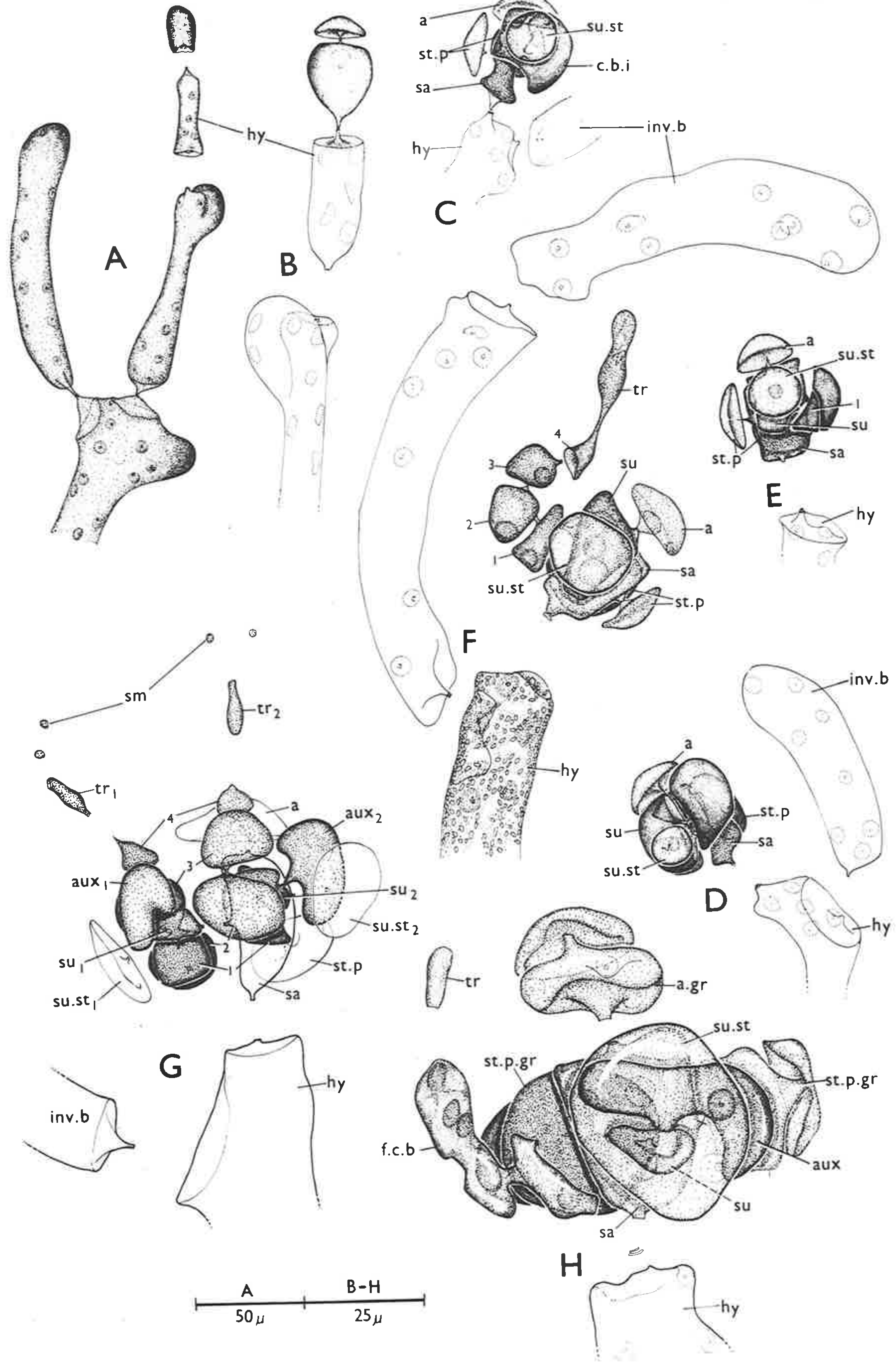

hy
A
B
a
su.st
st.p
c.b.i
sa
hy
inv.b
C
tr
4
3
2
1
su
a
sa
su.st
st.p
F
a
su.st
1
su
st.p
sa
E
hy
sm
tr₂
tr₁
4
a
aux₂
3
aux₁
su₂
su.st₂
2
su₁
1
st.p
su.st₁
sa
G
inv.b
hy
hy
a
su
st.p
sa
su.st
D
inv.b
hy
tr
a.gr
su.st
st.p.gr
st.p.gr
f.c.b
aux
su
sa
H
hy
A
B-H
50µ
25µ

FIGURE 14

Mazoyera protensa (Harvey) comb. nov.

A.	A26,719	Connecting cells produced from the expanded ends of the fused carpogonial branch.
B.	"	Fusion occurring between the elongate auxiliary cell and nearer connecting cell.
C.	"	Primary gonimolobe initials produced from the ends of the auxiliary cell.
D.	"	Young carposporophyte showing one gonimolobe, fusion between the auxiliary cell, supporting cell and subapical cell. Two of the four inner involucral branchlets are shown. The involucral branchlet on the hypogenous cell has been omitted.

FIGURE 14

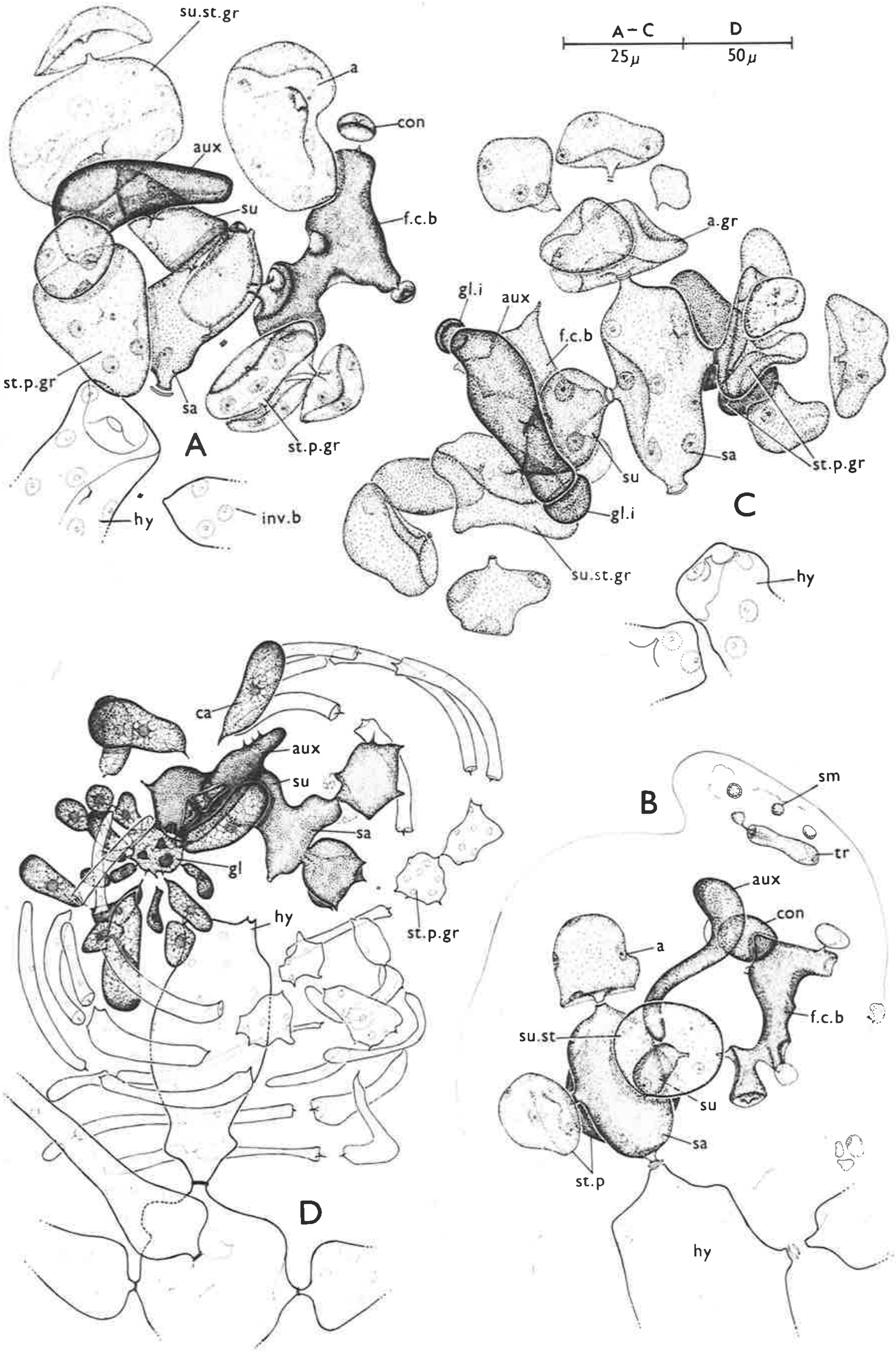

A – C
25μ
D
50μ
su.st.gr
a
con
aux
su
f.c.b
st.p.gr
sa
st.p.gr
A
hy
inv.b
a.gr
gl.i
aux
f.c.b
sa
st.p.gr
su
gl.i
C
su.st.gr
hy
ca
aux
su
sa
gl
hy
st.p.gr
D
sm
B
tr
aux
con
a
f.c.b
su.st
su
sa
st.p
hy

FIGURE 15

Mazoyera halura (Harvey) comb. nov.

A.	A27,887	Habit of plant showing imbricating whorl-branchlets.
B.	A30,629	Prostrate and erect axes with haptera.
C.	A19,301	Whorl-branchlet with tetrasporangia.
D.	MEL15,359	Young stage in the development of spermatangial heads.
E.	"	Longitudinal section of a mature spermatangial head.

FIGURE 15

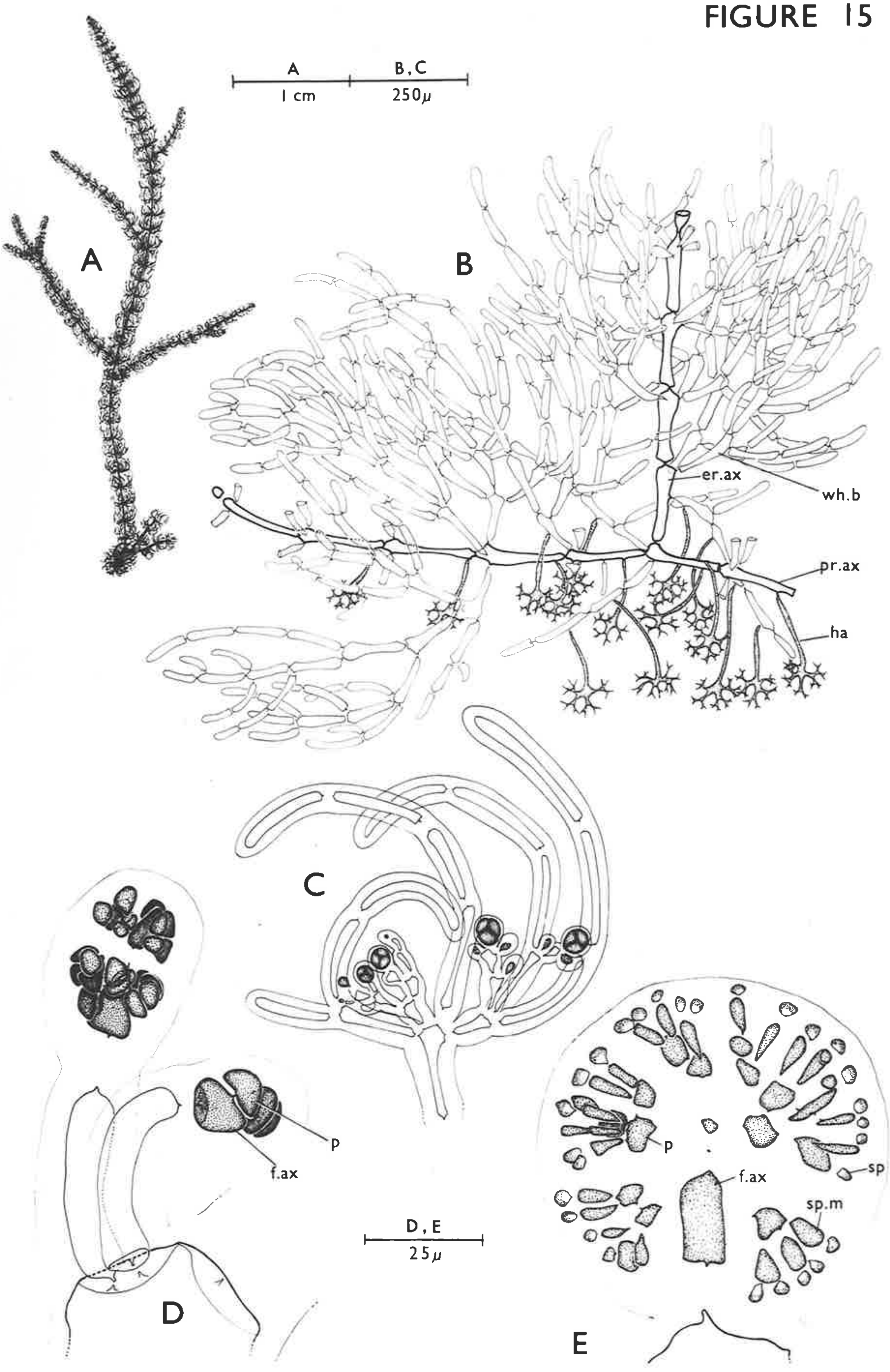


FIGURE 16

Mazoyera halura (Harvey) comb. nov.

A.	A28,003	Mature procarp system.
B.	"	Post fertilization stage - production of auxiliary cell.
C.	"	Fusion of cells of carpogonial branch.
D.	"	Segmentation of auxiliary cell and division of sterile cells associated with the procarp.
E.	"	Early stage in production of gonimolobes (N.B. inner involucral branchlet from supporting cell omitted).
F.	"	One gonimolobe showing production of carposporangia.

FIGURE 16

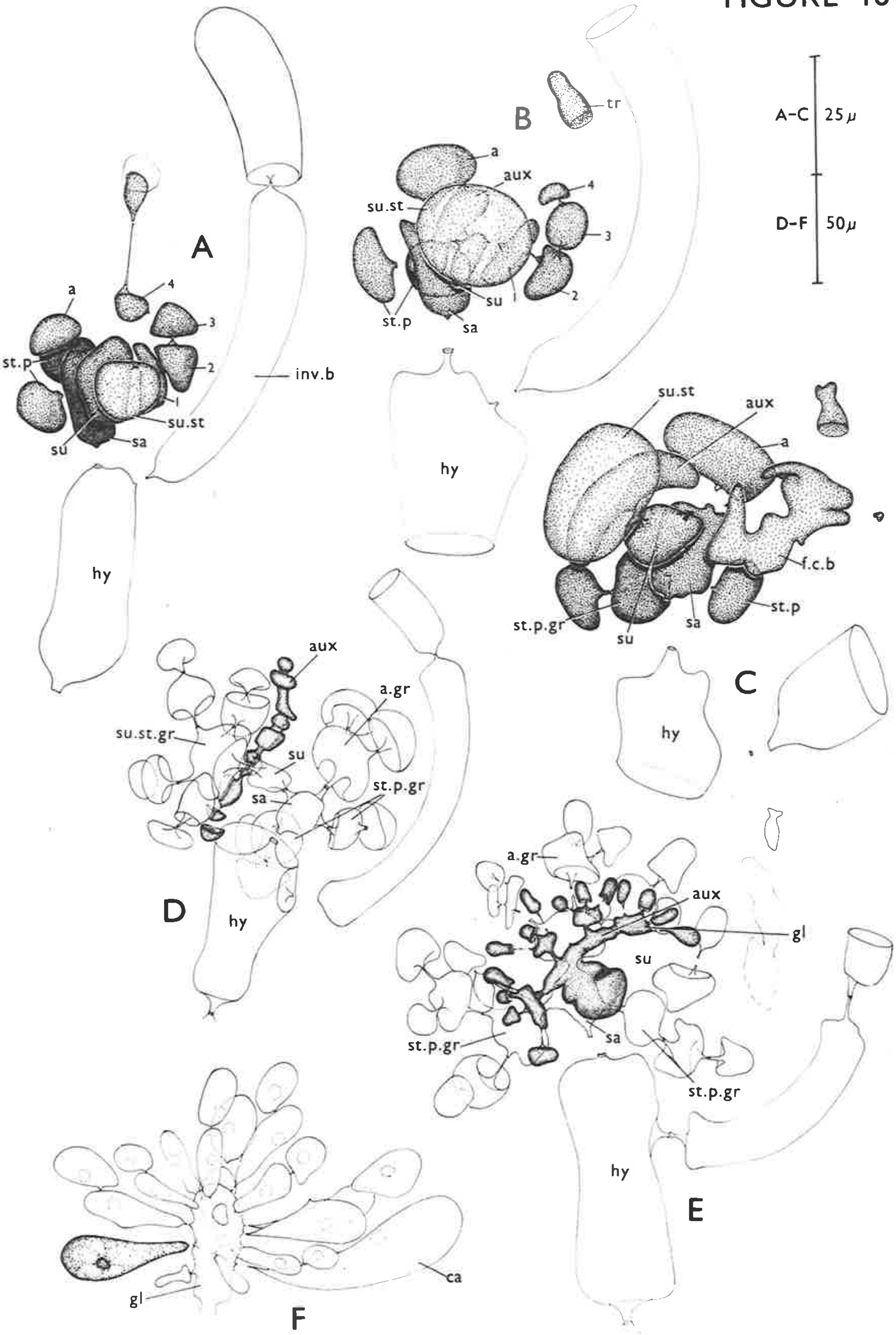

A
a
4
3
2
1
st.p
su
sa
su.st
inv.b
hy
B
tr
a
aux
su.st
4
3
2
1
su
st.p
sa
hy
A–C 25µ
D–F 50µ
C
su.st
aux
a
f.c.b
st.p
sa
su
st.p.gr
hy
D
aux
a.gr
su.st.gr
su
sa
st.p.gr
hy
E
a.gr
aux
gl
su
sa
st.p.gr
st.p.gr
hy
F
gl
ca

FIGURE 17

Mazoyera lyallii (Harvey) comb. nov.

A.	A29,774	Habit of plant.
B.	"	Prostrate and erect axes with haptera.
C.	"	Part of a main axis showing origin of cortical rhizoids.
D.	"	Whorl-branchlet bearing tetrasporangia.
E.	A21,354	Whorl-branchlet bearing tetrasporangia, 2-3 per cell.

FIGURE 17

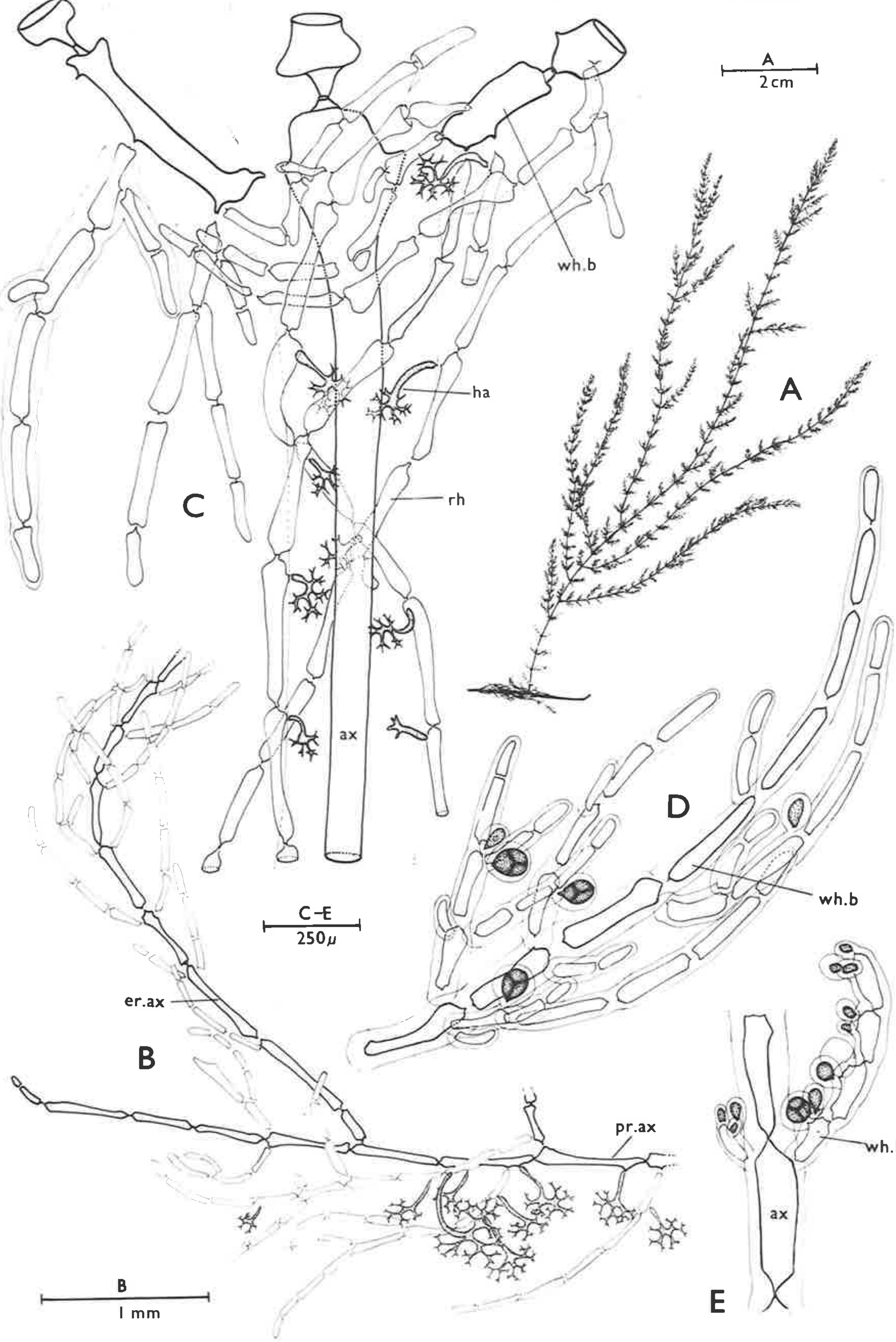


FIGURE 18

Mazoyera lyallii (Harvey) comb. nov.

A.	A29,774	Apex of indeterminate branch showing production of whorl-branchlets and position of spermatangial heads.
B-E	"	Stages in formation of spermatangial head.
E.	"	Longitudinal section of mature spermatangial head.
F.	"	Young stage in formation of procarp.
G.	"	Mature procarp system.
H.	"	Post fertilization stage showing auxiliary cell and fusion of cells of the carpogonial branch.

FIGURE 18

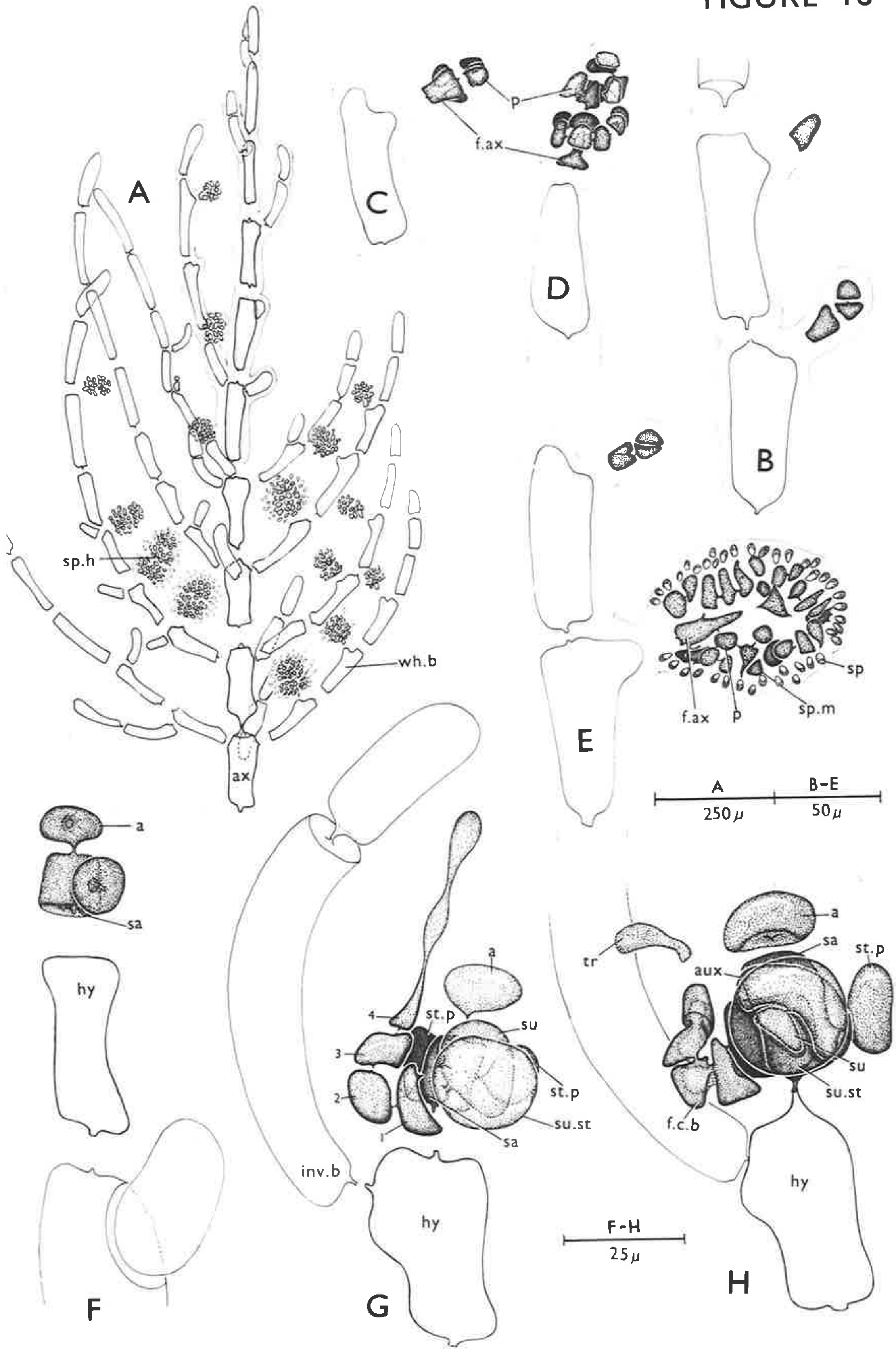

A
sp.h
wh.b
ax
C
p
f.ax
D
B
E
f.ax
p
sp.m
sp
A
250μ
B-E
50μ
a
sa
hy
F
4
3
2
1
st.p
su
a
st.p
su.st
sa
inv.b
hy
G
tr
a
sa
aux
st.p
su
su.st
f.c.b
hy
F-H
25μ
H

FIGURE 19

Mazoyera lyallii (Harvey) comb. nov.

A.	A29,774	Post fertilization stage showing gonimolobe initials and sterile groups produced by division of the sterile cells associated with the procarp.
B.	"	Further segmentation of auxiliary cell.
C.	"	Early stage in production of gonimolobes.
D.	"	Mature carposporophyte and involucral filaments.

FIGURE 19

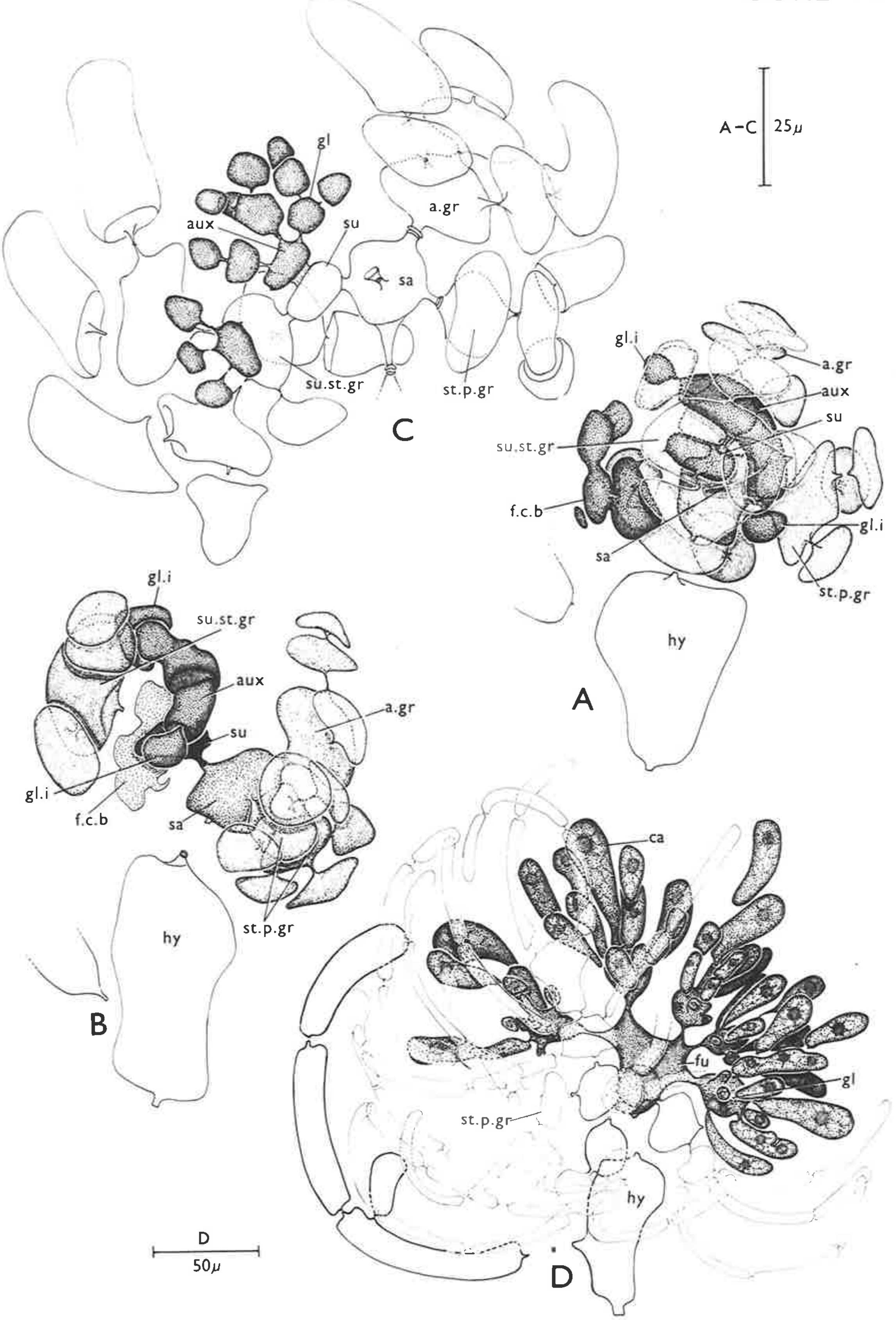

A–C 25μ
gl
aux
su
a.gr
sa
su.st.gr
st.p.gr
C
gl.i
a.gr
aux
su
su.st.gr
f.c.b
gl.i
sa
st.p.gr
hy
A
gl.i
su.st.gr
aux
a.gr
su
gl.i
f.c.b
sa
st.p.gr
hy
B
ca
fu
gl
st.p.gr
hy
D
D
50μ

FIGURE 20

Mazoyera repens sp. nov.

A.	A30,665	Habit of epiphyte on host.
B.	"	Prostrate axis bearing erect and prostrate whorl-branchlets.
C.	"	Whorl-branchlet bearing tetrasporangia.
D.	"	Early stages in the formation of the spermatangial head.
E.	"	Longitudinal section of a mature spermatangial head.

FIGURE 20

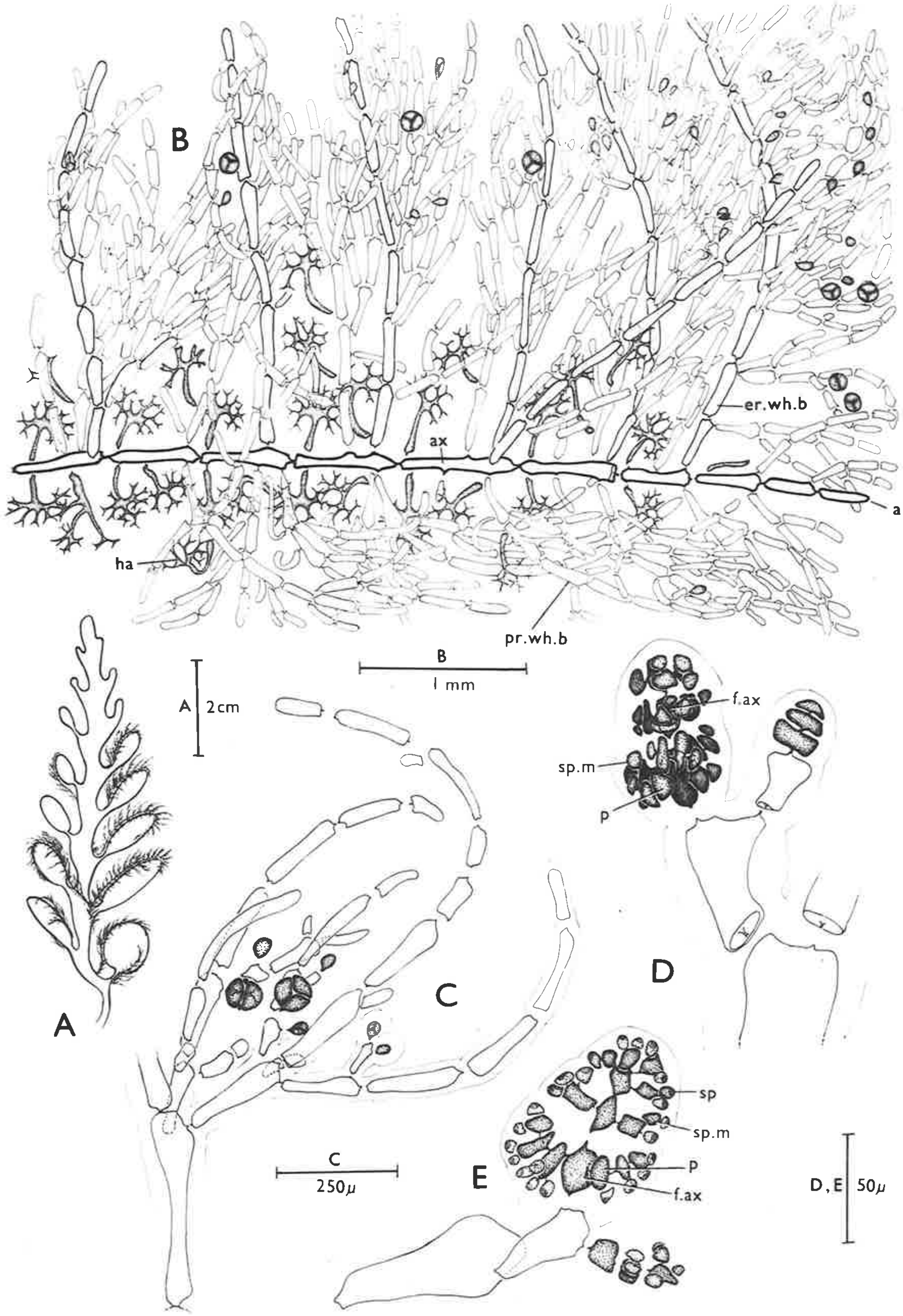

B
er.wh.b
ax
a
ha
pr.wh.b
B
1 mm
A 2cm
f.ax
sp.m
p
A
C
D
sp
sp.m
p
f.ax
C
250μ
E
D, E 50μ

FIGURE 21

Mazoyera repens sp. nov.

A-C.	A30,665	Stages in formation of procarp system.
C.	"	Mature procarp system.
D.	"	Post fertilization stage showing fused carpogonial branch.

FIGURE 21

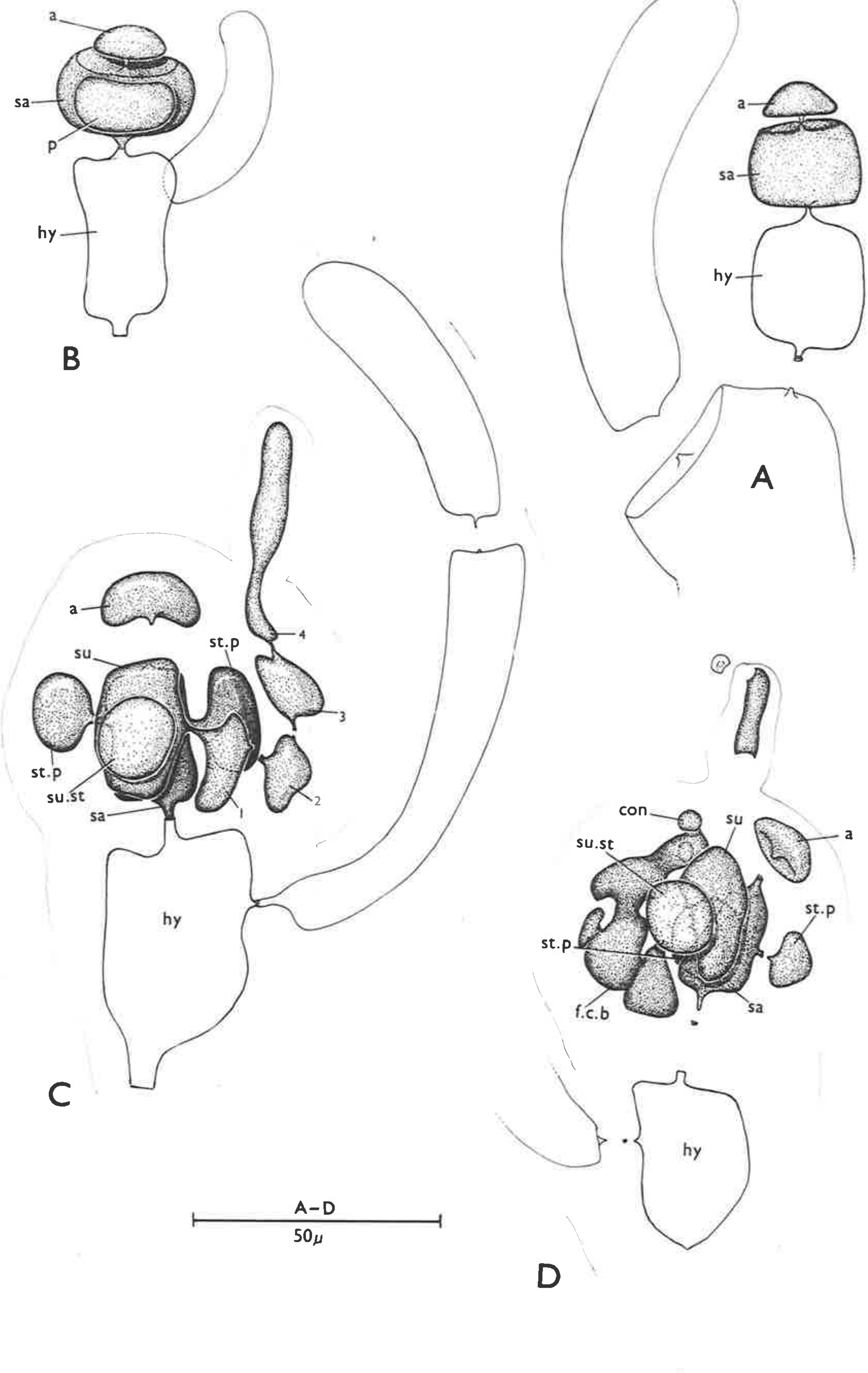

a
sa
p
hy
B
a
sa
hy
A
a
su
st.p
4
3
st.p
su.st
sa
1
2
hy
C
con
su
a
su.st
st.p
st.p
f.c.b
sa
hy
D
A–D
50μ

FIGURE 22

Mazoyera repens sp. nov.

A.	A30,665	Stage showing gonimolobe initials and division of sterile cells associated with the procarp.
B.	"	Early stage in the development of the carposporophyte and involucrum. One sterile pericentral cell remains undivided.
C.	"	Mature carposporophyte and involucral branchlets.

FIGURE 22

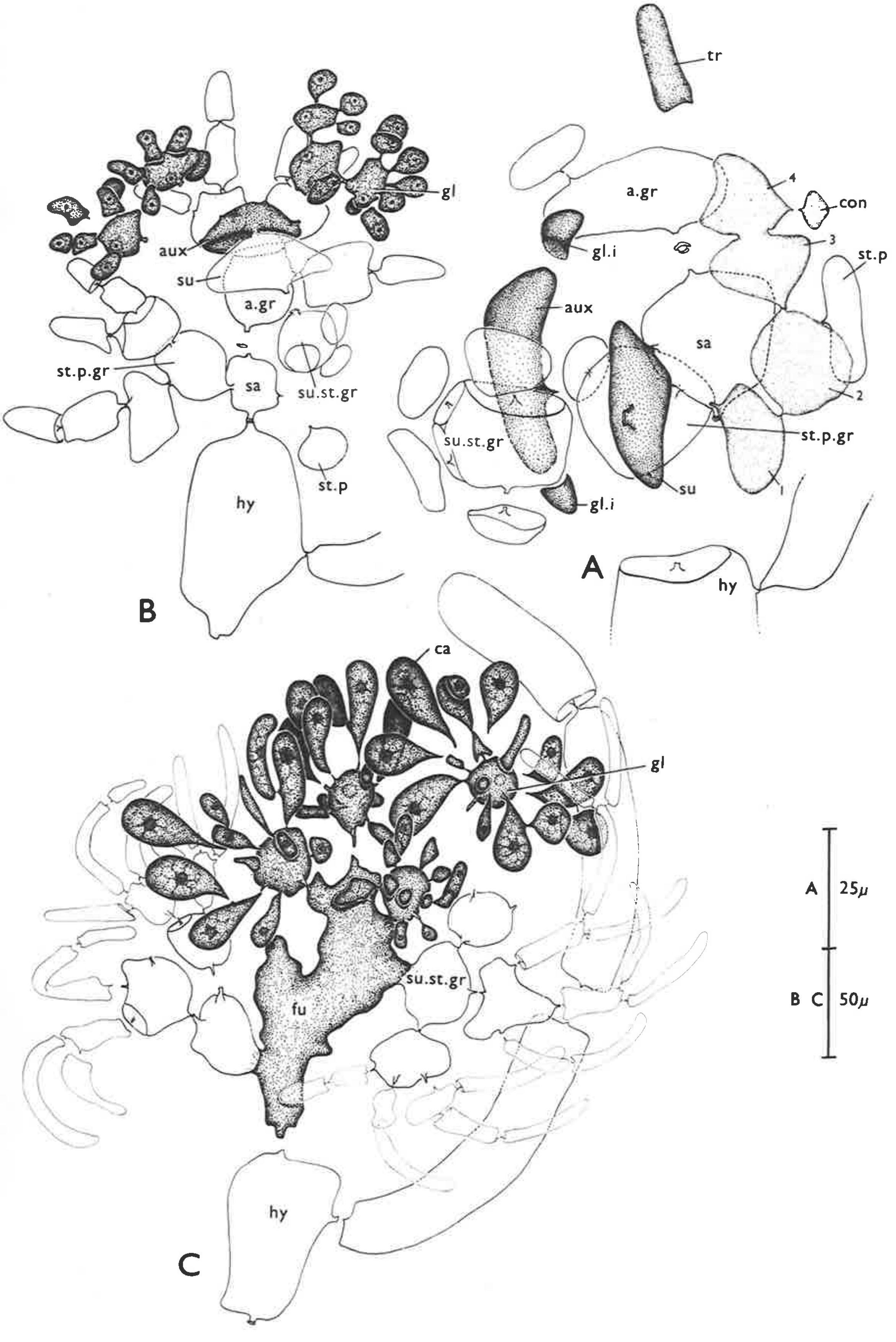

tr
a.gr
4
con
gl.i
3
st.p
aux
sa
2
st.p.gr
su.st.gr
su
1
gl.i
A
hy
gl
aux
su
a.gr
st.p.gr
sa
su.st.gr
st.p
hy
B
ca
gl
su.st.gr
fu
hy
C
A 25µ
B C 50µ

FIGURE 23

Shepleya wattsii (Harvey) comb. nov.

A.	A27,904	Apex of indeterminate branch showing transverse division of apical cell and production of whorl-branchlets (living condition).
B.	"	Similar to A but in plasmolysed condition.
C.	"	Part of a main axis showing the origin of a cortical rhizoid from the basal cell of a whorl-branchlet, and haptera from the proximal ends of rhizoidal cells.
D.	"	Small sporangial branchlets borne laterally on the cells of a whorl-branchlet.
E.	"	Whorl-branchlet bearing laterally small spermatangial branchlets.
F.	"	Early stage in development of a spermatangial head.
G.	"	Longitudinal section of a spermatangial head.

FIGURE 23

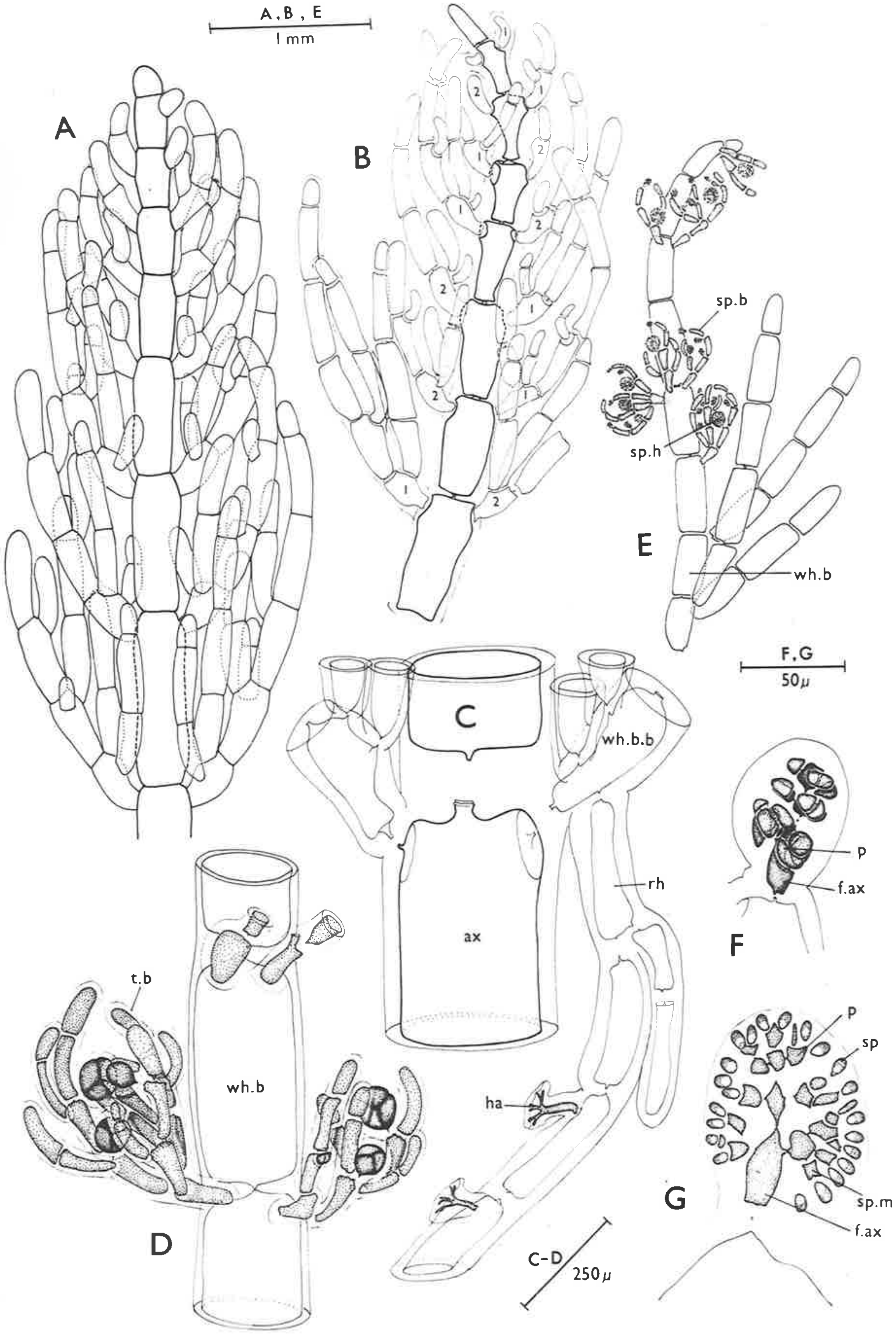

A, B, E
1 mm
A
B
1
2
E
sp.b
sp.h
wh.b
F, G
50μ
C
wh.b.b
ax
rh
ha
D
t.b
wh.b
F
p
f.ax
G
p
sp
sp.m
f.ax
C-D
250μ

FIGURE 24

Shepleya wattsii (Harvey) comb. nov.

A.	A27,904	Whorl-branchlet bearing small female branchlets.
B.	"	Early stage in formation of procarp system.
C.	"	Procarp system with three-celled carpogonial branch.
D.	"	Mature procarp system.
E.	A21,262	Post fertilization stage showing connecting cells and fusion of cells of carpogonial branch.
F.	A27,904	Post fertilization stage showing two auxiliary cells.
G.	A21,262	Early stage in gonimoblast formation and division of sterile cells associated with the procarp. The sterile group from the sterile pericentral cell has been omitted for clarity.

FIGURE 24

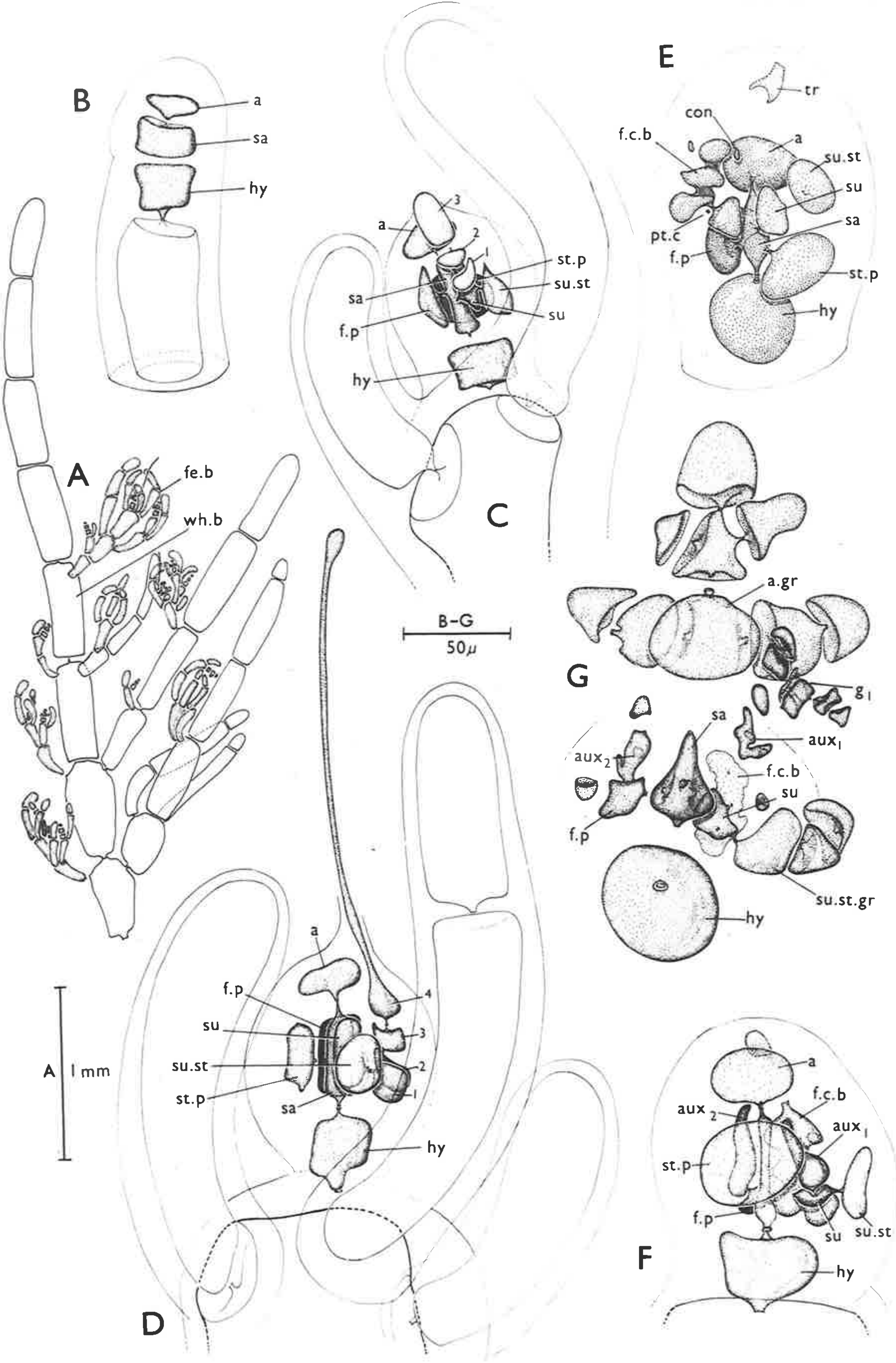

B
a
sa
hy
A
fe.b
wh.b
C
a
3
2
1
st.p
su.st
sa
su
f.p
hy
E
tr
con
f.c.b
a
su.st
su
sa
pt.c
f.p
st.p
hy
G
a.gr
g1
sa
aux1
aux2
f.c.b
su
f.p
su.st.gr
hy
B-G
50µ
A
1 mm
D
a
f.p
4
su
3
su.st
2
st.p
1
sa
hy
F
a
f.c.b
aux2
aux1
st.p
f.p
su
su.st
hy

FIGURE 25

Shepleya wattsii (Harvey) comb. nov.

A.	A21,262	Two armed fusion cell with immature carposporangia.
B-D.	"	Stages in maturation of carposporangia.
E.	"	Involucral branchlet formed from a sterile cell associated with the procarp.
F.	A31,422	Production of abnormal sporangial branchlets.
G.	"	Production of spermatangial heads and procarps on the one abnormal branchlet.

FIGURE 25

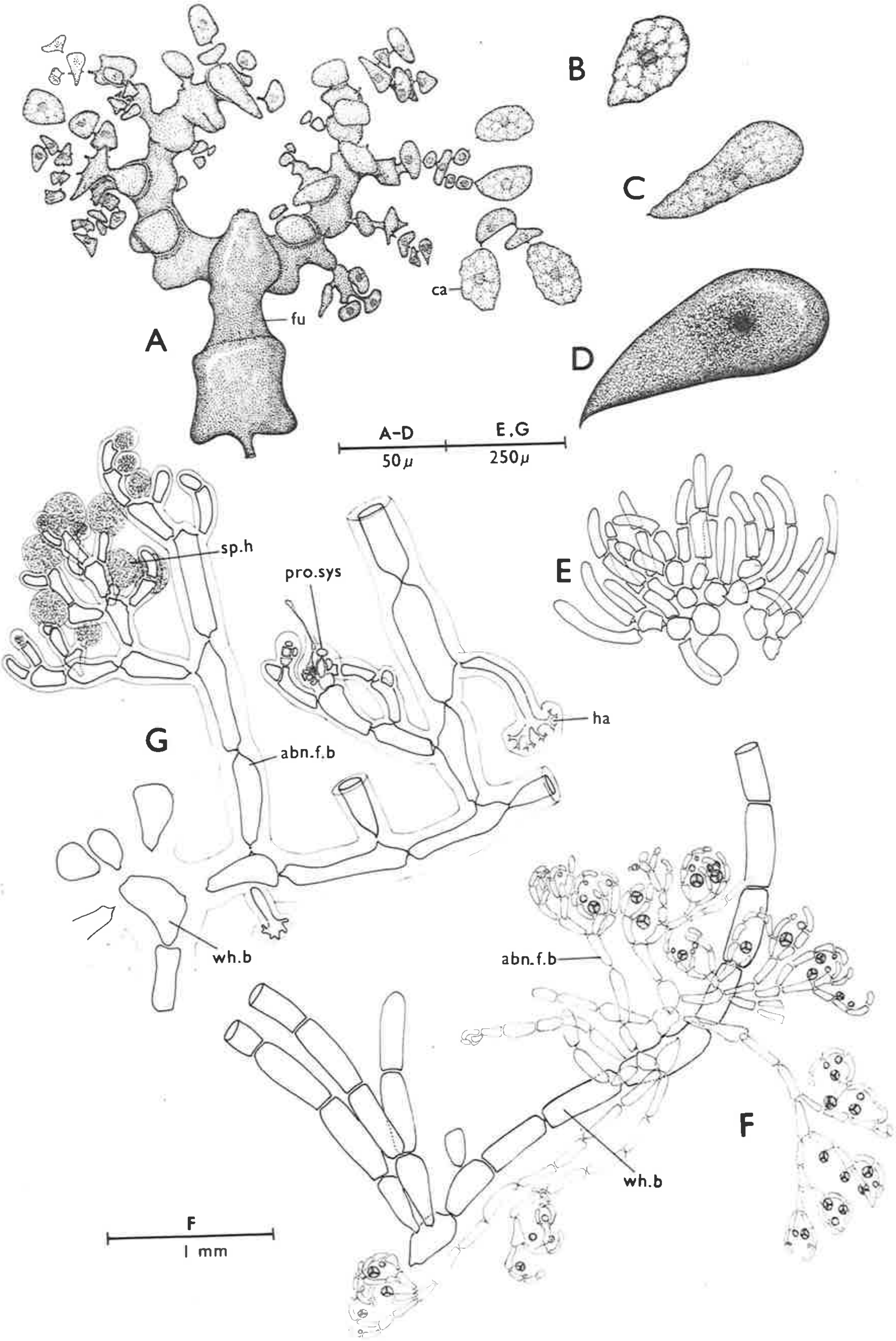
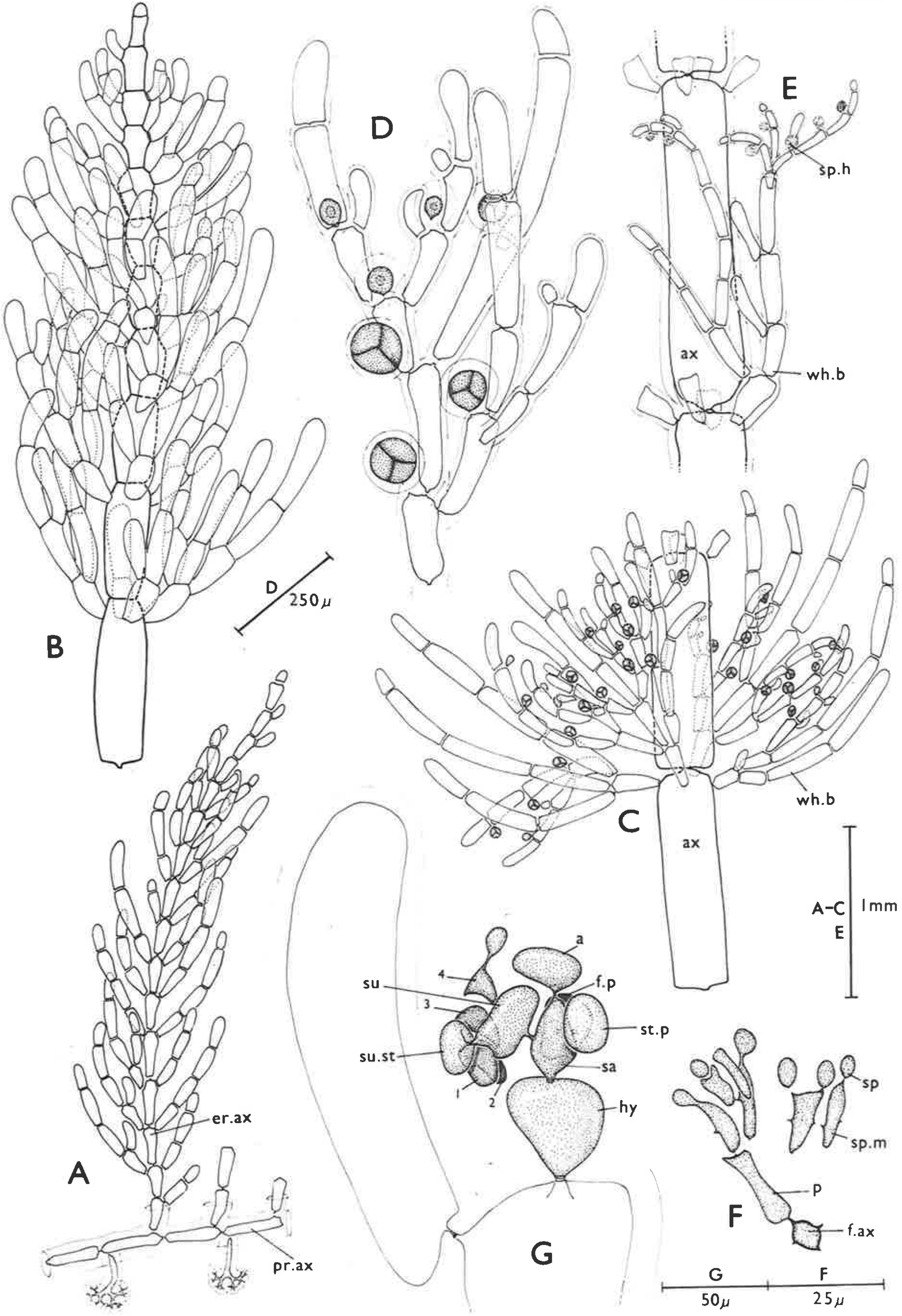

B
C
fu
ca
A
D
A–D
50 μ
E,G
250 μ
sp.h
pro.sys
E
ha
G
abn.f.b
wh.b
abn.f.b
F
wh.b
F
1 mm

FIGURE 26

Shepleya verticillata nom. nov.

A.	A31,420	Prostrate axis bearing young erect axis.
B.	A27,886	Apex of indeterminate branch showing production of whorl-branchlets.
C.	"	Part of main axis bearing whorl-branchlets with tetrasporangia.
D.	"	Part of whorl-branchlet with tetrasporangia.
E.	A10,984	Part of main axis with whorl-branchlet bearing spermatangial heads.
F.	"	Transverse section of fertile axial cell of spermatangial head, with one pericentral cell and derivatives.
G.	MEL15,325	Mature procarp system.

FIGURE 26



D
E
sp.h
ax
wh.b
B
D
250μ
C
wh.b
ax
A–C
E
1mm
er.ax
A
pr.ax
a
4
su
f.p
3
st.p
su.st
sa
1
2
hy
sp
sp.m
p
F
f.ax
G
G
50μ
F
25μ

FIGURE 27

Shepleya australe (J.Ag.) comb. nov.

A.	A31,007	Apex of indeterminate branch showing production of whorl-branchlets and haptera.
B.	"	Axis with whorl-branchlets bearing tetrasporangia.
C.	"	Longitudinal section of mature spermatangial head.
D-F.	"	Stages in development of procarp system.
F.	"	Mature procarp system.
G.	"	Post fertilization stage showing fused carpogonial branch and connecting cells.
H.	"	Post fertilization stage showing enlarged supporting cell and fertile pericentral cell.

FIGURE 27

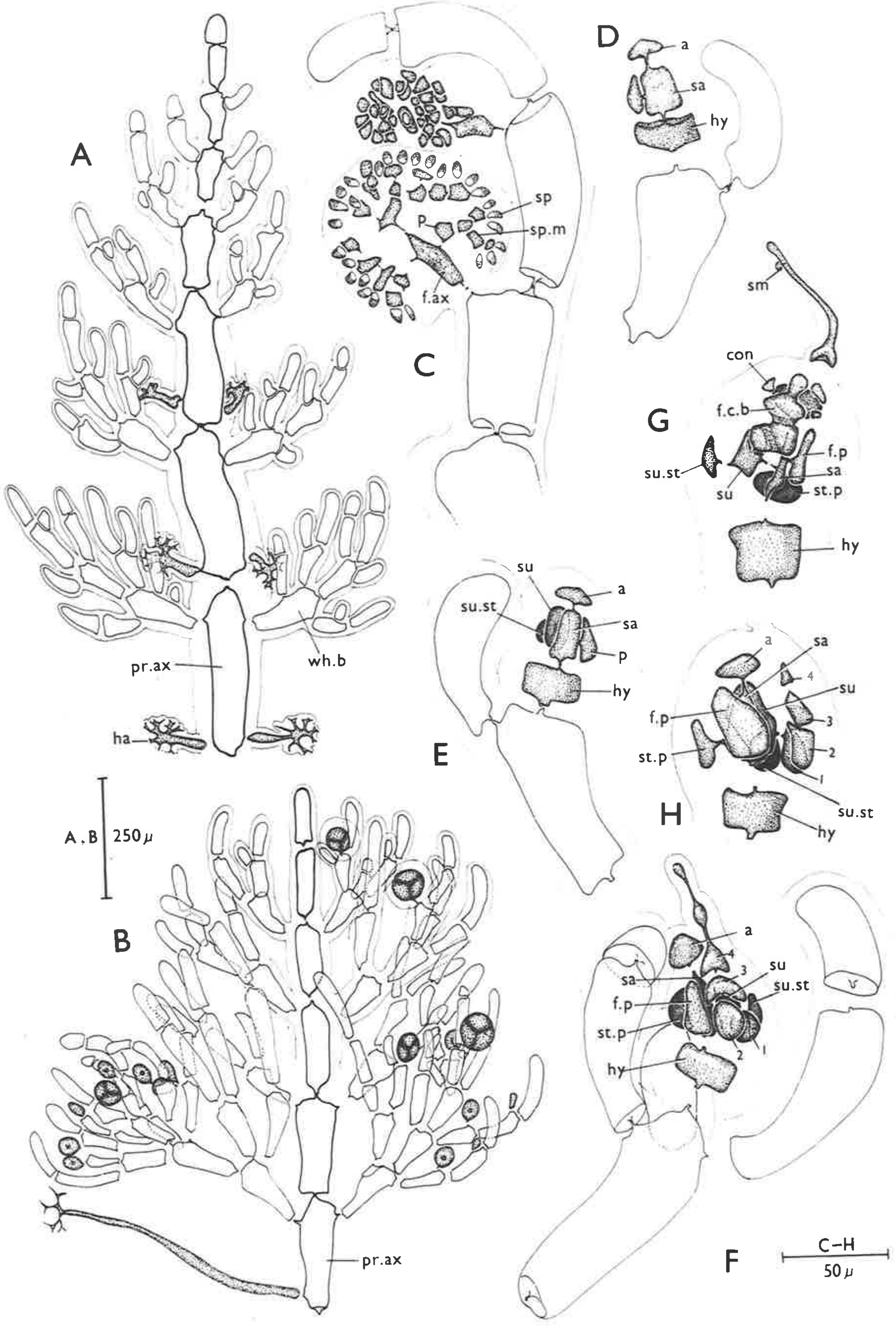

A
pr.ax
wh.b
ha
A.B 250μ
B
pr.ax
C
sp
P
sp.m
f.ax
D
a
sa
hy
G
sm
con
f.c.b
su.st
f.p
sa
su
st.p
hy
E
su
su.st
a
sa
P
hy
H
a
sa
4
su
f.p
3
st.p
2
1
su.st
hy
F
a
4
3
sa
su
su.st
f.p
st.p
2
1
hy
C–H
50μ

FIGURE 28

Shepleya australe (J.Ag.) comb. nov.

A.	A31,007	Post fertilization stage showing two auxiliary cells.
B.	"	Post fertilization stage showing first gonimolobe initial, and apical and sterile pericentral groups.
C.	"	Early stage in gonimoblast development.
D.	"	Fusion cell with carposporangia.

FIGURE 28

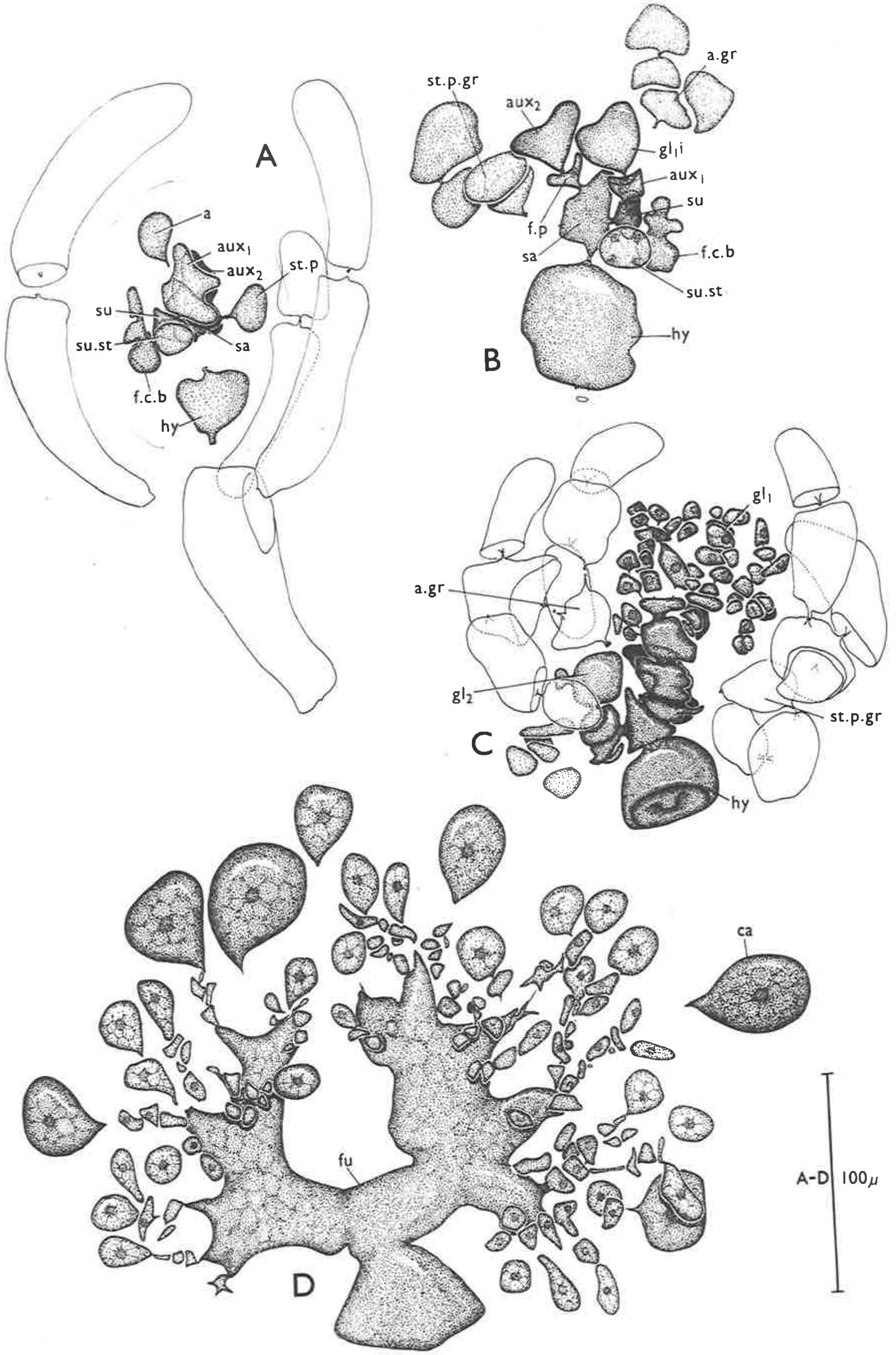

A
a
aux_1
aux_2
st.p
su
su.st
sa
f.c.b
hy
B
a.gr
st.p.gr
aux_2
gl_1i
aux_1
su
f.p
sa
f.c.b
su.st
hy
C
gl_1
a.gr
gl_2
st.p.gr
hy
D
ca
fu
A-D 100μ

FIGURE 29

Shepleya claviformis sp. nov.

A.	A31,008	Apex of indeterminate branch showing production of whorl-branchlets.
B.	"	Part of prostrate axis with haptera.
C.	"	Range in rhodoplast shape in vegetative cells.
D.	"	Whorl-branchlet bearing tetrasporangia.

FIGURE 29

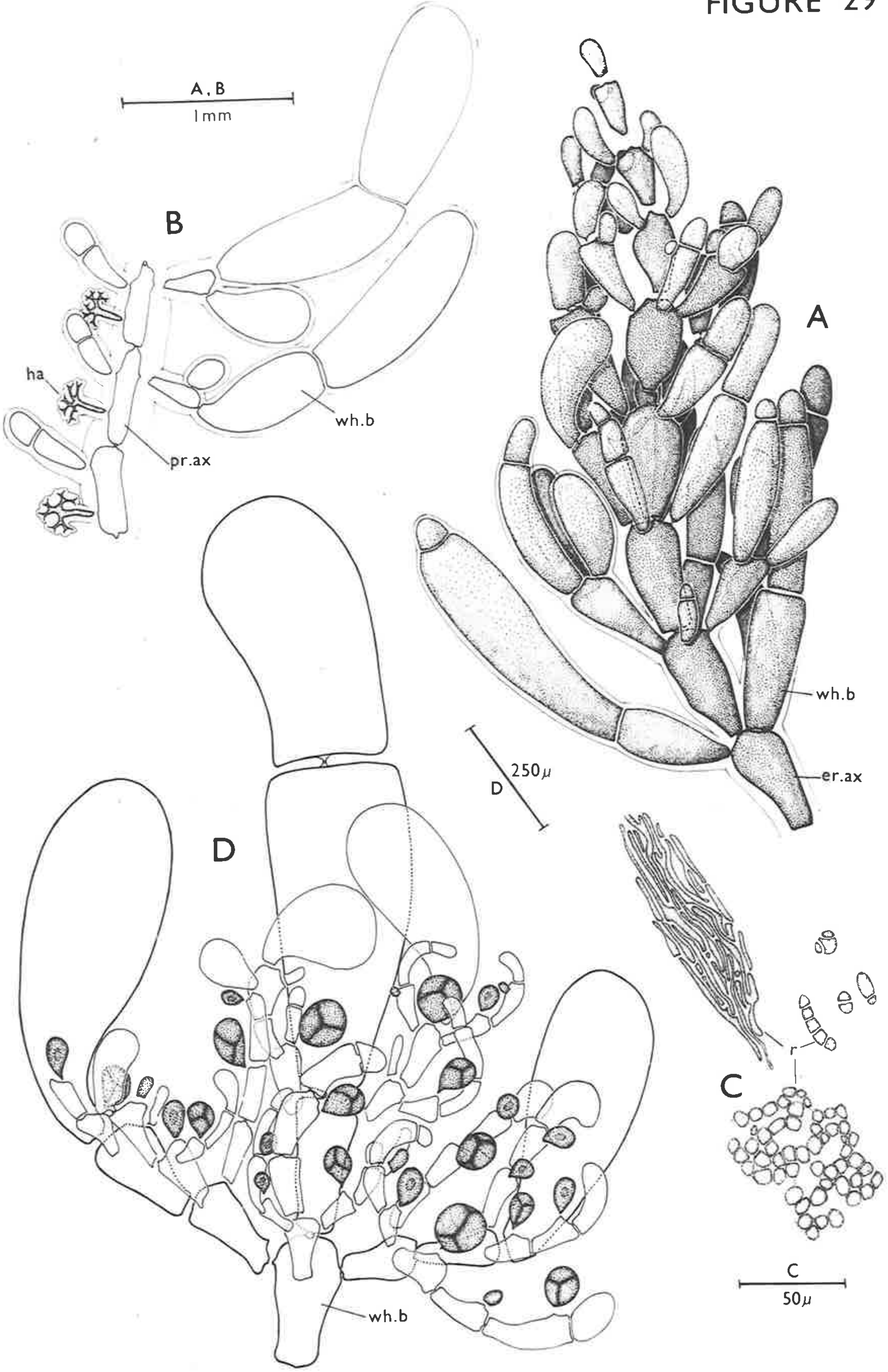


FIGURE 30

Shepleya claviformis sp. nov.

A.	A31,008	Part of an indeterminate axis showing sterile and fertile whorl-branchlets bearing spermatangial heads.
B.	"	Mature procarp system.
C.	"	Post fertilization stage showing two auxiliary cells.
D.	"	Early stage in production of gonimoblast.

FIGURE 30

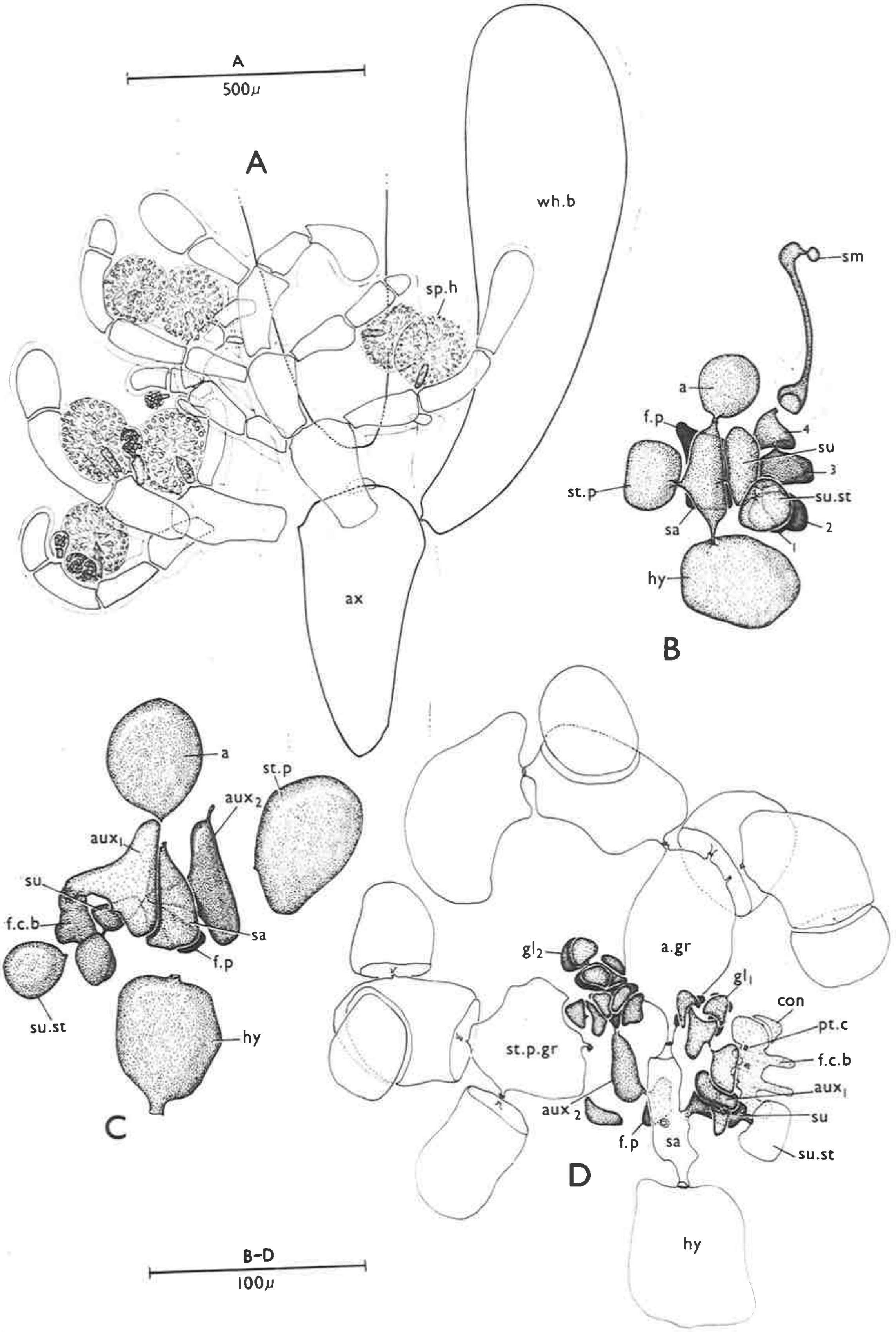

A
500µ
A
wh.b
sp.h
ax
sm
a
f.p
4
su
3
st.p
su.st
sa
2
1
hy
B
a
st.p
aux₂
aux₁
su
f.c.b
sa
f.p
su.st
hy
C
a.gr
gl₂
gl₁
con
pt.c
f.c.b
aux₁
st.p.gr
aux₂
su
f.p
sa
su.st
D
hy
B-D
100µ

FIGURE 31

Wollastoniella myriophylloides (Harvey) comb. nov.

A.	A31,432	Habit of plant.
B.	A30,667	Apex of indeterminate branch showing production of whorl-branchlets.
C.	"	Mature whorl-branchlet.
D.	"	Transverse section of a main axis showing arrangement of the four whorl-branchlets and four potentially indeterminate branches.

FIGURE 31

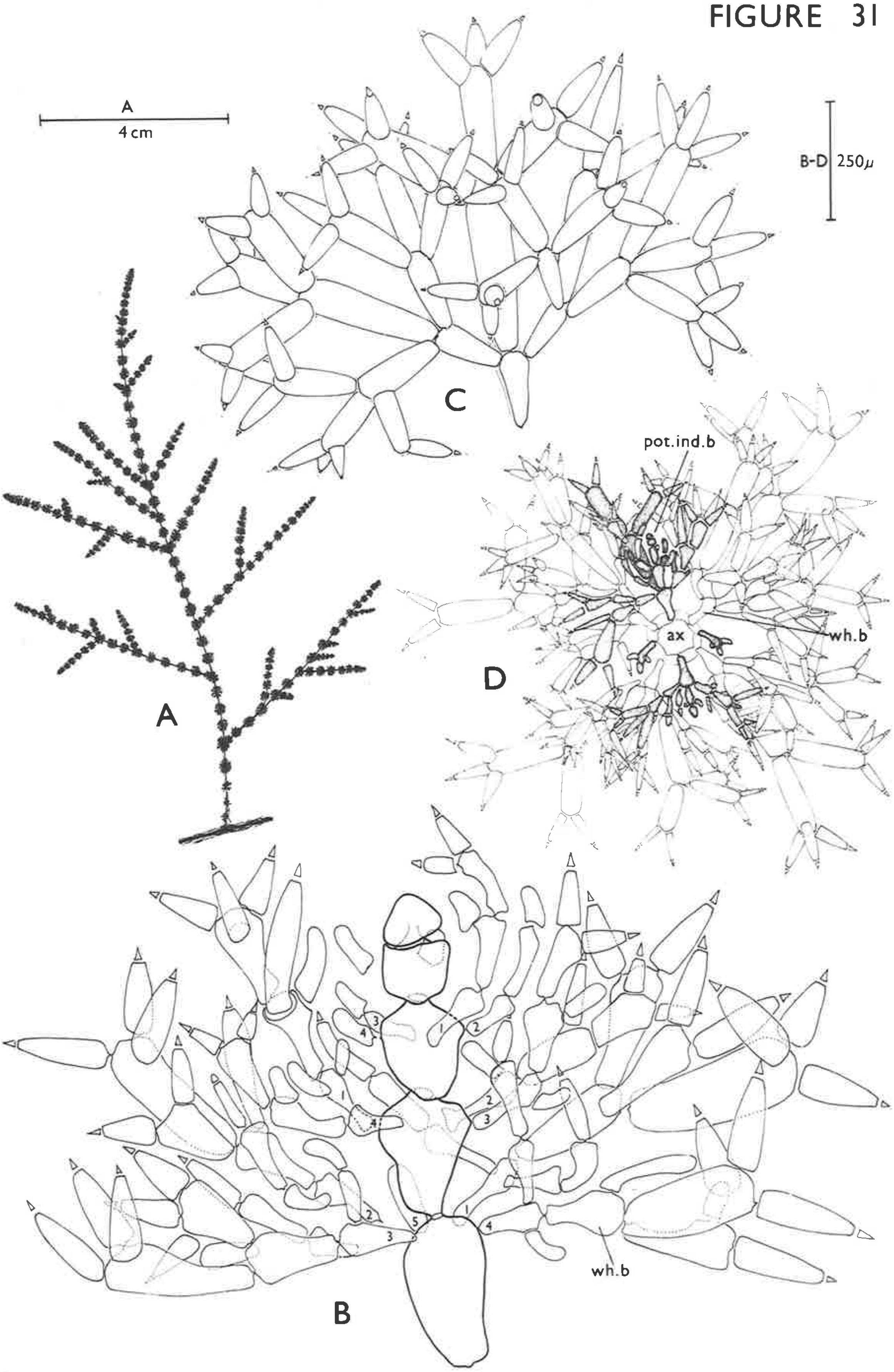


FIGURE 32

Wollastoniella myriophylloides (Harvey) comb. nov.

A.	A27,888	Potentially indeterminate branch becoming villose.
B.	A12,732	Part of an indeterminate axis showing origin of cortical rhizoids from proximal end of axial cell, and haptera from the proximal ends of rhizoidal cells. Young potentially indeterminate branch borne on one rhizoid. Whorl-branchlets on lower axial cell omitted.
C.	A12,731	Whorl-branchlet bearing tetrasporangia.
D.	A32,167	Villose whorl-branchlet bearing spermatangial heads.
E.	"	Longitudinal section of a spermatangial head.

FIGURE 32

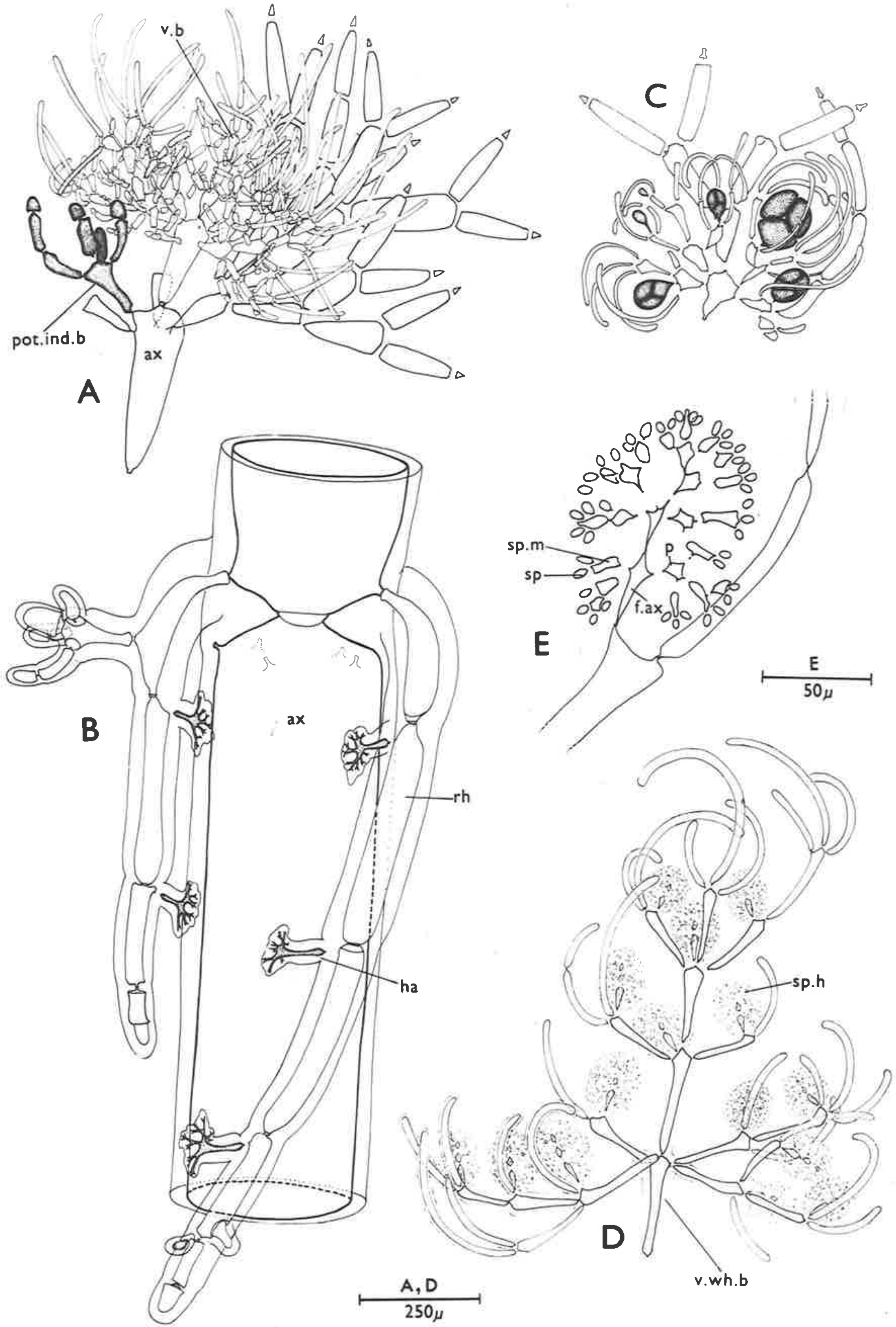


FIGURE 33

Wollastoniella myriophylloides (Harvey) comb. nov.

A.	A12,732	Apex of fertile axis showing a whorl of three further 5-celled fertile axes on the sixth axial cell.
B.	A31,432	Procarp system with two carpogonial branches.
C.	A12,732	Post fertilization stage showing fused carpogonial branch and connecting cells.
D.	"	Post fertilization stage showing a connecting cell fusing with the auxiliary cell and early divisions of sterile cells.
E.	"	Early stage in carposporophyte development. Involucral filaments from one sterile pericentral cell and the apical cell are omitted.

FIGURE 33

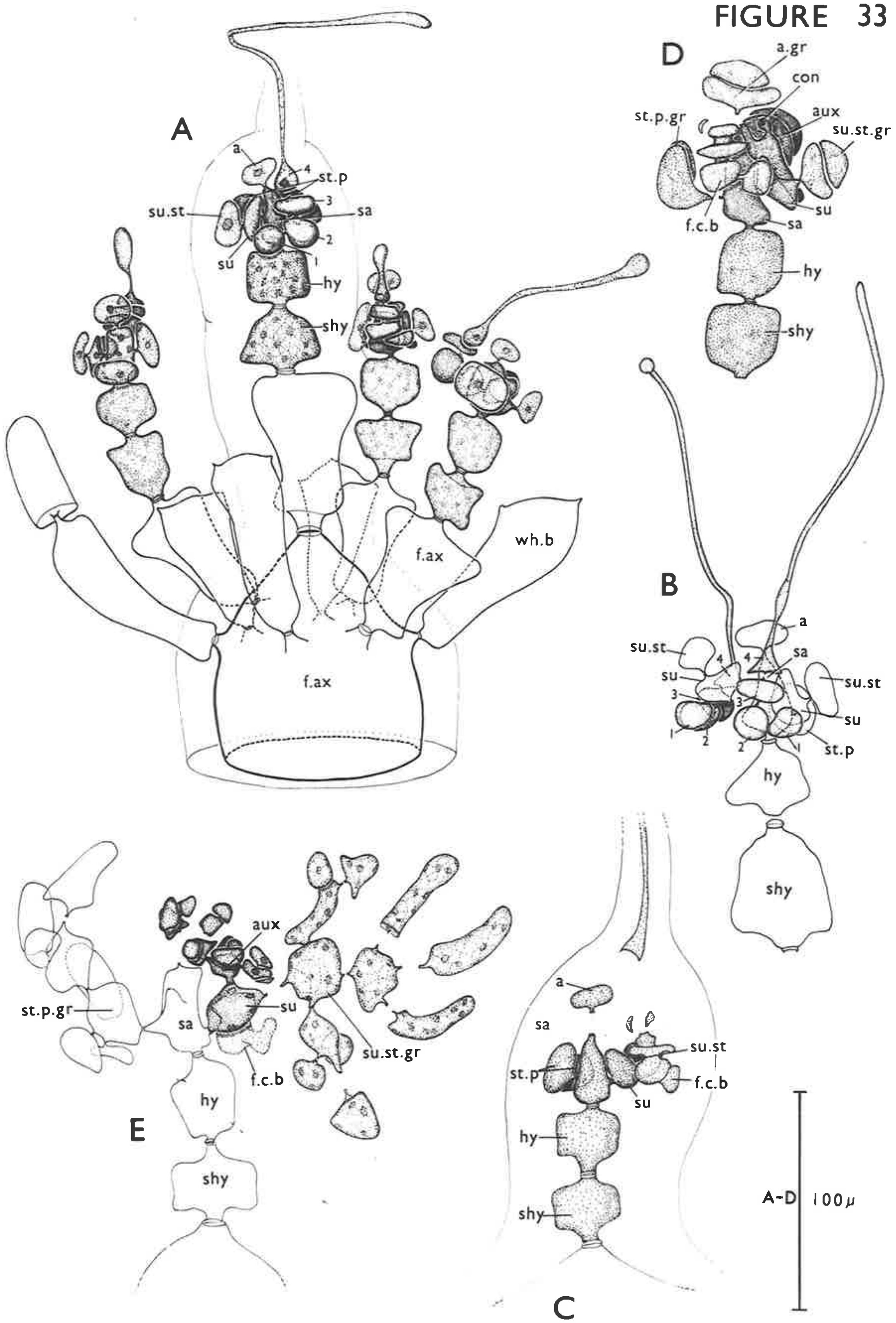

A
a
4
st.p
3
su.st
sa
2
su
1
hy
shy
f.ax
wh.b
f.ax
D
a.gr
con
aux
st.p.gr
su.st.gr
su
f.c.b
sa
hy
shy
B
a
su.st
sa
4
4
su
su.st
3
3
su
1
2
2
1
st.p
hy
shy
E
aux
su
st.p.gr
sa
su.st.gr
f.c.b
hy
shy
C
a
sa
su.st
st.p
f.c.b
su
hy
shy
A-D
100μ

FIGURE 34

Wollastoniella myriophylloides (Harvey) comb. nov.

A.	A12,732	Mature carposporophyte with involucrum.
B.	"	Detail of carposporangium formation.

Wollastoniella mucronata (Harvey) comb. nov.

C.	A18,987	Habit of plant.
D.	"	Apex of indeterminate branch showing origin of whorl-branchlets.

FIGURE 34

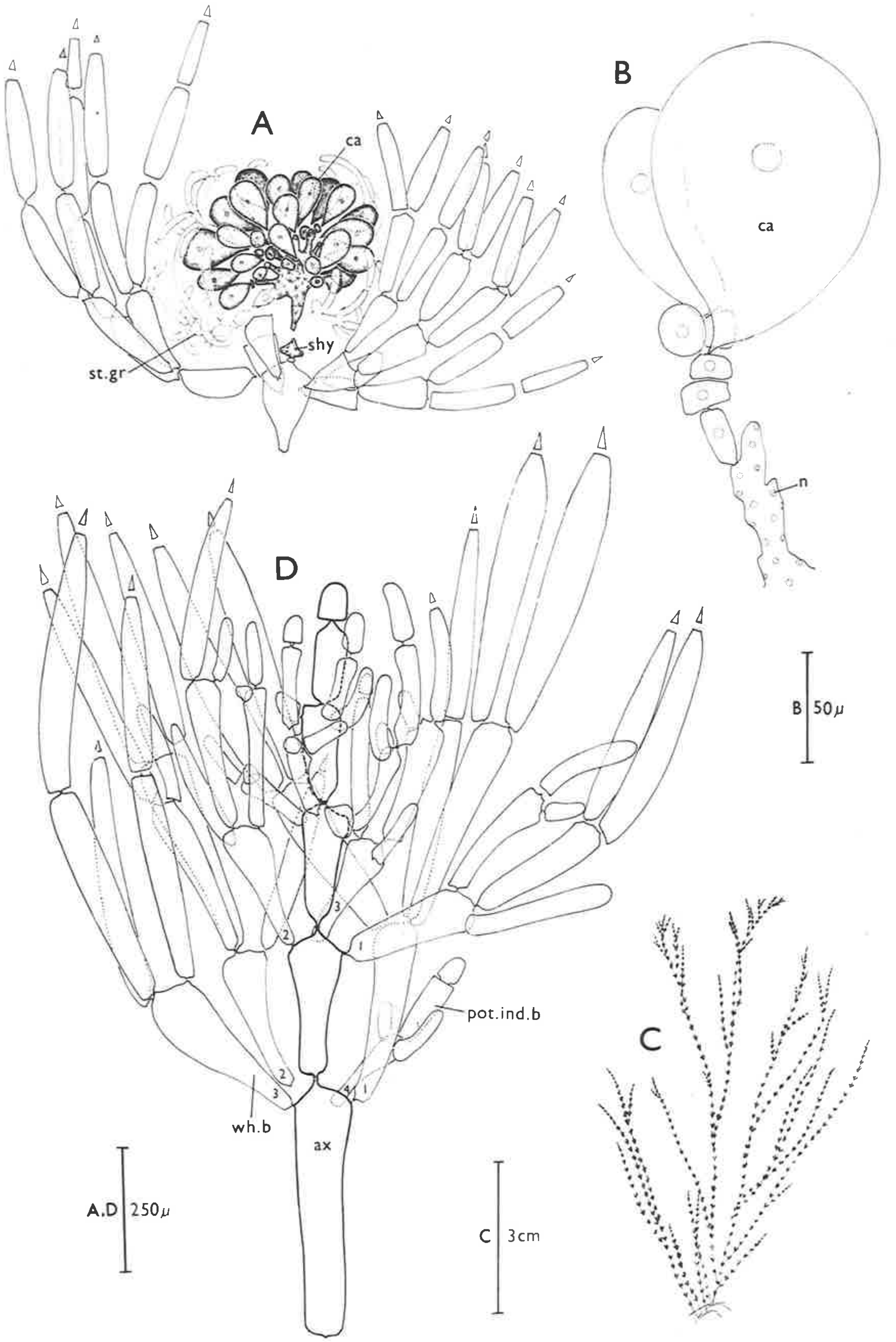


FIGURE 35

Wollastoniella mucronata (Harvey) comb. nov.

A.	A18,987	Apex of branch becoming villose. Growth being taken over by an indeterminate branch on a lower axial cell.
B(i)	"	Part of an axis with whorl-branchlets bearing tetrasporangia.
B(ii)	"	Sporangium with eight spores.
C.	MEL15,322	Mature procarp system.
D.	"	Post fertilization stage showing auxiliary cell and fusion of cells of the carpogonial branch.
E.	"	Post fertilization stage showing division of sterile cells associated with the procarp.
F.	"	Young carposporophyte, fusion cell and part of the inner involucrum.

FIGURE 35

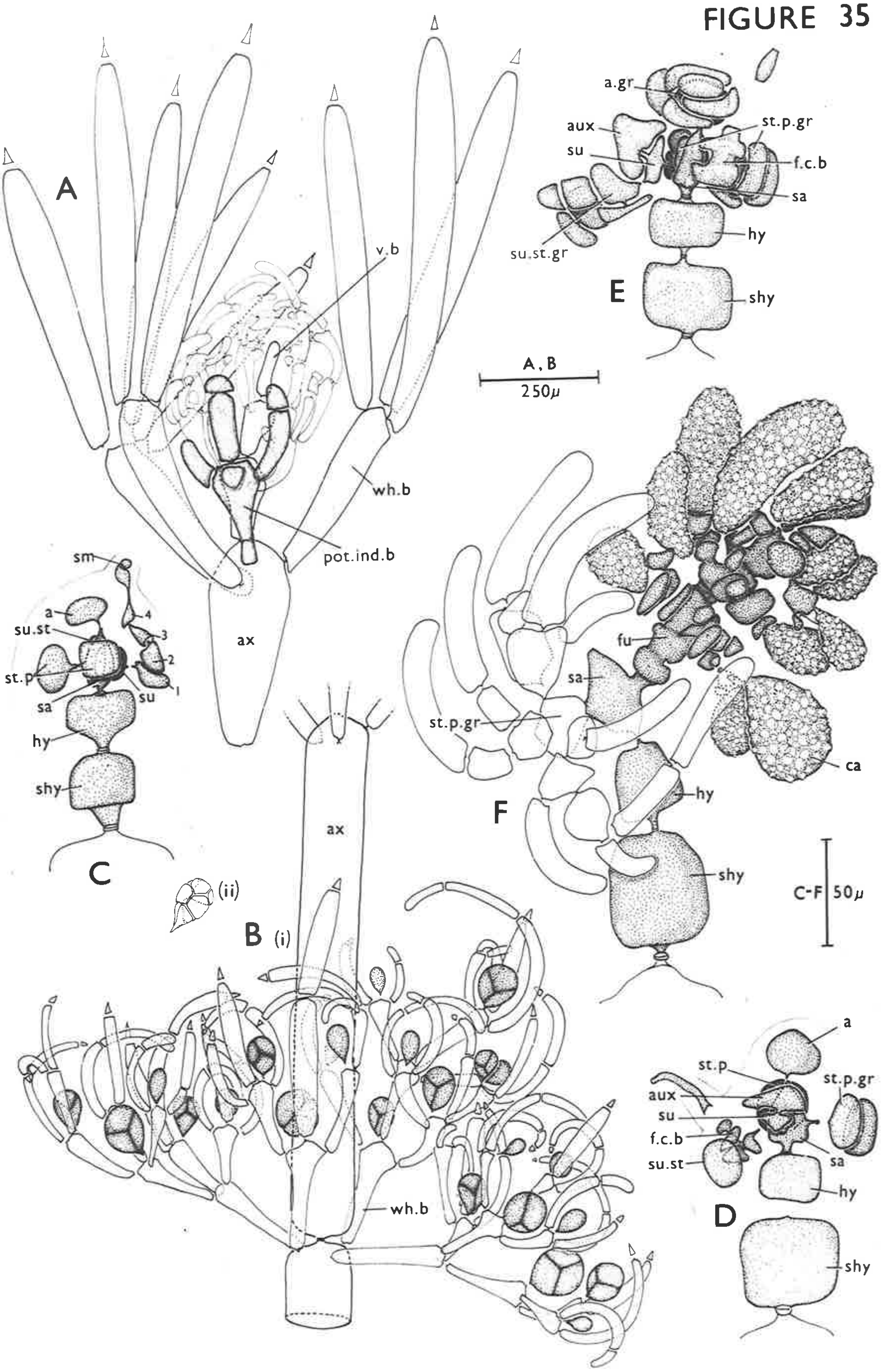

A
v.b
wh.b
pot.ind.b
ax
A, B
250μ
a.gr
aux
su
st.p.gr
f.c.b
sa
hy
su.st.gr
E
shy
sm
a
su.st
4
3
2
1
st.p
sa
su
hy
shy
C
ax
(ii)
B (i)
wh.b
fu
sa
st.p.gr
ca
hy
F
shy
C-F
50μ
a
st.p
st.p.gr
aux
su
f.c.b
su.st
sa
hy
D
shy

FIGURE 36

Drewiana nitella (Harvey) comb. nov.

A.	MEL15,320	Part of a creeping prostrate axis bearing lateral branches with curled tips.
B.	A29,688	Apex of an indeterminate branch showing production of whorl-branchlets and tetrasporangia.
C.	"	Whorl-branchlet bearing tetrasporangia.
D.	NSW	Mature procarp system.
E.	"	Post fertilization stage showing auxiliary cell and fused carpogonial branch.
F.	"	Early stage in development of carposporophyte and involucral branchlets.
G.	"	Mature carposporophyte and involucrum.

FIGURE 36

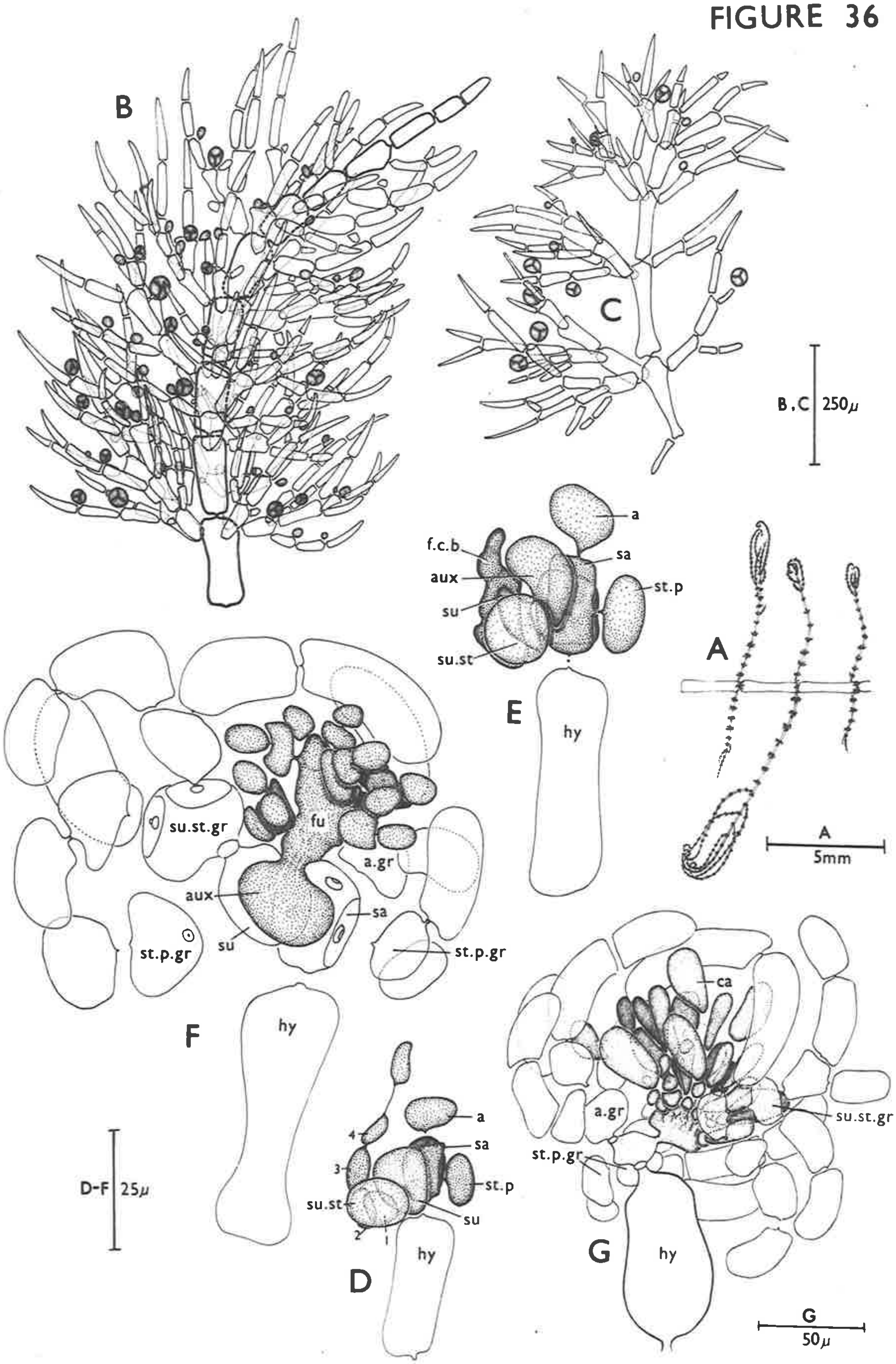

B
C
B, C 250µ
a
f.c.b
sa
aux
st.p
su
su.st
A
E
hy
A
5mm
su.st.gr
fu
a.gr
aux
sa
su
st.p.gr
st.p.gr
F
hy
ca
a
4
sa
3
st.p
su.st
su
2
1
hy
D
a.gr
su.st.gr
st.p.gr
G
hy
D-F 25µ
G
50µ

FIGURE 37

Involucrana crassa (Hooker f. et Harvey) comb nov.

A.	A31,159	Apex of indeterminate branch showing production of whorl-branchlets (living condition).
B.	A27,896	Apex of indeterminate branch (plasmolysed condition).
C.	NSW	Polysporangium with stalk cell and involucral branchlets.
D.	A31,009	Whorl-branchlet bearing spermatangial heads.
E.	"	Early stage in formation of spermatangial head.
F.	"	Part of spermatangial head showing some of division products of one pericentral cell.
G.	A25,467	Mature procarp system.
H.	"	Part of fusion cell with carposporangia.
I.	"	Involucral branchlet from a sterile cell associated with the procarp.

FIGURE 37

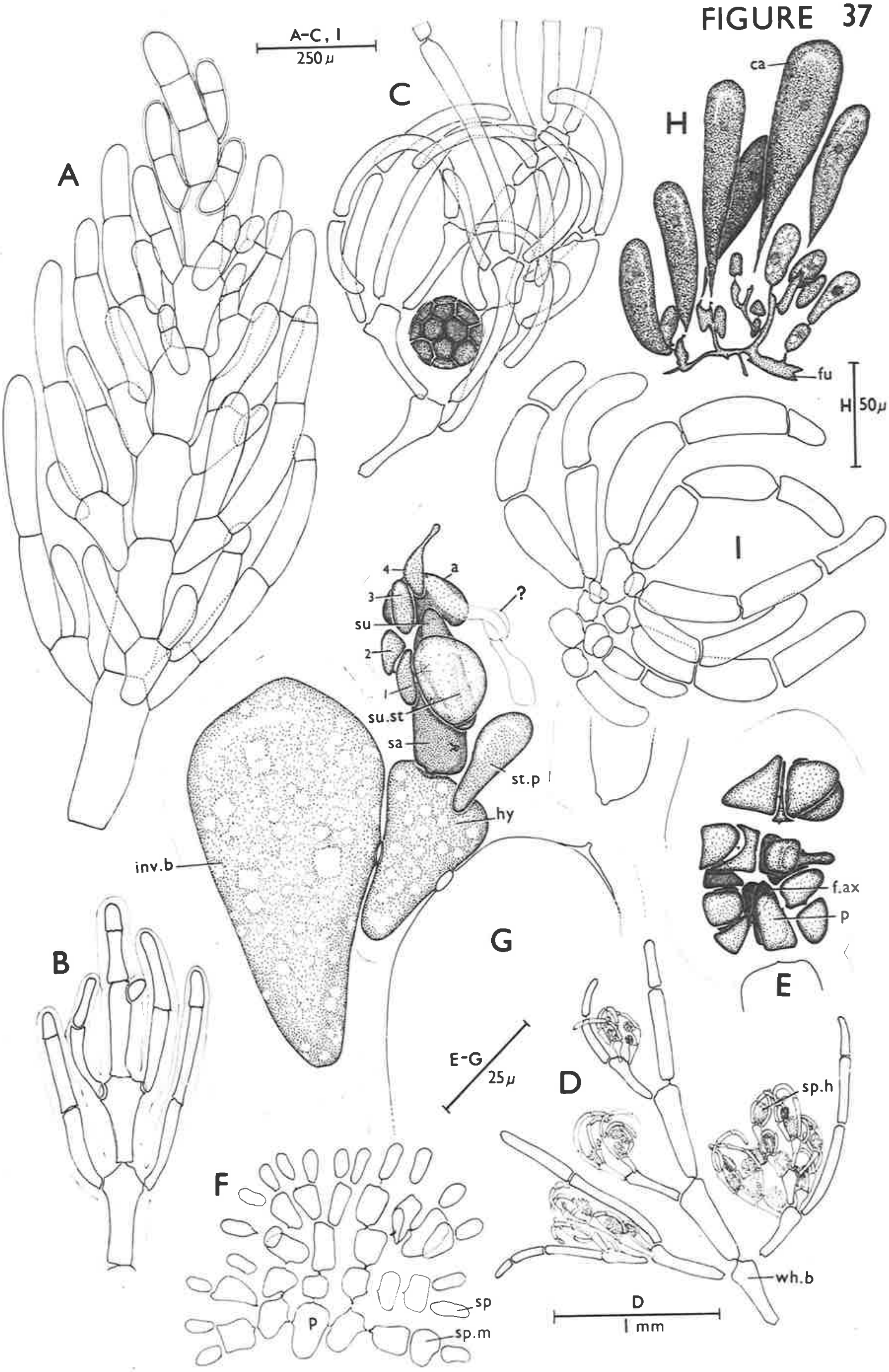

A-C, I
250 µ
A
B
C
H
ca
fu
H 50µ
I
4
a
?
3
su
2
1
su.st
sa
st.p
hy
inv.b
G
f.ax
p
E
E-G
25 µ
D
sp.h
F
sp
p
sp.m
wh.b
D
1 mm

FIGURE 38

Spermothamnion pinnatum sp. nov.

A.	A27,713	Prostrate axis bearing prostrate laterals.
B.	"	Prostrate axis bearing erect laterals with tetrasporangia.
C.	"	Prostrate axis bearing erect laterals.
D.	"	Erect axis with tetrasporangia.
E.	"	Upper part of an erect axis with spermatangial heads.
F.	"	Longitudinal section of a spermatangial head.

FIGURE 38

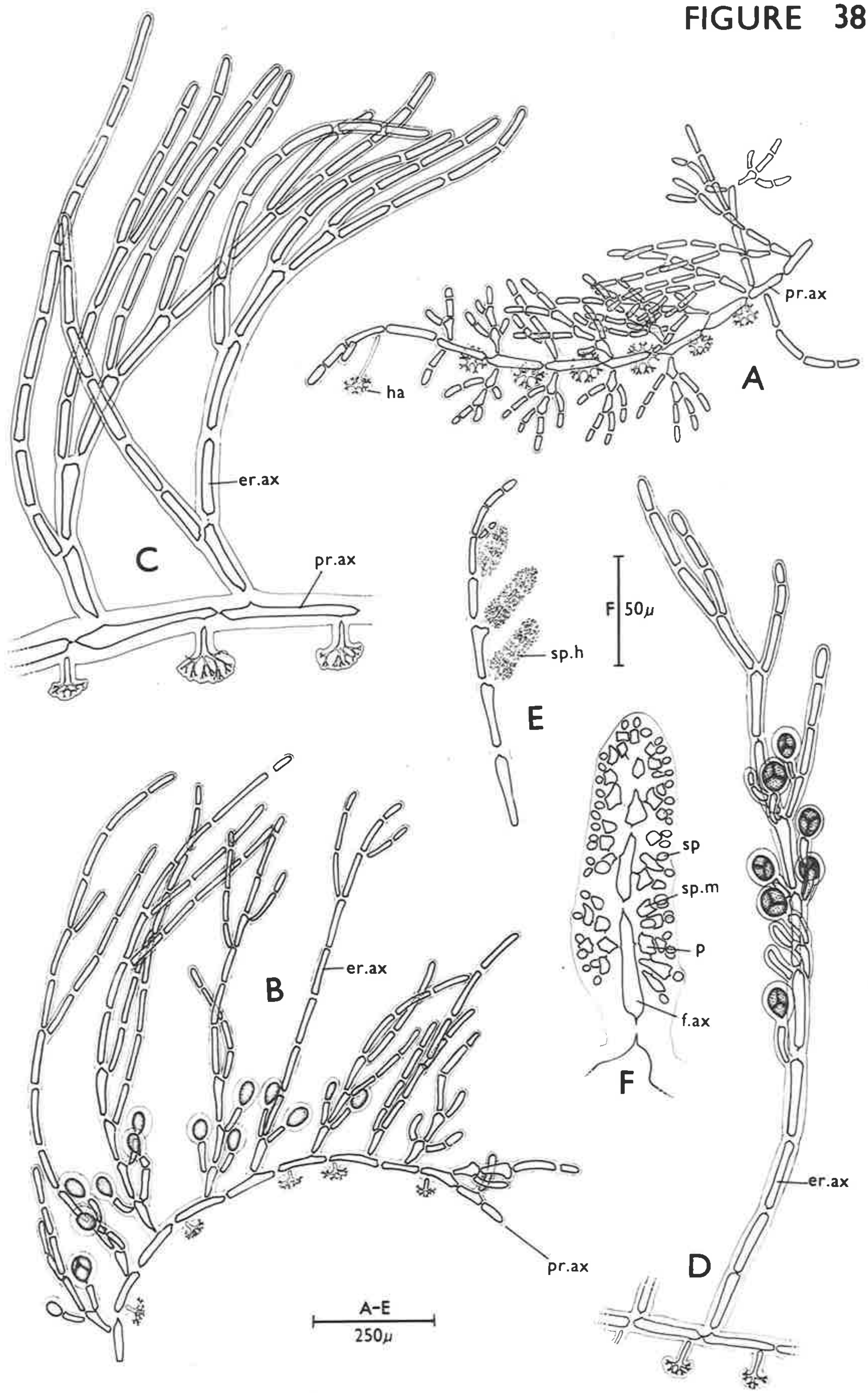

pr.ax
ha
A
er.ax
C
pr.ax
sp.h
E
F 50μ
sp
sp.m
p
f.ax
F
er.ax
B
pr.ax
er.ax
D
A–E
250μ

FIGURE 39

Spermothamnion pinnatum sp. nov.

A.	A27,713	Mature procarp system.
B.	"	Procarp system where the apical cell has divided giving a small group of cells.
C.	"	Post fertilization stage showing young gonimolobes.
D.	"	Young carposporophyte showing fusion cell and involucral branchlets.

Spermothamnion cymosum (Harvey) De Toni

E.	A18,288	Part of an erect axis with octosporangia.

FIGURE 39

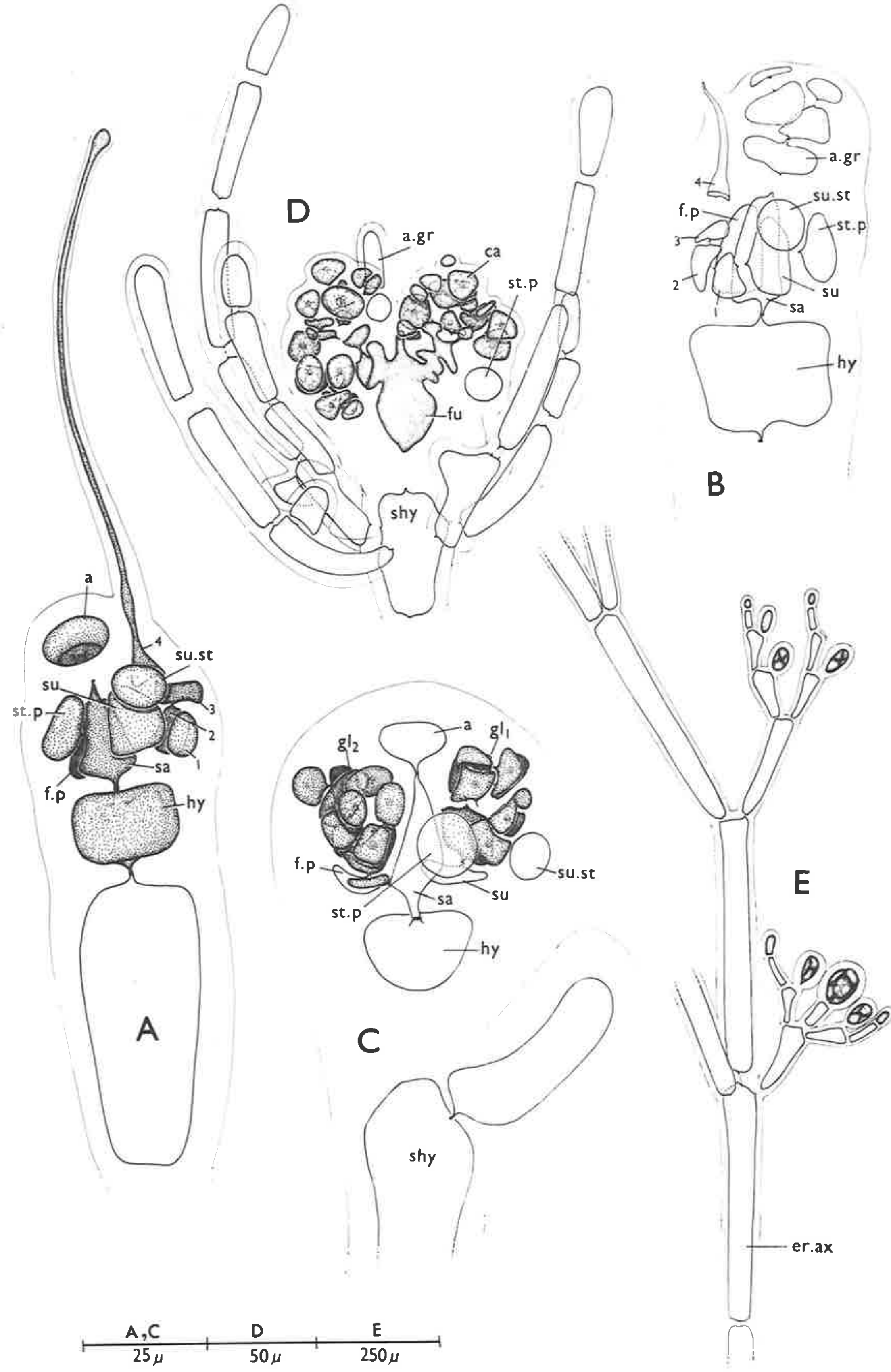

D
a.gr
ca
st.p
fu
shy
a.gr
4
su.st
f.p
st.p
3
2
su
1
sa
hy
B
a
4
su.st
su
st.p
3
2
sa
1
f.p
hy
A
a
gl2
gl1
f.p
su.st
st.p
sa
su
hy
C
shy
E
er.ax
A,C
25μ
D
50μ
E
250μ

FIGURE 40

Tiffaniella sacchoriza (Setchell et Gardner)
Doty et Menez

A.	A26,004	Mature procarp system.
B.	"	Post fertilization stage showing enlargement of supporting cell and fertile pericentral cell.
C.	"	Mature carposporophyte.

Tiffaniella cymodoceae (Boergesen) comb. nov.

D.	A32,149	Prostrate and erect axes.
E.	"	Part of an erect axis with undivided sporangia.
F.	"	Part of an erect axis with spermatangial heads.

FIGURE 40

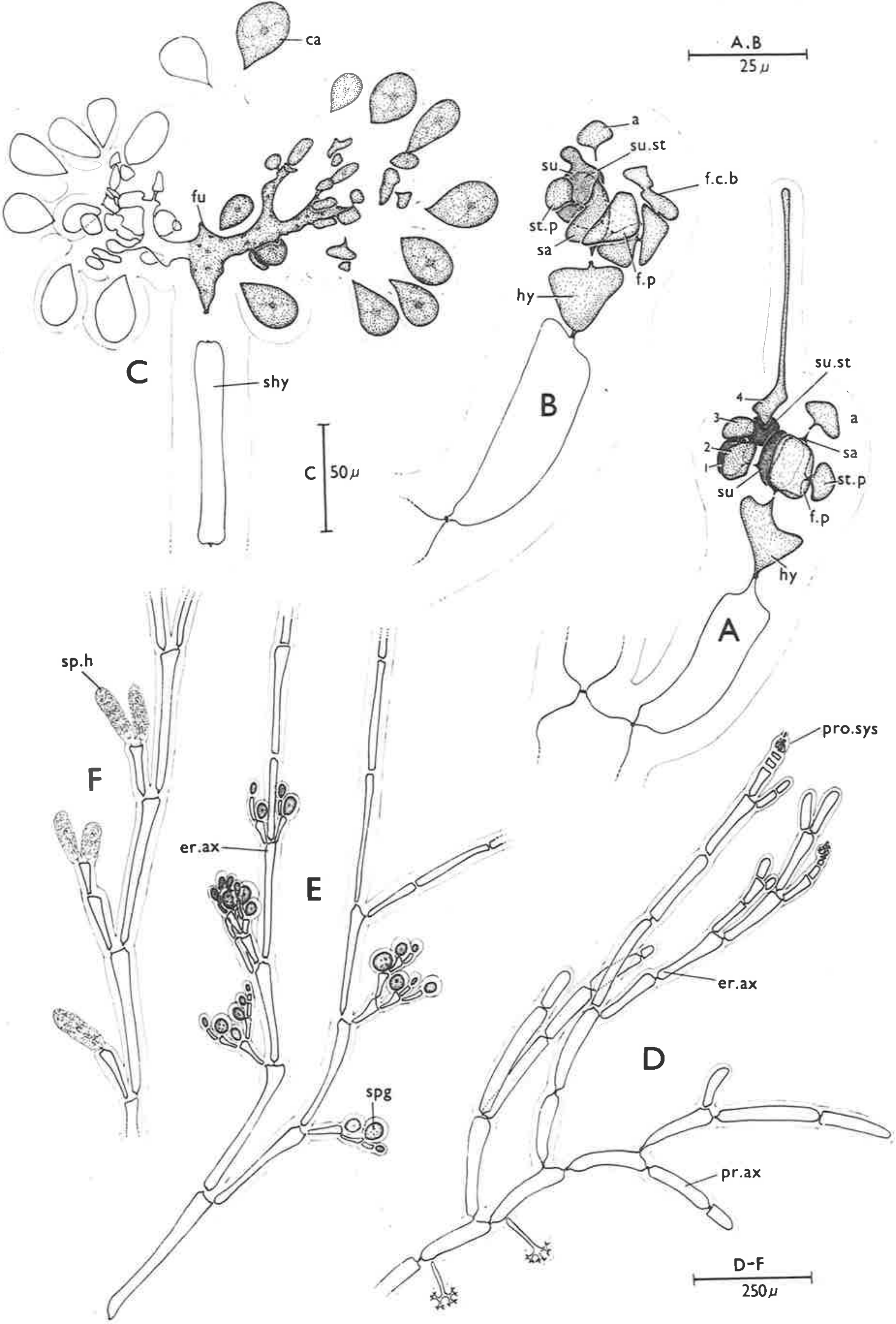

A.B
25 µ
ca
fu
C
shy
C 50 µ
a
su.st
su
f.c.b
st.p
sa
f.p
hy
B
su.st
4
3
2
1
a
sa
st.p
su
f.p
hy
A
sp.h
F
er.ax
E
spg
pro.sys
er.ax
D
pr.ax
D-F
250 µ

FIGURE 41

Tiffaniella cymodoceae (Boergesen) comb. nov.

A.	A32,149	Longitudinal section of a spermatangial head.
B.	"	Fertile axis with mature procarp system.
C.	"	Post fertilization stage showing fused carpogonial branch and two auxiliary cells.
D.	"	Early stage in gonimoblast development.
E.	"	Mature carposporophyte.

FIGURE 41

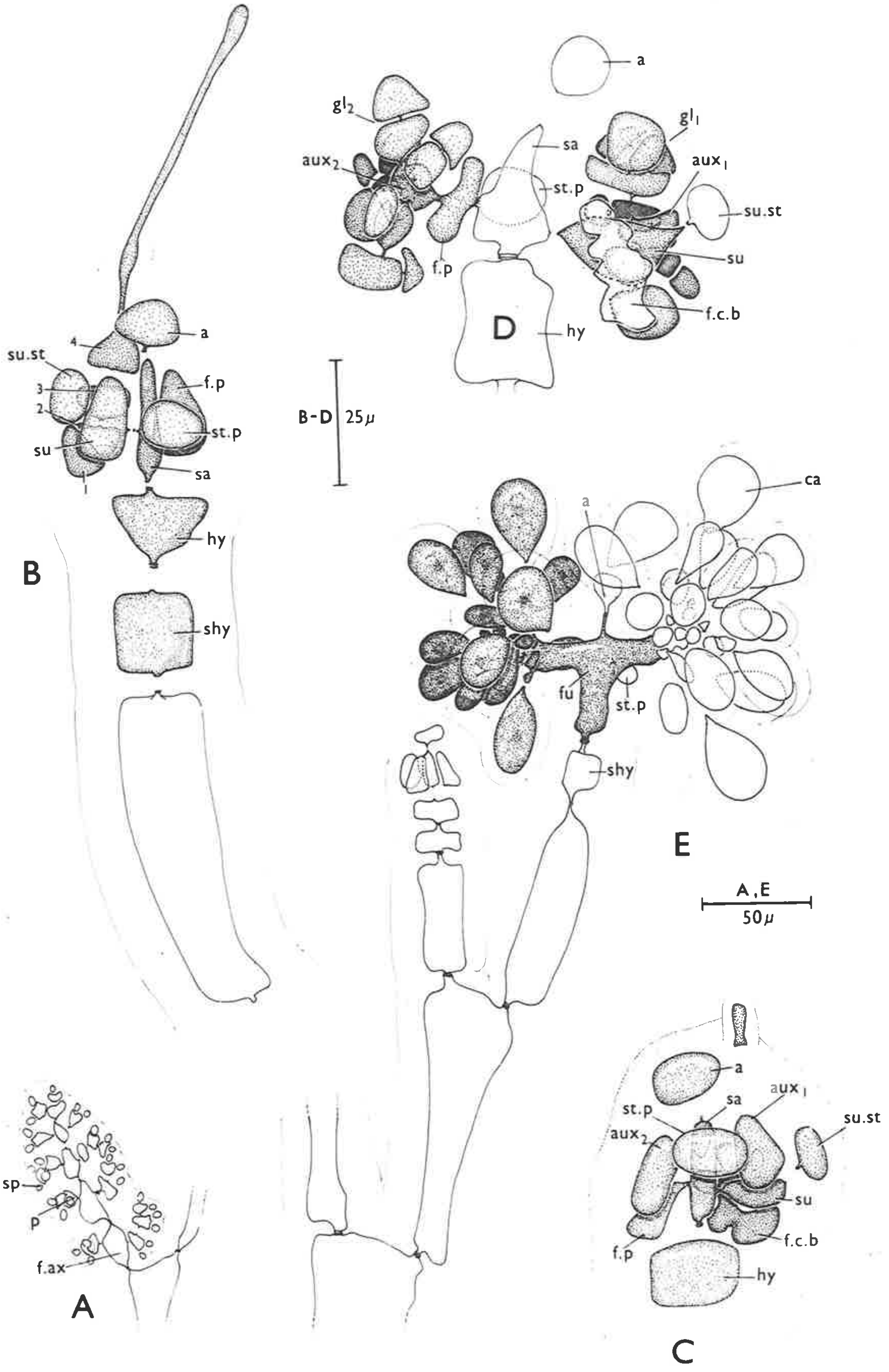

a
gl_2
gl_1
sa
aux_2
aux_1
st.p
su.st
su
f.p
f.c.b
D
hy
a
4
su.st
3
f.p
2
st.p
su
sa
1
hy
B
shy
B-D 25μ
ca
a
fu
st.p
shy
E
A, E
50μ
sp
p
f.ax
A
a
aux_1
st.p
sa
su.st
aux_2
su
f.c.b
f.p
hy
C

FIGURE 42

Lomathamnion epicodii sp. nov.

A.	A20,909	Prostrate and erect axes with tetrasporangia.
B.	A30,961	Prostrate and erect axes with spermatangial heads.
C.	"	Longitudinal section of a spermatangial head.
D.	A20,909	Mature procarp system.
E.	A30,961	Post fertilization stage showing auxiliary cell.
F.	A28,897	Young carposporophyte.

FIGURE 42

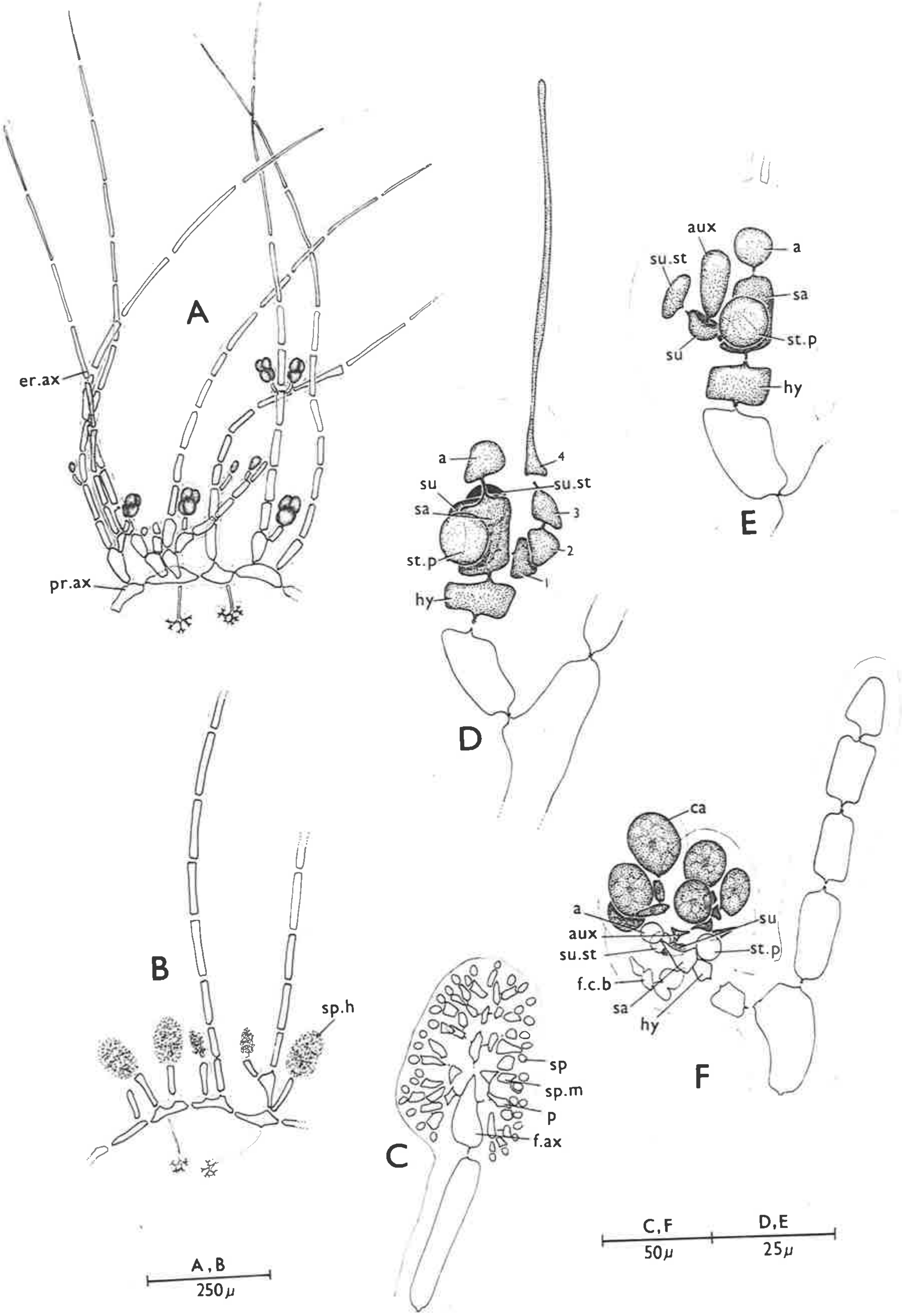

A
er.ax
pr.ax
B
sp.h
A, B
250μ
C
sp
sp.m
p
f.ax
D
a
su
sa
st.p
hy
su.st
4
3
2
1
E
aux
a
su.st
sa
su
st.p
hy
F
ca
a
aux
su.st
f.c.b
sa
hy
su
st.p
C, F
50μ
D, E
25μ

FIGURE 43

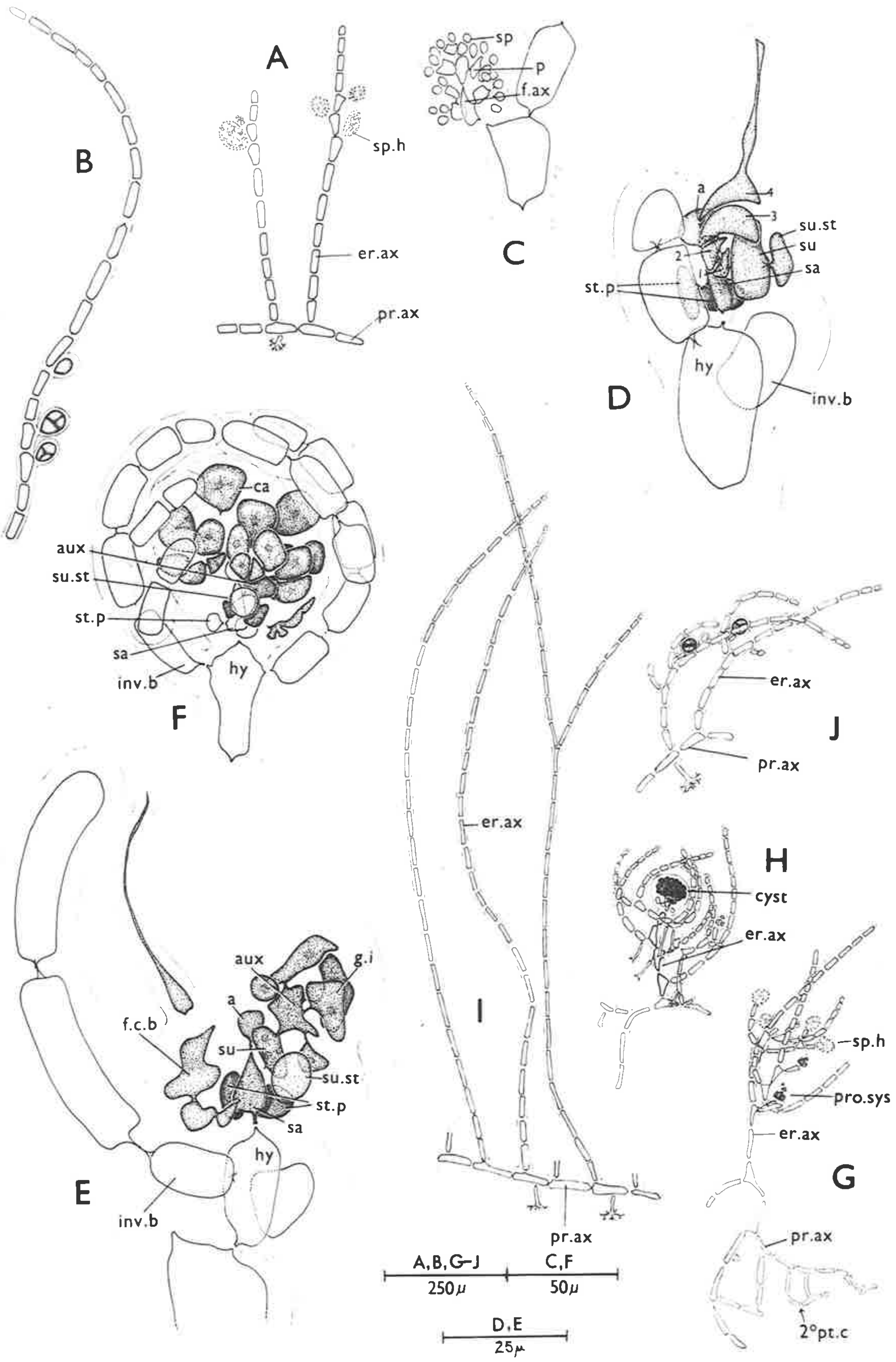
Ptilothamnion subsimplex sp. nov.

A.	A32,150	Prostrate axes and erect axes with spermatangial heads.
B.	"	Part of an erect axis bearing tetrasporangia.
C.	"	Longitudinal section of a spermatangial head.
D.	"	Mature procarp system.
E.	"	Early stage in gonimoblast development.
F.	"	Mature carposporophyte with involucrum.

Ptilothamnion schmitzii Heydrich

G.	A32,154	Prostrate and erect axes of form on stipes of host. Spermatangial heads and procarp systems on the same branch systems.
H.	"	Female gametophyte with a mature carposporophyte.
I.	A31,347	Prostrate and erect axes of form on frond of host.
J.	"	Prostrate and erect axes with tetrasporangia.

FIGURE 43



A
sp.h
er.ax
pr.ax
B
sp
p
f.ax
C
a
4
3
su.st
su
sa
2
1
st.p
hy
inv.b
D
ca
aux
su.st
st.p
sa
inv.b
hy
F
er.ax
I
pr.ax
er.ax
pr.ax
J
H
cyst
er.ax
aux
g.i
a
f.c.b
su
su.st
st.p
sa
hy
inv.b
E
sp.h
pro.sys
er.ax
G
pr.ax
2°pt.c
A,B,G–J
250μ
C,F
50μ
D,E
25μ

FIGURE 44

Ptilothamnion schmitzii Heydrich

A.	A31,347	Longitudinal section of a spermatangial head.
B.	"	Mature procarp system.
C.	"	Post fertilization stage showing auxiliary cell and fused carpogonial branch.
D.	"	Early stage in gonimoblast development.
E.	"	Carposporophyte showing two gonimolobes at different stages of maturity.

FIGURE 44

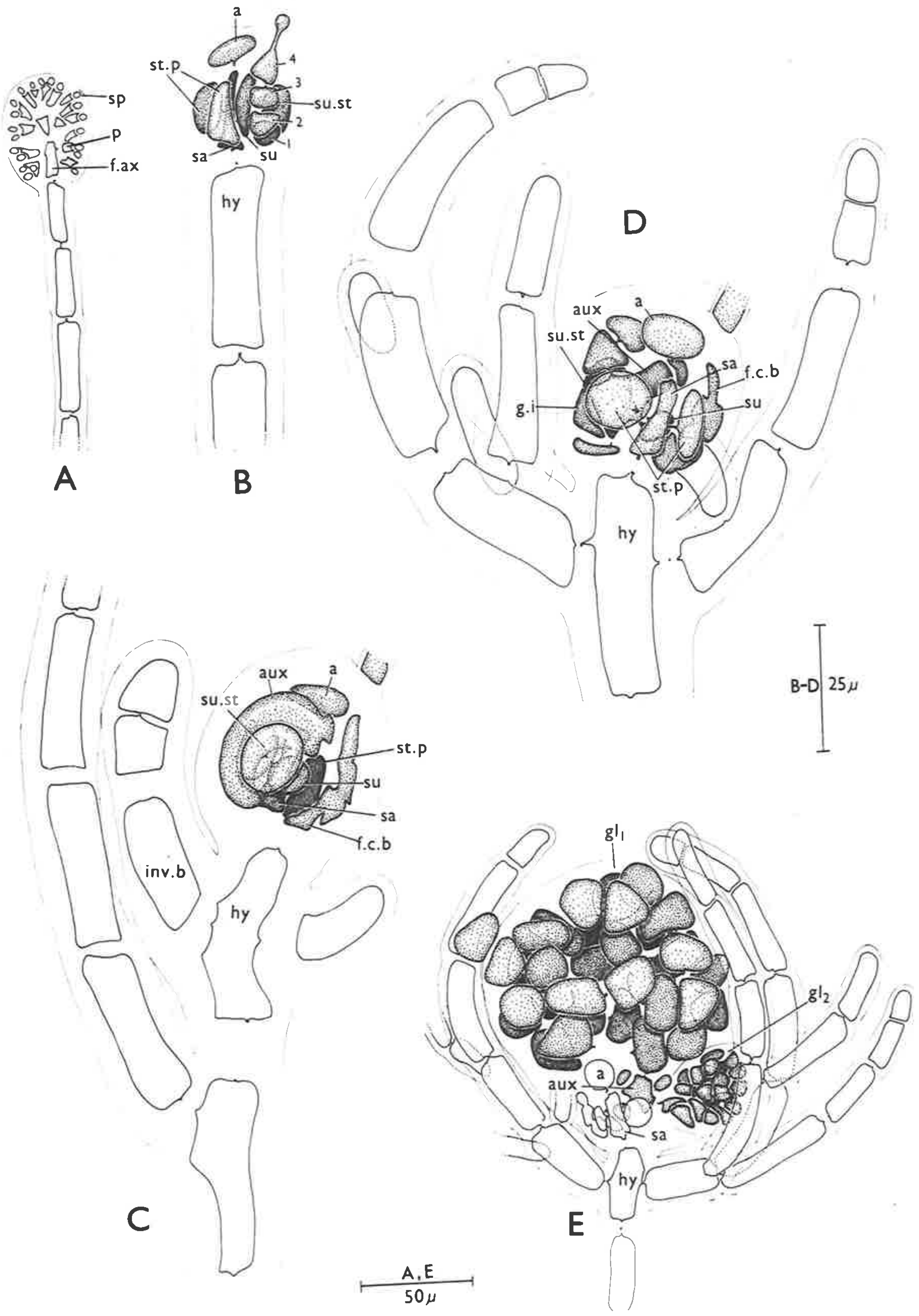

sp
p
f.ax
A
a
4
3
st.p
su.st
2
1
sa
su
hy
B
D
aux
a
su.st
sa
f.c.b
g.i
su
st.p
hy
B-D
25μ
aux
a
su.st
st.p
su
sa
f.c.b
inv.b
hy
C
gl$_1$
gl$_2$
a
aux
sa
hy
E
A, E
50μ

FIGURE 45

Interthamnion attenuata sp. nov.

A.	A29,616	Prostrate and erect axes.
B.	"	Erect axes bearing tetrasporangial branchlets.
C.	"	Longitudinal section of a spermatangial head.
D.	"	Post fertilization stage showing connecting cells and fusion of cells of carpogonial branch.
E.	"	Post fertilization stage showing two auxiliary cells.
F.	"	Mature carposporophyte showing groups of sterile cells.
G.	"	Part of gonimoblast showing carposporangium formation.

FIGURE 45

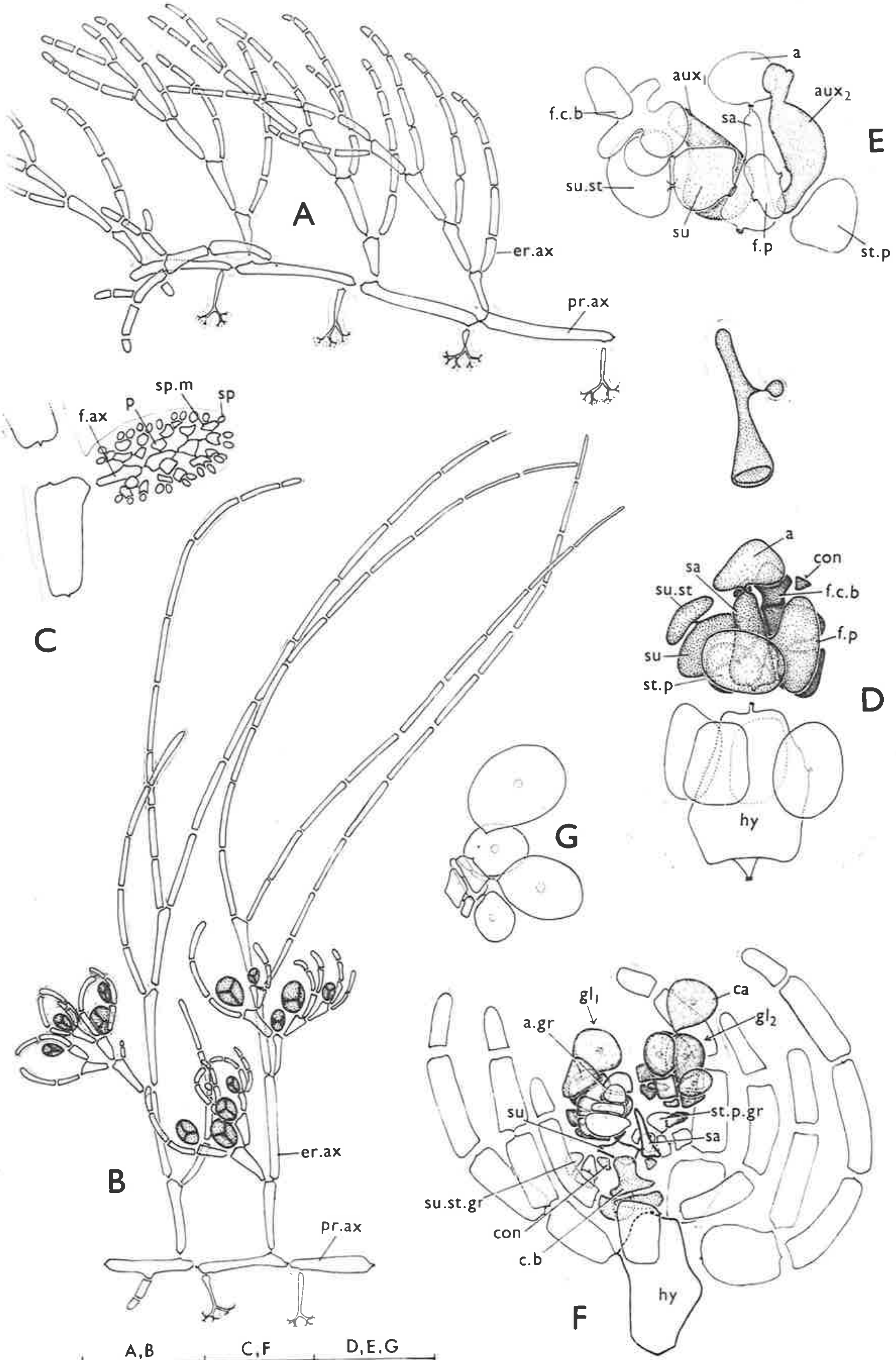

A
er.ax
pr.ax
a
aux1
aux2
f.c.b
sa
E
su.st
su
f.p
st.p
C
f.ax
p
sp.m
sp
a
con
sa
su.st
f.c.b
f.p
su
st.p
D
hy
G
B
er.ax
pr.ax
ca
gl1
a.gr
gl2
su
st.p.gr
sa
su.st.gr
con
c.b
hy
F
A,B
250µ
C,F
50µ
D,E,G
25µ

FIGURE 46

Lejolisia aegagropila (J.Ag.) J.Ag.

A.	A19,502	Prostrate and erect axes with cystocarps.
B.	"	Erect axis with branched hair-like apices.
C.	A18,689	Part of an erect axis of a larger celled form.
D.	A32,161	Part of an erect axis of a smaller celled form.
E.	A19,502	Part of an erect axis bearing tetrasporangia.
F.	"	Part of an erect axis bearing both spermatangial heads and procarp systems.
G.	"	Longitudinal section of a spermatangial head.

FIGURE 46

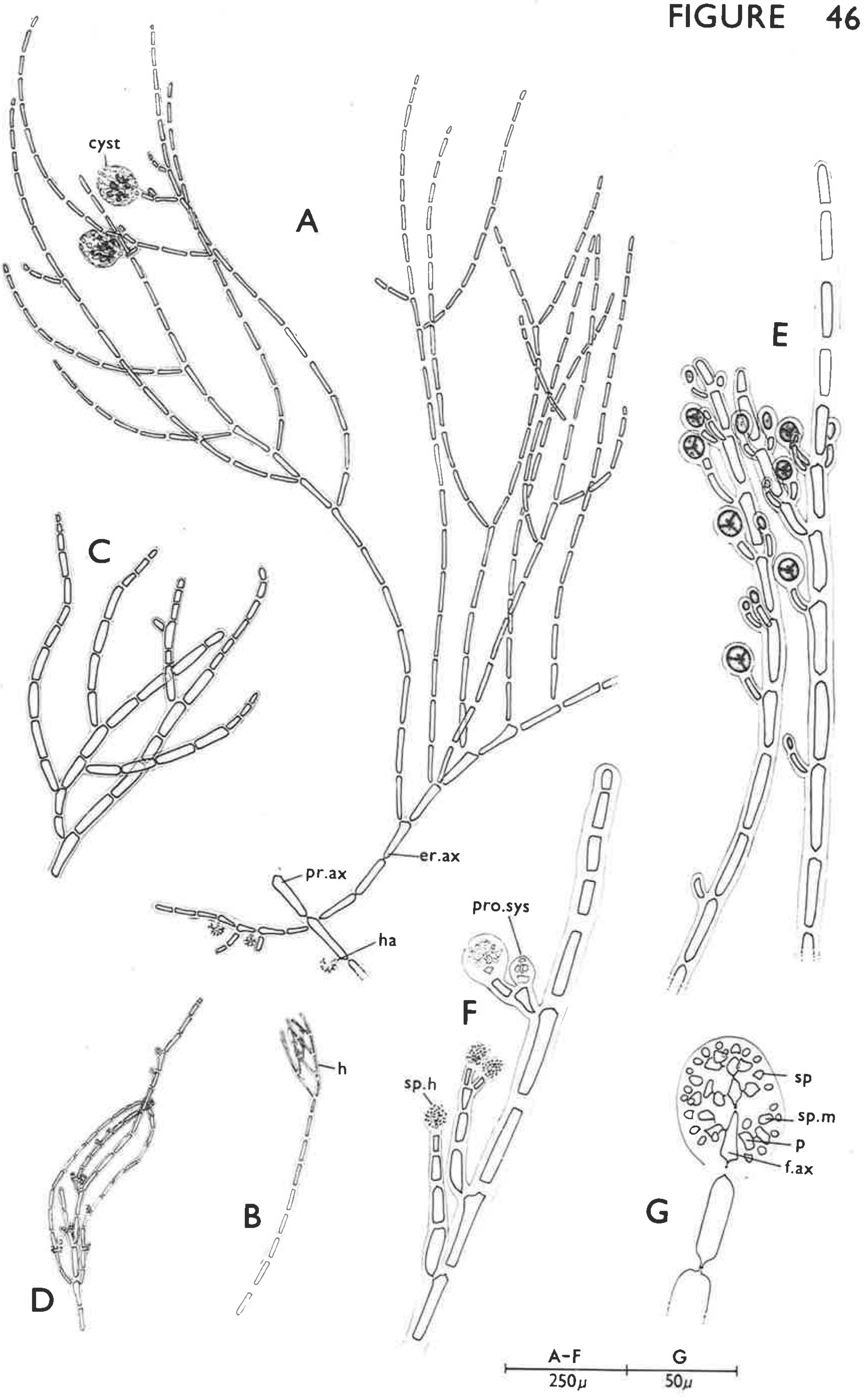

cyst
A
C
pr.ax
er.ax
ha
E
pro.sys
F
sp.h
h
B
D
sp
sp.m
p
f.ax
G
A–F
250µ
G
50µ

FIGURE 47

Lejolisia aegagropila (J.Ag.) J.Ag.

A.	A19,502	Mature procarp system.
B.	"	Post fertilization stage showing auxiliary cell, fused carpogonial branch and division of sterile cells associated with the procarp.
C.	"	Early stage in the development of gonimoblast and pericarp.
D.	"	Later stage in development of gonimoblast. Pericarp omitted.
E.	"	Mature cystocarp.
F.	"	Fusion cell with carposporangia.

FIGURE 47

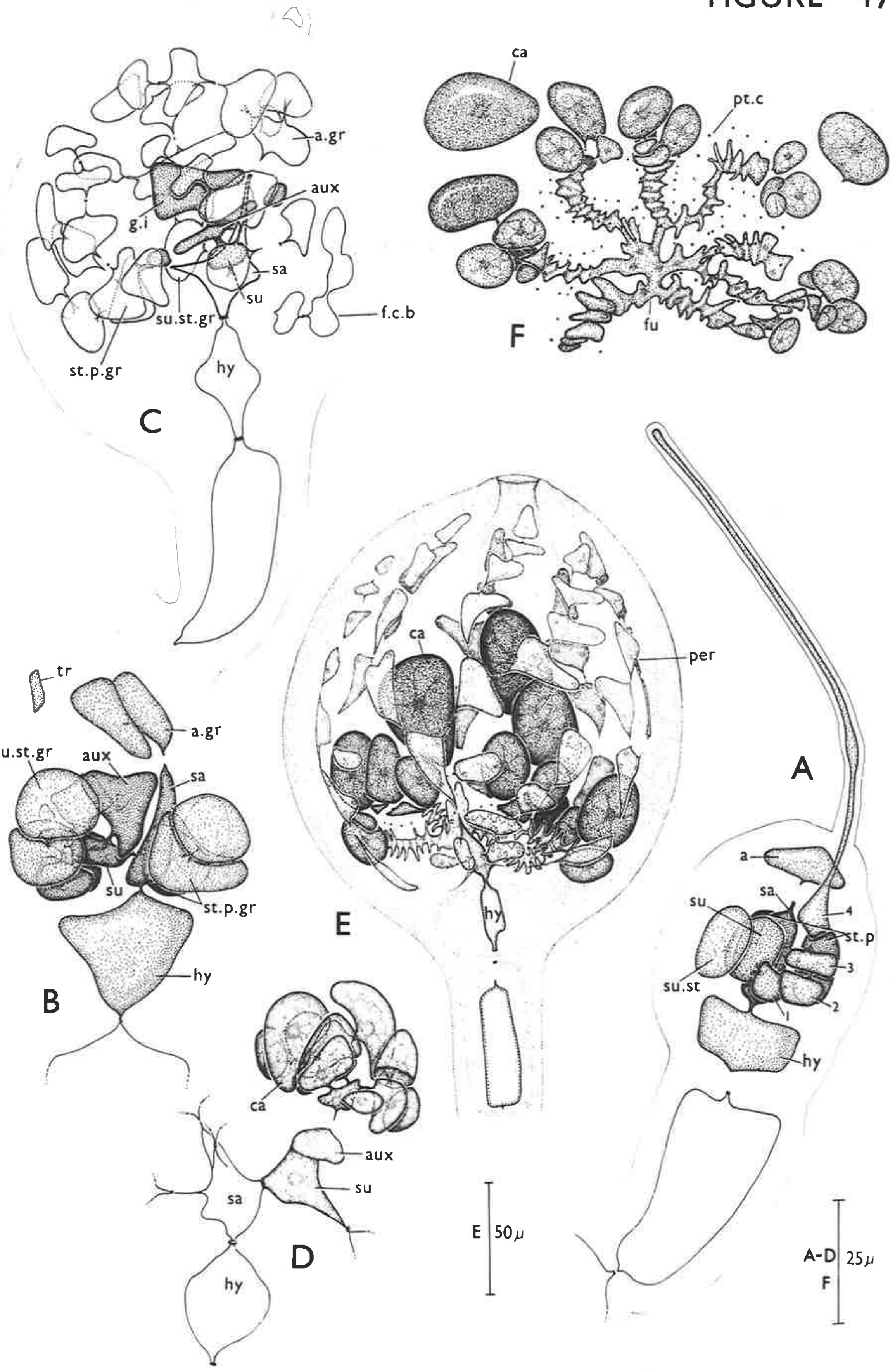
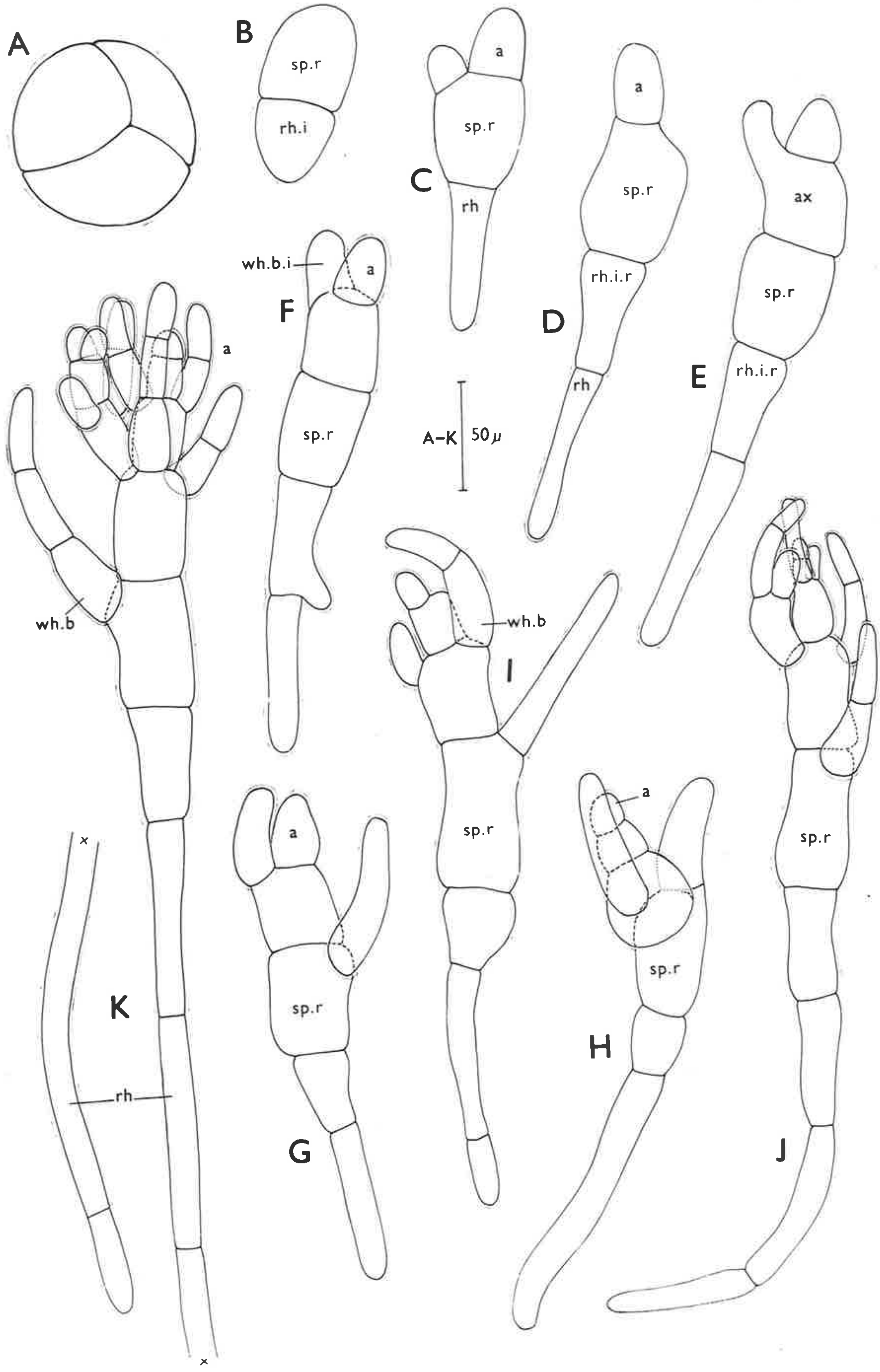

a.gr
aux
g.i
sa
su
su.st.gr
f.c.b
st.p.gr
hy
C
ca
pt.c
fu
F
ca
per
hy
E
a
sa
su
4
st.p
3
su.st
2
1
hy
A
tr
a.gr
su.st.gr
aux
sa
su
st.p.gr
hy
B
ca
aux
su
sa
hy
D
E 50μ
A-D
F
25μ

FIGURE 48

Wrangelia plumosa - stages in germination of tetraspores.

A.	A31,065	Mature tetrasporangium.
B.	"	Two-celled stage.
C.	"	Four-celled stage - first whorl-branchlet initial produced.
D.	"	Four-celled stage.
E.	"	Five-celled stage - rhizoid developing.
F.	"	Six-celled stage.
G.	"	Seven-celled stage.
H.	"	Eight-celled stage - sporeling growing from an oblique to an erect position.
I.	"	Eleven-celled stage.
J.	"	Nineteen-celled stage.
K.	"	Twentynine-celled stage.

FIGURE 48



A
B
sp.r
rh.i
a
sp.r
C
rh
a
sp.r
rh.i.r
D
rh
ax
sp.r
rh.i.r
E
wh.b.i
a
F
sp.r
a
wh.b
A–K
50 µ
wh.b
I
sp.r
a
sp.r
H
sp.r
J
a
sp.r
G
K
rh
×
×

FIGURE 49

Wrangelia plumosa - tetrasporelings

A.	A31,065	48-celled stage - total length of rhizoid not shown.

Lejolisia aegagropila - stages in germination of tetraspores

B.	A32,170	Germinating tetraspore.
C.	"	Three-celled stage.
D.	"	Five-celled stage.
E.	"	Six-celled stage - two free branches arising from the spore residual cell.
F.	"	Young sporeling - one "erect" axis growing horizontally.

FIGURE 49

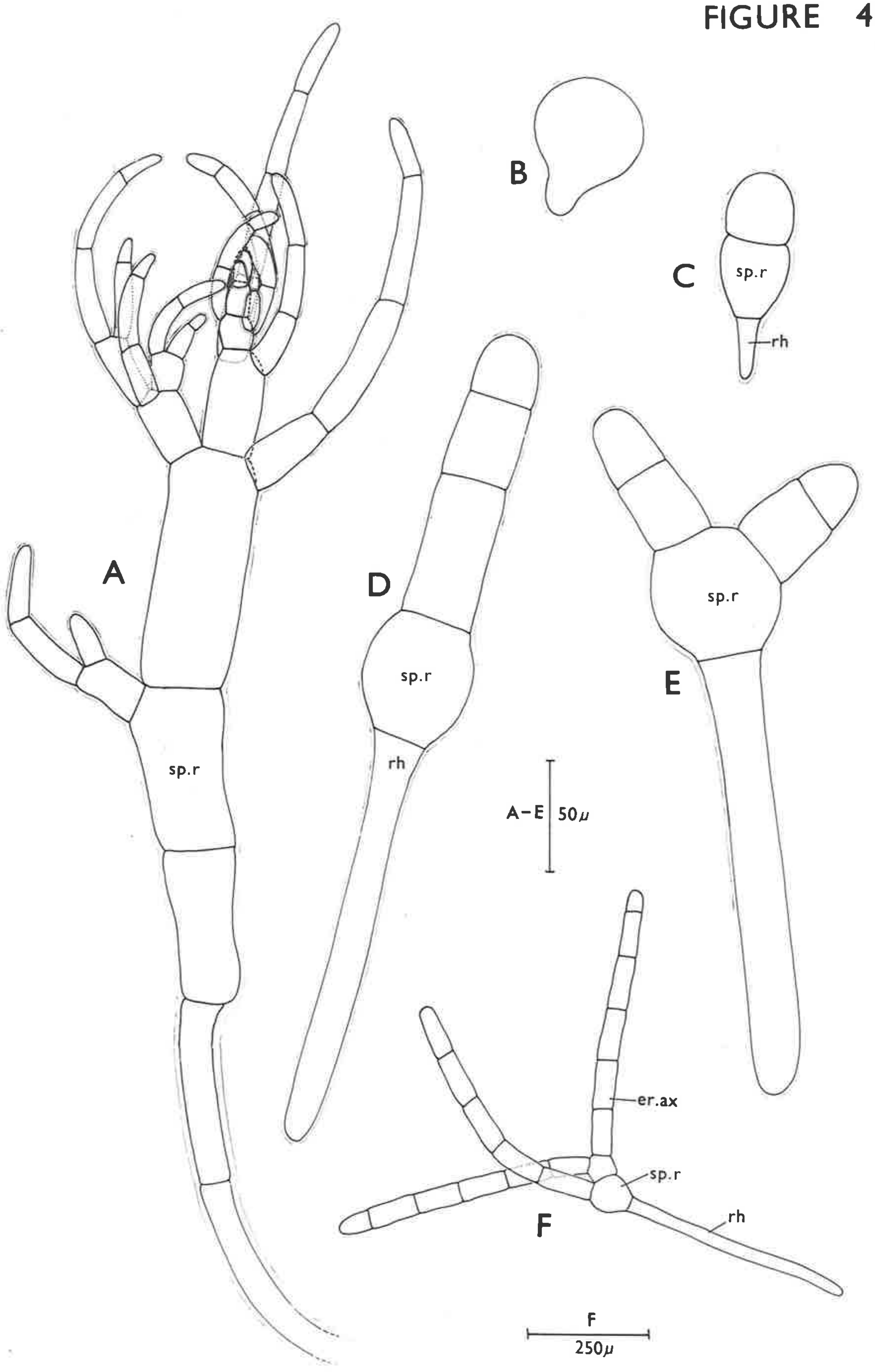


FIGURE 50

Wrangelia plumosa - uninucleate

A.	A31,387	Small dividing cells of whorl-branchlet showing nuclear detail.
B.	"	Part of a median cell of a whorl-branchlet showing nuclear detail and rhodoplasts.

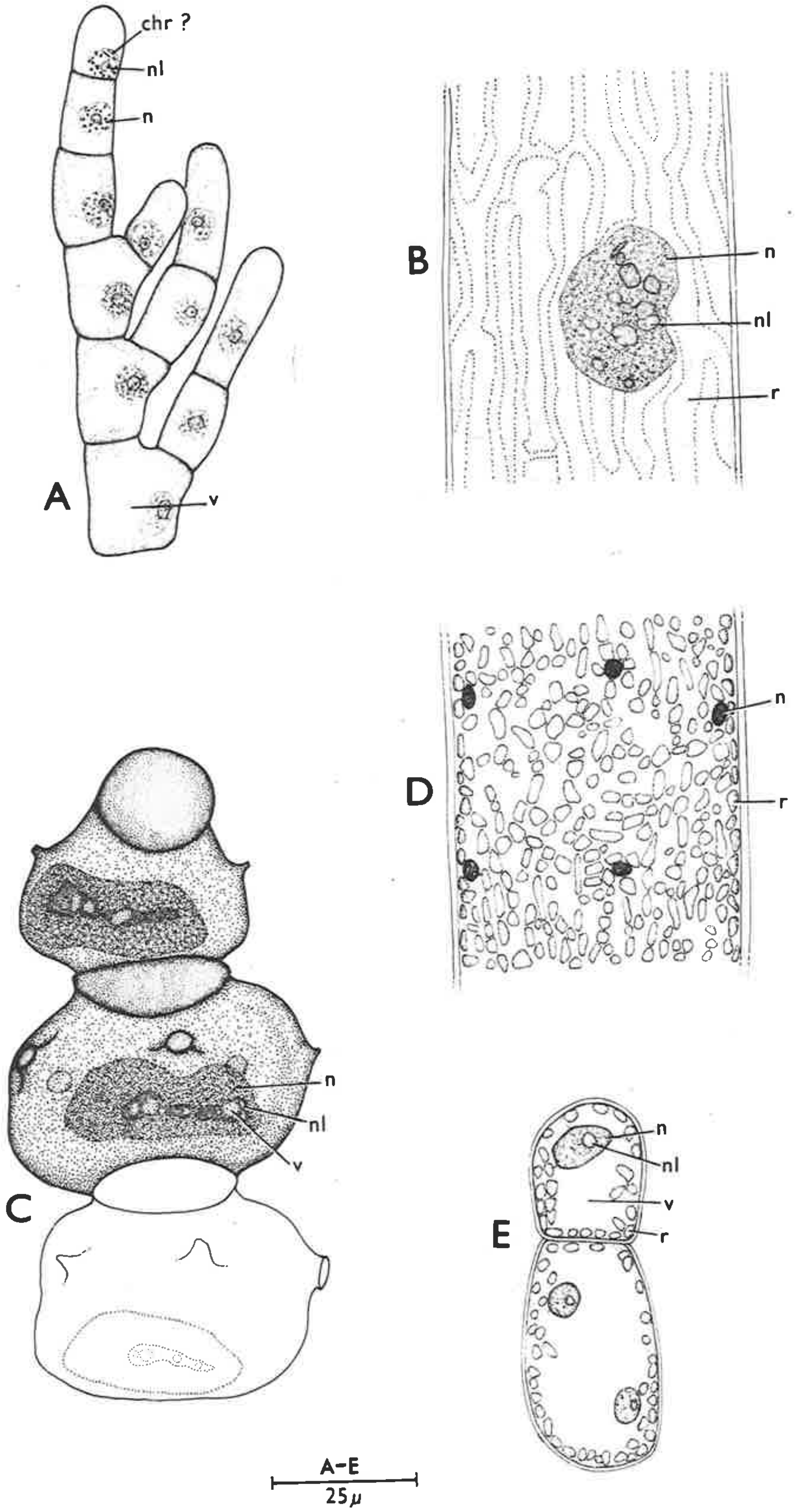
Wrangelia velutina - uninucleate

C.	A32,156	Part of fertile axis of cystocarp showing nuclear detail.

Mazoyera halura - multinucleate

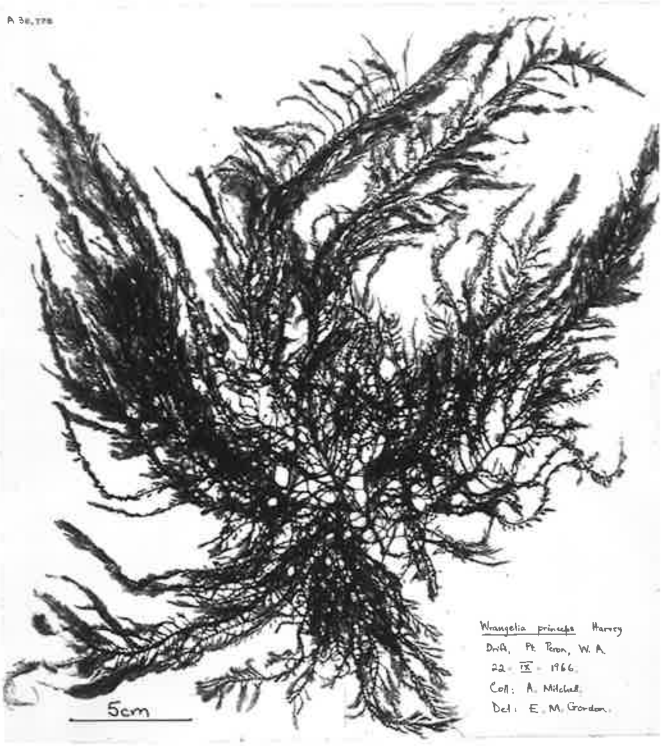
D.	A32,143	Part of a median cell of a whorl-branchlet showing nuclei and rhodoplasts.
E.	"	Longitudinal sections of a tetrasporangial initial and stalk cell showing nuclei and rhodoplasts.

FIGURE 50



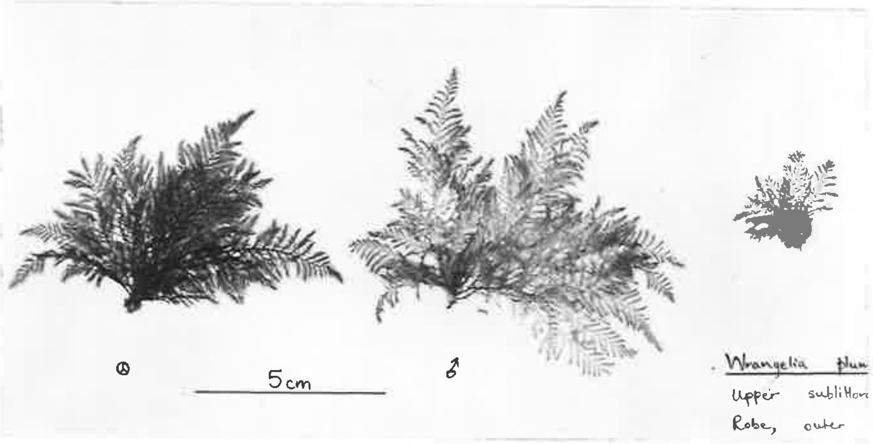
PLATES 1 - 14.

PLATE 1



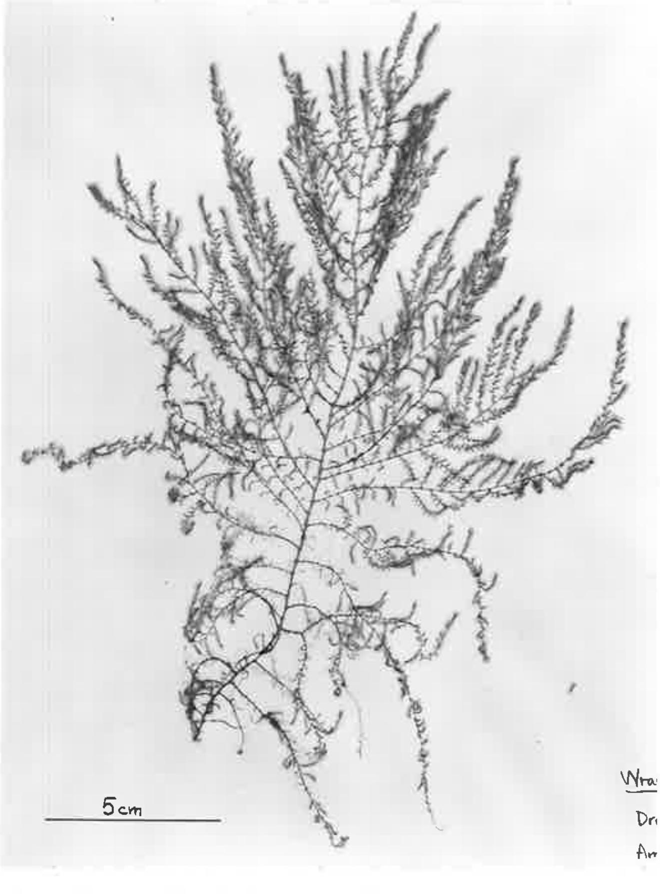
Wrangelia princeps Harvey

ADU, A30,770, Pt. Peron, W. Aust.
Mitchell, 22.ix.1966.



A, Wrangelia plumosa Harvey

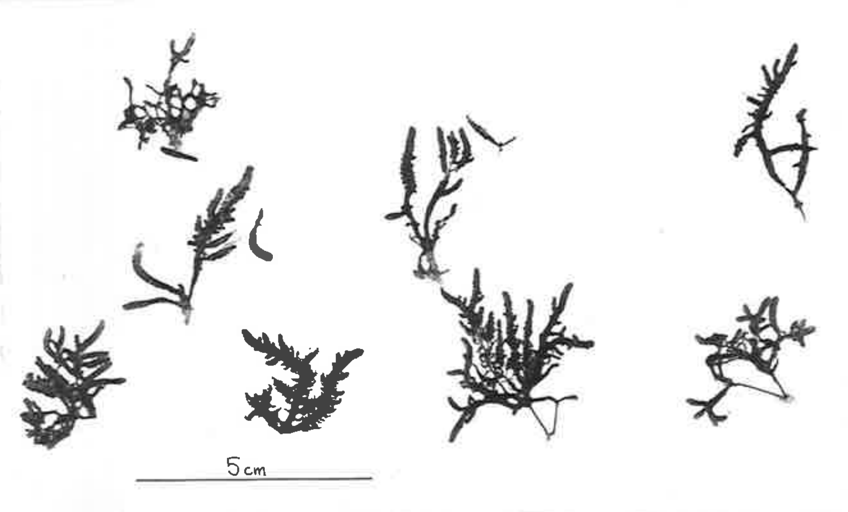
ADU, A31,163, lower littoral plants,
Robe, S. Aust., Gordon, 26.i.1967.



B, Wrangelia plumosa Harvey

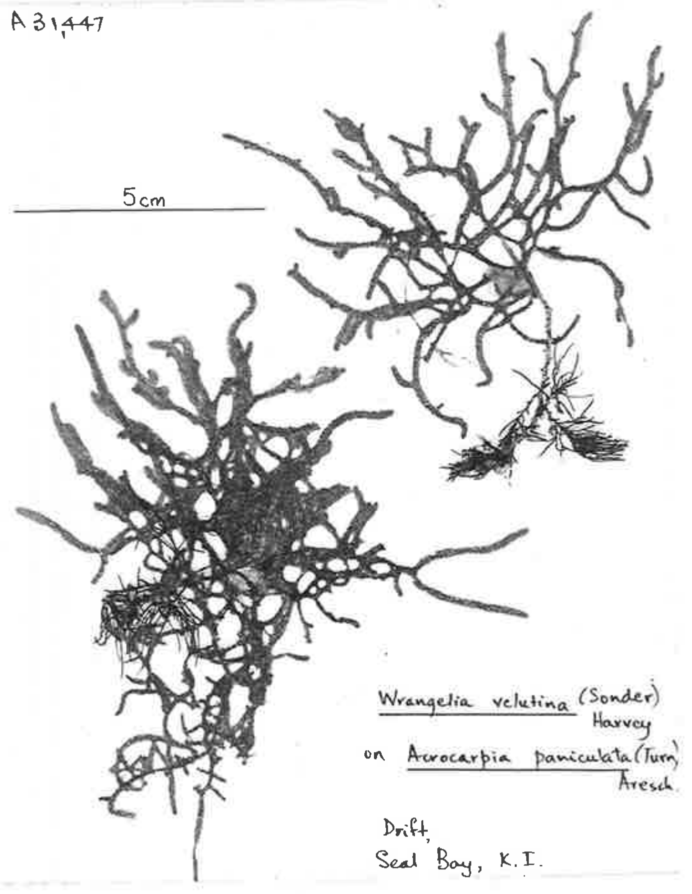
ADU, A30,823, dredged from about 3m, American
River Inlet, Kangaroo Is., S. Aust.,
Gordon, 31.x.1966.

PLATE 3



A. Wrangelia velutina (Sonder) Harvey

ADU, A26,348, lower littoral plants,
Pondalowie Bay, Yorke Pen., S. Aust.,
Womersley, 14.iv.1963



B. Wrangelia velutina (Sonder) Harvey

ADU, A31,447, drift on Acrocarpia, Seal
Bay, Kangaroo Is., S. Aust., Gordon, 20.xi.1967.

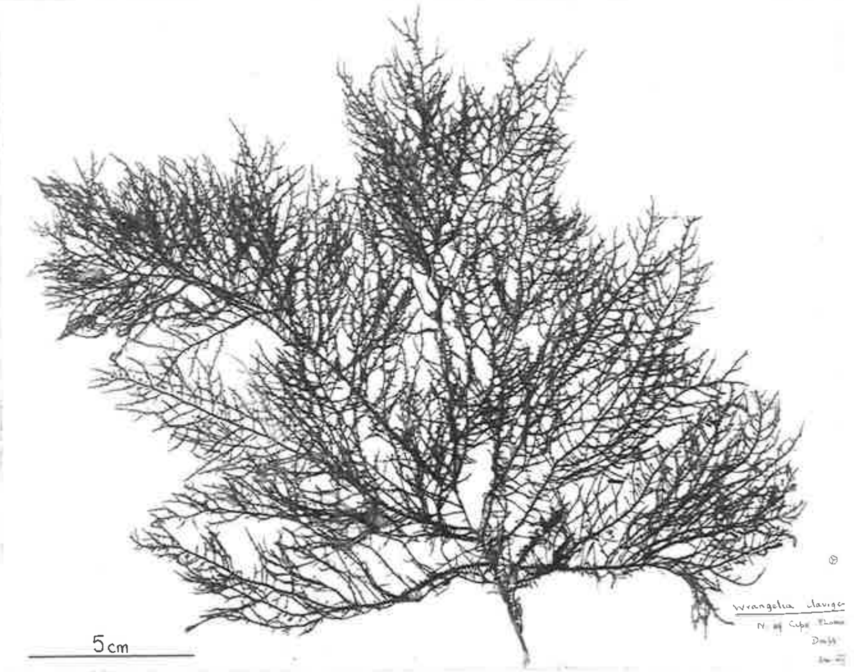
PLATE 4

A. *Wrangelia nobilis* Hooker et Harvey

ADU, A18,294, deep water form,
Georgetown, Tas., Harvey, no. 2691.

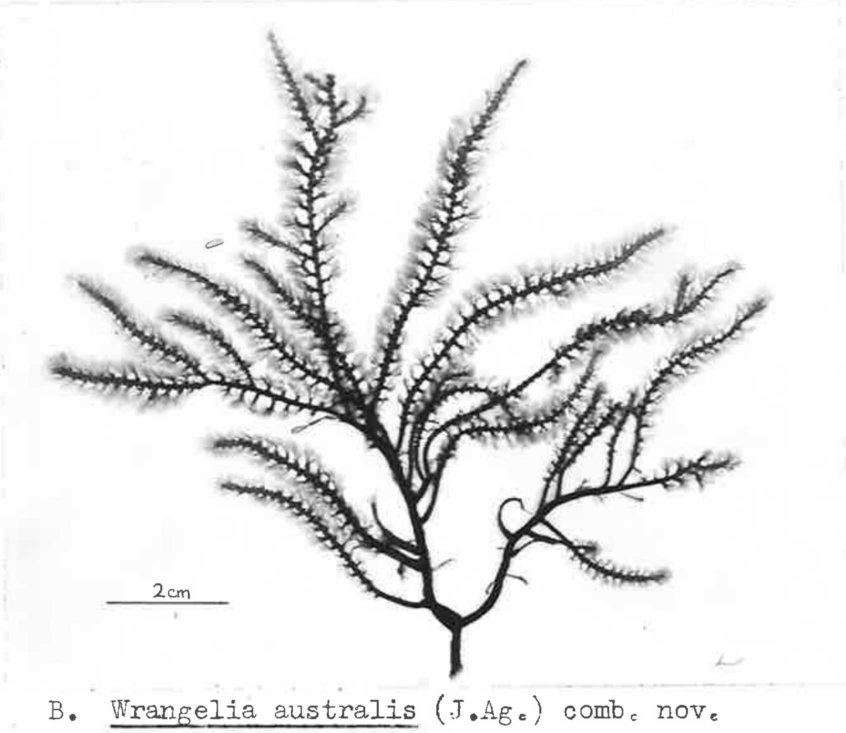
B. *Wrangelia nobilis* Hooker et Harvey

ADU, A30,530, shallow water form,
Seal Bay, Kangaroo Is., S. Aust.,
Gordon, 29.x.1966.



A. Wrangelia nobilis Hooker et Harvey

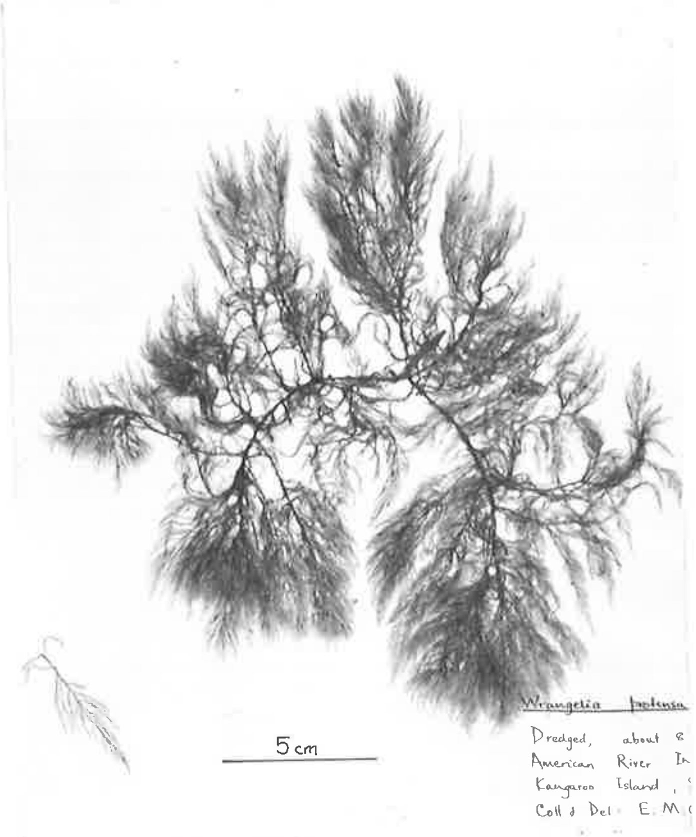
ADU, A24,383, fertile plant, Guichen Bay,
S. Aust., Womersley, 24.viii.1960.



B. Wrangelia australis (J.Ag.) comb. nov.

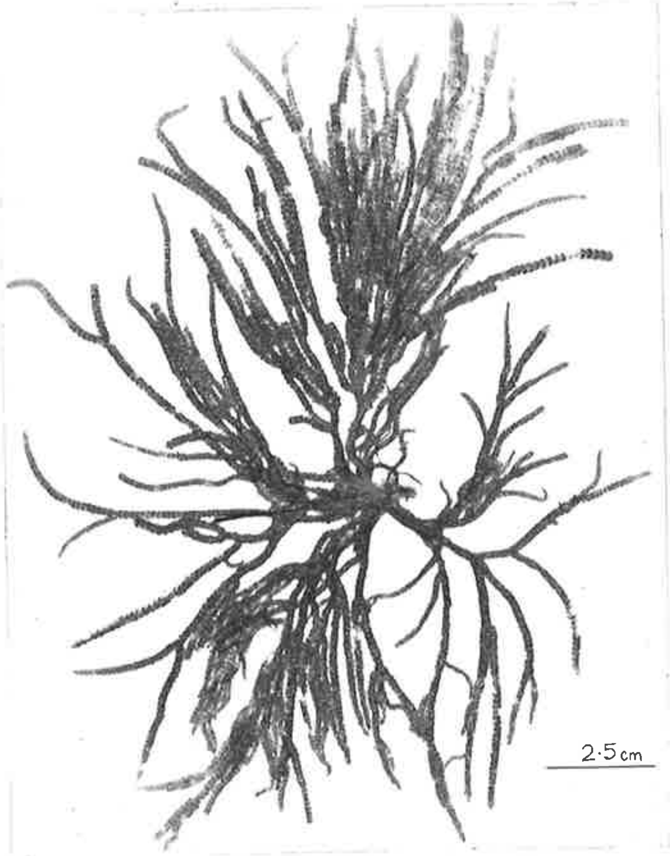
ADU, A32,174, Seal Bay, Kangaroo Is.,
S. Aust., Womersley, 22.xi.1968.

PLATE 6



A. Mazoyera protensa (Harv.) comb. nov.

ADU, A30,877, American River Inlet, Kangaroo Is., S. Aust., Gordon, 30.x.1966.

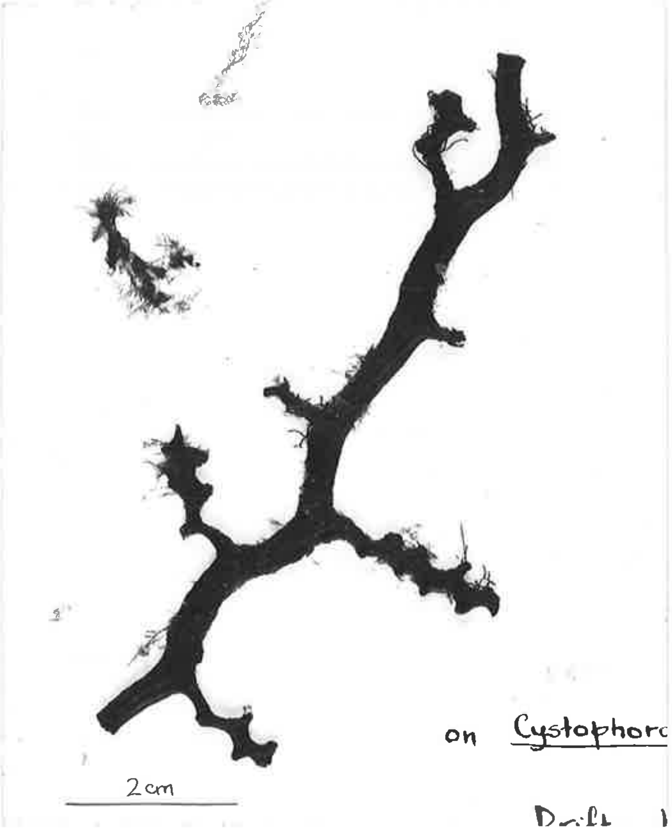


B. Mazoyera halura (Harvey) comb. nov.

ADU, A30,666, Stinky Bay, S. Aust., Gordon, 20.viii.1966.

A. Mazoyera lyallii (Harvey) comb. nov.

ADU, A4063, Timaru, New Zealand,
27.xii.1945 (Herb. Lindauer).

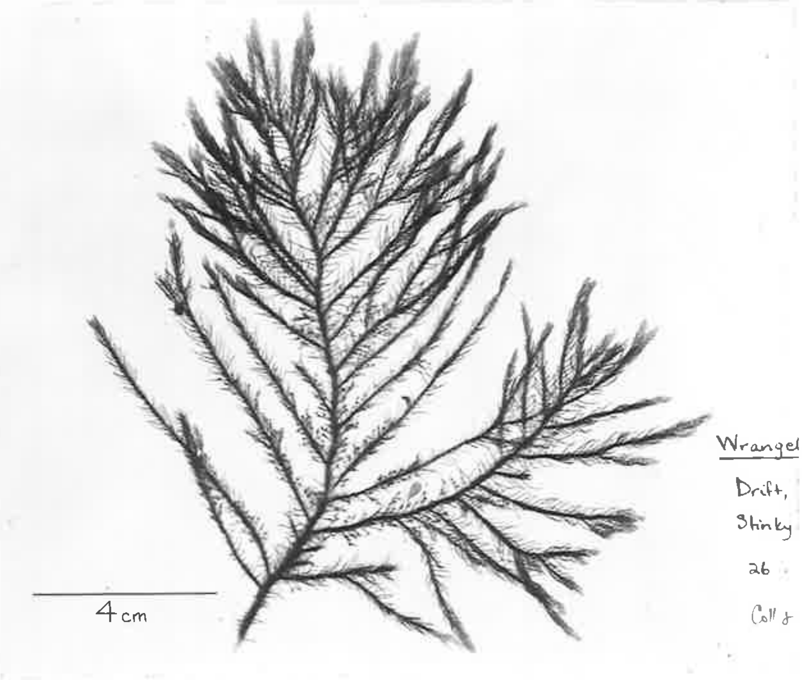


B. Mazoyera repens sp. nov.

ADU, A30,665, on Cystophora,
Kingston, S. Aust.,
Womersley, 19.viii.1966.

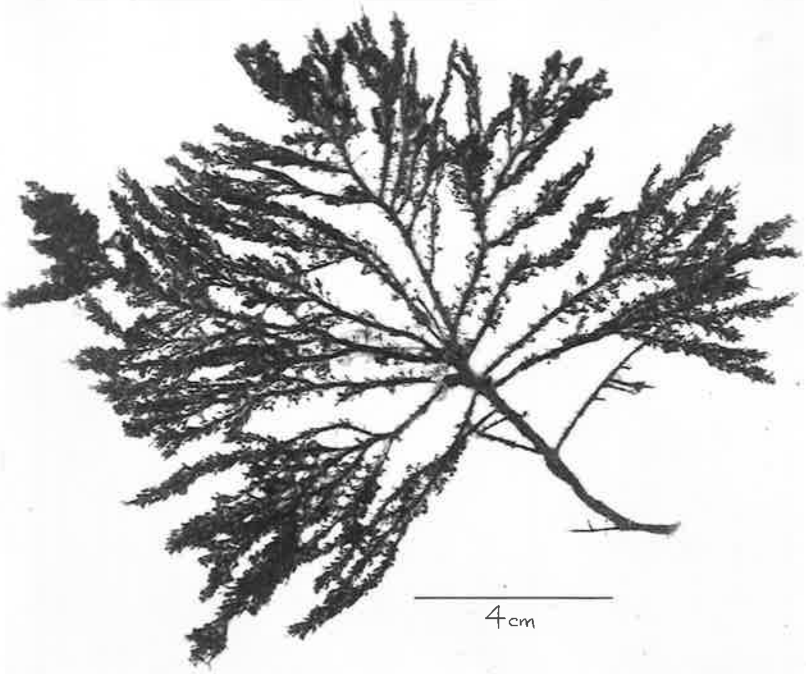
PLATE 7

PLATE 8



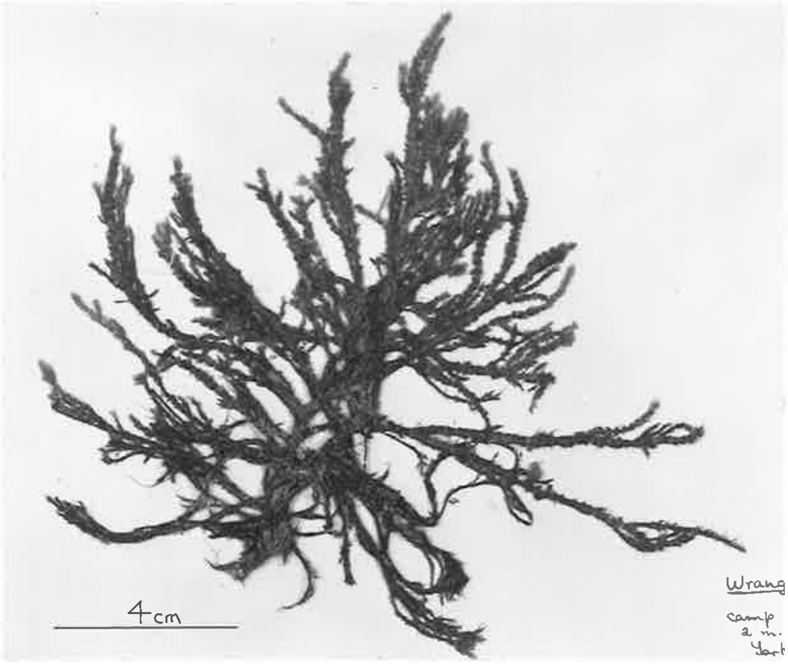
A. Shepleya wattsii (Harvey) comb. nov.

ADU, A31,162, sterile plant, Stinky
Bay, S. Aust., Gordon, 26.i.1967.



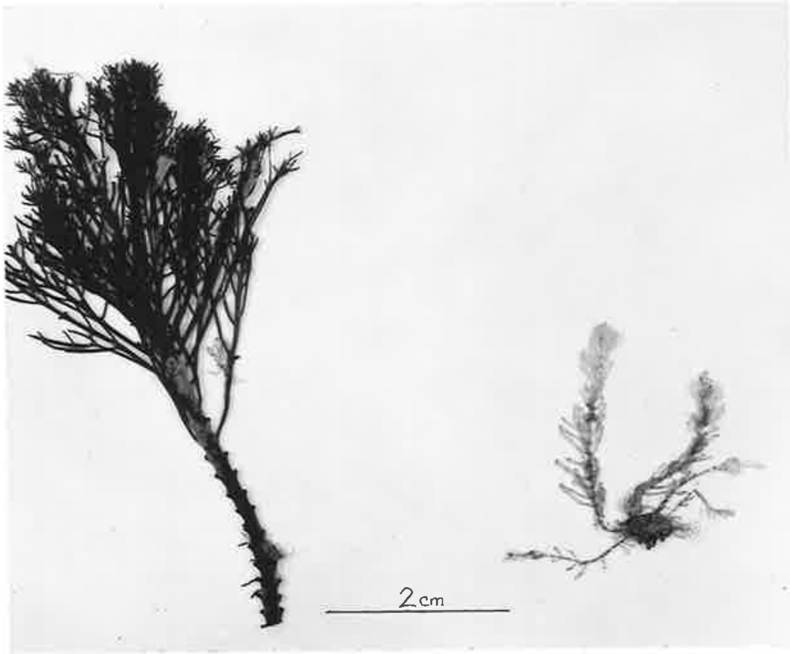
B. Shepleya wattsii (Harvey) comb. nov.

ADU, A30,531, fertile plant, Stinky
Bay, S. Aust., Mitchell, 20.viii.1966.



A. Shepleya verticillata nom. nov.

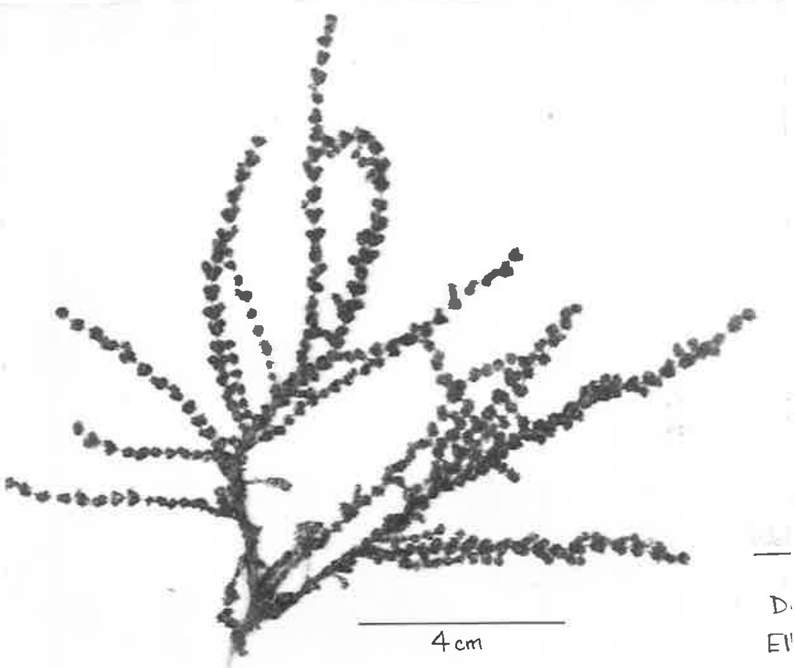
ADU, A26,574, Brown Beach, Yorke Pen., S. Aust., Shepherd, 14.iv.1963.



B. Shepleya claviformis sp. nov.

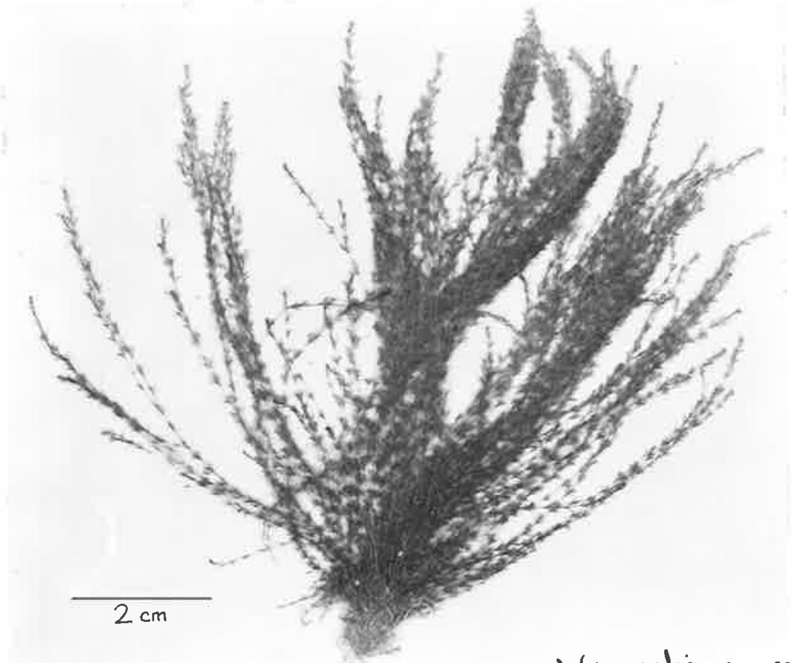
ADU, A32,179, on Callophycus, Pt. Denison, W. Aust., Gordon, 8.xi.1968.

PLATE 10



A. Wollastoniella myriophylloides (Harvey) comb. nov.

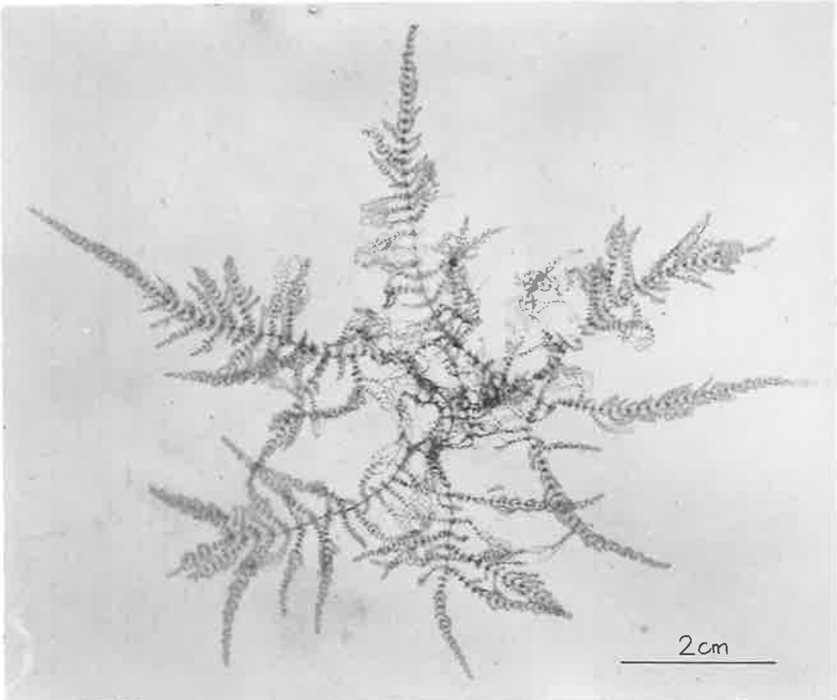
ADU, A31,432, Elliston, Eyre Pen., S. Aust., Parsons, 23.viii.1967.



Wrangelia muci

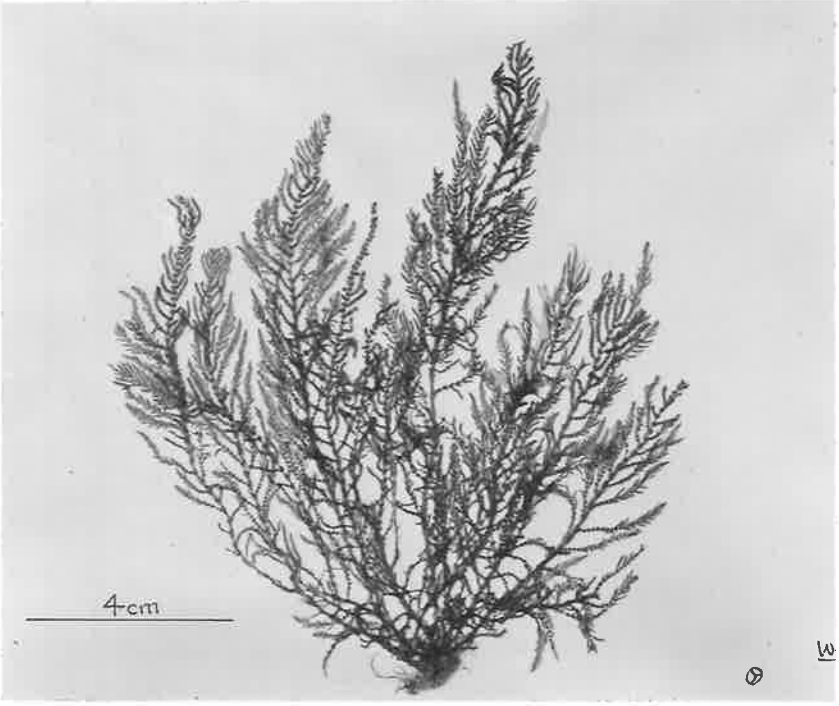
B. Wollastoniella mucronata (Harvey) comb. nov.

ADU, A18,987, Pt.MacDonnell, S. Aust., Womersley, 19.viii.1953.



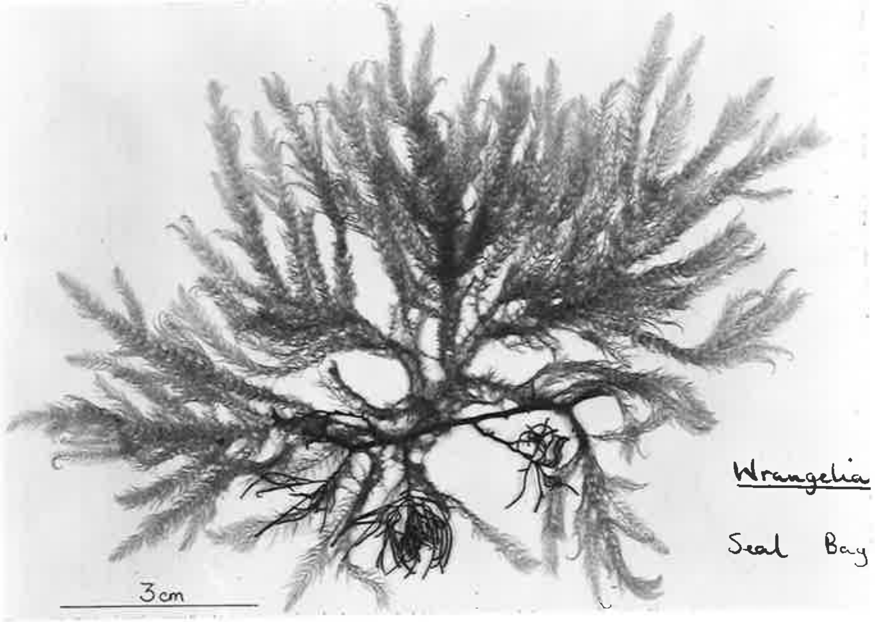
A. Drewiana nitella (Harvey) comb. nov.

ADU, A18,252, plant with creeping prostrate axes, W. Aust., Clifton.



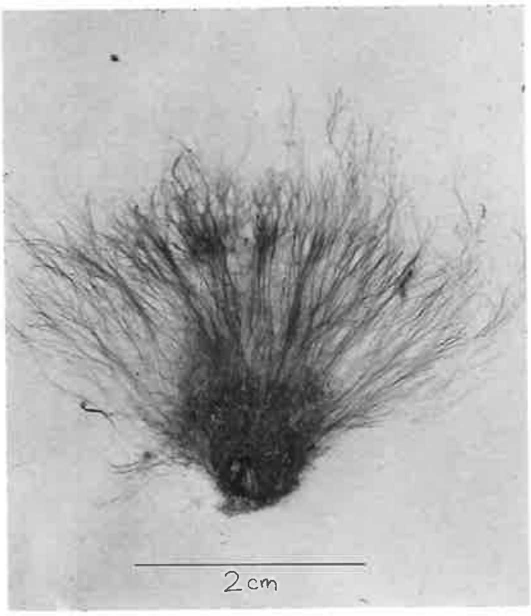
B. Drewiana nitella (Harvey) comb. nov.

ADU, A29,688, plant with compact holdfast, Middleton, S. Aust., Womersley, 14.xi.1965.



A. Involucrana crassa (Hooker f. et Harvey) comb. nov.

ADU, A28,625, Seal Bay, Kangaroo Is., S. Aust., Gordon, 21.i.1965.



B. Spermothamnion cymosum (Harv.) De Toni

ADU, A18,288, King George's Sound, W. Aust., Harvey.

C. Lejolisia aegagropila (J.Ag.) J.Ag.

ADU, A19,502, on Cymodocea, Venus Bay, Kangaroo Is., Womersley, 12.ii.1954.

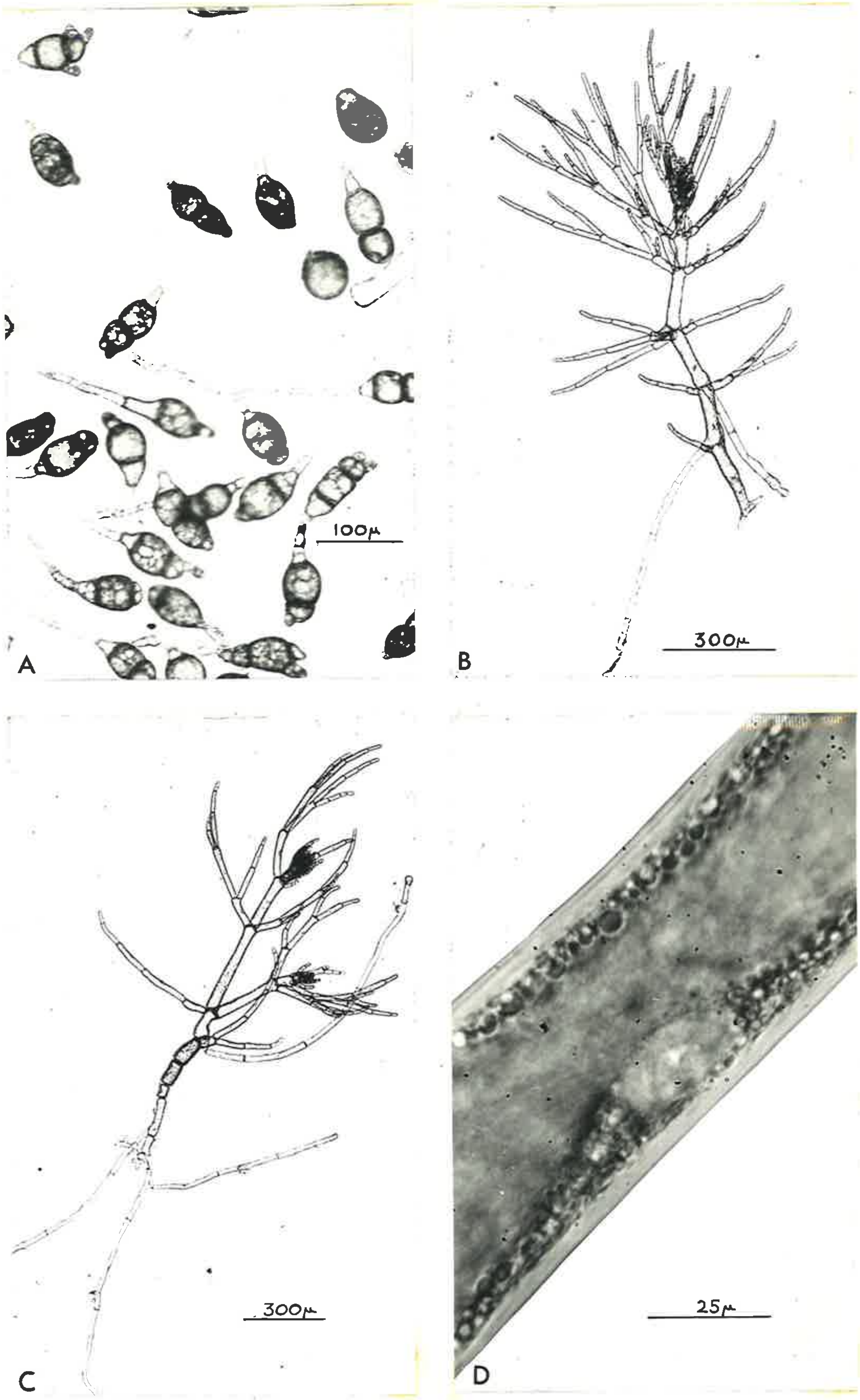
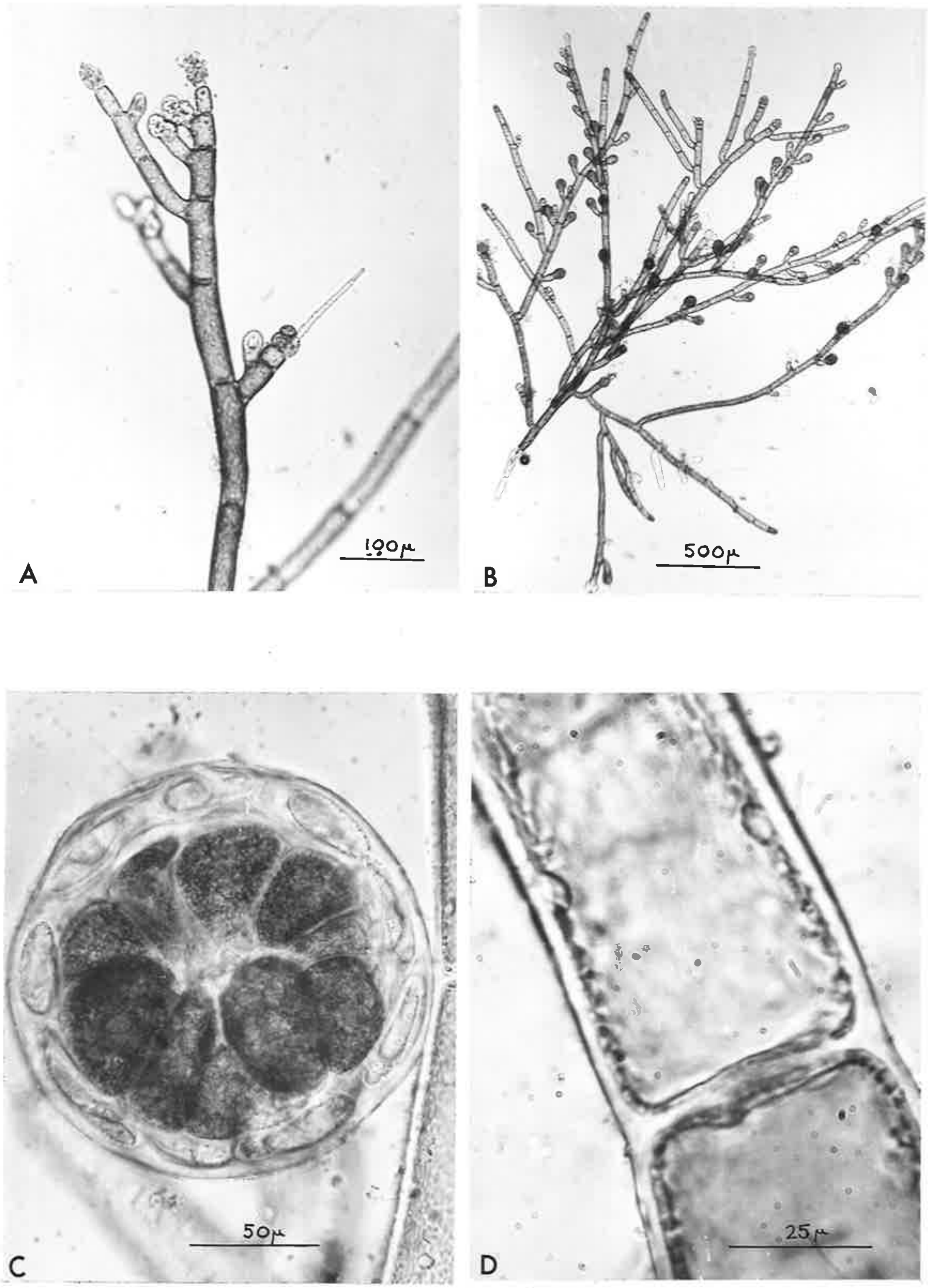

100μ
A
300μ
B
300μ
C
25μ
D

PLATE 14



APPENDIX

Gordon, E. M. & Womersley, H. B. S. (1966). The morphology and reproduction of *Sphondylothamnion multifidum* (Hudson) Naegeli (Ceramiaceae). *British Phycological Bulletin, 3*(1), 23-30.