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fulfilled the requirements for the degree of
Doctor of Philosophy.

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INTRODUCTION

*Riccia* is a widespread genus in tropical and temperate regions. There are more than 200 species recorded: 138 species by Stephani (1900, 1917), and about 100 species subsequently by other authors. All, except the *R. fluitans*-complex, are terrestrial plants usually growing on damp soil and rocks scapage. Some species grow in exposed localities and are drought resistant (Schuster 1957).

In the past hundred years much information has been accumulated dealing with the life-history, structure, distribution, cytology and taxonomy of the Ricciaceae, mainly referring to the European, North and South American, African and Indian representatives. Little is known of Taylor (1864) and Stephani (1900, 1917) of the species in Australia beyond the superficial descriptions, mostly without illustrations. Much of the type material lacks spores which provide more reliable characters than those of the gametophyte. Furthermore, little attempt was made to compare the Australian species with those from other parts of the world.

Stephani lists 23 species of *Riccia* in Australia in his *Species Hepaticarum* (1900, 1917), excluding 5 unpublished species which occur in his drawings in Incones Hepaticarum Volume IV and some in his letters to Dr. Levis. The 23 species recorded are:


The other 5 unpublished species are:
1) *R. burrowensis* St., 2) *R. perthiensis* St.,
3) *R. inoiso-sulcata* St., 4) *R. spongiosa* St., and
5) *R. wattsiana* St.

"All of these species are not clarified in their taxonomy and need careful revision" (Schuster, 1963).

Previously, the treatment of the genus Riccia was mainly based on vegetative characters which have proved to be extremely variable and unreliable. Vegetative characters used appear to show considerable variation in
one species due to different environmental conditions, i.e. the ratio of the width and the thickness of the thallus, thus this method is open to considerable confusion. Furthermore, most of the description were usually with formalized and often meaningless diagnosis; lack of illustrations and no keys.

It has been extremely difficult to define many of these species owing to the unsatisfactory and vague diagnoses provided by Stephani and Taylor, their failure to give adequate spore descriptions and the poor quality of much of the type materials. Therefore an attempt is made here to re-examine all the Australian species of *Riccia* from Stephani's and Taylor's herbariums and to compare these with old and new collections from various places in Australia. Field collections of much new material have been assembled. The aim of this work is:

1. To provide descriptions and illustrations of the Australian species in attempt to clarify their taxonomy.
2. To provide a key for identification of the species;
3. To study their cytology for a better understanding of their taxonomy and their evolution.
4. To study their polyploidy with a view to clarify the relationship between some closely related species.
5. To study the fine structures of the spore wall of various group of *Riccia* and to relate this to the external ornamentation of the spore and
6. To incorporate all the above investigations into a study of their possible phylogeny.
STUDIES IN AUSTRALIAN MARCHANTIALES, THE GENUS RICCIA.

BY

ORBANT NA-THALANG

A THESIS
SUBMITTED TO THE UNIVERSITY OF SYDNEY
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

NOVEMBER 1969.
DECLARATION

I hereby declare that the studies reported in this thesis have been carried out through my own observations, guided by my supervisor, and in the light of subsequently published works. All investigations were carried out in the Botany Department, University of Sydney between March 1966 and November 1969. None of this work has been previously submitted as a requirement for any degree in this or any other University.

Obhanth Na-Thalang.
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INTRODUCTION

Riccia is a widespread genus in tropical and temperate regions. There are more than 200 species recorded: 138 species by Stephani (1900, 1917), and about 100 species subsequently by other authors. All, except the R. fluitans–complex, are terrestrial plants usually growing on damp soil and rocks seapage. Some species grow in exposed localities and are drought resistant (Schuster 1957).

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Previously, the treatment of the genus *Rhodioia* was mainly based on vegetative characters which have proved to be extremely variable and unreliable. Vegetative characters used appear to show considerable variation in
one species due to different environmental conditions, i.e. the ratio of the width and the thickness of the thallus, thus this method is open to considerable confusion. Furthermore, most of the description were usually with formalized and often meaningless diagnosis; lack of illustrations and no keys.

It has been extremely difficult to define many of these species owing to the unsatisfactory and vague diagnoses provided by Stephani and Taylor, their failure to give adequate spore descriptions and the poor quality of much of the type materials. Therefore an attempt is made here to re-examine all the Australian species of Riccia from Stephani's and Taylor's herbariums and to compare these with old and new collections from various places in Australia. Field collections of much new material have been assembled. The aim of this work is:

1. To provide descriptions and illustrations of the Australian species in attempt to clarify their taxonomy.

2. To provide a key for identification of the species.

3. To study their cytology for a better understanding of their taxonomy and their evolution.

4. To study their polyploidy with a view to clarify the relationship between some closely related species.

5. To study the fine structures of the spore wall of various group of Riccia and to relate this to the external ornamentation of the spore and 6. To incorporate all the above investigations into a study of their possible phylogeny.
II.

MORPHOLOGY

A. CHARACTERS USED IN TAXONOMY.

The characters used for defining Riccia spp.
are based on both vegetative and spore features, the
latter are more reliable at the specific level because
of the rather constant sculpturing on the distal and
proximal faces of the fully mature spore, apparently
regardless of environmental situation. Only the size
of the spores seems to be very variable in the same
species. Nevertheless, the size of spores together with
the form, colour and sculpturing on both surfaces are
very useful in distinguishing the species, especially with
herbarium material as the spore is usually the only part
of the plant which has retained its characteristics.
However, the vegetative or gametophyte features are
still adequate for distinguishing between the subgenera
and the groups.

The vegetative or gametophyte characters:

1. HABIT - The gametophyte in this genus is
dichotomously branched and occasionally forming
complete or incomplete rosettes; mainly, they are
annual in the subgenus Ricciella while most species
in subgenus Riccia are perennial.

2. PHOTOSYNTHETIC ZONE - In the majority of species
the green or photosynthetic zone occurs on the upper part
of the thallus, but in one species the photosynthetic
tissue occurs on the ventral side, mainly at the scales
of the thallus with hyaline compact tissue on upper part. The species with photosynthetic tissue at upper part of the thallus can be divided into two main groups: one with green tissue arranged in vertical columns each terminated by a hyaline epidermal cell (Fig. 2.3, a, b, & c), the other consisting of reticulate, one-layered cell plates forming polyhedral air chambers, each normally is roofed over by green epidermal cells with an air pore in the centre (Fig. 2.3, j, k & l). The first type of photosynthetic tissue occurs in subgenus Riccia, the second in subgenus Ricciella.

3. FORM OF THALLUS AND OF SEGMENT — The frequency of branching varies from furcate to bi- or trifurcate, and one group is multifurcate (R. fluitans-complex). For the form of the segment, it is slightly varied from obconic to obconic-oblanceolate, oblanceolate, narrowly and broadly oblong to broadly and narrowly linear.

4. SIZE — The dimensions of the thallus; both length and breadth are necessary to give the general appearance of the thallus; but the ratio of the width and the thickness shows considerably variation depending on the environment, i.e. in moist conditions the thallus is less thick (Abeywickrama, 1945).

5. UPPER SURFACE — a) A dorsal groove (Fig. 2.1, c) is present in almost all Riccia spp. and is rather invariable. b) The outline of the air chamber areas is visible on the upper surface in the subgenus Ricciella, whilst the surface pattern on the thallus of subgenus Riccia is due to the epidermal cells.
FIG. 2.1

Diagram of the transverse section of the thallus.

a - antheridium
b - basal portion of thallus
c - channel or dorsal groove
m - margin
p - photosynthetic part of thallus
r - rhizoid
s - scale
Diagram of the transverse sections and outline of the thallus to illustrate terms used in descriptions.

a. Margin rounded, ascending, with cilia; channel broad.

b. Margin acute; scale extending beyond the margin, channel narrow.

c. Margin obtuse or rounded, slightly raised up; channel broad.

d. Margin rounded, flat.

e. Margin rounded, flat.

f. Margin rounded or obtuse, raised up or tumid; channel very broad.

g. Margin acute, attenuate; channel narrow and shallow.

g, h and i. Position of capsules.

g. Capsule prominent on ventral surface.
h. Capsule prominent on upper surface.
i. Capsule embedded in the thallus.

j, k and l. Thallus.

j. Thallus with cilia at the margin.
k. Thallus with scales at the margin.
l. Thallus without cilia or scales.
FIG. 2.3

Characters of epidermis and airchambers.

a, b and c Subgenus *Riccia*

a. Portion of the epidermis of the typical *Riccia*, surface view.
b. Portion of paradermal section of the thallus.
c. Portion of transverse section of the thallus.

j, k and l Subgenus *Ricciella*

j. Portion of the epidermis, surface view.
k. Portion of paradermal section of the thallus.
l. Portion of transverse section of the thallus.

e  - epidermal cell
g  - photosynthetic cell
h  - airchamber
p  - airpore
6. SCALES – The lateral–ventral scales (Fig. 2.1, 5 & Fig. 2.2, k) are well developed in some species, but almost rudimentary in others. The character of scales such as the size, colour and its persistent are slightly changed under moist or shady conditions (see below), but in the normal habitats these characters are rather constant and can readily distinguish the groups in the field.

7. CILIA (Fig. 2.2, a & j) – The presence of cilia in certain groups is relatively constant, but again the length and the density also vary under different growing conditions (see below).

8. THE POSITION OF THE CAPSULE – This character is very distinct in the R. fluitans–complex group in which the capsule bulges out on the ventral surface (Fig. 2.2, g) can separate this group from others in the subgenus Ricciella. In the subgenus Riccia it can be used at the specific level, especially among the group with cilia at the margins.

9. THE MARGIN – As seen from the dorsal surface, there are two types: 1) with plane or flat margin (Fig. 2.2, c, d, f, g & i), 2) with swollen or raised up margin (Fig. 2.2, a & e). In vertical section, the margin is acute and attenuate (Fig. 2.2, f), acute (Fig. 2.2, c, g & i), obtuse (Fig. 2.2, c & e), or rounded (Fig. 2.2, d & h).

10. THE APEX – The character of the apex is normally of 2 types, obtuse and truncate (Fig. 2.2, k, j & l).

The spore characters:

1. FORM – a) The spores of Riccia are normally
FIG. 2.4

Spore types and patterns.

a - globose spore.
b - triangular-globular or subtriangular, proximal face showing triradiate ridge (mark).
c - the profile of triangular-globular spores.
d, e, f, g, h and i pattern on sculpturing of spores:— (Ca x 730).
d - reticulate with high and thick ridges at the corners of areola.
e - reticulate, areola with smooth and narrow borders which project at the corners.
f - reticulate with vermicula ridges.
g - reticulate, areola with smooth and narrow borders not projecting at the corners.
h - reticulate, areola with broad border.
i - di-trichotomous branching ridges.
tetrahedrally arranged, the tetrad usually separating at maturity (except in *R. curtisii* Jam., *R. personii* Khan, *R. compacta* Garside and *R. arnelli* Khan in which the spores are permanently united in tetrads), which results in a tetrahedral spore with a convex distal face and a proximal face marked by triradiate ridge (Fig. 2.2, b & c). This type of spore is triangular or triangular-globular or sometimes almost circular as it is seen from distal or proximal face (Fig. 2.4, a & b), but pyramid-like in profile (Fig. 2.4, c, b). In some groups of *Riccia* spp. the spores are probably separating during the early stage of development resulting in each spore having a globular shape without distinct distal or proximal faces (Fig. 2.4, a).

2. SIZE - The size of the spore is measured at the maximum width from distal or proximal face (Fig. 2.4, b).

3. COLOUR AND OPACITY - The colour and opacity of spores vary from species to species but remain rather constant in each species. Most of the species have brown spores; in some species the spores are reddish-brown or purplish-brown, others are dark-brown and still others are quite opaque at maturity.

4. WING - The wing or the margin is a hyaline membrane surrounding each spore of many species at the equatorial rim separating the distal face from proximal face, sometimes with enlarged marginal angles or "pole" or "mucilage plug" (Fig. 2.4, b & c). In some species, it appears as a thin membrane attached to the ridge of spore, e.g. *R. billardieri* Mont. et N. (Pl. 3.10, c), but it is not present in others, e.g. *R. genetica* Ahmad (Pl. 3.9, c).
5. SCULPTURE — The sculpture on the proximal face is as important for identification as that on the distal face. Normally, the sculpture on the distal face is reticulate (RETICULATE — consisting of net-work, reticulum, formed by anastomosing ridges; enclosing small, frequently more or less irregular space (Erdtman, 1947)), e.g. R. duplex Lorb. (Fig. 2.4, e); the small areas formed by the reticulation are called areolae (AREOLA — a space marked out on a surface by (crack) ridges (Stern, 1966)), e.g. R. duplex Lorb. (Fig. 2.4, e). In most species, the ridge at the corners of the areola is raised up forming "papillae" or projecting processes, e.g. R. marginata Carr. et P. (Fig. 2.4, a); in some species, however, the ridge is not raised up at the corners and only forms a smooth border to each areola, e.g. R. blackii 0. NT. sp. nov. (Fig. 2.4, g & h). In still other species, the ridge is arranged in a irregular form and is said to be "vermicular" e.g. R. limbata Bisch. (Fig. 2.4, f). There are some Riccia spp. in which the spore does not form definite areolae, but the surface is marked out by regular or irregular branched ridges, e.g. R. cavernosa Hoffm. (Fig. 2.4, i), and one species, only, has a smooth spore wall, e.g. R. albida Sull. On the proximal face, the presence of a distinct or indistinct triradiate mark is rather stable in each species as well as the reticulation, but the latter is normally less distinct than that of distal face and sometimes consists of different types of ridges (see Chapter III; descriptions of species).
B. EFFECT OF ENVIRONMENT ON SOME OF THE VEGETATIVE CHARACTERS.

The vegetative structures of the genus *Riccia* are very variable under different circumstances and this has caused a great deal of taxonomic complexity in the group. Mainly owing to the lack of comparative studies of the species growing in different habitats, and in different geographical locations, probably an undue emphasis has been given to minor differences in size etc. The size of the thallus is considerably variable in terms of width, length and thickness, as well as the form of the thallus, apex, margin and colour. Many attempts, both observational and experimental have been carried out to provide a definite delimitation of species of the "*R. fluitans*-complex" (Torka, 1905, 1911; Donaghy, 1916; Gaisbery, 1921; Carter, 1935; Klingmüller, 1958; Müller, 1941). Whilst many species of the rest of this genus still need a careful re-investigation in the same way.

Pande (1924) noted the change of colour and width of the thallus in *R. sanguinea* Kash. The male thalli, which normally develop a red colour in nature, becoming green when growing under different conditions of light and moisture and thalli of both male and female plants are narrower when moisture is in excess.

Similar investigations on the effect of light and moisture on thalli of *R. crispatula* Mitt. have also been reported by Abeywickrama (1945). He observed that "In shade plants it is seldom or never produced dark purple colour at the margin and ventral surface" and
"When plants were grown in strong sunlight, whether on dry or moist soil, the colour was always produced". For the width and the thickness of the thallus, he says "Increasing the moisture-content of the habitat, whilst still keeping the plants exposed, caused the thallus to become narrower, but the thickness remained unchanged. Increase in moisture accompanied by shading resulted in the thallus becoming broader and thinner, and finally when plants were given an excess of moisture the thallus became narrow".

As it seems that changing conditions of light and moisture play an important part in the variation of the vegetative characters, it was decided to use the apparently more stable characters of cilia and scales in an investigation on the effect of the environment on taxonomically useful characters.

A. CILIA

Materials and Methods.

Two species of Riccia which normally produced cilia at the margins viz. R. crinita Tayl. and R. asprella Carr. et P. were used for the observation. Each species was treated with the same method by planting 6 thalli (which have similar characters of cilia, i.e. density and length and almost the same size of the thallus) on soil in the closed chamber of crystal dish (ca. 5 cm. diam.,
4 cm. high), for each treatment. They were treated with two conditions of light and two conditions of moisture in a constant temperature room (25°C). Each treatment has two replicates.

In Table 2.1 and 2.2

$I_1 = \text{high light (50 foot candles) with maximum moisture.}$

$I_2 = \text{high light (50 foot candles) with minimum moisture.}$

$II_1 = \text{low light (5 foot candles) with maximum moisture.}$

$II_2 = \text{low light (5 foot candles) with minimum moisture.}$

The measurement of cilia was taken from 10 thalli in each treatment after growing for 90 days.

$m = \text{mean of length of the cilia in each plant.}$

The density of the cilia per 10 mm. was the average number taken from the same plant used for measuring the length of the cilia.
These values were then compared between treatments by the F test and t test, and the correlation of the length and the density of cilia were compared in each treatment by correlation coefficient.

\[ x_{ij}^2 = \text{sum of 40 of } x^2 = \xi (x_i^2) \]

\[ \text{correction factor} = (\xi (x_i))^2/rt \]

\[ \xi x_i^2 = \xi (x_i)^2 \]

\[ T = \text{Treatment mean square} \]

\[ E = \text{Error mean square} \]

The hypothesis being that there is no difference in cilia length or density between each treatment, i.e. \( T_i = 0 \) (where \( T_i = \text{treatment } T_i \) mean square).
$0 \neq \frac{\text{Repeet Hypothese or Teo}}{\text{a parameter in hypothesis test}}$  

\[
\begin{align*}
\frac{37.3}{19} &= (p) \times \frac{24.225}{32.75} \\
\frac{10.909}{4} &= (p) \times \frac{923.5}{73.5} \\
\frac{24.225}{19} &= (p) \times \frac{24.225}{32.75} \\
\frac{10.909}{4} &= (p) \times \frac{923.5}{73.5} \\
\frac{24.225}{19} &= (p) \times \frac{24.225}{32.75} \\
\frac{10.909}{4} &= (p) \times \frac{923.5}{73.5} \\
\end{align*}
\]
There is the difference in cilia length and density between each treatment. In other words the length and the density of cilia in *R. crinita* differ under different conditions of light and moisture.

For comparing the difference of length and density of cilia between each treatment:

The null hypothesis being that there is no difference in cilia length or density between each treatment; i.e., \( \mu_{I_1}(l) = \mu_{I_2}(l) \);
\( \mu_{I_1}(d) = \mu_{I_2}(d) \);
\( \mu_{II_1}(l) = \mu_{II_2}(l) \);
\( \mu_{II_1}(d) = \mu_{II_2}(d) \);
\( \mu_{I_1}(l) = \mu_{I_1}(l) \);
\( \mu_{I_1}(d) = \mu_{I_2}(d) \);
\( \mu_{I_2}(l) = \mu_{II_2}(l) \) and
\( \mu_{I_2}(d) = \mu_{II_2}(d) \).

When \( \mu_{IJ}(l) \) = mean of the length of cilia in Treatment \( IJ \)
\( \mu_{IJ}(d) \) = mean of the density of cilia per 10mm. in treatment \( IJ \)

where \( i = 1 \) or 2

\[
t = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}}
\]

\( (\bar{x} = \text{mean}, \ s^2 = \text{variance}) \)
Comparative results between each treatment in *R. crinita*.

<table>
<thead>
<tr>
<th>I₁(l) &amp; I₂(l)</th>
<th>I₁(d) &amp; I₂(d)</th>
<th>II₁(l) &amp; II₂(l)</th>
<th>II₁(d) &amp; II₂(d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.249</td>
<td>2.479</td>
<td>17.135</td>
<td>5.798</td>
</tr>
</tbody>
</table>

(significant values are underlined in the Table).

T \( .05 d(9) = 2.262 \)

The different conditions of light did not affect the length and density of cilia, but the moisture seems to be an important factor determining the length and density of cilia in *R. crinita*.

The equation for \( r \) in this notation gives:

\[
\rho = \frac{\sum dxdy}{(\sqrt{\sum dx^2} \cdot \sqrt{\sum dy^2})}
\]

The equation for \( r \) express the relationship between \( x \) (length of cilia) and \( y \) (density of cilia per 100mm.) in terms of the variances within \( x \) and with \( y \).

\[
\sum \Delta x = \sum x^2 - (\sum x)^2/n
\]

\[
\sum \Delta y = \sum y^2 - (\sum y)^2/n
\]

\[
\sum \Delta xy = \sum xy - (\sum x)(\sum y)/n
\]
\[ T I_1 \quad r = \frac{379266.70 - 3796924.56/10}{(751269.23-7397638.4196/10)(213102-1948816/10)} = -0.294 \]

\[ T I_2 \quad r = \frac{911785.43 - 9226376.25/10}{(2238142.68-21388312.5625/10)(432447-3980025/10)} = -0.1855 \]

\[ T II_1 \quad r = \frac{127757.32 - 1260347.4/10}{(466808.59-4641611.7136/10)(46251-342225/10)} = 0.3053 \]

\[ T II_2 \quad r = \frac{726083.55 - 7230729.66/10}{(1773355.24-17631852.94/10)(319144-2695284/10)} = 0.1985 \]

In the example, \((n-1) = 9\) and when probability = 0.01, \(r = 0.735\).

The calculated value of \(r\) not exceeds this, so there is no positive correlation between the length and the density of cilia at the 1% level. Increased length is not correlated with increased density in any treatment.
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<tbody>
<tr>
<td>I</td>
<td>19.6</td>
<td>19.5</td>
<td>19.3</td>
<td>19.7</td>
<td>19.6</td>
<td>19.5</td>
</tr>
<tr>
<td>II</td>
<td>21.0</td>
<td>21.0</td>
<td>20.8</td>
<td>21.1</td>
<td>21.0</td>
<td>21.0</td>
</tr>
</tbody>
</table>

**TABLE 5.2**

After growing 90 days.

R: Rapata - Tenth of tissue in different treatments.
There is a difference in cell length and density between the treatments.

Studentized values are underlined in the table.

\[ P \cdot 0.05 (z) = 2.87 \]

\[ P(1) = \frac{17.796}{36} = 0.4936 \]

\[ P(2) = \frac{11.602.54}{10} = 1.1602.54 \]

\[ \frac{P(2)}{P(1)} = \frac{1.1602.54}{0.4936} = 2.343.9819 \]

Mean square

\[ 4 - 1 = 3 \]

\[ \frac{1}{3} \sum (x_i - \bar{x})^2 = 41.7945.9788 \]

\[ \frac{1}{3} = 13.9245.9788 \]

Source of Variation

\[ 4 - 1 = 3 \]

\[ \frac{1}{3} \sum (x_i - \bar{x})^2 = 41.7945.9788 \]

\[ 41.7945.9788 \]

\[ 13.9245.9788 \]

\[ 2.343.9819 \]

\[ 0.4936 \]

\[ 1.1602.54 \]

\[ \frac{1}{3} = 13.9245.9788 \]

\[ 41.7945.9788 \]

\[ 13.9245.9788 \]

\[ 2.343.9819 \]

\[ 0.4936 \]

\[ 1.1602.54 \]
Comparative results between each treatment in *R. asprenna*.

<table>
<thead>
<tr>
<th>I₁(1) &amp; I₂(1)</th>
<th>I₁(d) &amp; I₂(d)</th>
<th>II₁(1) &amp; II₂(1)</th>
<th>II₁(d) &amp; II₂(d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.161</td>
<td>1.118</td>
<td>1.033</td>
<td>4.721</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>I₁(1) &amp; II₁(1)</th>
<th>I₁(d) &amp; II₁(d)</th>
<th>I₂(1) &amp; II₂(1)</th>
<th>I₂(d) &amp; II₂(d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.737</td>
<td>4.263</td>
<td>3.999</td>
<td>0.189</td>
</tr>
</tbody>
</table>

Significant values are underlined in the Table.

In *R. asprenna*, the length of cilia differ under different conditions of light, but were not affected by different moisture situations. The density of cilia seemed to be affected by the condition of low light with maximum moisture.

\[
T \text{ } I₁ \quad r = \frac{641544.29 - 630847.90/10}{(1041845.5193-10254533.1529/10)(422750-3880900/10)} = 0.44878
\]

\[
T \text{ } I₂ \quad r = \frac{610695.25 - 6006812.25/10}{(1248546.9541-12125786.4841/10)(308125-2975625/10)} = 0.5138
\]

\[
T \text{ } II₁ \quad r = \frac{276586.77 - 2690562.75/10}{(651295.7497-6382444.3225/10)(119839-1134225/10)} = 0.8229
\]

\[
T \text{ } II₂ \quad r = \frac{487791.19 - 4767472.32/10}{(759442.6942-7404711.7451/10)(319282-3069504/10)} = 0.72204
\]
In the example, \((n-1) = 9\) and when probability = 0.05, 0.01, \(r = 0.602\) and \(0.735\) respectively. At the \(p = 0.05\). The calculated value of \(r\) in treatment \(I_1\) and \(I_2\) exceeds this, so there is a positive correlation between the length and the density of cilia in treatment \(I_1\) and \(I_2\), but for treatment \(I_1\) and \(I_2\) the calculated value \(r \ldots\) does not exceed \(r\) at \(p = 0.01\) and \(0.05\) there is no positive correlation between the length and the density of cilia in these treatments.

At \(p = .01\), \(r = 0.735\), the calculated value of \(r\) in treatment \(I_1\) exceeds this, there is positive correlation between the variables, significant at the \(1\%\) level. Increased length is correlated with increased density.

B. SCALES

Materials and Methods.

The experiments have been carried on in the same way as for those on cilia. \(R.\ macrospora\) St. and \(R.\ limbata\) Bisch., which normally produce purple scales, were used.

Observations.

\(R.\ macrospora\): The colour of the scales of this species is very sensitive to light and moisture differences, under high light condition with maximum moisture the scales are still slightly extended beyond the margin but become hyaline, the purple colour
is sometimes developed on the dorsal surface of the thallus in older parts. With the high light and minimum moisture, all the scales are purple. When it was growing under low light with higher conditions of moisture no purple colour develops in either of them.

*R. limbata*: It appears that the colour of the scales in this species is rather constant. None of the plants under the different conditions produce wholly hyaline scales.

CONCLUSION.

From the above observations, it shows that the conditions of light and moisture affected each species differently. Therefore the usefulness of these characters varies from species to species and the situation where the plants grow. This confirms the idea that the definite determination of *Riccia* spp. cannot rely on vegetative characters only, but the use of vegetative features at the group or subgroup levels is still significant, especially with the careful observation of the habitats. However, the average length of cilia between subgroups in nature shows a greater difference than in the experiment, especially when combined with the position of cilia.
III.

TAXONOMY

The first information on the Ricciaceae is that given by Ray (1696) in which he classifies the genus with the lichens (this plant was later found by Lindberg (1877) to be Riccia glauca L.)

Dillenius (1718, 1724) and others described many species of Riccia under various genera like Lichen, Lichenastrum, Hepatica and Ulva.

In 1729, Micheli was the first botanist who delimited and described the genus Riccia (it was named after P.F. Ricci, an Italian botanist) and divided this genus into two groups depending on the position of the sporogonia as follows:

1. 'Ricciae fructu e rimis foliorum surgente, et supra eorum rem foliorum planum se extollente,' included Corsinia Berck and Oxymitra Bisch.


Linnaeus (1737, 1753, 1784 and 1789-1791) in his edition of "Genera Plantarum" interpreted the structure of reproductive organs in terms of the flowering plants and accepted Micheli's genus Riccia. He included only 4 species of Riccia in his "Species Plantarum", 1st ed., i.e. R. crystallina L., R. minima Linderb., R. glauca L. and R. fluitans L.

Schmidel (1793-1797) illustrated and described
several species of Riccia with solid thallus and those with large air chambers which was later subgenus Riccia and Ricciella.

Raddi (1818) separated the genus Corinna from genus Riccia basing this on the position of the sporogonia. His interpretation of genus Riccia is 'Sporangia integra intra frondis substantiam, nec visibilia nisi per frondis dissolutionem', contains R. crystallina Raddi, R. lamellosa Raddi, R. ciliata Raddi, R. michelii Raddi, R. glauca Raddi, R. minima Raddi and R. cavernosa Raddi, whilst he places R. fluitans in "Species dubii generis".

Braun (1821) defined Riccia as "Capsula frondis immersa stylo emergente fugaci coronata", and Ricciella as "Capsula in inferiori frondis pagina sessilis, stylo destituta". The latter was instituted as a new genus from R. fluitans L.

Dumortier (1822) remarked "Le genre Riccia qui fait aussi partie de cette famille a besoin d'être étudié de nouveau, on doit en former deux genres, savoir: 1er. Riccia, fruits enfonce dans le thalle; 2eme. Tessellina, fruit sortant par une fente; on doit rapporter à ce dernier la R. reticulata Poir. no SW = Tessellina coriandri nob. et la R. pyrimidata Willd. = Tessellina pyrimidata nob". His classification seems to be uncertain and no detailed description of his new genus Tessellina.


Bischoff (1805) divided the genus Riccia Mich. (sensu stricto) into three sections:

Section 1. Riccia verae S. Lichenoides.
Fructus plerumque in pagina frondis superiore protuberantes et illa fatiscente supra prorumpentes. This section was subdivided into (a) "Frond margine glabra"? with R. sorocarpa Bisch. and R. glauca. (b) "Frond margine ciliata" with R. ciliata Hoffm. and R. bischofii.

Section 2. Ricciellae. "Fructus in pagina frondis inferior protuberantes et illa fatiscente subtus prorumpentes". The name R. eudichotoma was given with two varieties (a) fluitans and (b) canaliculata.


Lindenburg (1836) published "Monographie der Riccieen" which was the first attempt to give a complete account of the Ricciaceae of the world, but in fact it dealt mainly with the European flora. He provided keys to the twenty described species of Riccia which were primarily based upon the presence or (supposed) absence of ventral scales and did not divide Riccia into subgenera. In the Ricciaceae, Riccia (Mich) L., Corsinia Reddi, Oxymitra Bisch., and Sphaerocarpus Mich. are included, but R. fluitans (Ricciella) and Ricciocarpus (R. natoms) were not given generic status as he regarded their fruits insufficient for such an action.

In 1838, Nees who was working on European liverworts, accepted Bischoff's three sections and added a fourth section, "Spongodes", in it. His divisions are:

1. "Lichenoides - Frons solidus (i.e. cavitatibus æreis haud intercepta). Fructus plerumque in pagina superiori frondis protuberantes et illa diarumpente aut fatiscente demum denudati. Terrestres, arete repentes".
This group includes eleven species, e.g. *R. glauca* L.

(2) "*Spongodes* - Frons cavernosa, laxa. Fructus latentes aut in pagina superiori frondis protuberantes illaque fatiscente demum denudati. Terrestres, limicolas, arcte repentes." In which only two species are mentioned, i.e. *R. crystallina* L. and *R. bullosa* Link.

(3) "*Ricciella* - Frons cavernosa. Fructus in pagina frondis inferiori protuberantes et illa fatiscente subitus protumpentes. Natantes, aut in limo molli repentes". Three species in this group are: *R. huebeneriana* Lind., *R. fluitana* L., and *R. nodosa* D.C.

(4) "*Hemiseuma* - Frons cavernosa. Fructus in neutra frondis pagina protuberantes, demum ob frondis incisuram profundis penetrantem in sulco medio demudati, geminati. Natantes". With only one species, *R. natans* L.

These 4 sections were divided on the basis of air chambers and the liberation of the spores in relation to the thallus surfaces and were used for classifying *Riccia* by Gottsehe, Lindenberg and Nees in "Synopsis Hepaticarum" (1844, p. 47).

Lindenberg (1974), in his "Bryophyta of Soandinavia", divided the genus *Riccia* into two subgenera:

A. **Ricciocarpus** (Corda) Lindb. including only *R. natans* L.

B. **Euriccia** Lindb. which was subdivided into 3 groups:
   (a) *Terrestres* Lindb., with e.g. *R. sorocarpa*, *R. glauca* R. ciliata, etc.
   (b) *Spongodes* Ness. with *R. crystallina* L.
   (c) *Ricciella* (Braun) Bisch., with *R. huebeneriana* and *R. canaliculata var. b. fluitans.

Stephani (1898, 1900, 1917) is the first bryologist who gave the account of the Ricciaceae of the world in "Species Hepaticarum". (1900 & 1917) and there is
no other complete record since then. He gave the Latin
diagnosis and geographical distribution of Riccia Mich.
(138 species), Ricciocarpus and Rupinia (Oxymitra).
For the genus Riccia it was divided into two sections under
the heading:

A. Riccia - with solid thallus, including
83 species.
B. Riccia B. Ricciella - thallus with large
air chambers, including 45 species.

He provided clear descriptions for the genus
Riccia and also of the two sections; but for further
subsections (13) his classification was entirely based
on the vegetative characters as given below:

A. RICCIA

a. Ciliatae

I. Frons tenuis, multo latior quam crassa. (4 species)
II. Frons crassa, abrupte alata. (2 species)
III. Frons crassa, marginibus acutis vel obtusis,
nusquam abrupte alata. (16 spp.)

b. Innermes

IV. Frons minus crassa, subtenuis, antice plana vel late
concava, marginibus longe attenuatis (in una tantum
obtusatis). - (12 species)

V. Frons minus crassa (pro more quintuplo latior
quam crassa) antice sultata, marginibus plus minus
attenuatis. - (11 species)

VI. Frons crassa (pro more triplo latior quam crassa)
abrupte alata. - (11 species)
VII. Frons crassa (pro more triplo latior quam crassa) marginibus crassis acutis vel obtusis. — (14 species)

VIII. Frons maxime crassa, pro more diametro parum humilior.

> Frons antice plana vel canaliculata (haud sulcata). — (7 species)

< Frons antice sulcata. — (6 species)

B. RICCIELA

IX. Frons tenerrima, membranae — (6 species)

X. Frons magis costata, alis attenuatis costam late superantibus. — (6 species)

XI. Frons angusta, magis incrassata, antice plana. (15 species)

XII. Frons magis incrassata, antice sulcata vel canaliculata. — (10 species).

XIII. Frons valde incrassata, pro more duplo latior quam alta. — (9 species)

These characters vary with differing environment conditions and are not appropriate for classification at any level. Since Stephani used them as the important features for identifying groups and species, this has resulted in many taxonomic synonyms, which still need a careful reinvestigation.

In 1904, Bauley subdivided the genus Riccia into three subgenera, Ricciocarpus Corda (R. natans L.), Ricciella Bisch. (R. crystallina L., R. huebeneriana Lind. and R. fluitans L.), and Euriccia Lindb. (14 species, including R. sorocarpa, R. glauca, R. nigrella, etc.). His Euriccia Lindb. is not the same as that of the original author which includes all Riccia spp. Boulay's Euriccia is described in the sense now being used by almost every
author, which applied to those species with compact thalli and with narrow airspaces. His subgenus Ricciella is defined as "texture des frondes spongieuse, avec grandes chambers à air, appareil sporifère s'ouvrant du côte ventral."

Schiffner (1909) reverted to the older treatment of the genus, dividing Riccia into Euriccia Lindb., and Ricciella with only R. fluittans L. Schiffner’s Euriccia was the same as that of Lindberg, but Ricciella was treated as a sub-genus.

In 1926, Sim adapted those classifications which have been described for the local South African Flora. His synopsis is as follows:

1. Lichenoïdes – Thallus without air-cavities further than perpendicular spaces between individual rows of cells.
   a) Epidermal cells, or some of them, elongated or mamillate and free, including 3 species viz. R. coronata Sim., R. natalensis Sim., R. albumarginata G.L.N.
   b) Epidermal cells not much elongated; thallus provided with ventral marginal scales. With 5 species viz. R. potathiana Sim., R. africana Sim., R. atropurpurea Sim., R. limbata G.L.N. and R. concava G.L.N.

2. Favoides – Thallus with one layer of air-cavities; these deeply cylindrical, hexagonal, separated by walls one cell thick, and when young furnished with roof and minute apical pore. This resembles a honeycomb – R. bullose Link., R. gargidei Sim.

3. Spongodes – Thallus mostly composed of numerous large superimposed air-cavities, separated by walls one cell thick; capsules eventually opening to the upper surface – R. crystallina L.

4. Ricciella – Thallus cavernose; capsules formed in a swelling on the under-surface and eventually bursting to
the under surface. – *R. fluitans* L. var. *limicola* var. *aquatica*, *R. purpureascens* L. et L.

5. *Ricciocarpus* – Thallus composed mostly of superimposed air-cavities, with connecting and external pores; sexual organs in several rows in a ridge immersed under the mid-furrow; ventral scales numerous, independent, narrow. – *R. natans* var. *limicola* and var. *aquatica*.

In the modern classification of the genus *Riccia*, the terms "*Euriccia*" and "*Ricciella*" have been used in a more limited and yet more comprehensive sense than before. The subgenus or section *Euriccia* was that described by Bauley (1904) and by Stephani (1900) under the name *Riccia*. For subgenus *Ricciella* which was erected as a new genus by Braun (1821) containing *R. fluitans* L., has been modified and used in a broader interpretation.

Subsequent workers seem to separate *Riccia* into two groups with and without cilia, i.e., Macvicar (1926) – subgenus *Euriccia* (Lindb.) Boulay and subgenus *Ricciella* (Braun) Boulay; Frye and Clark (1937) – Section *Euriccia* and Section *Ricciella*; Arnell (1963) – subgenus *Euriccia* Lindb. and subgenus *Ricciella* Braun. Lately, Augler (1966) divided *Riccia* into five series: series I. *Euriccia* – thallus winged, series II *Euriccia* – thallus not winged with papillae or cilia, series III *Euriccia* – thallus hardly or not ciliated, margin acute, series IV *Euriccia* – thallus ciliated or not so, margin rounded, and series V *Ricciella*.

In the following treatment the species are separated into "groups" and "subgroups". These are considered to be units with some biological significance and, indeed, the separation is made in order that their biological and phylogenetic relationships can be discussed. They are not, however, given formal taxonomic status here.
since it is considered that an overall world-wide appraisal is necessary before taxa below the level of subgenus become formalized.

GENERIC DESCRIPTION

Nomenclatural synonyms from Frye and Clark (1937)
(Type not seen)
**Thallicarpus** Lindb. in Nat. Saellsk. Fauna et Fl. Fenncia 13: 337 (1894)
**Angiocarpus** Trev. in Mem. Instit. Lomb. 13: 444 (1877)

**Gametophyte** monoeocious or dioeocious, forming complete or incomplete rosette or in gregarious patches, mostly land forms (except *R. fluitans-complex*), annual or perennial; upper surface normally sulcate. **Branches** furcate or bi- or trifurcate, and some multifurcate; segment ovate, ovoidate, oblong or linear; apex obtuse or rounded or truncate; margin attenuate, acute, obtuse or rounded, sometimes attached with cilia or scales arising from lateral-ventral side of the thallus or from the margin itself. **Scales** of various sizes and present in almost of the species. **Dorsal part of the thallus** of two types: 1) with compact tissue which more or less arranged in vertical column and 2) with rather loosely arranged tissue forming polyhedral air chambers. **Ventral part of the thallus** mainly composed of compact parenchymatous tissue. **Rhizoids** of two types smooth and tuberculate, almost absent or absent in aquatic forms. **Sporogonia or capsules** with neither seta nor foot, normally
embed in the thallus; capsule wall unistratose. **SPORES** triangular-globular or globose, 40–150 μ diameter; sterile cells (elators) absent.

**HAPLOID CHROMOSOME NUMBER** mainly 8.

**TYPIFICATION** Riccia Lectotype. *R. glauca* L. Howe (1923) has selected *R. crystallina* L. as the type. He gives no reason for this selection. However, this is contrary to previous practice.

Since A. Braun (1821) the supra-specific taxon *Ricciella* had been recognized, based upon the presence of large air-chambers as opposed to the narrow air-channels of the true *Riccia*. Sometimes this was recognized at subgeneric level and sometimes as a genus. Stephani's (1900) is the first treatment which is comprehensive enough to include *R. crystallina* and place it correctly in *Ricciella*. Baulay (1904) also unequivocally places it within *Ricciella*.

Thus the practice, before Howe, was to recognize *R. crystallina* and its relatives as members of the subgeneric or generic taxon *Ricciella* and to refer to the other species as belonging to *Eu-Riccia*.

Howe's action in selecting *R. crystallina* as the lectotype of Riccia is thus contrary to previous practice, indeed, no-one since seems to have followed up the nomenclatural implication and changed the subgeneric names.

Linnaeus' description in *Genera Plantarum* is not much help in choosing a lectotype from amongst the species in *Species Plantarum*. *R. fluitans* can probably be excluded since the generic description makes no reference to sterile plants. The lectotype should be selected if possible to promote stability of nomenclature and this would eliminate *R. crystallina* without doing any injustice.
to Linnaeus' descriptions. There remains R. minima and R. glauca. R. glauca is selected to replace the Howe's Lectotype which is herewith rejected.

I. Subgenus RICCIA

Riccia "Capsula in inferiori frondis pagina sessilia, stylo destituta" Braun Flora I: 756-759 (1821)


**SUBGENUS RICCIA** - Upper part of the thallus composed of compact tissue which almost arranged in vertical columns; air chambers narrow without special air pores; epidermal cells hyaline.

Section *Viridisquamata* sect. nov.
Thallus viridis no visi ventraliter et in squamis.

Holotypus - *R. caroliniana* sp. nov.

Chlorophyll-bearing layer at ventral side of the thallus and mainly at the scales, dorsal part of the thallus consists of compact and hyaline tissue.

Section *Riccia* - Chlorophyll bearing layer at dorsal part of the thallus.
I. THE SUBGENUS RICCIA

SECTION VIRIDESQUAMATA.

There is only one species belongs to this section and is only found growing abundantly in the Northern Territory especially around Darwin and is still found about 400 miles south, but no other records are known. This species shows a different adaptation to environmental situation in having scales containing chloroplasts which appear to be responsible for the major part of photosynthesis. The transparent upper part of the thallus seems to be adapted for protecting the green ventral part. In dry state, these upper cells collapse, but they are easily regain water when moistened. Its apex also develops tubers for greater drought resistance.

SECTION RICCIA.

This section is divided into three major groups here for the classification of Australian species.

1. "CILIATA". The species in this group are mostly rather small, usually grow in open area and under rather dry habitat. In dry state, cilia usually long and dense, but in some species in moistened condition or in shady area produce shorter and less dense cilia while rather stable in others. Among the species which occur in Australia: R. crinita Tayl., R. asprella Carr. et P., R. longiciliata sp. nov., R. blackii sp. nov. and R. ascolata sp. nov. are probably endemic; 1 species, R. crozalsii Lev. is an European plant and is rather rare in Australia. They are divided into two subgroups: 1) Ciliata group - long cilia and capsule bearing cilia, and 2) Ciliata group - short cilia, capsule not bearing cilia.
2. "SQUAMATA". This group has the largest number of species which here are separated into three subgroups.

(1) "R. macrospora". The plants belong to this subgroup react sensitively to environmental change, i.e. the change of colour of the scales in R. macrospora St. (see Chapter II). R. discolor L. et L., R. billardieri Mont. et N. and R. gangetica Ahmad are the tropical monsoon species which appear to be plants of the same habitat and usually growing intermingled in nature. R. macrospora St. is found growing abundantly in Central part of Australia and has various habitats. When growing in dry habitat and under strong light thalli are bluish-green, scales dark purple and show less frequent branching, but in shady area or moistened condition, thalli are normally green with hyaline scales and bi-trifurcal branched. The first 2 species R. discolor and R. billardieri are usually forming tubers after growing season, but this habit is not occurred in R. gangetica and R. macrospora. The latter two species are surviving from dry situation by having both lateral-ventral sides of the thallus curved inward protecting the living ventral parts.

(2) "R. limbata". This subgroup is very closely related to the "R. macrospora" in vegetative characters, but the colour of the scales of "R. limbata" are not easily changed according to environmental conditions. R. limbata Bisch. is found growing widely in Australia, i.e. New South Wales, South Australia and Western Australia. The wide distribution of this species shows a successfully adapted character of this taxa to different situations of environment. In dry state, the thallus is protected by the scales which curved inward and covered the whole dorsal surface. The other species of this subgroup is R. nigrella DC.
which is rather rare in Australia.

(3) "R. sorocarpa". This subgroup including:
1 world-wide species, R. sorocarpa Bisch.; 1 European
species, R. lamellosa Raddi and 3 probably Australian
species viz. R. marginita Carr. et P., R. olgensis sp. nov.
and R. rorida sp. nov. The distribution of the latter 3
is very limited as R. marginata is only found growing in
New South Wales, R. olgensis in Central Australia and
R. rorida in Canberra A.C.T. Most of them except R. marginata
are annual species.

3. "LAEVIGATA". There are only 2 species belonging
to this subgroup. R. bifurea Hoffm. is an European species
and rare in Australia, normally growing among grass and
under rather moistened condition. R. albida Sull. which
is only reported from Texas is also found in Australia
and seems to be confined to one place only (Palm Valley,
Northern Territory). Its geographical distribution is
very peculiar and such data may be rather incomplete.

SECTION VIRIDESQUAMATA. Chlorophyll bearing layer at
ventral side of the thallus.

1. R. caroliniana sp. nov.

Dioecae, gregaria, hyalo-viridis. Thallus 5-15 mm
longus, 2-5 mm latus pagina dorsali anguste sulcata ad
apicem sed plana vel convexa alibi. Rami furcati vel
bifurcati, extendentes. Squamae anguste oblongae, viridis
interdum plus minusve purpureae. Epidermis et par
dorsalis thalli hyalina: cellulae interdum in columnis
verticalibus dispositae. Antheridia collis longis.
Archeonia in serie una disposita. Sporae ± 100 μ diam.,
impolishes fuscae, deltalo-globulares, reticulatae cristas
crassis humilibus. Chromosomata 10.
**Gametophyte** dioecious, in gregarious patches, crystalline green, thallus 5-15 (20) mm long, 2-4 (5) mm broad, 2-3 times as broad as thick in transverse section (Fig. 3.1, a, b, c & d); upper surface almost flat in dry condition and convex in moistened state, narrowly sulcate towards the apex. **Branches** furcate or bifurcate, divergent; segment elliptical-oblong or obcuneate-oblong; apex obtuse or rounded or truncate (Pl. 3.1, a); margin acute, 2-3 cells thick (Fig. 3.1, f). **Scales** narrowly oblong (Fig. 3.1, h), green, cells containing chloroplasts, imbricate and persistent (Pl. 3.1, a), 1-2 layers of cells in thickness (Fig. 3.1, i), in dry state upper part of scales near the margins becoming purple. **Epidermal Cells** hyaline, irregularly arranged and very varied in sizes (Fig. 3.1, g); airpore not developed. Tissue of almost the whole thallus pellucid (except scales), destitute of chloroplast except few towards the apex, the margins and ventral layer next to the scales; 8-10 cells in thickness, occasionally not arranged in columns; no airspace in between (Fig. 3.1, 2). **Male Plant** slightly smaller than female plant, easily distinguished from the latter by its persistent antheridial necks, 0.7-1.2 mm long, hyaline in moistened condition, purple in dry state, arranged in 2-3 rows along the middle part of the thallus (Pl. 3.1, a). **Female Plant** with a single row of archegonia, archegonial necks hyaline or purple, not prominent (Pl. 3.1, a). **Capsules** in single row, 2-3 in each segment, clearly seen through the transparent tissue of the thallus, with 174-276 spores per capsule. **Spores** 85-100 /µ (150) diameter, dull brown, triangular-globular or almost circular when looking from distal or proximal face; wing smooth 2-3 /µ wide; distal face
reticulate forming 9-10 areolae across the diameter, areola almost rounded. 6-10 μ diameter with rather thick and low ridges (Pl. 3.1, b); proximal face with triradiate mark, the rest reticulate similar to the distal ones but less distinct (Pl. 3.1, c).

**CHROMOSOME NUMBER** n = 10. **Voucher:** Northern Territory, Robin Water Fall, O. Na-Thalang No. 288, 28.1.1969 (SYD)

**RANGE** Northern Territory

**HABITAT** open grassland, under shade of tree, growing mixed with *R. discolor*, *R. billardieri* and *R. gangetica*; firmly fixed to soil.

**TYPIFICATION** *R. caroliniana* sp. nov. Holotype – Northern Territory, Robin Water Fall, O. Na-Thalang No. 288, 28.1.1969 (SYD). Name in honour of Professor R.C. Carolin.

**DISCUSSION** *R. caroliniana* is not closely related to any species of *Riccia* described before. It is different from the rest in having a photosynthetic part on ventral side of thallus and mainly at the scales, the hyaline upper part making this plant look like green glass crystal. When growing in nature it is hardly distinguished from the soil. Besides its unusual photosynthetic part, it is also the only *Riccia* collected so far in Australia that has haploid chromosome number n = 10 with seven long and three small chromosomes.

**SPECIMENS EXAMINED:** Northern Territory: Coomalie Creek, O. Na-Thalang No. 258, 19.1.1969 (SYD); Mt. Bundey, O. Na-Thalang No. 270, 22.1.1969 (SYD); Darwin River Road, O. Na-Thalang No. 276, 24.1.1969 (SYD); Darwin River, South of the Quatery, O. Na-Thalang No. 280, 24.1.1969 (SYD); South of Adelaide River, O. Na-Thalang No. 282, 26.1.1969 (SYD); Robin Water Fall, O. Na-Thalang No. 283, 26.1.1969 (SYD); 2 miles from Robin Water Fall, O. Na-Thalang
FIG. 3.1

*R. caroliniana* sp. nov.

a, b, c & d – transverse sections of the thallus from 4 plants. x10

e – portion of transverse section of the thallus. x50

f – epidermal cells. x100

g – scale x25

h – the section of the scales. x100

ep = epidermal cell

ch = chlorophyll bearing cells.
PL. 3.1

*R. caroliniana* sp. nov.

a - plant, x4
b - spore, distal face. x730
c - spore, proximal face. x730
d - spore, optical section. x730
No. 288, 28.1.1969 (SYD); Daly River Road near Adelaide River, O. Na-Thalang No. 289, 28.1.1969 (SYD); Green Jungle, South Darwin, O. Na-Thalang No. 291, 28.1.1969 (SYD); South of Pine Creek, O. Na-Thalang No. 296, 29.1.1969 (SYD); 150 miles south of Darwin, O. Na-Thalang No. 298, 29.1.1969 (SYD); Borriol Creek, O. Na-Thalang No. 302, 30.1.1969 (SYD); 270 miles South Darwin, Stuart Highway, 3.2.1969 (SYD); Maluka Cemetery, O. Na-Thalang No. 310, 3.2.1969 (SYD); Mataranka Creek, O. Na-Thalang No. 313, 3.2.1969 (SYD); 380 miles Stuart Highway, South of Darwin, O. Na-Thalang No. 316, 4.2.1969 (SYD); 370 miles Stuart Highway, South Darwin, O. Na-Thalang No. 318, 4.2.1969 (SYD); 5 miles South Katherine, O. Na-Thalang No. 323, 5.2.1969 (SYD).

SECTION RICCIA

Chlorophyll bearing layer at dorsal part of the thallus consists of compact vertical columns of green cells which terminated by hyaline epidermal cells, each airspace normally enclosed by four vertical columns (except in some species the air chambers close to the margin may be enlarged and in that case it is surrounded by 5-6 columns).

1. "CILIATA" group - Thalli bearing cilia at the margins sometimes on dorsal surface.

   (1) "Ciliata" group - long cilia and capsule bearing cilia.
2. R. longiciliata Sp. nov.

Monoica gregaria viridis vel glauco-viridis. Thallus 3-5mm. longus, 1-1.5mm. latus. Segmenta ovata vel obovato-elonga, anguste canaliculata; apice leste obtuso vel truncato: margo tumidus, prominens ciliis aggregatis 200-1000 μ longis in seriisus 4-6. Capsula valde exserta ex pagina superiore qui est ciliata supra capsulam. Sporae pro parte maxima 80 μ latae, atrofuscæ triangulo-globulares alae 2-3 μ latae. Areolae 6-8 μ latæ margine tenui humili aliquando imperfectae superficie distali. Superficies proximalis exsesta triradiata distincta. GAMETOPHYTE monosечно, in gregarious patches, glaucous green; thallus 3-5mm. long, 1-1.5mm. broad, 2-3 times as broad as thick in transverse section (Fig. 3.1, a, b, c); upper surface finely reticulate; channel narrow.

BRANCHES furcate, divergent; segment ovate or obovato-oblong; apex rounded or truncate; margin tumid, rounded, slightly raised up from both sides of channel, with crowded cilia at lateral-ventral sides arranging in 4-6 rows, 200-1000 μ long (Pl. 3.2, a). SCALES small, hyaline, present only under the apex. EPIDERMAL CELLS globose, 20-30 μ. PHOTOSYNTHETIC CELLS 20-25 μ, longer than broad, 5-6 cells in each vertical column (Fig. 3.2, d).

ANTHHERIDIA at both sides of archegonia along the furrow close to the apex; antheridia and archegonial necks not prominent. CAPSULES large, protruding on upper surface (Fig. 3.2, c, Pl. 3.2, a), with long cilia over it about 900-1000 μ long. Tissue over capsule separating tardily, with 120-170 spores per capsule. SPORES 70-100 μ, dark brown, triangular-globular with almost entire wing 2-3 μ wide; distal face (Pl. 3.2, b) reticulate, forming 9-10 rather rounded areolae across the diameter, each areola
FIG. 3.2

*R. longiciliata* sp. nov.

a - Transverse section of the thallus close to the apex.

b - Transverse section of the thallus at the middle part of segment.

c - Transverse section of the thallus at the place where the capsule is present.

a, b, c - x50.

d - Transverse section of the thallus,
(e) epidermal cell, (f) photosynthetic column x200
PL. 3.2

*R. longicilliata*

a. Plant x10
b. Spore, distal face. x730
c. Spore, proximal face. x730
8-12 μm wide with smooth and narrow border; proximal face (pl. 3.2, o) nearly the same as distal, but with distinct triradiate ridge.


**HABITAT** Open sandy soil, often in rather dry situations.

**TYPOFICATION** - *R. longiciliata*. Holotype: Northern Territory, Palm Valley, O. Na-Thalang No. 100A, 15.8.1966 (NSW); isotype (SYD).

**DISCUSSION:** *R. longiciliata* is closely related to *R. crinita Tayl.* in the character of gametophyte in having long and crowded cilia, but its spore are larger and clearly reticulate on both sides; further more, the haploid chromosome number is 16 whilst that of *R. crinita* is 8.

Comparing with other oiliates group with long cilia: *R. crenescens* St. has inflexed margin and broad channel; *R. ciliata* Hoffm. has thick but not elevated margin, channel broad, capsule easily broken; *R. trichocarpa* Howe has large spores without wing; and *R. henriquesii* Lev. is dioecious: the character of *R. longiciliata* does not agree with any of those mentioned.

**SPECIMENS EXAMINED:** See typification.


**GAMETOPHYTE** monoeocious, in gregarious patches or forming a rosette 15-25mm. diameter, green to dark green, thallus 3-6mm. long, 1-1.5mm. broad, 2-3 times as broad as thick in transverse section; upper surface finely and compactly reticulate, shining (Fig. 3.3, a, b & c); channel narrow
and shallow throughout. **BRANCHES** furcate or bifurcate, slightly divergent; segment ovate, or obtuse-oblong; apex obtuse or rounded to truncate, usually bilobed; margin tumid near the apex, the rest flat, obtuse or rounded with numerous long cilia on lateral-ventral side scales throughout the thallus (Pl. 3.3, a & b); cilia in 4-6 rows on purple or hyaline scales, crowded and curved, 200-1000 μ long. **SCALES** purple or hyaline, slightly overlapping each other, not reaching beyond the margin, partly joined to the lateral-ventral side, persistent. **EPIDERMAL CELLS** 35-40 μ, globose or pyriform (Fig. 3.3, d). **PHOTOSYNTHETIC CELLS** 25-30 μ, almost isodiametric, 7-9 cells in each vertical column (Fig. 3.3, d). **ANTHERIDIA** at both sides of archegonia along the furrow, close to the apex, antheridial and archegonial necks not prominent. **CAPSULES** numerous, slightly protruding, ciliated, easily exposed by rupture of tissue over it (Pl. 3.3, a & b); cilia straight or curved, 400-1000 μ, nearly the same length as marginal cilia; with 136-224 spores per capsule. **SPORES** 55-85 μ, dark brown, becoming opaque when fully mature, almost rounded from distal face with narrow and slightly crenate wing of 2-4 μ wide; distal face (Pl. 3.3, c) reticulate, forming incomplete rounded areolae about 10-12 across the diameter; areola 3-5 μ wide; ridge around each areola narrow and thin, sometimes slightly raised up at the corners; proximal face (Pl. 3.3, d) less distinctly reticulate, with faint triradiate mark.

**CHROMOSOME NUMBER** n=8. **Voucher:** New South Wales. Balonne H'way. J. Jacob (O. Na–Thalang No. 24), 3.5.1966 (SYD); Tummallallee Creek, O. Na–Thalang No. 217, 26.3.1967 (SYD); Northern Territory, Alice Springs,
R.C. Carolin No. 5393, 7.8.1966 (SYD).

**Range:** New South Wales, Northern Territory, Western Australia.

**Habitat:** On open grassland or sandy soil, in dry state forming silver-white patches caused by inflexed cilia over the thallus, in moistened state cilia straight, often in dry situations.

**Typification — R. crinita Tayl.** Holotype — Western Australia, Swan River, W.T. Drummond, 1843 (K); isotype (MEL 19788).

**Discussion:** R. crinita Tayl. is very close to R. trichocarpa Howe in having crowded and long cilia both at the margin and over the capsule, but R. trichocarpa has narrower thallus and larger size of spores, 90-120 μ, which are wingless.

The other closely-related species is R. ciliata Hoffm., but R. ciliata has a different character of spore in forming 9-11 areolae across the diameter, bluntly papillose in profile, while R. crinita forms rather incomplete rounded areolae, not highly papillose and cilia are more crowded.

**Specimens Examined:** Typification and:— South Australia, West of Coober Pedy, T.R.N. Lothian No. 2834, 10.5.1964 (AD 21); Western Aust., Balladonia, Arthur Bunyan's Exped., 20.5.1953 (MEL 19786); Near Balmoral station, A. Bunbury, 8.7.1953 (MEL 19787); Northern Territory, Alice Springs, R.C. Carolin, No. 5202, 13.8.1966 (SYD); Alice Springs, R.C. Carolin No. 5393, 7.8.1966 (SYD); New South Wales, Balonne H'way, J. Jacob (O. Na-Thalang No. 24), 3.5.1966 (SYD); Razor-back Ridge, O. Na-Thalang No. 36, 11.7.1966 (SYD); Barralier, O.Na-Thalang No. 37, 12.7.1966 (SYD); Tumwallalle, O. Na-Thalang No. 217, 26.3.1967 (SYD).
FIG. 3.3

R. crinita Tayl.

a, b, c. - Transverse sections of the thallus from close to the apex, the middle part of segment, in old part respectively. x50

d. - Portion of transverse section of the thallus.
(e) epidermal cell,
(f) photosynthetic column. x200
PLATE 3.3

R. crinita Tayl.

a. Plant x 4
b. Plant x 27.5
c. Spore, distal face. x 730
d. Spore, proximal face. x 730


GAMEOTYPY monosocious, forming an incomplete rosette or scattered, green to dark green, shiny, 5–6mm. long, 1.5–2mm. broad, 2–3 times as broad as thick in transverse section (Fig. 3.4, a, b & c); upper surface finely and compactly reticulate; broadly channelled, narrowed and apparently closed in front by convergence of margins, becoming suddenly broad and almost flat towards the base. BRANCHES single or furcate, slightly divergent; segment oblong with obtuse or rounded apex; margin tumid at apex, the rest almost flat, crowded with long cilia throughout (Pl. 3.4, a); cilia 200–800 /μ long, in 4–5 rows at lateral–ventral sides, the uppermost cilia usually the longest, often curved and covering the thallus in dry state. SCALES small, hyaline or sometimes tinged with purple, not reaching beyond the margin, present under the apex only. EPIDERMAL CELLS 30–40 /μ, globose (Fig. 3.4, d). PHOTOSYNTHETIC CELLS 25–30 /μ, 6–7 cells in each vertical column (Fig. 3.4, d). ANTERIDIA at both sides of archegonia along the furrow, antheridal and archegonial necks not prominent.
FIG. 3.4

_R. arsolutea_ sp. nov.

a, b, c. - Transverse sections of the thallus from younger to older parts. x40

d. - Portion of transverse section of the thallus.

(e) epidermal cell,
(f) photosynthetic column. x200
PLATE 3.4

*R. areolata*

a. Plant x15
b. Spore, distal face x730
c. Spore, proximal face x730
CAPSULES numerous, ciliated; cilia 300–500 μ, persistent; tissue over capsule easily ruptured with 362–668 spores per capsule. SPORES 55–85 μ, dark brown, opaque when fully mature, irregular in form from triangular-globular to almost oval with smooth wing 3–4 μ wide; distal face (Pl. 3.4, b) reticulate, forming 5–9 rather rounded areolae across the diameter, each areola 7–14 μ wide with smooth and narrow border slightly raised up at the corners; proximal face (Pl. 3.4, c) similar to the distal one but with a distinct triradiate ridge.


RANGE: New South Wales.

HABITAT: Open grassland, rare.


DISCUSSION: R. areolata is closely related to R. crinita Tayl. in the character of the gametophyte, but the spore has larger areolae and is clearly reticulate on both sides. SPECIMENS EXAMINED: Typification and New South Wales, Luddenham, O. Na-Thalang No. 244, 15.6.1967 (SYD).

(2) "Ciliata" group – short cilia, capsule not bearing cilia.

5. R. crozalsii Levev. Revue Bryol. p. 73, 1902;
GAMETOPHYTE monoecious, seldom forming complete rosette 15-20mm. in diameter with 16-18 bilobed branches in one rosette, pale or glaucous green; thallus 4-6mm. long, 1-1.5mm. broad, almost as thick as broad in transverse section (Fig. 3.5, a, b, c); upper surface finely reticulate, sharply furrowed at the apex, the channel becoming broader and shallower throughout. BRANCHES furcate to bi- or trifurcate, divergent, usually overlapping in old patches, segment linear-ovate or obcumsate; apex rounded; margin obtuse, ascending with a series of short cilia (Pl. 3.5, a & b); cilia 200-500 /μ long, most numerous towards the apex, sometimes absent elsewhere, but frequently extending along the whole length of the thallus when in dry conditions (MacVicar 1926). SCALES small, hyaline, occasionally purple, present only under the apex, not reaching over it. EPIDERMAL CELLS thin walled, globose (Fig. 3.5, d), 25-45 /μ. PHOTOSYNTHETIC CELLS 25-40 /μ, 5-7 cells in each vertical column (Fig. 3.5, d). ANTERIDIA frequently close to the apex. ARCHEGONIA in 2 rows along the furrow, necks sometimes purple, slightly projecting over the upper surface. CAPSULES many, often two together, without cilia over it, not protruding, tissue over capsule not easily ruptured; with 108-195 spores per capsule. SPORES 65-85 /μ, dark brown, triangular-globular with almost entire wing of 2-3 /μ wide, marginal angles enlarged; distal face (Pl. 3.5, c) regularly reticulate forming 8-10 angular areolae across the diameter, each areola 5-7 /μ wide with smooth and narrow border slightly raised up at the corners; proximal face (Pl. 3.5, d) similar to distal one with distinct triradiate ridge.

CHROMOSOME NUMBER n=8. Voucher: New South Wales,
FIG. 3.5

R. crozalsii Levier

a, b, c. - Transverse sections of the thallus, from close to the apex, middle part of segment, and in old part with capsule respectively. x40

d. - Portion of the transverse section of the thallus, (e) epidermal cell (f) photosynthetic column, (g) air chamber. x200
Fig. 3.5

a.

b.

c.

d.

- e
- f
- g
PLATE 3.5

*R. crozalsii* Levier

a. - Plant  x4
b. - Plant  x20
c. - Spore, distal face  x730
d. - Spore, proximal face  x730
MacArthur's Flat, Nattai River, R.C. Carolin No. 5414, 3.10.1966 (SYD); North Bulahdelah, D.A. Anderson (Q. Na-Thalang No. 174), 17.2.1967 (SYD).

RANGE: New South Wales.

HABITAT: shady area, among grass, rare.


DISCUSSION: R. crozalsii Leviey can be distinguished from other species in the same "ciliata" group by its small size, few and inflexed cilia at apex which are 200–500 μ long, although no cilia are present over the scarcely protruding capsule.

R. longiciliata, R. areolata and R. crinita have longer and more crowded cilia both at the margin and over the capsules.

R. blackii also has short cilia near the apex, but the size of the thallus is larger, the margin very tumid and raised up, the channel very broad, the capsule protruding on dorsal surface, and the spores 100–115 μ.

SPECIMENS EXAMINED: Europe: Tenerife, Bufadero, C.J. Pilard 750, 1.1906 (G 13135); England, Merionethshire, D.A. Jones, 12.1912 (G 13136); San Giorgio, A. Letzel, 19.11.1909 (G 13137)

Australia - see chromosome voucher.

6. R. blackii Sp. nov.

Monoica, flavovirens vel pallide viridis.

Thallus 3–7mm. longus, 1.5–2mm. latus. Segmenta obovata vel obovata–oblonge apica late obtuso vel truncato marginibus tumidis elevatis breviter distantier ciliatis; cilis 150–350 μ longis: pagina superior late canalicula

GAMETOPHYTE monoecious, in gregarious patches or sometimes forming a small rosette of 6-8 branches, pale green or yellowish green; thallus 3-7 mm. long, 1.5-2 mm. broad, 2-3 times as broad as thick in transverse section (Fig. 3.6, a, b & c); upper surface finely reticulate, papillate in young part; broadly channelled in the first segment, the rest becoming almost flat or slightly convex (Pl. 3.6, a).

BRANCHES single or furcate, rarely bifurcate, divergent; segment obovate or obovate-oblong, deeply divided; apex emarginate or truncate; margin tumid, elevated near the apex but flattening towards the end of first segment, with few and scattered short cilia; cilia 150-350 μ long usually present towards the apex. SCALES hyaline or purple, small, rare, under the apex only. EPIDERMAL CELLS pyriform or globose (Fig. 3.6, d), 20-30 μ in diameter, occasionally up to 60 μ near the apex. PHOTOSYNTHETIC CELLS 30-40 μ wide, 8-10 cells in each vertical column (Fig. 3.6, d), cells almost as broad as long. ANtheridia 2 rows at both sides of archegonia, close to the young part, antheridial and archegonial necks not prominent.

CAPSULES single, 1-3 in one thallus, protruding, without cilia over it, usually not easily exposed; with 90-280 spores per capsule. SPORES 100-115 μ, dark brown, nearly opaque when fully mature, triangular-globular or almost rounded from distal or proximal face, with broad and
rather smooth wing 6-7 μ wide; distal face (Pl. 3.6, b) forming 10-11 rather rounded areolae across the diameter, each areola 8-10 μ wide with thick border usually incomplete thickening; proximal face (Pl. 3.6, c) similar to distal one but with distinct triradiate ridge.


RANGE: Central Australia.

HABITAT: On fine sandy soil, near creeks.

TYPIFICATION: R. blackii sp. nov. Holotype - Central Australia, Mt. Olga, D. Black (O. Na-Thalang No. 87), 11.8.1966 (NSW).

DISCUSSION: R. blackii is close to R. bifurca Hoffm. in having tumid and raised margin, but the presence of marginal cilia differentiate it from the latter, the size of the spore is larger, 100-115 μ while that of R. bifurca is 70-85 μ.

Among the 22 short cilia species (Steph. Sp. Hep. I, 1900, pp. 314-322, plus the new records after 1900: R. crozalii Levier., R. donnellii Aust., R. subbifurca Warnst., and R. natalensis Sim.), 5 species, viz.: R. breidleri Jurczka, R. spinosissima St., R. stromarginata Levier, R. papillosa Morias, and R. pseudopapillosa St., have no description of spores which makes it hard to compare them; 10 species have small spores, less than 90 μ in diameter; the other 7 species have larger spores, that is, more than 90 μ, viz.: R. asprella Carr. et P., R. beyrichiana Hampe., R. natalensis Sim., R. lusitanica Levier, and R. donnellii.
FIG. 3.6

*R. blackii* sp. nov.

a, b, c. — Transverse sections of the thallus at different parts, a. close to the apex, b. at the middle part of segment, c. at basal part of segment. x20

d. — Portion of transverse section of the thallus, (e) epidermal cell, (f) photosynthetic column, (g) airchamber. x200
Fig. 3.6
PLATE 3.6

*R. blackii* sp. nov.

a. Plant x14
b. Spore, distal face x730
c. Spore, proximal face x730
Aust., which also are larger plants than the one under discussion. The remaining two, R. gaugetiana Mont. and R. michellii Raddi, which show the closest affinity with R. blackii but the latter is monoecious while the former two species are dioecious. Furthermore R. gaugetiana has a winged thallus, spore 136 μ, and R. michellii has a deeply immersed capsule, the epidermal cells are not marrillate. Thus, this specimen from Mt. Olga differs from all the known species of the genus. It is named after Miss D. Blacki who collected the holotype.

**SPECIMENS EXAMINED:** see typification.

7. R. asperella Carr. et P. Proc. Linn. Soc. N.S.W. II. p. 1059, (1887); Steph. Sp. Hep. I. p.8 (1900). **GAMETOPHYTE** monoecious, usually forming flabellate patches, but occasionally forming a rosette 20-30mm. in diameter with 6-12 branches; glaucous green or pale green, sometimes tinged with brown. colour over the capsule and in old parts; thallus 4-10mm. long, 2.5-3.5mm. broad, 3-4 times as broad as thick in transverse section (Fig. 3.7, a, b, c & d) upper surface finely reticulate, reticulum along the middle part arranged perpendiculary to the apex, and obliquely on swollen margin (Pl. 3.7, a); channel narrowed and apparently closed at the apex by convergence of margins, becoming suddenly broad about one half the width of the thallus (Pl. 3.7, a). **BRANCHES** furcate or bifurcate, slightly divergent; segment broadly obovate-oblong or oblong with rounded apex; margin acute, raised up and tumid forming broad edges along both sides of the thallus, always with short, stout and straight cilia (Fig. 3.7, b). **CILIA** 200-300 μ
long, arranged in 2–4 rows at the margins and lateral-ventral sides (Pl. 3.7, a). SCALES hyaline, delicate, present only under the apex. EPIDERMAL CELLS in young parts papillate or mammilate (Fig. 3.7, g), 55–80 μ, soon collapsing. PHOTOSYNTHETIC CELLS 40–60 μ, 5–6 cells in each vertical column (Fig. 3.7, e), cells almost isodiamic or slightly longer than broad. ANThERIDIA arranged in two rows along the furrow with 1–2 rows of archegonia between, antheridial and archegonial necks not prominent.

CAPSULES many, slightly protruding, not ciliated, exposed only in older parts of the thallus with 176–388 spores per capsule. SPORES 90–100 μ, brown or dark brown, almost triangular–globular; wing crenate or uneven with 1–2 poles which usually interrupted, 4–5 μ wide; distal face (Pl. 3.7, b) reticulate, forming 6–7 areolae across the diameter; areola 10–15 μ wide, angular with high ridges at the border and corners; proximal face (Pl. 3.7, c) similar to distal one but less distinctly reticulate, sometimes with short ridges and a well-defined triradiate ridge.


RANGE: New South Wales.

HABITAT: Dry open grassland or water seepages on rocks.


DISCUSSION: R. asprella is completely different from
FIG. 3.7

*R. asprella* Carr. et P.

a, b, c, d. Transverse sections of the thallus from younger to older parts. x20

g. Portion of transverse section of the thallus,
(e) epidermal cell,
(f) photosynthetic column. x200
PLATE 3.7

R. asprella Carr. et P.

a. Plant x16
b. Spore, distal face x730
c. Spore, proximal face x730
other members of the "ciliated group" in Australia with its large size and stout cilia.

The other closely related species are
R. beyrichiana Hempe, and R. californica Aust., but
R. beyrichiana has curved and fewer cilia with thallus
1-2.5mm. broad and spores nearly smooth on proximal face;
R. californica sometimes has cilia on dorsal surface and
the spore has 8-10 areolae across the diameter.

SPECIMENS EXAMINED: New South Wales; Barralier,
O. Na-Thalang No. 56, No. 60, 12.7.1966 (SYD); Jibbon
Head, National Park, O. Na-Thalang No. 128, 3.9.1966 (SYD);
Nattai River, R.C. Carolin No. 5415, 3.10.1966 (SYD);
Cox River, Blue Mts., D. Black (O. Na-Thalang No. 200),
12.3.1967 (SYD); North Bulahdelah, D. J. Anderson
(O. Na-Thalang No. 196), 17.2.1967, (SYD); Coonabarabran,
O. Na-Thalang No. 210, 26.3.1967 (SYD); Prospect Reservoir,
O. Na-Thalang No. 237, 15.6.1967 (SYD); Luddenham,

2. "SQUAMATA" group – thalli with scales extending
beyond the margins or reach at the margins.

(1) Subgroup "R. macrospora" – thalli with variable purple
scales, spores globose with similar reticulation on all
the surfaces.


1900; Arnell S.

R. sellingii S. Arn. Botanisk Notiser 115:
311-313, 1962

GAMETOPHYTE monoecious, in gregarious patches, green to
dark green; thallus 7-12mm. long, 3-4mm. broad, 2-3
times broader than thick in transverse section (Fig. 3.8, a, b, c, & d); upper surface finely reticulate, narrowly sulcate throughout. **BRANCHES** single or furcate to bifurcate (Pl. 3.8, a), usually equal, divergent; segment obovate-oblong, apex rounded; margin flat, acute, attenuate. **SCALES** (Fig. 3.8, h) dark red-purple, large overlapping each other, persistent, extending beyond the margins. **EPIDERMAL CELLS** 50-60 μ, globose or papillate (Fig. 3.8, g) at apex, soon collapsing. **PHOTOSYNTHETIC CELLS** 20-30 μ, usually longer than wide, 6-7 cells in each vertical column (Fig. 3.8, g). **ANTHERIDIA** at both sides of archegonia along the furrow; antheridial and archegonial necks sometimes purple, slightly prominent. **CAPSULES** single or two together, numerous in the same thallus, exposed along the channel in older parts; with 132-244 spores per capsule. **SPORES** (Pl. 3.8, b & c) 90-120 μ, occasionally up to 150 μ, dark red-purple, becoming dark and opaque when fully mature, rounded or globular without wing, regularly reticulate forming 8-12 areolae across the diameter, each areola 7-13 μ wide with prominent and equally high ridges all over the surface, in optical section looking like cog-wheel, no triradiate mark on proximal face.

**CHROMOSOME NUMBER** n=48. **Voucher:** Central Australia, Ayers Rock, O. Na-Thalang No. 95, 12.8.1966 (SYD); Northern Territory, Alice Springs, R.C. Carolin, No. 5031, No. 5080, No. 5082, 2.8.1966 (SYD).

**RANGE:** Northern Territory.

**HABITAT:** on sandy soil, open areas or at the base of rocks, along creek bank, often in dry situations.

**TYPOGRAPHICAL:** R. macrosperma St. **Holotype:** Central Australia, Arco-ellina Well, R. Helms, 27.5.1891.
(G.12730); isotype (AD 19); R. runssorensis St.

Holotype: Central Africa, Mt. Runssoro, Scott Elliott, Nov. - (G.13176); R. sellingii S. Arnell Holotype:

Central Australia, bank of Finoke River, Olaf Selling, 3.4.1949 (S-PA).

DISCUSSION: R. rubrispora St. (Stephani, 1900) has the vegetative features and structure of spores (Incone. Hep. vol. IV P. 362 fig. 7) and his description is strongly reminiscent of R. macrospora. Stephani, however, describes it as a dioecious species which is hardly reliable since he only writes "antheridia unknown". As long as no type specimens of R. rubrispora can be found and the description agrees with that of R. macrospora, R. rubrispora should be reduced to a synonym.

An examination of the type material of R. runssorensis St. and R. sellingii S. Arnell, both appear to be the same plant and have the same characters as R. macrospora.

R. macrospora is very variable in the size of spores, if the spores are large then the number of spores are less per capsule than those plants with smaller spores. The typical globose spore without a wing separates this plant from R. limbata Bisch., which is easily confused with R. macrospora in having the same character of purple scales extending beyond the margins; furthermore the haploid chromosome number of R. macrospora is 48, but in R. limbata 16.

SPECIMENS EXAMINED: Africa, Mt. Ruscenzori Riuani, Scott Elliott (G.13175); Northern Territory, Mt. Olga, O. Na-Thalang No. 91, 11.8.1966 (SYD); Ayers Rock, O. Na-Thalang. No. 95, 12.8.1966 (SYD); Palm Valley, O. Na-Thalang No. 99, 15.8.1966 (SYD); Dahle Gorge, Alice Springs, R.C.Carolin
FIG. 3.8

R. macrospora St.

a, b, c, d. Transverse sections of the thallus from younger to older parts. x20

g - Portion of transverse section.
e - epidermal cell.
f - photosynthetic column (in part) x200

h - scale x50
75.
PLATE 3.8

R. macrospora St.

a. Plant x4.5
b. Spore x730, (distal and proximal face are the same).
c. Spore x730, optical section.
No. 5031, No. 5032, No. 5033, No. 5034, No. 5080, No. 5082, 2.8.1966 (SYD); Stuart's Wall, Alice Springs, R.C. Carolin 5021, 13.8.1966 (SYD); Emily Gap, Alice Springs, R.C. Carolin, No. 5396, 5400, 5399, 7.8.1966 (SYD).


GAMETOPHYTE monoecious, normally forming a rosette 15-25 mm. diameter, dull green or bluish-green, developing dark purple colour over the capsules and in older parts under strong light intensity; thallus 5-8 mm. long, 1.5-2.5 mm. broad, 1.5-2 times as broad as thick in transverse section (Fig. 3.9, a, b, c); upper surface narrowly sulcate throughout. BRANCHES 1-3 furcate, closed together (Pl. 3.9, a); segment elliptical-oblung; apex obtuse or rounded; margin acute. SCALES hyaline or reddish-purple (Fig. 3.9, f) slightly reach over the margin in dry state. EPIDERMAL CELLS 20-25 μ wide, oval or papillate near the apex, soon collapse (Fig. 3.9, d & e). PHOTOSYNTHETIC CELLS 15-20 μ wide, 5-6 cells in each vertical column (Fig. 3.9, d). ANtheridia and ARCHEGONIA in 2-3 rows along the mid dorsal line; antheridial and archegonial necks hyaline or purple, slightly projecting above the thallus surface.

CAPSULES large, 2-4 in each segment, sometimes confine to the lateral sides of the thallus; tissue above the capsule normally becoming purple and easily ruptured; 32-136 spores per capsule. SPORES 75-135 μ, dark brown and becoming opaque at maturity; subglobose, unwinged, finely reticulate all over the surface, forming 8-16 areolae across the diameter, areola 5-8 μ wide, ridges
thick and low slightly projecting at each corner
resulting a coarsely dentate rim around the spore in
optical section (Pl. 3.9, b & c).

CHROMOSOME NUMBER n=16 Voucher: Northern Territory,
Mt. Bundeey, 0. Na–Thalang No. 267, 22.1.1968 (SYD);
Stuart Highway ca. 270 miles (South), 0. Na–Thalang
No. 307, 3.2.1969 (SYD); Daly water, 0. Na–Thalang No. 317,
4.2.1969 (SYD); Eda River, 0. Na–Thalang No. 320,
5.2.1969 (SYD).

RANGE: Northern Territory

HABITAT at the base of rocks, alluvial deposit, growing
mixed with other Riccias i.e. R. billardieri, R.
R. junghuhniara.

TYPOIFICATION The type material of R. gangetica Ahmad
has not been located. The original description and
illustrations provided by Ahmad (1942), however, and
subsequently by Pandi et Udar (1957) are adequate to
decide that the Australian specimens are conspecific.

DISCUSSION In moistened state, R. gangetica resembles
R. sorocarpa Bisch. in vegetative characters, except the former
is slightly larger than the latter; but in dry state
one can recognize it as R. macrospora St. in having
purple scales at the margins and thallus is of the same
bluish-green. In fact, it differs from R. sorocarpa and
R. macrospora in the spore characters. R. sorocarpa has
triangular-globular spore with triradiate mark on proximal
face and winged. R. macrospora has the globose spore
and unwinged like R. gangetica but the spore of the former
with high and prominent ridges while the latter with
very low ridges.

This species is only reported from India
(Ahmad, 1949; Pandi et Udar, 1957, Srivastava, 1964)
FIG. 3.9

*R. gangetica Ahmad.*

a, b & c. - Transverse section of the thallus from younger to older parts. \(x\times10\)

d - Portion of vertical column; ep = epidermal cell, ch = chlorophyll bearing cell. \(x\times100\)

e - epidermal cells near the apex. \(x\times100\)

f - scale \(x\times50\)
PL. 3.9

*R. gangetica* Ahmad.

a. Plant x4
b. & c. Spores. x730 (distal and proximal faces are the same).

b. Surface.
c. Optical section.
and Java (Meijer, 1958). Udar and Chopra (1957) showed the haploid chromosome number n=24. It was found to have only 16 from several thalli and antheridia squashes from plants collected in Northern Territory. This is rather unusual in that the difference in chromosome numbers are not simple multiples. The vegetative and spore characters of this plant collected in India and in Australia are agreed in every aspect according to the original descriptions.

SPECIMENS EXAMINED: Northern Territory: Pinkerton Range, R.C. Carolin, No. 6679, 11.5.1968 (SYD); and also chromosome vouchers.


Tax. syn. from Pande et Udar (1957, 1958)

GAMETOPHYTE monocious, generally forming incomplete rosette, light green or yellowish-green; thallus 10-15 mm. long, 2-4mm. broad, 3-4 times as broad as thick in transverse section (Fig. 3.10, a, b, c); upper surface almost flat and narrowly sulcate throughout the thallus, pitted by 1-2 alternated rows of antheridial and archegonial ostioles. BRANCHES 1-3 furcate, deeply divided; segment oblong or elliptical-oblong, apex rounded or truncate (Pl. 3.10, a); margin acute, slightly attenuate.

SCALES (Fig. 3.10, d) slightly overlapping each other, reach at the margins; pinkish-purple in dry state,
becoming hyaline under moistened condition. **EPIDERMAL CELLS** hyaline, oval-spherical or papillate, 15-20 μm wide (Fig. 3.10, e). **PHOTOSYNTHETIC CELLS** 15-20 μm diameter, 5-6 cells in each vertical column (Fig. 3.10, e). **ANTHERIDIA** and **ARCHEGONIA** arranged in 1-3 rows along the middle part of thallus; antheridial and archegonial necks slightly projecting above thallus surface. **CAPSULES** 1-4 in each segment, prominent on ventral surface, tissue above them easily breakdown; 64-184 spores per capsule. **SPORES** 85-145 μm (± 115 μm), purplish-brown and becoming almost opaque at maturity, subglobose or globose, regularly reticulate all over the surface, no triradiate mark; 5-8 areolae across the diameter, each areola 12-15 μm wide with thin and high border, projecting at the corners, a thin membrane surrounding the spore attached to these projections (Pl. 3.10, b, c).

**CHROMOSOME NUMBER** n=8,16

Voucher: Northern Territory; 40 miles East of Pine Creek, O. Na-Thalang No. 297 (n=16), 29.1.1969 (SYD); Robin Water Fall, O. Na-Thalang No. 287 (n=16), 28.1.1969 (SYD); Mt. Bunderay, O. Na-Thalang No. 272 (n=16), 22.1.1969 (SYD); South of Katherine, O. Na-Thalang No. 319 (n=16), 5.2.1969 (SYD); West of El Sharana, O. Na-Thalang No. 293 (n=8), 29.1.1969 (SYD).

**RANGE** Northern Territory

**HABITAT** at the base of rocks, among grass, alluvial among limestone and sandstone rocks.

**TYPOGRAPHIC** The type of R. billiarderi Mont. et N. was not seen. Although Meijer (1958), states that it is at Strasbourg a search there did not reveal it. To date it has not been located. Pande and Udar’s description and photographs of this plant, however, leave little doubt that the plants collected in Australia can be
referred to *R. billardieri* Mont. et N.

**DISCUSSION** *R. billardieri* normally grows mixed with *R. gangatica* and *R. discolor* as it is found in India. The plants collected from Northern Territory appear to have two chromosome numbers, some with n=16 and others n=8. These two types have the same spore character and only slightly different vegetative features: the one with n=16 is slightly larger than the latter. The diploid species may have evolved from the haploid one by a simple doubling of the chromosome set.

**SPECIMENS EXAMINED** Northern Territory: Darwin, Home Jungle, O. Na-Thalang No. 261, 20.1.1969 (SYD); Darwin Harbour, O. Na-Thalang No. 264, 21.1.1969 (SYD); Elizabeth River, O. Na-Thalang No. 266, 21.1.1969 (SYD); Mt. Bundey, O. Na-Thalang No. 268, 22.1.1969 (SYD); Robin Water Fall, O. Na-Thalang No. 284, 26.1.1969 (SYD); Daly River Road, O. Na-Thalang No. 290, 28.1.1969 (SYD); South Alligator River, O. Na-Thalang No. 292, 29.1.1969 (SYD); South of Pine Creek, O. Na-Thalang No. 295, 29.1.1969 (SYD); ca. 150 miles Stuart Highway (south), O. Na-Thalang No. 299, 29.1.1969 (SYD); ca. 25 miles South of Pine Creek, O. Na-Thalang No. 305, 30.1.1969 (SYD); Maluka Cemetery, O. Na-Thalang No. 309, 3.2.1969 (SYD); 1 mile South of Maluka, O. Na-Thalang No. 311, 3.2.1969 (SYD); and also chromosome vouchers.
FIG. 3.10

*R. billardieri* Mont. et N.

a, b & c - Transverse sections of the thallus from younger to older parts. x10

d & c - scales x50

f - portion of transverse section of the thallus showing epidermal cells (ep) and photosynthetic part (ch). x100
PL. 3.10

*R. billardieri* Mont. et N.

a - Plant x4, left - ventral surface, right - dorsal surface.
b - Spore, surface x730
c - Spore, optical section x730

Taxonomic synonym: from Pande et Udar (1957, 1958)
R. himalayensis St. (MS) in Kashyap's J.

GAMETOPHYTE dioecious, light green or yellowish green, easily develop purple colour over thallus surfaces under strong light intensity; forming a well-developed rosette or in gregarious patches; thallus 5-12 mm. long, 2-3 mm. broad, 3-4 times as broad as thick in transverse section (Fig. 3.11, a, b, c); upper surface roughly reticulated almost flat in male plant, narrowly sulcate in female plant. BRANCHES bi-trifurcate, deeply divided; segment elliptical-oblong; apex obtuse (Pl. 3.11, a); margin acute. SCALES (Fig. 3.11, d), deep pink or purplish-pink, overlapping in dry state and distant in moistened state, extending beyond the thallus margins (Pl. 3.11, a).

EPIDERMAL CELLS 20-30 μ, hyaline, oval shape, papillate around antheridial necks (Fig. 3.11, f).
PHOTOSYNTHETIC CELLS slightly smaller than epidermal cells, 4-5 cells in each vertical column. MALE PLANT with conspicuous hyaline or purplish-pink antheridial necks in 1-3 rows along the middle part of thallus (Pl. 3.11, a (right)). Female plant slightly larger, without prominent archegonial necks (Pl. 3.11, a (middle)).
CAPSULES single or two together, 2-4 in a segment,
prominent on ventral surface (Pl. 3.11, a (for left)), with 46-244 spores per capsule. **Spores** vary in sizes, 80-155 \( \mu \) (± 115) diameter, purplish-brown and rather opaque at maturity, subglobose, roughly reticulate all over the surfaces, no triradiate mark, forming 5-6 areolae across the diameter, areola 15-20 \( \mu \) wide, ridges around each areola almost equally high and attached to the thin membrane covering the spore (Pl. 3.11, b & c).


**RANGE** Northern Territory

**HABITAT** on bare soil among grass.

**TYPOIFICATION** *R. discolor* L. et L. Holotype: Nepal, Wallich (G) (not seen). Since this specimen is sterile Pande and Udar have used Dehra Dun, Duthie (G 008310) for their amended description; this specimen has been examined.


**DISCUSSION** *R. crispulata* Mitt. is the closest species to *R. discolor* L. et L. in being dioecious and has almost the same spore characters except the former has broader membranous part, the number of areolae only 2-4 and the ridges around areolae higher than those found in *R. discolor*.

FIG. 3.11

*R. discolor* L. et L.

a, b & c - Transverse sections of the thallus from younger to older parts. x10

d - scales x50

e - portion of transverse section of the thallus x200; ep = epidermal cell

ch = chlorophyll-bearing cells

f - epidermal cells around antheridial ostiole. x100
PL. 3.11

*R. discolor* L. et L.

a - Plants x4; left - female plants,
   right - male plants.

b - Spore, surface x730

c - Spore, optical section x730
(2) Subgroup "R. limbata" Thalli with dark purple scales, spores triangular-globular, proximal face with triradiate mark.


GAMETOPHYTE monoecious, occasionally forming a complete rosette 15-40mm. diameter or scattered, yellowish-green or glaucous dull-green, very variable in size from 5 to 10 or 15mm. long, 2-4mm. broad, 2-3 times as broad as thick in transverse section (Fig. 3.12, a, b, c, d, & e); upper surface finely and compactly reticulate, channel narrow and deep towards the apex, the rest becoming shallower and almost flat, pitted by antheridial and archegonial necks. BRANCHES radiate, bi-trifurcate, close together, usually unequal (Pl. 3.12, a); segment obcunate-oblong; apex rounded or shortly bilobed; margin flat, acute, attenuate. SCALES dark purple half almost opaque and other half hyaline (Fig. 3.12, h), shiny, imbricate and reaching beyond the margin, when dry inflexed and covering the upper surface. EPIDERMIS slightly papillate in younger parts, epidermal cells 30-70 μ, globose or mammilate, soon collapse (Fig. 3.12, g). PHOTOSYNTHETIC CELLS 30-70 μ, 6-7 cells in each vertical column (Fig. 3.12, f & g), usually longer than wide. ANHERIDIA in 2 rows along the furrow, archegoria in single row between; antheridial and archegonial necks colourless or purple, prominent.
CAPSULES usually many, deeply embedded, exposed only in older parts; with 148-228 spores per capsule.

SPORES 85-130 μ, dark brown, triangular-globular or irregular in form with the wing 4-7 μ wide; distal face reticulate (Pl. 3.12, b) forming 9-15 areolae across the diameter, border of areola thin and faintly marked, with prominent vermicular ridges; proximal face (Pl. 3.12, c) similar to distal one but less distinctly reticulate, triradiate ridge distinct.


RANGE: New South Wales, South Australia, Victoria, Central Australia.

HABITAT: Open grassland, nearly everywhere, abundant, often in dry situations, perennial.

TYPIFICATION R. limbata Bisch. Holotype - Cape Spei, Krauss (G.13163); R. lata Tayl., Holotype - Australia, Swan River, W.J. Drummond, 1843 (K.), isotype (MEL 19780); R. inflexa Tayl. Holotype - Australia, Swan River, W.J. Drummond, 1843 (K.), isotype (MEL 19781); R. punctata Tayl. Holotype - Australia, Swan River, W.J. Drummond, 1843 (K).

DISCUSSION: R. inflexa Tayl., R. punctata Tayl., and R. lata Tayl. are no doubt the same as R. limbata Bisch. These 3 species are vaguely described by Taylor and Stephani. From the type specimens, they are very similar to each other and bearing in mind the wide variation of this species as shown by more than 20
specimens from different places, it is quite clear that all of them belong to the same species.

The other closely related species is *R. macrosperma* St., but the characters of spores of the letter are very different from *R. limbata* in having no wing but with very high ridges.

**SPECIMENS EXAMINED:** Africa:— Cape Province, S. Arnell 778, 1951 (G.13164); Cap. Gaurdenthal, Breute (G.13167); Gaurdathal, Breutel (G.13168).


Victoria: County of Lowan, F.M. Reader, 13.7.1896 (MEL 19773).

FIG. 3.12

*R. limbata Bisch.*

a, b, c, d. - Transverse sections of the thallus from younger to older parts. x20

f, g. - Portion of transverse section of the thallus.
(h) epidermal cell in young part.
(i) photosynthetic column.
(j) air chamber.
(k) epidermal cell collapse, leaving irregular vestiges. x200

1 - scale x50
93.
PLATE 3.12

R. limbata Bischof.

a. Plant x4.5
b. Spore, distal face x730
c. Spore, proximal face x730


**GAMETOPHYTE** monoecious, forming a rosette 10-15mm. diameter or scattered in an incomplete rosette, dark green, usually rusty-coloured over capsule and in older parts; thallus 3-6mm. long, 1-1.5mm. broad, 1-2 times as broad as thick in transverse section (Fig. 3.13, a, b & c); upper surface finely and compactly reticulate, shining; channel deep and narrow at apex, becoming gradually broader and almost flat towards the base, pitted by gametangial necks. **BRANCHES** (Pl. 3.13, a) furcate or bifurcate, slightly divergent; segment at first obovate, finally oblong or obcuneate-oblong; apex obtuse or rounded to truncate; margin flat, acute, ascending. **SCALES** (Fig. 3.12, h) dark purple, arranged in two lateral-ventral rows, not extending beyond the margin, persistent. **EPIDERMAL CELLS** almost isodiametric (Fig. 3.13, d), 20-30 μ wide, filled with fluid which reacts strongly with iron-haematoxylin stain (Frye & Clark 1937) and
safranin 0. **PHOTOSYNTHETIC CELLS** 20–30 \(\mu\), 7–9 cells in each vertical column (Fig. 3.13, d). **ANtheridIa** at both sides of archegonia along the furrow; antheridial and archegonial necks prominent. **Capsules** large, almost occupying the whole width of the thallus, exposed by ruptured of upper surface in older parts leaving a large black pit filled with spores; 208–368 spores per capsule. **Spores** 70–75 \(\mu\), dark brown, triangular-globular with nearly smooth wing 1–2 \(\mu\) wide; distal face (Pl. 3.13, b) irregularly reticulate with thin vermiculate ridges radiating from the central part or scattered; proximal face (Pl. 3.13, c) almost the same as distal one, but less distinctly ridged, faintly marked by triradiate ridges.

**Chromosome Number** n=8 Voucher: New South Wales, Prospect Reservoir, O. Na-Thalang No. 240, 15.6.1967 (Syd); Corowa, D. Black (O. Na-Thalang No. 255), 8.1967 (Syd).

**Range:** New South Wales, South Australia, Western Australia.

**Habitat:** Open grassland, rare, perennial.

**Typification** A request to Geneva did not produce type material. However authentic named specimens were forwarded and there is no doubt that these belong to the species under discussion. They are cited under "specimens examined".

**R. porosa** Tayl. Holotype: Swan River, W.J. Drummond, (Pro parte) (K); isotype (MEL 19794).

**Discussion:** *R. nigrella* DC is easily distinguished from others by its small size and the purple lateral scales which do not extend over the margin. It also has persistent epidermis which in section seems to be filled with a clear cell sap which reacts strongly with
Safranin O and iron-haematoxylin.

*R. porosa* Tayl. is a doubtful species. There are two specimens in the same package: one of them is *R. nigrella*, the other is in subgenus *Ricciella* (without capsule) which is close to *R. musciculosa* St. Both specimens from Kew Herbarium and Victorian National Herbarium are the same in having two plants in the same package. According to the description, *R. porosa* is close to *R. nigrella*, and from the material, Swan River, W.J. Drummond (K) and (MEL 19794) both *Eriococcia* in those two packages are exactly the same as *R. nigrella* DC. Since there are 2 discordant elements and it is impossible to determine to which one Taylor's description applies, this name *R. porosa* Tayl. must be rejected (Art. 56).

**SPECIMENS EXAMINED:** Europe and America:— Calif., Soboda Hot Springs, Lee Bonar, 1957 (G.13169); Morocco, S. Jovet-Ast, 1955 (G.13170); Frankreich, A. Crozala, 1902 (G.13171); Florenz, Dr. E. Levier, 1888 (G.13172); Calif., Annetta M. Carter 252, 1933 (G.13173); France, Husnot, 1891 (G.13174).

New South Wales, Australia:— Barralier, O. Na-Thalang No. 54, 72, 12.7.1966 (SYD); Prospect Reservoir, O. Na-Thalang No. 240, 15.6.1967 (SYD); Corowa, D. Black (O. Na-Thalang No. 255), 8.1967 (SYD).


Western Australia:— in loc. cit.
FIG. 3.13

*R. nigrella DC.*

a, b, c. Transverse sections of the thallus from younger to older parts. x40.

d. - Portion of transverse section of thallus, (e) epidermal cell, (g) photosynthetic cell, (f) vacuole x200.

h. - Scale x50 (shadowed - dark and almost opaque part).
PLATE 3.13

_R. nigrella DC._

a. Plant x4
b. Plant x16
c. Spore, distal face x730
d. Spore, proximal face x730
(3) Subgroup *"R. sorocarpa"* Thalli with hyaline scales.


GAMETOPHYTE monocious, scattered, whitish green or green; thallus 6-12 mm. long, 3-4 mm. broad, 2-3 times as broad as thick in transverse section (Fig. 3.14, a, b, c & d); upper surface loosely reticulate, usually with a wax-like powder over it; channel narrow at apex, suddenly becoming broader andrather flat pitted by antheridial and archegonial necks. BRANCHES single or furcate (Pl. 3.14, a), divergent, segment obovate-oblong or oblong with rounded apex; apex acute, obtuse to rounded; margin flat, acute, attenuate, hyaline.

SCALES (Fig. 3.14, h) hyaline, large, extending beyond the margins, overlapping each other, persistent.

EPIDERMAL CELLS (Fig. 3.14, g) 50-60 μ, globose or mammillate, soon collapsing and leaving irregular vestiges. PHOTOSYNTHETIC CELLS 40-50 μ, about 11 cells in each vertical column, almost isodiametric. ANThERIDIA at both sides of archegonia which are in 2 rows along the furrow; antheridial and archegonial necks prominent.

CAPSULES usually single, many in the same thallus, not easily exposed; with 198-386 spores per capsule.

SPORES 100-128 μ, golden brown to dark brown, mostly globular with a finely dentate or nearly smooth wing of 3-4 μ wide; distal face (Pl. 3.14, b) faintly reticulate with irregular high ridge radiating from the central part of the spore or sometimes forming 8-10 irregular
areolae across the diameter, each areola 10-12 μ wide with broad and incomplete border; proximal face (Pl. 3.14, c) similar to distal one but with distinct triradiate ridge.


**RANGE**: New South Wales, Northern Territory, Southern Australia.

**HABITAT**: Open grassland, rare.

**TYPIFICATION** The type of *R. lamellosa* Raddi was not seen. It has been sought in herbarium of Conservatoire et Jardin Botaniques, Geneve. There seems little doubt that those authentic materials and the plants collected in Australia refer to *R. lamellosa* Raddi according to its distinct characters in having large imbricate hyaline scales and its spores scarcely form perfect areolae.

**DISCUSSION** *R. lamellosa* is rather rare in Australia, it is easily differentiated from others by its large size, persistent hyaline scales extending beyond the margins and upper surface in dry state usually with a wax-like powder on it.

Its closely related species are *R. austini* St., *R. alboclimbata* Arnell, *R. albosquamata* Arnell and *R. albomarginata* Bischo. For the first 3 species, they differ from *R. lamellosa* in the spores characters which all are clearly reticulate. *R. albomarginata* has smaller spores, only 60-70 μ with narrow and crenulate wing which is not so in *R. lamellosa*.

**SPECIMENS EXAMINED**: Europe: Frankreich, A. Crozals, 1902 (G.13151); Italy, Egidio Barsali, 1902 (G.13152); Morocco, S. Jovet-Ast, 1955 (G.13153); Florenz, O. Becchari, 1888 (G.13154); Jarozita Palermo, Prof. Ross, 1889
101.
FIG. 3.14

R. lamellosa Raddi

a, b, c, d. Transverse sections of the thallus from younger to older part. x20

g. Portion of transverse section of the thallus.
   (e) epidermal cell,
   (f) photosynthetic cell.
   x200

h. Scale x50
PLATE 3.14

*R. lamellosa* Raddi

a. Plant x8
b. Spore, distal face x730
c. Spore, proximal face x730
(G.13155); Villa Beocari, Dr. Levier, 1888 (G.13156); Sardinia (?), Moirs, (G.13157); Niopania, Lange, 1852 (G.13158); Herb. Taylor proparte majore (R. acuminata Tayl.) (G.13159); Picarazzi, E. et A. Hast du Pavillon, 1855 (G.13160); Coimbra, Moller No. 4, 1900 (G.13161); Corte, Evisa, 1901 (G.13162).


Tax. Synonym from Frye & Clark. Hepaticae of North America, p. 19, 1937 (Type has not been seen).

R. lindenbergiana Sauter, Flora 28: 132, 1845

R. epicarpa Wallr., G.L. & N. Syn. Hep. 600, 1846
GAMETOPHYTE monococious, forming a rosette 10–20mm. diameter or in gregarious patches, pale green or yellowish-green or somewhat crystalline; thallus 3–7mm. long, 1.5–2mm. broad, 2–3 times as broad as thick in transverse section (Fig. 3.15, a, b & c); upper surface regularly and compactly reticulate, papillate towards the apex, channel narrow and acute throughout. BRANCHES (Pl. 3.15, a & b) furcate or bifurcate, deeply divided, divergent, about 8–12 segments in a rosette; segment narrowly oblong or obovate-oblong with a narrow to subacute apex; margin sharply acute, hyaline membranous, commonly ascending, slightly incurved in dry situations, making upper surface resemble a broad V-shape in transverse section. SCALES (Fig. 3.15, i) hyaline often extending to the margin at or near the apex, slightly overlapping each other. EPIDERMAL CELLS 20–30 μ diameter, globose or mammillate soon collapsing leaving persistent cups attached to the thick-wall sub-epidermal layer (Fig. 3.15, d & g). PHOTOSYNTHETIC CELLS 20–30 μ, about 8–10 cells in each vertical column, longer than wide. ARCHEGONIA 1–2 rows along the furrow with antheridia at both sides; antheridial and archegonial necks not prominent. CAPSULES numerous, easily ruptured, usually exposed even in younger parts, with 248–528 spores per capsule. SPORES 70–85 μ, rarely up to 100 μ, dark red-brown, almost opaque when fully mature, triangular-globular with slightly crenulate wing 4–6 μ wide; distal face (Pl. 3.15, c) regularly reticulate forming 5–7 angular areolae across the diameter; areola 14–15 μ wide with a rather thick and complete border which is raised up at the corners; proximal face (Pl. 3.15, d) with indistinct triradiate
ridges, densely and minutely punctate or with short and numerous minute ridges, not forming areolae.

CHROMOSOME NUMBER n=8
Voucher: New South Wales, Cooleman Creek, O. Na–Thalang No. 185, 26.1.1967 (SYD);
Prospect Reservoir, O. Na–Thalang No. 235, 15.6.1967 (SYD);

RANGE: New South Wales, Victoria, Western Australia, A.C.T.

HABITAT: Open grassland, nearly everywhere, abundant.

TYPOIFICATION: The type of R. sorocarpa Bisch. was not seen. It was sought at the herbarium of Conservatoire et Jardin Botanique, Geneve. R. acuminata Tayl., Holotype – Swan River, W.J. Drummond, 27.6.1845 (FH).

DISCUSSION: Taylor's description of R. acuminata is so incomplete that it is very hard for anyone to determine what that plant looks like. He says only: "frond 1 inch in diameter, when moistened the lobes swell and their margins are so closely inflexed: under surface is quite destitute of scales; frond pale green look as if sprinkled with powder; lobes acuminated"; there is no description of the spores at all. From the type specimens there are two plants in the same package: one is R. lamellosa Raddi, the other is R. sorocarpa Bisch. It is possible that Taylor has used both plants' characters for R. acuminata, because "frond pale green look as if sprinkled with powder" is the character of R. lamellosa and the size of frond is that of R. sorocarpa. This name must therefore be rejected as invalid (Art. 66).

R. sorocarpa Bisch. is a very common species and can be easily recognised by its narrow oblong segment, narrowly channelled throughout, scales reaching the apex,
hyaline and acute margin. It differs from *R. lamellosa*
its closely related species in the character of the
scales and the spores. In the latter it has large
imbricate scales extending beyond the margin, the spore
is larger and not forming perfect areolae.
*SPECIMENS EXAMINED:* Europe & America: Nyland, Harald
Lindberg, 1902 (G.13177); North Austria, A. Zahlbruckner,
(G.13178); G.T. Doward Hill, Herefordshire, C.M. Watkins,
1874 (G.13179); Prov. Brandenburg, O. Jaap, 1904
(G.13180); Bayern, Ig. Famieller, 1901 (G.13181);
Niederösterreich, V. Schiffer & J. Baumgartner, 1902
(G.13182); Calif., Annette M. Carter 408, 1933 (G.13183);
de Condille, Iamy? (G.13184); Akersleiss I.
Frenzen, 1912 (G.13185); Am Scharnik, 1898 (G.13186);
Stocksund, 1926 (G.13187); Kirchzaten, Mully, 1898
(G.13188); Sibiria, N. Wilh. Arnell, 1876 (G.13189);
Genico, Reuter, 1855 (G.13191); Myazaki, T. Kurata &
S. Hattori, 1950 (G.13192); Zealand, O. Jensen, 1906
(G.13193); North Austria, A. Zahlbruckner 281 (BRI 061836).
Australia: North West Victoria, P. Bibby, 10.10.45
(MEL 19792); Swan River, Drummond (MEL 19794);
Melbourne, Ral. Bastow, 5.11.1896 (MEL 19795); New South
Wales: Bullio, O. Na-Thalang No. 27, 11.7.1966 (SYD);
Picton, O. Na-Thalang No. 30, 11.7.1966 (SYD); Razor-
back Ridge, O. Na-Thalang No. 34, 11.7.1966 (SYD);
Barallier, O. Na-Thalang No. 38, No. 45, No. 58, No. 71,
12.7.1966 (SYD); Wombyan Creek, O. Na-Thalang No. 75,
13.7.1966 (SYD); Thredo River, O. Na-Thalang No. 184,
25.1.1967 (SYD); Cooleman Creek, O. Na-Thalang No. 185,
26.1.1967 (SYD); Prospect Reservoir, O. Na-Thalang No. 235,
15.6.1967 (SYD); Luddenham, O. Na-Thalang No. 241,
15.6.1967 (SYD); Jerricknorra, R. Selkirk (O. Na-Thalang
FIG. 3.15

R. sorocarpa Bisch.

a, b & c. - Outline of the transverse sections of the thallus from younger to older part.  x40

d & g. - Portion of transverse section of the thallus, (e) epidermal cell, (f) photosynthetic cell, (h) air chamber.  x200

i - scale  x50
PLATE 3.15

*R. sorocarpa* Bisch.

a. Plant x4
b. Plant x15
c. Spore, distal face x730
d. Spore, proximal face x730
Canberra ACT, Cotter River, O. Na-Thalang No. 189,
27.1.1967 (SYD).

16. *R. marginata* Carr. et P. Linn. Soc. N.S.W. II,
Tax. Syn.: *R. cartilaginosa* St. Hedwigia p. 44, 1889;

**GAMETOPHYTE** monoeious, forming a rosette 25-50mm.
diameter or in gregarious patches, dark green; thallus
7-10-15mm. long, 4-5mm. broad, 2-5 times as broad as
thick in transverse section (Fig. 3.16, a, b & c);
upper surface finely and compactly reticulate, shiny;
channel narrow and deep at the apex, the rest almost flat
and pitted by the projecting antheridial and archegonial
necks. **BRANCHES** (Pl. 3.16, a) furcate or bifurcate,
slightly divergent; segment obtuse-oblanceolate or oblong;
apex rounded or truncate; margin slightly undulate,
yellow, acute and attenuate. **SCALES** (Fig. 3.16, i)
large, hyaline, join with the margin. **EPIDERMAL CELLS**
(Fig. 3.16, d & f) 20-40 μ, not papillate; air-pore
in young part covered with 4 thin and hyaline membranes
soon disintegrated. **PHOTOSYNTHETIC CELLS** 20-30 μ,
10-12 cells in each vertical column, longer than wide,
sometimes with special thickening on adjacent walls
resembling a simple pit. **ANTHERIDIA** at both sides of
archegonia along the furrow; antheridial and archegonial
necks prominent. **CAPSULES** deeply embedded in the thallus,
numerous, exposed in older part only; with 192-592
spores per capsule. **SPORES** 70-85 μ (occasionally up to
100 μ), brown, triangular-globular with slightly crenate
wing 4–5 μ wide; distal face (Pl. 3.16, b) regularly reticulate forming 8–10 areolae across the diameter, each areola 8–12 μ wide; border of the areola usually incompletely thickened with high ridges at the corners; proximal face (Pl. 3.16, c) with a distinct triradiate mark and scattered high ridges not forming definite areolae.

**CHROMOSOME NUMBER** n=16  
**Voucher:** New South Wales, Parramatta Lake, O. Na-Thalang No. 4, 21.6.1966 (SYD); Luddenham, O. Na-Thalang No. 243, 15.6.1967 (SYD).

**RANGE:** New South Wales.

**HABITAT:** nearly everywhere in open grassland, abundant.

**TYPOIFICATION:** *R. marginata* Carr. et F. Holotype — New South Wales, Parramatta, Whitelegge, 9.1889 (NSW H. 89); Isotype (NSW H. 91), (SYD T.W.4); *R. cartilaginosa* St. 120 Queensland, F.H. Bailey (G.12726).

**DISCUSSION:** The large size of the thallus and the very shiny upper surface with hyaline and wavy margins distinguishes this plant from others. It has some characters close to *R. bistriata* Evans (Evans, 1919), but is different in its smaller size of spore. The spore of *R. bistriata* is 110–130 μ while that of *R. marginata* is 70–85 μ and not opaque even when fully matured, wing not interrupted, and inner face with high ridges which is not so in *R. bistriata*.

*R. cartilaginosa* St. is very similar to *R. marginata*, the characters of the type specimens and the descriptions agree with those of *R. marginata*.

**SPECIMENS EXAMINED:** New South Wales: Parramatta Lake, O. Na-Thalang No. 4, 21.6.1966 (SYD); Balone H'way, J. Jacob (O. Na-Thalang No. 23), 9.5.1966 (SYD); Picton,
111.
R. marginata Carr. et P.

a, b & c. Outline of the transverse sections of the thallus from younger to older parts. x20

d. - Portion of epidermis, surface view, (e) epidermal cell, (p) airpore. x134.

j. - Portion of the transverse section of the thallus, (e) epidermal cell, (g) photosynthetic cell, (h) airchamber x200

i. - scale x50
Fig. 3.16
PLATE 3.16

R. marginata Carr. et P.

a. Plant x4.5
b. Spore, distal face x730
c. Spore, proximal face x730
Razor-back Ridge, O. Na-Thalang No. 32, 11.7.1966 (SYD); Barralier, O. Na-Thalang No. 48, No. 51, No. 61, No. 70, 12.7.1966 (SYD); Wombeyan Creek, O. Na-Thalang No. 77, No. 79, 13.7.1966 (SYD); Nattai River, R.C. Carolin No. 5418, 3.10.1966 (SYD); Glen Davis, Blue Hts., O. Na-Thalang No. 146, 12.10.1966 (SYD); Berry's Island, D.A. Adamson (O. Na-Thalang No. 231), 28.5.1967 (SYD); Luddenham, O. Na-Thalang No. 243, 15.6.1967 (SYD); Camden, O. Na-Thalang No. 248, 15.6.1967 (SYD).

17. R. olgensis sp. nov.

Monoica, viridis, gregaris; thallus 7-10mm. longus, 3-5mm. latus; segmenta obcuneato-oblongo apice late obtuso vel truncato marginibus sublacerates. Columnae cellularum 4-6 cavernulam aeriam unamquamque angustam verticalem cingentes. Squmae hyalinae vel interdum purpurarsentes 2-cellulis crassae haud imbricatae vix ad marginem extensae. Sporae 70-100 μ latae, atrofuscæ suborticulares ala crenata 2-3 μ lata; superficies distalis obscure areolata cristis brevibus crassis: superficies proximalis cristis indistinctis.

GALETOPHYTE, monoecious, in gregarious patches, green; thallus 7-10mm. long, 3-5mm. broad, 2-4 times as broad as thick in transverse section (Fig. 3.17, a, b & c); upper surface loosely reticulate; channel narrow and deep only near the apex, the rest broad or almost flat pitted by antheridal and archegonial necks.

BRANCHES (Pl. 3.17, a) single or furcate, divergent; segment obcuneato-oblong; apex rounded or truncate; margin usually curved downwards, acute, attenuate.

SCALES (Fig. 3.17, i) hyaline or sometimes tinged with
purple, 2 layers thick, not overlapping each other, present near the apex, reaching at the margin. 

**EPIFERMAL CELLS** 30-40 μ, not papillate, airpore surrounded by 4-6 cells (Fig. 3.17, h). **PHOTOSYNTHETIC CELLS** 40-50 μ, 10-11 cells in each vertical column (Fig. 3.17, d), usually longer than broad. **ANTHERIDIA** of both sides of archegonia along the furrow; antheridal and archegonial necks prominent. 

**CAPSULES** slightly protruding, numerous, 5-10 in each segment, tissue over them spongy, easily ruptured; with 412-737 spores per capsule. **SPORES** 70-80 μ, dark brown, almost rounded with crenate wing 2-3 μ wide; distal face (Pl. 3.17, b) reticulate forming 9-10 areolae across the diameter, areola 5-6 μ wide with thin and short irregular ridges; proximal face (Pl. 3.17, c) roughened by indistinct ridges.

**CHROMOSOME NUMBER** n=8 Voucher: Central Australia, Mt. Olga, D.R. Selkirk (O. Na-Thalang No. 136), 20.8.1966 (NSW).

**RANGE:** Mt. Olga, Central Australia.

**HABITAT:** on fine red sandy soil, along the creek.

**TYPOIFICATION:** R. olgensis sp. nov. Holotype - Central Australia, Mt. Olga, D.R. Selkirk, (O. Na-Thalang No. 136) 20.8.1966 (NSW); isotype (SYD).

**DISCUSSION:** R. olgensis is similar to R. marginata Carr. et P. in size and form of thallus, but its scales are not joined with the margin as in R. marginata, the scales are 2 cell-layers in thickness, the upper surface is less compact, the pattern of the spore is less distinct and the haploid chromosome number is 8, while in R. marginata it is 16.

**SPECIMENS EXAMINED:** See Typification.
FIG. 3.17

*R. olgensis sp. nov.*

a, b, c. Transverse sections of the thallus from younger to older parts. x20

d. – Portion of transverse section of the thallus, (e) epidermal cell, (f) photosynthetic column, (i) air chamber. x200

g. – Scale (section) x200

h. – Part of epidermis, (e) epidermal cell, (p) air pore. x200

i. – Scale (whole scale) x. 50
PLATE 3.17

*R. olgensis* sp. nov.

a. Plant x4
b. Spore, distal face x730
c. Spore, proximal face x730
18. *R. rorida* sp. nov.

Monoecia. Thalli rosulam perfectam vel imperfectam 12-18 mm. latam, glaucum formans, 5-10 mm. longi, 2-3 mm. lati pagina dorsali canaliculata lati ad apicem. Rami 1-2 furcati extendentes. Squamas hyalinae exsertae ultramtrans marginem ad apicem. Sporae ± 75 μ diam., deltato-glabulares sine areolis distinctis sed cum ala crenulata 3-5 μ lata et cristis irregularibus prominentibus. Chromosomata 16.

GAMETOPHYTE monoecious, forming complete or incomplete rosette with 4-6 branches, 12-18 mm. diameter, glaucescent green; thallus 5-10 mm. long, 1-3 mm. broad, almost 2 times as broad as thick in transverse section (Fig. 3.11, a, b, c), upper surface roughtened by papillated epidermal cells, broadly channelled at apex, the rest more or less flat or convex (Pl. 3.18, a). BRANCHES 1-2 furcate, divergent; segment obcuneate or oblong; apex round or truncate-emarginate, margin acute or obtuse, slightly curved downward. SCALES (Fig. 3.18, d) hyaline, slightly extending beyond the margin at the apex, only reach at the margin in older part. EPIDERMAL CELLS dew-drop like, hyaline, globose or papillate, sparsely persistent, 25-30 μ wide (Fig. 3.21, e). PHOTOSYNTHETIC CELLS 15-25 μ wide, 4-5 cells in each vertical column (Fig. 3.18 e). ANTHERIDIA and ARCHEGONIA arranged in 2-4 rows along the middle part of thallus, antheridial and archegonial necks not prominent. CAPSULES many, 4-8 in each segment, embedded in the thallus, 212-300 spores per capsule.

SPORES almost 75 μ, brown or dark brown, triangular-globular with crenulate wing, 3-5 μ wide; distal face faintly reticulated not forming definite areolae, but with irregular, thin and high ridges (Pl. 3.18, b); proximal
FIG. 3.18

*R. rorida* sp. nov.

a, b & c. Transverse sections of the thallus.  
x10

d. Portion of transverse section of the thallus, ep = epidermal cell,  
   ch = chlorophyll bearing cell.  
x100

e. scale  x50
PLATE 3.18

**R. rorida** sp. nov.

a. Plant x
b. Spore, distal face x730
c. Spore, proximal face x730
face similar to the distal one, triradiate mark narrow (Pl. 3.18, c).


RANGE: Canberra, A.C.T.

HABITAT: open grass land.


DISCUSSION: R. rorida resembles R. crystallina L. in the upper surface of the thallus, but the latter has a polyhedral air chamber type and differs from the former in all other aspects. In the subgenus Riccia, it is rather closely related to R. lamellosa Raddi in the whitish-green or glaucous green colour of the thallus and the presence of hyaline scales, but R. rorida is comparatively smaller than R. lamellosa and its spores are completely different (see Pl. 3.14, a, b & c and Pl. 3.18, a, b & c).

SPECIMENS EXAMINED: see typification.

3. "LAEVIGATA" group - thalli without cilia at the margin, scales small and present under the apex only.


(Types not seen)

R. marginata Lindberg
from Frye & Clark: Hepaticae of North America, p.15, 1937


GAMETOPHYTE monoecious, forming incomplete rosette or gregarious overlapping patches, light green, thallus 5–8 mm. long (rarely up to 10 mm. long), 1.5–2.5 mm. broad, fleshy, 2–3 times broader than thick in transverse sections (Fig. 3.19, a, b, c & d); upper surface finely reticulate, papillate in the younger parts, deeply and narrowly channelled at the apex where the tumid margins meet, abruptly broad and flat towards the base.

BRANCHES (Pl. 3.19, a) single or furcate, deeply divided, divergent, segment obovate–oblong or oblong; apex rounded or emarginate; margin obtuse, tumid, raised up in the first segment and disappearing in the rest of the thallus. SCALES hyaline, small, on ventral side close to the apex. EPIDERMAL CELLS (Fig. 3.19, f) 20–30 μm, globose, soon collapsing. PHOTOSYNTHETIC CELLS 20–30 μm, slightly longer than broad, 6–7 cells in each vertical column (Fig. 3.19, f). ANTERIDIA at both sides of archegonia along the furrow close to the apex; antheridial and archegonial necks prominent. CAPSULES solitary or two together, slightly protruding, not easily exposed; with 224–336 spores per capsule.

SPORES 70–85 μm, dark brown, triangular–globular with crenate or nearly smooth wing 3–4 μm wide usually broader at the corners; distal face (Pl. 3.19, b) regularly reticulate forming 6–7 areolae across the diameter, each
areola 10-12 μ wide with a thin and almost complete
border slightly raised at the corners; proximal face
(Pl. 3.19, c) similar to distal one but less distinctly
reticulate, sometimes with high ridges, triradiate mark
distinct.

CHROMOSOME NUMBER n=8 Voucher: New South Wales,
Bells Creek, O. Na-Thalang No. 7, 21.6.1966 (SYD);
Luddenham, O. Na-Thalang No. 245, 15.6.1967 (SYD).
RANGE: New South Wales, South Australia.
HABITAT: among grass, rather shady and moistened area.

TYPOIFICATION Stafleu (1968) states that the location of
Hoffmann's types is unknown. It is possible that they
are at Göttingen since he was professor there in 1795.
Attempts are being made to locate it. However it is a
fairly well known and distinctive species with its typical
swollen margin, broadly channelled upper surface, small
and few scales separating it from other species. There
seems little doubt that the description and illustrations
of R. bifurca Hoffm. given by Stephani (1900), Arnell
(1956), Freye and Clark (1937) and Macvicar (1926) refer
to these specimens collected in Australia.

DISCUSSION R. bifurca is a rather distinct species. Its
closely related species i.e. R. blackii, R. asprella are
of the "ciliata" group and R. albida is completely
different in being dioecious and having smooth rounded
spores.

SPECIMENS EXAMINED: Europe: Italy, Etruria, E.G., 21.
May 1888 (G.13124); Scandinavia, Hassletrolm, J. Persson,
7.11.1887 (G.13125); Coimbra, Henriques (G.13126);
Bechlin, 11.1885 (G.13127); German, Dr. Giessler
(G.13128); Fontainebleau (G.13129); England, Barmouth,
Jack, 4.1876 (G.13131); German, Oberh. Stauteich, H.J.E.
FIG. 3.19

R. bifurca Hoffm.

a, b, c & d. Outline of transverse sections of the thallus from younger to older part. x20

f. — Portion of transverse section of thallus.
   (e) epidermal cell,
   (g) photosynthetic cell,
   (h) airchamber. x200
PLATE 3.19

*R. bifurca Hoffm.*

a. Plant  x17  
b. Spore, distal face  x730  
c. Spore, proximal face  x730
Australia: New South Wales: Bells Creek, O. Na–Thalang No. 7, 21.6.1966 (SYD); Barralier, O. Na–Thalang No. 49, No. 50, No. 59, No. 62, 12.7.1966 (SYD); Luddenham, O. Na–Thalang No. 245, 15.6.1967 (SYD); South Australia, Mt. Lofty, R.H. Kuchel No. 1193, 6.9.1963 (AD 53); Clare Agri. & Hor. Soc. ground 0. Na–Thalang No. 127, 22.8.1966 (SYD).


GAMETOPHYTE dioecious, in gregarious patches, whitish-green or normally almost white in dry state; thallus 4-6mm. long, 1.5-2mm. broad, 2-3times as broad as thick in transverse section (Fig. 3.20, a, b, c); upper surface finely reticulate or alveolate-reticulate or spongiose when dry (Frye & Clark, 1937), narrowly sulcate throughout except at the place where capsule present (Pl. 3.20, a). BRANCHES single or furcate, rarely bifurcate, divergent; segment obconic-oblong or obovate-oblong; apex rounded or truncate; margin rounded (Pl. 3.20, a). SCALES rare, small, hyaline.

EPIDERMAL CELLS 20-30 /μ, colourless, persistent, rounded to mamillate, variable in form (Fig. 3.20, d & f); air pores and air chambers often enlarged.

PHOTOSYNTHETIC CELLS 25-30 /μ wide, about 9 cells in each vertical column, almost isodiametric or slightly longer than broad in vertical section (Fig. 3.20, d & f); in dry state, these cells usually colourless for 1-6 layers giving the whitish thallus appearance. MALE plant similar
to FEMALE one, except the former upper surface are pitted by antheridial ostioles (Pl. 3.20, a (left)). CAPSULE rare, single, deeply embedded in thallus or sometimes protruding on dorsal surface, 70-148 spores per capsule. SPORES 70-85 μ, almost rounded, dark-red and becoming opaque at maturity; smooth all over the surface, sometimes showing low irregular wrinkles or warts (Pl. 3.20, b).

CHROMOSOME NUMBER n=8 Voucher: Northern Territory, Palm Valley, O. Na-Thalang No. 100, 15.8.1966 (SYD).

RANGE: Northern Territory, Palm Valley.

HABITAT: on red fine sandy soil, open area.

TYPIFICATION R. albida Sull. Holotype: Texas, Ch. Wright, 1849 (FH No. 1325).

DISCUSSION R. albida is rather distinct from others in its whitish-green thallus with narrow furrow and rounded margin. The only Riccia with smooth and rounded spore. Frye and Clark (1937) and MacGregor (1961) give the description of R. albida that "epidermis is decolorized and with calcified walls". The plants collected from Palm Valley are less calcified and spores are slightly smaller, but all other characters agree with those previous descriptions (there is no mature spore on the holotype).

SPECIMENS EXAMINED: Northern Territory, Palm Valley, O. Na-Thalang No. 100, 15.8.1966 (SYD).
FIG. 3.20

R. albida Sull.

a, b, c. Transverse sections of the thallus from younger to older parts. x50

d, f. - Portion of the thallus,
    (e) epidermal cell,
    (g) photosynthetic column,
    (h) air chamber. x200
PLATE 3.20

R. albida Sull.

a. Plant, (left) female plant, male plant (right). x12

b. Spore. x730
II. Subgenus RICCIELLA (Braun) Baulay Musc. de la France II: CIXIV (1904).

Riccia sect. 2 "Spongodes" (Bisch) Nees, sect. 3 "Ricciella" (Bisch) Nees. Naturgeschichte der Europaischen Lebermoose IV (1838). Berlin.

Riccia subgen. Ricciella (Braun) Müller in Rabenhorsts Kryptogämen Flora VI: 421 (1954)

SUBGENUS RICCIELLA. Upper part of the thallus composed of rather loosely arranged chlorophyll-bearing tissue forming reticulate one-layered cell plates; air chambers polyhedral, normally roofed over by green epidermal cells with an air pore in the centre.

II. THE SUBGENUS RICCIELLA

In the subgenus Ricciella, there are 18 taxa so far collected; 3 species viz. R. duplex Lorb., R. crystallina L. and R. cavernosa Hoffm. seems to be a world-wide species; R. junghuhniana Nees et Lindb. was only reported from Java; the other 9 species and 5 varieties are probably found only in Australia. Here, this subgenus is separated into two major groups.

1. "Terrestrial" group which the majority of the subgenus are land-form; few species are semi-terrestrial-form growing on mud but are not an aquatic plant. This group is divided into:

(1) "R. crystallina" group is the semi-terrestrial plants and are found growing on mud, at the edge of swamps, creek banks. They can be easily recognized by the form of almost rounded and compact rosette. R. crystallina L. and R. cavernosa Hoffm. had been misidentified for a long time, i.e. most of the authors described R. cavernosa Hoffm. as R. crystallina L.
and _R. crystallina_ L. itself was considered as _R. plana_ Tayl.

(2) "_R. papulosa_" group including _R. papulosa_ St. and _R. spongiosa_ St. which probably are the largest plants of the genus. They can be found growing even in the rather dry places and are widely distributed in New South Wales.

(3) "_R. vesiculosa_" group which are hygrophyllus plants, comprising one dioecious species and 5 monoecious species. They are found in moistened areas, some are growing under the shade but some are heat resistant growing under strong light. _R. vesiculosa_ Carr. et P. and _R. collata_ sp. nov. (dioecious) are of the former type and also _R. muscicola_ St. which is growing among mosses (as the source of its name); _R. deserticola_ St., _R. oressa_ St. and _R. junghuhniana_ Nees et Lindb. are of the latter type which are normally found growing in Central Australia and Northern Territory.

2. "Aquatic-Terrestrial" group or _R. fluitans-complex_ group which includes 3 species and 4 varieties. Found on mud along creek banks, waterfalls and occasionally as an aquatic. For identification the plants of this group, it is necessary to use the spore characters for a definite determination unless the chromosome numbers must be counted.
1. "TERRESTRIAL" group.
   (1) Subgroup "R. crystallina" - semi-terrestrial plants, normally forming rounded and compact rosette.


   Taxonomic synonym: Jovet—Ast, Rev. Bryol. et Lichenol.,


*CAMESTROPHE* monoeious, usually in compact rosette or half a rosette 7-25 mm. diameter, sometimes forming a scattered rosette, young thallus broadly bi-tetralobed; pale green or glaucous green; thallus 5-7 mm. long, 2-4 mm. broad, 3-5 times as broad as thick in transverse section (Fig. 3.21, a); upper surface strongly papillate, not marked with air chamber area, slightly grooved or channelled at apex; the rest almost flat (Pl. 3.21, a).

*BRANCHES* short, divergent, overlapped when forming a rosette; segment obcuneate with shortly bilobed apex; margin rounded, thick. *EPIDERMAL CELLS* papillate, collapsed in older parts (Fig. 3.21, b), air chambers appearing as 1-3 layers in transverse section (Fig. 3.21, b & c), with 1-2 layers of compact cells. *ANTHERIDIA* and *ARCHEGONIA* present close to the apex; antheridial and archegonial necks not prominent. *CAPSULES* numerous, embedded in the thallus, 380-546 spores per capsule.
SPORES 70–85 μ, dark-grey or dark-brown, triangular-globular with finely crenulate wing 4–6 μ wide; distal face finely reticulate, forming 8–10 areolae across the diameter, areola 7–10 μ wide with thin and high ridge around the border, prominently papillate at the corners (Pl. 3.21, b); proximal face similar to distal one but less distinctly reticulate, triradiate mark prominent (Pl. 3.21, c).

RANGE: New South Wales, Western Australia, South Australia.

HABITAT on mud along creek bank, edge of water hole, always confined to places that flooded occasionally, annually.

TYPIFICATION There is no type specimens in Linnean Herbarium in London (S. Garside, 1957). Specimens identified as R. crystallina from Conservatoire et Jardin Botaniques Herbarium, Geneva, showed that they are a mixture of R. crystallina and R. cavernosa.

R. plana Tayl. Holotype: Western Australia, Swan River, W.J. Drummond, 1843 (K); isotype (MEL 19775).

DISCUSSION R. crystallina L. had been misidentified for a long time since there is no type specimen. The recent studies by Jovet-Ast (1964–65, 1967) clarified this species as well as R. cavernosa Hoffm. emend Raddi, two closely related species. Her discussion in some detail and her conclusions as to the specific characteristic are accorded here.


Fig. 3.21

*R. crystallina* L.

a. Transverse section of the thallus  x  20
b. Portion of transverse section  x  200
c. Portion of paradermal section  x  50
e. epidermal cell
g. photosynthetic cell
h. airchamber
PLATE 3.21

R. crystallina L.

a. Plant x 16
b. Spore, distal face x 730
c. Spore, proximal face x 730
Canada, Dufferin Co., Ontario, 10.8.1948 (G.13527); Europe, Coimbra, Moller, 5.1886 (G.13528); U.S.A., California, Dr. Bolander, No. 28, 9.1866 (G.13529); Coofre, Spathijs (G.13530); Odenwald, Erback (G.13531); Arabia Felix, G. Schweinfurt, 2.1889 (G.13532); Baden (G.13533); Glersdorf, Ulmy 35 (G.13534); T. Arcaugel, 4.1888 (G.13535); Keuruppi, Swamraerf, 9.1879 (G.13536); Keuruppi, G.W. Puarudloof, 28.1877 (G.13537); Treburg, G. Scunholz (96), 10.1882 (G.13538); Tonanz, O. Faup, 9.11.1900 (G.13539); Alger, Trabut, 1904 (G.13540); Pisa, Erbar, Gittogam Kal. 2.1861/62 (G.13541); Seine et Marne, Dr. Duclos, 10.20.1944 (G.13542); Dresden, 1855-1877 (G.13543); South America, Paraguari, 1882 (G.13544); U.S.A., Montana, P.W. Anderson, 10.1888 (G.13545); Europe, Schiteam, G. Schweinfurt, 2.1889 (G.13545).


(Types not seen)


R. tenllimi Gola Ibid.
GAMETOPHYTE monoeocious, usually forming a compact spongy rosette 10-25mm. diameter, bright green or yellowish green, sometimes tinged with red or purple colour on upper surface and at the edge of thallus; 5-7mm. long, 2-4mm. broad, 2-3 times broader than thick in transverse section (Fig. 3.22, a & b); upper surface cavernose, slightly channelled at the apex only.

BRANCHES (Pl. 3.22, a) shortly divided or if deeply divided then close together or overlapping each other; segment obconic or obconic-obleng; apex truncate or emarginate; margin thick, rounded. EPIDERMIS easily ruptured, almost completely disintegrating behind the apex (Pl. 3.22, a), air chambers appearing as 1-3 layers in transverse section (Fig. 3.22, c), basal part more compact (Fig. 3.22, d). ANTERIDIA and archegonia close to the apex; antheridial and archegonial necks not prominent. CAPSULES many, deeply embedded; 84-812 spores per capsule. SPORES 70-85 /μm, occasionally up to 100 /μm, yellow brown or dark brown. Transparent when not fully mature, triangular-globular with finely crenulate wing 4-6 /μm wide; distal face (Pl. 3.22, b) not reticulate but with the ridge bi-trichotomously branched, rarely forming areolae, proximal face (Pl. 3.22, c) with distinct triradiate ridge and roughened by high ridges but without definite areolae.

CHROMOSOME NUMBER n=8 Voucher: Western Australia, Glen Cummins, R.C. Carolin No. 6154, 8.19677(SYD).

RANGE: Palm Valley, Northern Territory, South Australia.

HABITAT: On mud along creeks or moist shady places, annual, occasionally flooded.

TYPOIFICATION: The type of R. cavernosa Hoffm. has not been traced. The existence of type specimens is doubtful.

R. multilamellata St.: Holotype Finke River, W.F. Schwarz, 8.1886 (G.12732); isotype (MEL 19779).

DISCUSSION: R. multilamellata St. in another species first described by Stephani. His description of the gametophyte and spores is quite unlike the type. From his type (G.12732 & MEL 19779), the spores are 100-120 /µ in diameter while in his description (Sp. Hep. I p. 373, 1900) the spore is only 60 /µ. He does not state any characteristic feature of R. multilamellata such as the air chambers which are usually exposed by rupture of the epidermis over each of them or the normal rosette habit usually tinged with red or purple. After comparing the type of R. multilamellata St. with the description of R. cavernosa Hoffm. emend Raddi (S. Jove-ast. 1964-65), Stephani's plant is doubtless R. cavernosa.

SPECIMENS EXAMINED: South Australia, Murray River, R. Schodde No. 512, 14.10.1957 (AD 27); Western Australia, Glen Cummins, R.C. Carolin No. 6154, 8.1967 (SYD); Northern Territory, Palm Valley, C. Na-Thalang No. 98, 15.8.1966 (SYD); Palm Valley, H. Allan Morrison, 25.7.1964 (MEL 19802); Emily Gap, J.H. Willis, 15.11.1965 (MEL 19799).

(2) Subgroup "R. papulosa" - thalli large 8-15mm. long, 2.5-6mm. broad. Spores ± 100 /µ.
FIG. 3.22

*R. cavernosa* Hoffm.

a,b. Transverse sections of the thallus,
   a. close to the apex,
   b. behind the apex,

(h). air chamber

(f). capsule  x 20

c. Portion of transverse section
   of the thallus  x 200

d. Portion of paradermal section
   of the thallus  x 200

(g) photosynthetic cell
PLATE 3.22

R. cavernosa Hoffm.

a. Plant x 16

b. Spore, distal face x 730

c. Spore, proximal face x 730

GAMETOPHYTE monoeocious, sometimes forming a rosette 30-50mm. diameter, whitish-green or green; thallus 8-15mm. long (up to 20 mm.), 2.5-5mm. broad, 2-4 times as broad as thick in transverse section; upper surface finely marked by airchannel areas; narrowly sulcate at apex, becoming broader and shallower towards the base, almost flat, pitted by archegonial and antheridial ostioles along the middle part of thallus. BRANCHES furcate or bi- or trifurcate; segment broadly oblong, or ovate-oblong; apex rounded or truncate; margin varied from thin and attenuate to acute. SCALES small, hyaline, present only under the apex. EPIDERMS persistent, slightly raised up over each airchannels; airpole small, surrounded by 4-7 hyaline cells; airchannels appearing as 2-3 layers in transverse section.

ANTHERIDIA arranged in 2 rows at both sides of ARCHEGONIA along the furrow; antheridial and archegonial neck slightly prominent. CAPSULE many, easily exposed by ruptured of upper surface along the channel with 132-372 spores per capsule. SPORE 100-140 μ, brown, almost rounded from distal face with or without wing; distal face finely reticulate forming 12-15 areolae across the diameter, areola 5-6 μ wide with a thick broad incompletely thickened border, ridges thick and short at the corners; proximal face with distinct triradiate mark or sometimes indistinctly mark.

CHROMOSOME NUMBER n=8, n=16.

RANGE: New South Wales, Victoria, Northern Territory.

HABITAT: among grass, seapage of rocks, in shady or open area.
DISCUSSION see R. spongiosa St.

23A. R. papulosa var. papulosa.
GAMETOPHYTE thallus 10–20mm. long, 3–5mm. broad, 3–4 times as broad as thick in transverse sections (Fig. 3.23A, a, b & c). BRANCHES (Pl. 3.23A, a) furcate or bifurcate, divergent; segment broadly oblong or ovate-oblong; apex rounded or truncate; margin thin, slightly undulate, attenuate. EPIDERMIS persistent, slightly raised up over each areolam; air pore small, surrounded by 4–7 hyaline cells in 1–2 series with 6–7 cells between each air pore (Fig. 3.23A, f); air chambers narrow, (Fig. 3.23A, d), appearing as 2–3 layers in transverse section. CAPSULES many, 4–6 in a segment, easily exposed by ruptured of upper surface along the channel; 160–372 spores per capsule. SPORES 100–140 μ, brown, almost rounded from distal or proximal face with crenulate wing 2–3 μ wide; distal face (Pl. 3.23A, b) reticulate forming 12–15 areolae across the diameter, areola 5–6 μ diameter with a thick but incomplete border, ridges thick and short; proximal face (Pl. 3.23A, c) faintly marked into areolae; triradiate mark distinct.
RANGE: New South Wales, Victoria.
HABITAT: Among grass, seapage of rocks or in shady areas. TYPIFICATION: R. papulosa St. Holotype.
Fig. 3.23-A

*R. papulosa St. var. papulosa*

a,b,c. Transverse sections of the thallus from younger to older parts \( \times 20 \)

d. Portion of transverse section of the thallus,

(e) epidermal cell

(g) chlorophy bearing cells

(h) airchamber \( \times 50 \)

Portion of the epidermis

(e) epidermal cell

(p) airpore \( \times 134 \)
PLATE 3.23A

*R. papulosa* St, var. *papulosa.*

a. Plant x 4
b. Spore, distal face x 730
c. Spore, proximal face x 730
SPECIMENS EXAMINED: Victoria: Graytown, J.H. Willis, 8, 1939; New South Wales: Bullio, O. Na-Thalang No. 26, 11.7.1966 (SYD); Barralier, O. Na-Thalang No. 42, 12.7.1966 (SYD); Hickey’s Waterfall, Goonabarabran, O. Na-Thalang No. 203, No. 206, 25.3.1967 (SYD); 42½ miles from Goonabarabran, O. Na-Thalang No. 213, 26.3.1967 (SYD); Tunmallallee, O. Na-Thalang No. 224, 226, 26.3.1967 (SYD); Jerricknorra Creek, R. Selkirk, 14.8.1967 (SYD); Nattai River, R.C. Carolin No. 5416, No. 5417, 3.10.1966 (SYD).

23B. R. papulosa var. variabilis var. nov.

Monoecos. Thallus variabilimus. 8-15mm. longus, 2.5-3.5mm. latus pagiana dorsali anguste sulcata nitida Ramii radiati unoquoque segmento anguste oblongo obtuso vel rotundo acuto vel nonnullum attenuato ad marginem. Sporae ssepe sinu ala.

GAMETOPHYTE thallus 8-15mm. long, 2.5-3.5mm. broad, 2-3 times as broad as thick in transverse section (Fig. 3.23B, a, b & c). BRANCHES (Pl. 3.23B, a) bi-trifurcate, deeply divided; segment oblong; apex obtuse or rounded; margin acute. EPIDERMIS not raised up over airchambers; airpore small, surrounded by 4 hyaline cells with 2-5 epidermal cells between each airpore (Fig. 3.23B, e); airchambers narrow, 20-24 across the width of the thallus (Fig. 3.23B, d), appearing as 2-3 layers in transverse section.

CAPSULES single or two together, 2-4 in a segment, slightly prominent on ventral surface; 156-244 spores per capsule. SPORES 100-115 /µ, brown to dark brown, almost rounded from distal or proximal face; wing very narrow and often absent; distal face (Pl. 3.23B, b) similar to that of var. papulosa; proximal face (Pl. 3.23B, c) rather
distinctly reticulate, occasionally with short and thick ridges; triradiate mark distinct.

**CHROMOSOME NUMBER** n=8  **Voucher:** Northern Territory, West El Sharana, O. Na-Thalang No. 294, 29.1.1969 (SYD);
Darwin, Harbour, O. Na-Thalang No. 265, 21.1.1969 (SYD);
Woolner Road, O. Na-Thalang No. 274, 22.1.1969 (SYD);
Darwin River, O. Na-Thalang No. 279, 24.1.1969 (SYD);
Stuart Highway, O. Na-Thalang No. 300, 29.1.1969 (SYD);
South Pinkerton Ranges, R.C. Carolin No. 6677, 11.5.1968 (SYD).

**RANGE:** Northern Territory.

**HABITAT:** growing on sandy soil, swamp, granite soil along stream bank, rather open area.

**TYPOIFICATION:** *R. papulosa var. variabilis*  **Holotype:**
Northern Territory, South of Darwin, ca. 150 miles on Stuart Highway, O. Na-Thalang No. 300, 29.1.1969 (SYD).

**DISCUSSION:** The vegetative character of *R. papulosa var. variabilis* is very varied under different environmental condition. In the dry state the thallus narrow and thick, yellowish-green or whitish-green; but in the moistened state the thallus is thinner, margin gradually winged, green and less shining. The spore characters resemble that of var. *papulosa* in every aspect except the wing which is normally absent in the type variety. Its thallus is smaller and the haploid chromosome number is eight. This seems very likely that the diploid *R. papulosa* may arise from the haploid variety.

**SPECIMENS EXAMINED:** Northern Territory, Pinkerton Range, Timber Creek, R.C. Carolin No. 6677, 11.5.1968 (SYD);
and also chromosome voucher in loc. cit.
Fig. 3.23B.

R. papulosa var. variabilis.

a, b, c. Transverse sections of the thallus from younger to older parts x 10

d. Portion of the transverse section of the thallus showing alveolombers x 50

e. Portion of the epidermis

ch = chlorophyll bearing cell
ep = epidermal cell
p = air pore x 100
PLATE 3.23B.

*R. papulosa* var. *variabilis.*

a. Plant x 4

b. Spore, distal face x 730

c. Spore, proximal face x 730
24. *R. spongiosa* St. in litt. ad Dr. Levier, 1906.
Sp. nov.

Monoica gregaria, viridis vel alba-viridis.
Thallus 10-12mm. longus, 4-6mm. latus, spongiosus, carnosus; pagina superior anguste profundeque caniculata ad apicem sed latior et planior ad basin ocellulis aeris distincte manifestis. Rami singulares vel furcati plus minusve divergentes; segmenta late obcuneata vel obovato-oblonga apice trunciato vel late obtuso plerumque bilobato; margo acutus plus minusve attenuatus. Cavemula aeris profunde inclusa. Sporae 100-130 μ latae fuscae triangulo-globulares ala 7-8 μ lata; superficies distalis regulatim reticulata areolis 6-8 diametro; superficies proximalis crista triradiata indistincta.

GAMETOPHYTE monoeious, in gregarious patches, green or whitish-green; thallus 10-12mm. long, 4-6mm. broad, fleshy and spongy, 2-3 times as broad as thick in transverse section (Fig. 3.24, a, b & c); upper surface with distinct end large aircambrer areas (Pl. 3.24, a); channel narrow and deep at the apex, becoming broader and almost flat towards the base, pitted by archegonial and antheridial ostioles. BRANCHES (Pl. 3.24, a) single or furcate, slightly divergent; segment broadly obcuneate or obovate-oblong; apex truncate or rounded, usually bilobed; margin flat, acute, slightly attenuate. SCALES hyaline, small, present only under the apex. EPIDERMIS raised up over aircambrer, easily ruptured in older parts, exposing the whole chamber; airpore surrounded by 6-8 thin and hyaline cells in 1-2 series, with 6-10 epidermal cells between each pore (Fig. 3.23, d); aircambrer large and
high (Fig. 3.23, f) appearing as 1-2 layers in transverse section. ANtheridia along both sides of archegonia which are in 1-2 rows along the furrow; antheridal and archegonial necks not prominent. CAPSULES many 3-8 in each segment deeply embedded in the thallus, hardly visible from upper surface; 346-708 spores per capsule. SPORES 100-130 /μ, brown, triangular-globular with crenate wing 7-8 /μ wide; distal face (Pl. 3.24, b) regularly reticulate forming 6-8 areolae across the diameter; each areola 14-20 /μ wide with thin and incomplete thickening border, ridges high and thick at the corners of areola; proximal face (Pl. 3.24, c) with triradiate ridge, the rest indistinctly roughened. CHROMOSOME NUMBER: n=8 Voucher: New South Wales, Cox's River, D. Black (O. Na-Thalang No. 198), 12.3.1967 (SYD); Prospect Reservoir, O. Na-Thalang No. 239, 15.6.1967 (SYD). RANGE: New South Wales. HABITAT: Open grassland. TYPIFICATION: R. spongiosa St. Holotype: New South Wales, Jubbul, W.W. Watts 144, 22.7.1903 (NSW H.97). DISCUSSION: R. spongiosa is one of the two largest Riccia species in Australia. This species was first named by Stephani in his letter to Dr. Levier and in his unpublished drawings. (Incote Hepaticarum IV p.388, fig. 14). There is no capsule in the type material, but the character of the gametophyte is quite different from others in having a clearly marked upper surface which is usually cavernose and resembles a honey-comb, thallus single or furcate rarely bifurcate. Its closest affinity is with R. papulosa St. which has thimer, usually furcate or bifurcate thallus, smaller aircamber
FIG. 3.24.

*R. spongiosa* St.

a,b,c. Transverse sections of the thallus

from younger to older parts $\times$ 20.

d. Portion of the epidermis

(a) epidermal cell

(p) airpore $\times$ 134

f. Portion of transverse section of the thallus

(e) epidermal cell

(h) airchamber

(g) photosynthetic cell $\times$ 200
PLATE 3.24.

*R. spongiosa* St.

a. Plant  x  4

b. Spore, distal face  x  730

c. Spore, proximal face  x  730
and rather persistent epidermis. The characters of the spores are completely different: *R. spongiosa* has a triangular-globular spore, 6-7 areolae across the diameter but in *R. papulosa* the spore is rather rounded with 12-15 areolae. The haploid chromosome number of *R. spongiosa* is 8 while that of *R. papulosa* is 16.

**SPECIMENS EXAMINED**: New South Wales: Picton, Razor-back Ridge, O. Na-Thalang No. 31, 11.7.1966 (SYD); Jomah Creek, O. Na-Thalang No. 69, 12.7.1966 (SYD); Cox's River, D. Black (O. Na-Thalang No. 198), 12.3.1967 (SYD); Prospect Reservoir, O. Na-Thalang No. 239, 15.6.1967 (SYD); Corowa, D. Black (O. Na-Thalang No. 256), 3.9.1967 (SYD).

(3) Subgroup "*R. vesiculosa*" - thalli 5-10mm. long (rarely up to 15mm.) 2-3mm. broad. Spores 75-85 μ.


**GAMETOPHYTE** monoeocious, bright green or yellowish-green occasionally developed bluish-purple colour in older parts, in large patches or forming an incomplete rosette; thallus 8-15mm. long, 3-4mm. broad, 4-5 times as broad as thick in transverse section (Fig. 3.25, a, b, c & d); upper surface clearly marked out by airohambor areas; channel deep and narrow at apex, shallower and faintly marked elsewhere, pitted by archegonial & antheridial necks.

**BRANCHES** (Pl. 3.25, a) single or furcate, rarely bifurcate, very divergent; segment oblong with rounded or truncate apex, or shortly bilobed; margin acute, gradually attenuate, slightly undulate. **SCALES** many and rather large (Fig. 3.25, g), hyaline or bluish-purple, slightly
overlapped, join with the margin. **EPIDERMIS** slightly raised up over air chambers, persistent; airpore surrounded by 4–6 hyaline cells, about 5–7 epidermal cells between each pore (Fig. 3.25, f); air chambers apparently 2–3 layers in transverse section, about 20 across the thallus (Fig. 3.25, c). **ARCHEGONIA** in single or alternate row along the furrow with antheridia at both sides; antheridial and archegonial necks prominent. **CAPSULES** single or two together, deeply embedded, exposed by rupture of tissue over it in older parts; 432–560 spores per capsule. **SPORES** 70–85 μ, rarely up to 100 μ, yellow brown, irregular in form with crenate wing 4–6 μ wide; distal face (Pl. 3.25, b) regularly reticulate forming 7–9 angular areolae across the diameter, each 10–15 μ wide, the border of areola thin and low sometimes incomplete, raised up at the corners; proximal face (Pl. 3.25, c) with distinct triradiate ridge, the rest being roughened by less distinct areolae and scattered high ridges.

**CHROMOSOME NUMBER** n=8 Voucher: New South Wales, Berkshire Park, O. Na-Thalang No. 10, 21.6.1966 (SYD); Jibbon Head, National Park, O. Na-Thalang No. 130, 3.9.1966 (SYD); Coolemen Creek, O. Na-Thalang No. 186, 21.1.1967 (SYD).

**RANGE:** New South Wales.

**HABITAT:** Among moss, grass, on creek banks or on seepage of rock; rather moist and shady areas.

**TYPIFICATION:** A request for the type material at Geneva has resulted in neither of the syntypes being located. Since this species is so distinctive in the features of the upper surface of the thallus and the margin, even Stephani's description of "alis tenerrimis,..........., ob
FIG. 3.25.

*R. muscicola* St.

a, b, c, d. Outline of transverse sections of the thallus from younger to older parts x 20

f. Portion of the epidermis,

(e) epidermal cell

(h) airpore  x 134

g. Scale  x  50
156.
PLATE 3.25
R. muscicola St.

a. Plant x 4

b. Spore, distal face x 730

c. Spore, proximal face x 730
lamellas perlucentes pulchre reticulatis" indicates that he was dealing with the species under discussion here.

**DISCUSSION**: From Stephani's unpublished drawings (Incone Hep. Vol. IV, p. 372, fig. 1) of *R. muscorica*, it is very similar to the specimens O. Na-Thalang No. 186 but in his description "Sporae 60 µ, late alatae, dense lamellatae, lamellis reguliter remosis, ad retum, seape interruptum confluentibus" does not agree with his drawing.


**GAMETOPHYTE** monoecious, in compact patches, pale green or whitish-green; thallus 9-12mm. long, 3-4mm. broad, 3-4 times as broad as thick in transverse section. (Fig. 3.26, a, b & c), upper surface spongyose with distinct airchamber area at apex; channel narrow at apex, broader and almost flat towards the base.

**BRANCHES** (Pl. 3.26, a) furcate or bifurcate, divergent; segment oblong or obovate-oblong, usually broadened at the place where the developing capsules are present; apex usually bilobed, rounded; margin obtuse. **SCALES** small, hyaline, rare. **EPIDERMIS** almost hyaline, shining, with a few chloroplasts, not raised up over airchambers;
airpore surrounded by 4 cells, with 6-7 epidermal cells between each pore (Fig. 3.26, d); airchambers 15-20 across the breadth of the thallus, apparently 2-3 layers in transverse section (Fig. 3.26, c). ANTHERIDIA at both sides of archegonia along the furrow; antheridial necks prominent. CAPSULES numerous 4-8 in a segment, tissue over it usually spongiosely, easily exposed; 432-740 spores per capsule. SPORES 60-85 µ, brown, triangular-globular with crenate interrupted wing 2 µ wide; distal face (Pl. 3.26, b) regularly reticulate forming 6-7 areolae across the diameter, each areola 7-8 µ wide; the border of areola thin, incomplete thickening, slightly raised up at the corners; proximal face (Pl. 3.26, c) forming faint and rounded areolae with broad borders, triradiate ridge indistinctly marked.

CHROMOSOME NUMBER n=8 Voucher: Central Australia, Mt. Olga, C. Na-Thanlang No. 90, 11.8.1966 (SYD); Western Australia, Poison Creek, R.C. Carolin No. 5827, 8.1967 (SYD).

RANGE: Southern Australia, Northern Territory.

HABITAT: along pool or creek banks and on rock seepage.

TYPIFICATION: R. deserticola St. Holotype - South Australia, Arco-eillina Well, R. Helms, 27.5.1891 (AD 48); isotype (MEL 19766).

DISCUSSION: R. deserticola St. is very close to R. crassa St. but the thallus surface is not shiny and less cavernous, the spores are smaller with smaller areolae on the distal face than those of the latter.

SPECIMENS EXAMINED: South Australia, Eversrd Range, D.J.E. Whibley No. 1137, 14.9.1963 (AD 45); Northern Territory; Mt. Olga, C. Na-Thalang, No. 90, 11.8.1966 (SYD); Alice Springs, R.C. Carolin No. 5076, 2.8.1966
FIG. 3.26

*R. deserticola* St.

a, b, c. Transverse sections of the thallus from younger to older parts x 20

d. Epidermis, (e) epidermal cell,
(p) air pore x 134

_R. deserticola St._

a. Plant x 16

b. Spore, distal face x 730

c. Spore, proximal face x 730

GAMETOphyte monoecious, green, forming complete or incomplete rosette, sometimes in gregarious patches; thallus 6–12 mm. long, 2.5–3 mm. broad, 2–3 times as broad as thick in transverse sections (Fig. 3.27, a, b & c); upper surface marked out into air chamber areas at apex, shiny; the rest pitted by enlarged air pores (Pl. 3.27, a), narrowly sulcate at apex, almost flat towards the base. BRANCHES furcate, hardly bifurcate, shortly bilobed; segment obtuse-oblong; apex obtuse or rounded, margin thick, obtuse. SCALES small, hyaline, rare, present only under the apex. EPIDERMAL CELLS 3–4 between each air pores; air pores becoming large behind the apex (Fig. 3.27, e & f); air chambers large (Fig. 3.27, d) about 20 across the width of the thallus. ANThEридIA and ARCHEGONTIA close to the apex, antheridial and archegonial necks slightly prominent. CAPSULES 2–3 in a segment, 152–344 spores per capsule. SPORES 70–90 /μ, brown or dark-brown, triangular-globular; wing rather smooth 4–5 /μ wide with 3 marginal poles; distal face with 6–8 incomplete areolae across the diameter, ridges irregular, but prominent (Pl. 3.27, b); proximal face faintly marked out or sometimes with indistinct ridges, triradiate mark not prominent (Pl. 3.27, c).

CHROMOSOME NUMBER n=8 Voucher: South Australia, near Port Augusta, 0. Na-Thalang No. 102, 18.8.1966 (SYD).
FIG. 3.27

*R. crassa St.*

a, b, c. Outline of the transverse sections of the thallus from younger to older parts x 20

d. Portion of the transverse section of the thallus

e. Portion of the epidermis near the apex

f. Portion of the part
PLATE 3.27

R. crassa St.

a. Plant x 16

b. Spore, distal face, x 730

d. Spore, proximal face, x 730

c. Spore, optical section, :
RANGE: South Australia.
HABITAT: on mud, at the edge of well.

TYPIFICATION: R. crassa St. Holotype: South Australia, Arkariaga, R. Helms, 15.5.1891 (G. 12729).
R. crassa St. isotype: (MEL 19765); (AD 47)

DISCUSSION: see R. deserticola St.

SPECIMENS EXAMINED: see chromosome voucher.


Nom. syn.: R. bullosa var. vesiculosa Carr. et P.

GAMETOPHYTE monocious, forming a complete rosette or incomplete rosette 20-40mm. diameter or usually in gregarious patches, green or silvery green; thallus 5-7mm. long, 2.5-3.5mm. broad, 3-4 times as broad as thick in transverse section (Fig. 3.28, a, b, c & d); upper surface clearly marked out with airchannel areas; channel deep and narrow at the apex; becoming shallower and almost flat towards the base, pitted by archegonial and antheridial necks. BRANCHES (Fl. 3.28, a) furcate or bifurcate, divergent; segment obcuneate-oblong or obovate-oblong; apex rounded or truncate; margin rounded and waved. SCALES small and hyaline, present on ventral side and close to the apex only. EPIDERMIS raised up over airchannel, about 4-6 cells between each air pore, 5-8 cells around the pore and hyaline (Fig. 3.28, f); airchambers about 20 in the breadth of the thallus apparently 3-4 layers in transverse section (Fig. 3.28, d).

ARCHEGONTIA in a single row between antheridia along the furrow; antheridial necks slightly prominent.
CAPSULES many 3-4 in a segment, with spongy tissue over it, easily exposed; 308-392 spores per capsule.
SPORES 55-75 μ, dark brown, almost triangular-globular with crenate or crenulate wing 3-4 μ wide; distal face (Pl. 3.28, b) finely reticulate forming 8-9 areolae across the diameter, each areola 6-8 μ wide, the border of areola thin with high ridges at the corners; proximal face (Pl. 3.28, c) with distinct triradiate ridge but more finely reticulate than distal face without high ridge, areola about 4 μ diameter.


RANGE: New South Wales, Queensland.

HABITAT: On mud creeks or in swamp.

TYPIFICATION: R. vesiculose Carr. et P. Holotype: New South Wales, Parramatta, Whitelegge, 8.1885 (NSW H.87); isotype (SYD TW/2).

DISCUSSION: The characters of spore described here are from the new material (O. Na-Thalang No. 2), owing to the absence of spores from the type material. The proximal face of the spore separates this species from others.

SPECIMENS EXAMINED: New South Wales: Parramatta Lake, O. Na-Thalang No. 2, 21.6.1966 (SYD); Badgerys Creek, O. Na-Thalang No. 234, 15.6.1967 (SYD); Lake Parramatta, O. Na-Thalang No. 247, 15.6.1967. (SYD); Tummallallee Creek, O. Na-Thalang No. 212, 26.3.1967 (SYD); Queensland, J. Keys 156 (MEL 19771); Northern Territory, Darwin, Rapid Creek, O. Na-Thalang No. 327 (SYD); Robin Water. Fall, O. Na-Thalang No. 285, 26.1.1969 (SYD); East Alligator River, R.C. Carolin No. 6879, 16.5.1968 (SYD).
FIG. 3.26

*R. vesiculosa* Carr et P.

a, b, c, & d. Transverse sections of the thallus from younger to older parts x 20

g. Portion of the epidermis,

(e) epidermal cell,

(p) air pore x 134
R. vesiculosa Carr. et P.

a. Plant  x  16

b. Spore, distal face  x  720

c. Spore, proximal face  x  730


**GAMETOPHYTE** monocious, in gregarious patches, green; thallus 5–10mm. long, 2–2.5mm. broad, 2–3 times as broad as thick in transverse section (Fig. 3.29, a, b, c, d); upper surface almost flat, not clearly marked out by airchamber area, narrowly sulcate throughout (Pl. 3.29, a). **BRANCHES** furcate or bifurcate, divergent; apex rounded or truncate; margin acute, gradually attenuate. **SCALES** small, hyaline, present only under the apex. **EPIDERMIS** not raised up over airchamber, airpore surrounded by 3–4 hyaline cells with 2–3 epidermal cells between each pore (Fig. 3.29, e & f); airchamber narrow, about 20 across the width of the thallus. **ANtheridIA** and **ARCHegONIA** arranged in 1–2 rows along the furrow, antheridial and archegonial necks not prominent. **CAPSULES** 2–5 in a segment, prominent on ventral surface; 84–228 spores per capsule. **SPORES** 60–70 μ, light brown to dark brown, triangular-globular or irregular shape; wing 3–4 μ wide, crenulate; distal face reticulate forming 6–8 areolae across the diameter, each areola 6–7 μ wide with thin and high border, papillate at the corners (Pl. 3.29, b); proximal face clearly reticulate areola 4–5 μ wide, sometimes with high ridges, tri-radiate mark distinct (Pl. 3.29, c).

**CHROMOSOME NUMBER** m=8 Voucher: Northern Territory, Mt. Bundey, O. Na–Thalang No. 271, 22.1.1969 (SYD).

**RANGE:** Northern Territory.
HABITAT: In grassland and on mud.

**TYPOIFICATION**: *R. junghuhniana* Nees & Lindenb.,
Holotype: Java, Junghuhn (STR).


**DISCUSSION**: *R. junghuhniana* was considered as an intermediate species between subgenus *Riccia* and *Ricciella* because of its narrow air chambers. This is not quite correct if the two subgenera are separated by the size of air chambers. The characteristics of the air chambers the pores and the epidermal cells should be considered more important than the size, and for *R. junghuhniana*, it certainly belongs to subgenera *Ricciella*.

In 1958, Meijer described a new species *R. applanata* which is in fact similar to *R. junghuhniana*. The thallus of *R. applanata* is not as big as Meijer mentioned. It is more or less the same size as *R. junghuhniana*, and its spores are not different from the latter; therefore, *R. applanata* Meijer is reduced to be a synonym of *R. junghuhniana*.

**SPECIMENS EXAMINED**: see chromosome number and typification; and.
FIG. 3.29.

*R. funghuhniana* Nees et Lindenb.

a, b, c, & d. Transverse sections of the thallus from younger to older parts x 10

e. Portion of the transverse section of the thallus x 50

f. Epidermis x 10

ep = epidermal cell

p = airpore

ch = chlorophyll bearing cell
PLATE 3.29.


a. Plant x 4

b. Spores, distal face x 730

c. Spores, proximal face x 730
30. R. collata. Sp. nov.

Dioces. Planta feminea gregaris vel rosularis. Thallus 5-8 mm. longus, 1.5-3 mm. latus. Segmenta elliptico-oblunga vel anguste oblonga apice acuto vel obtuso marginibus, acutis ascendentibus. Cavemula aeria 15-20 parva in latitudine thalli. Squamae + grandes, hyalinae non ad marginem extensae. Planta mascula quam femina parvior dispersa antheridiis in seriebus duabus secus medium thalli collis longis persistentibus ex foes profundis emergentibus. Sporae 70-85 μ, latae fuscae, triangulare-globulares ala 5-6 μ lata. Areolae regulares 10-12 μ latis cristis eunibus plerumque imperfectis prominentibus ad angulos insidentibus superficie distali; superficies proximalis crista triradiata distincta.

GAMETOPHYTE dioecious. FEMALE plant (Pl. 3.30, a) forming a rosette or in gregarious patches, whitish-green; thallus 5-8 mm. long, 1.5-3 mm. broad, 1-2 times as broad as thick in transverse section (Fig. 3.30, a, b, c); upper surface with distinct airchamber areas but only at the apex and the margins, median region usually spongiosa; channel narrow and shallow, ending at the place where developing capsule present. BRANCHES (Pl. 3.30, a) furcate or bifurcate, divergent; segment elliptical-oblung, or narrowly oblong with acute to truncate apex; margin acute, ascending. SCALES (Fig. 3.30, k) hyaline or purple, at both lateral-ventral sides not overlapping each other. EPIDERMIS not raised up over airchamber, smooth, shining, air pore surrounded by one layer of 4-5 hyaline cells with about 4 epidermal cells between each pore (Fig. 3.30, i); about 15-20 air chambers
across the breadth of the thallus (Fig. 3.30, o), apparently 1-2 layers in transverse section.

Archegonia in 1-2 rows along the furrow, necks not prominent. Male plant (Pl. 3.30, b) scattered, whitish-green or purplish-green, 5-7 mm long, 1.5-2.5 mm broad, almost as thick as broad in transverse section (Fig. 3.30, g, h & i); upper surface with distinct air chamber areas at the apex, the rest of the thallus honey-comb like; channel short, narrow and deep at the apex, behind that pitted by antheridial necks throughout the thallus.

Epidermal cells present only close to younger parts, not raised up over air chamber, soon rupturing, exposing the whole air chamber of which there are about 20 across the breadth of the thallus (Fig. 3.30, i).

Antheridia numerous, arranged in 2 rows along the median line, neck long and prominent, hyaline or purple, persistent, emerging from a large pit. Capsules deeply embedded in the thallus, with spongy tissue over it; 265-365 spores per capsule. Spores 80-85 µ, brown, triangular-globular or almost globular with a slightly crenate wing 5-6 µ wide; distal face (Pl. 3.30, c) regularly reticulate, 7-8 areoles across the diameter; each areola 10-12 µ wide with a thin usually incomplete border, which raised up at the corners; proximal face (Pl. 3.30, d) with distinct triradiate ridge, otherwise roughened by a faint suggestion of areoles or sometimes with scattered low ridges.


Range: New South Wales, Northern Territory.

Habitat: Rock seepage or in Pilliga Scrub.
FIG. 3.30.

R. collata, sp. nov.

a, b, & c. Transverse sections of the thallus (female plant) from younger to older parts x 20

g, h, & i. Transverse sections of the thallus (male plant) from younger to older parts x 20

j. Portion of epidermis,
   (e) epidermal cell
   (p) air pore x 134

k. Scale x 50
PLATE 3.30.

R. collata sp. nov.

b. Male plant x 12.5

c. Female plant x 5

c. Spore, distal face x 730

d. Spore, proximal face x 730
TYPIFICATION: Holotype – New South Wales, Tummallallee, O. Na-Thalang No. 220, 26.3.1967 (NSW); isotype (SYD).
DISCUSSION: R. collata is the other dioecious species in the subgenus Ricciella in Australia. It is easy to distinguish from others by the male plant which has long and prominent antheridial necks.

R. rubricollis S. Garside shows the closest affinity, but the thallus of the latter is larger 15mm. long, 4mm. broad, the male plant has 1 row of antheridia and the spores have larger areolae (4–5 areolae across the diameter).

SPECIMENS EXAMINED: New South Wales, Gunnamulla, J. Jacob (O. Na-Thalang No. 22), 3.5.1966 (SYD) and chromosome voucher, Northern Territory, near Daly Water, O. Na-Thalang No. 315, 4.2.1969 (SYD).


31. R. limicola sp. nov.

GAMETOPHYTE dioecious, forming incomplete rosette soon becoming gregarious, pale green or yellowish-green; thallus 6-12mm. long, 1-2mm. broad, 3-4 times as broad as thick in transverse section (Fig. 3.31, a, b); upper surface finely marked out into airchamber areas, narrowly sulcate throughout the thallus in female plant but almost flat in male plant (Pl. 3.31, a, b). BRANCHES multifurcate; segment obconical-oblong or oblong, apex truncate, margin acute, attenuate, undulate. SCALES small, hyaline, 1-2 under the apex. EPIDERMIS slightly raised up over airchambers; airpore small, surrounded by 4 hyaline cells; airchambers 12-16 across the width of the thallus (Fig. 3.31, a). MALE PLANT with 1-2 rows of antheridia along the middle part of thallus, antheridial necks slightly projecting above the thallus surface from rather large pits which are continuous throughout the segment (Pl. 3.31, a). FEMALE PLANT almost the same size as the male one, archegonial neck not prominent, thallus broadened at the capsule position (Pl. 3.31, b). CAPSULE single, 1-2 in a segment, bulging out on ventral surface similar to those of R. fluitans-complex group; 178-194 spores per capsule. SPORES 64-85 μ, yellowish-brown or brown, triangular-globular or almost rounded from distal or proximal face; wing crenulate, 3-4 μ wide; distal face reticulate forming 8-10 areolae across the diameter, each areola 6-7 μ wide with thin and high border, papillate at the corners (Pl. 3.31, c); proximal face similar to the distal one, triradiate mark rather distinct (Pl. 3.31, d). CHROMOSOME NUMBER n=8 Voucher: Northern Territory, South Katherine, O. Na-Thalang No. 321, 5.2.1969 (SYD).
FIG. 3.31.

*R. limicola, sp. nov.*

a, b. Transverse sections of the thallus x 50
   a - female plant
   b - male plant

c. Portion of the epidermis x 200
   ep = epidermal cell
   p = air pore
PLATE 3.31.

*R. limicola, sp. nov.*

a. Plant x 4
b. Male plant x 25
c. Female plant x 25
d. Spore, Distal face x 730
e. Spore, proximal face x 730
RANGE: Northern Territory.

HABITAT: at the edge of swamp, among grass.

TYPOIFICATION: R. limicola O. Na-Thalang sp. nov.

Holotype: Northern Territory, ca. 5 miles South of Katherine, O. Na-Thalang No. 321, 5.2.1969 (SYD).

DISCUSSION: R. limicola seems to be the largest species among the fertile "R. fluitans-complex" group and it is dioecious. The other dioecious species of this group is probably R. canaliculata Hoffm. which differs from the former in the smaller size of thallus and spores are larger ± 100 μ with only 3-4 areolae across the diameter, areola 20-25 μ wide with a protruberance in the centre.

R. limicola shares some vegetative characters with R. frostii Aust. in being dioecious and in the habit of growing on mud, but the latter has different sizes of male and female plants; antheridia in many rows; upper surface cavernous; capsule not prominent on ventral surface; and spores not forming definite areolae.

SPECIMENS EXAMINED: see Typification.


GAMETOPHYTE monocious, forming a rosette or in crowded irregular patches, green; thallus 10-15mm. long, ± 1mm. broad; upper surface not clearly marked out into siphonema areas, narrowly sulcate at the apex, the rest of the thallus almost flat. BRANCHES
multifurcate, divergent; segment obovate-linear, becoming linear or strap-like towards the older part; apex obtuse or rounded; margin obtuse or rounded. SCALES small, not separating into two by the growth of the ventral part of the thallus, hyaline, rare, one or two on ventral side of the first segment. ANTERIDIA single, normally only one in a segment. ARCHEGONTA single, archegonial neck not prominent. CAPSULES single, prominent on the ventral side of the thallus; 60-140 spores per capsule. SPORES 70-85 \(\mu\) (up to 100 \(\mu\)) brown; triangular-globular, distal and proximal faces reticulate.

CHROMOSOME NUMBER \(n=16\).

RANGE: New South Wales, Northern Territory.

HABITAT: In standing water, muddy soil, creek bank or swampy area.

TYPIFICATION: The type of \(R.\) duplex Lorb. has not been seen, but Müller's description is adequate to decide that the Australian specimens are conspecific.

32A. \(R.\) duplex var. duplex.

GAMETOPHYTE Thallus 10-15 mm long, ± 1 mm broad, 2-3 times as broad as thick in transverse section (Fig. 3.32A, a, b, & c). BRANCHES multifurcate; segment obovate-linear (Pl. 3.32A, a). EPIDERMIS not raised up over aircambers; aircamers small, surrounded by 3-4 hyaline cells (Fig. 3.32A, d); aircambers 8-12 across the width of the thallus (Fig. 3.32A, a, b & c). CAPSULE single, with 60-140 spores per capsule. SPORES 70-85 \(\mu\), rarely up to 100 \(\mu\), triangular-globular, wing crenulate 4-6 \(\mu\) wide with 2-3 enlarged marginal angles; distal face (Pl. 3.32A, b) forming
FIG. 3.32 A.

*R. duplex var. duplex.*

a, b, & c. Transverse sections of the thallus from younger to older parts x 100

d. Portion of the epidermis x 400

ep = epidermal cell

p = air-pore
PLATE 3.32 A

*R. duplex* Lorh. var. *duplex*.

a. Plant  x  27.5

b. Spore, distal face  x  730

c. Spores, proximal face  x  730
6-7 rather angular areolae across the diameter; areola 10-20 \( \mu \) wide, the central one occasionally larger than the outer; border of areola complete and highly raised up at the corners; proximal face (Pl. 3.32A, o) finer reticulate, areolae 6-7 \( \mu \) wide; triradiate mark distinct.

**CHROMOSOME NUMBER:** \( n=16 \)  
**Voucher:** New South Wales, Jomah Freek, Barralier, O. Na-Thalang No. 66, 12.7.1966 (SYD); Lake Parramatta, O. Na-Thalang No. 56, 21.6.1966 (SYD); Jibbon Head, O. Na-Thalang No. 129, 3.9.1966 (SYD); Lake Parramatta, O. Na-Thalang No. 246, 15.6.1967 (SYD).

**RANGE:** New South Wales.

**TYPIFICATION:** *R. duplex* Lorb.

**DISCUSSION:** *R. duplex* Lorb. is one of the species in the "*R. fluitans-complex" group having a haploid chromosome number of 16 besides *R. zhenana* Lorb. which is always sterile. Its spores are slightly different from the others in having rather large and distinct areolae. It is very hard to differentiate the plants of this group, unless the chromosome numbers can be counted and the plants grow under the same conditions. The examination of the spore characters must be at the fully matured stage, for in the younger stages they seem to be the same (see Table 3.1 for comparison between species and varieties).

**SPECIMENS EXAMINED:** in loc. dit. chromosome voucher.

32B. *R. duplex var. megaspora var. nova.*

Monoecia. Sporae \( \pm 100 \ \mu \) crenulata et plerumque interruptae ad angulum; areolae 6-9 \( \mu \) latae
complete vel incomplete 9-10 in diametro superficie
distalis, crista irregularis. Superficies proximalis
reticulata sine crista alitis: nota triradiata indistincta.

GAMETOPHYTE the same as R. duplex var. duplex.
CAPSULE with 60-116 spores per capsule. SPORES 85-106 /\mu
(mostly 100 /\mu), brown, triangular-globular, almost
circular when observe from distal or proximal face; wing
orenulate 3-4 /\mu wide, expand at the marginal angle and
usually interrupted (Pl. 3.32B, b) distal face reticulated
forming 9-10 complete or incomplete areolae across the
diameter, each areola 6-9 /\mu wide, border of areola thin
and incomplete, ridges irregular (Pl. 3.32B, a), proximal
face clearly reticulate, areola more or less the same
size as the distal ones, triradiate mark indistinct
(Pl. 3.32B, c).

CHROMOSOME NUMBER n=16 Voucher: Northern Territory, East
Alligator River, R.C. Carolin No. 6880, 15.5.1968 (SYD).
RANGE: Northern Territory.
HABITAT: Margin of lagoon.
TYPIFICATION: R. duplex var. megaspora Holotype:
Northern Territory, East Alligator River, R.C. Carolin
No. 6880, 15.5.1968 (SYD).
DISCUSSION: R. duplex var. megaspora differs from
R. duplex in the larger size of spore as well as the
number and characters of areolae. There is no
difference in vegetative characters.
SPECIMENS EXAMINED: see Typification.
PLATE 3.32 B.

_R. duplex_ var. _megaspore_

a. Spore, distal face.

b. Spore, optical section

c. Spore, proximal face

_all x 730_


**GAMETOPHYTE** monoecious, forming a complete or incomplete rosette when young, soon spread out, green or pale green, when growing under strong light developed purple colour at the edge of the margins or on dorsal surface in the older parts; thallus 10-15mm. long, 1mm. broad; upper surface with or without distinct airchamber areas. **BRANCHES** multifurcate; segment obovate-linear or narrowly linear, slightly enlarged at the lateral side where the capsule is present. **SCALES** small, hyaline, 1-2 under the ventral part of the first segment. **AIRCHAMBERS** 7-10 across the width of the thallus. **CAPSULES** single, prominent on ventral surface. **SPORES** 65-100 μm diam.; reticulate on both sides.

**CHROMOSOME NUMBER** n=8

**RANGE:** New South Wales, Queensland, Northern Territory, Western Australia.

**TYPIFICATION:** *R. multifida* St. Holotype: Queensland, West Ballenger Ker Range, Karsten 3000 (MEL 19777).

*R. burnettensis* St. Holotype: Queensland, Burnett River, J. Keys 157, 10.1889 (G.12727).

**DISCUSSION:** *R. multifida* is a monoecious species as is *R. duplex*, but the haploid chromosome of the former is eight whilst that of the latter is sixteen. These two plants also differ in spore features (see Table 3.1 for comparison).

From the type material, there are mature spores which were unfortunately, not observed by Stephani.
R. burnettensis St. is in fact not different from R. multifida. Spores from the type material are rather small, but have the same character as that of R. multifida. In nature, the size of the spores varies under different conditions and this was also observed from the collections, especially specimen 0. Na-Thanlang No. 233. The spores when first observed similar to those from the type material of R. burnettensis, but after growing under the same condition as R. multifida, it produced the larger spores.

33A. R. multifida var. multifida.
GAMETOPHYTE thallus ± 7mm. broad, 2-3 times as broad as thick in transverse section (Fig. 3.33A, a, b, & c); upper surface marked out by air chamber areas, narrowly sulcate at the apex (Pl. 3.33A, a); apex obtuse or shortly bilobe, margin obtuse and thick (Fig. 3.33A, a, b & c). EPIDERMIS slightly raised up above air chambers; air pore small, surrounded by 4 hyaline cells (Fig. 3.33A, d); air chambers 8-10 across the width of the thallus (Fig. 3.33A, a). ANtheridium and ARCHEGONIUM close to the apex, usually single, necks not prominent.
CAPSULE with 56-290 spores per capsule. SPORES 65-100 μm diam., mostly 80 μm, brown to dark-brown, triangular-globular with crenulate wing 3-4 μm wide which normally complete, marginal angles enlarged (Pl. 3.33A, d); distal face forming 7-8 regular areolae across the diameter, areola 7-8 μm wide with high ridges at the corners (Pl. 3.33A, b); proximal face (Pl. 3.33A, c) clearly reticulate, areola 6-7 μm wide without high ridge or papillae; triradiate mark distinct.
FIG. 3.33 A

*R. multifida, St. var. multifida*

a, b, & c. Transverse sections of the thallus from younger to older parts × 100

d. Portion of the epidermis × 400

ep = epidermal cell

p = air pore
PLATE 3.33 A

*R. multifida St.* var. *multifida.*

a. Plant x 27.5

b. Spore, distal face x 730

c. Spore, proximal face x 730

d. Spore, optical section x 730

33B. R. multifida var. filiforme var. nov. Monoecia. Thallus ± 0.5mm. latus pagina dorsalis anguste sulcata reticulata ob cavermulum aeriam cellulisque epidermalibus laevibus. Archegenium unumquidque colla indistincto. Sporae ± 70 μ latae laeves polis tribus marginibus alasque 4–5 μ latae; areolae 6–8 μ latis, 6–7 in diametro superficie distalis: superficies proximalis indistincte reticulata.

GAMETOPHYTE thallus 5–10mm. long, less than 1mm. broad (mostly 0.5mm.), 1.5–2.5 times as broad as thick in transverse section (Fig. 3.33B, a, b, c & d); upper surface narrowly sulcate throughout, not marked out by air-chamber areas (Pl. 3.33B, b). BRANCHES multifuroate, filiform, divergent; segment narrowly linear; apex truncate; margin obtuse. SCALES hyaline, persistent, 3–6 in a segment (Pl. 3.33B, a). EPIDERMIS smooth; air pore many (Fig. 3.33B, e); air chambers small, 6–7 across
the width of the thallus (Fig. 3.33B, d).

**ANTHERTIDIA** single or two together, neck not prominent.
**ARCHEGONIA** single, neck hyaline or purple slightly protruding above the thallus surface. **CAPSULE** single, bulging out on ventral face, 20–140 spores per capsule.
**SPORES** 65–85 μ, mostly 70 μ, brown; triangular-globular with broad and smooth wing 4–5 μ wide and enlarged at 3 marginal angles (Pl. 3.33B, e); distal face regularly reticulate, forming 6–7 areolae across the diameter, areola 5–8 μ wide with thin and low border (Pl. 3.33B, c); proximal face less distinct than the distal ones, triradiate mark distinct (Pl. 3.33B, d).

**CHROMOSOME NUMBER** n=8  
**Voucher:** New South Wales, Coonabrabran, Mallalas Creek, O. Na-Thalang No. 215, 26.3.1967 (SYD); Tummallal Creek, O. Na-Thalang No. 222, 26.3.1967 (SYD).

**RANGE:** New South Wales.

**HABITAT:** on mud along dry creek.

**TYPOIFICATION:** R. multifida var. filiforme var. nov.
**Holotype:** New South Wales, Coonabrabran, Mallalas Creek, O. Na-Thalang No. 215, 26.3.1967 (SYD).

**DISCUSSION:** R. multifida var. filiforme has a typical narrowly linear thallus and small spores with a smooth wing. This can easily be separated from others of the same group. The vegetative and spore features are rather constant under different condition (see Table 3.1 for comparison with other varieties).

Bapna (1952) reported R. abuensis Bapna sp. nov. from India. The vegetative characters are quite similar to R. multifida var. filiforme except the former has
FIG. 3.33 B

*R. multifida var. filiforme* var. nov.

a, b, c, & d. Transverse sections of the thallus from younger to older parts  x  100

e. Position of the epidermis  x  400

ep = epidermal cell

p = air pore

f. Portion of the transverse section of the thallus  x  200
PLATE 3.33 B.

*R. multifida var. filiforme* var. nov.

a. Plant x 27, ventral surface showing scales.
b. Plant x 27, dorsal surface
c. Spore, distal face x 730
d. Spore, proximal face x 730
e. Spore, optical section x 730
only smooth rhizoid and no scales. For the spore characters R. abuensis is closer to R. multifida St. than any other species.

**SPECIMENS EXAMINED:** see chromosome voucher.

**33C. R. multifida var. divaricata var. nov.**

Monoecia. Thallus ± 0.7mm. latus pagina dorsalis anguste sulcata cellulisque epidermalibus tumidis. Archegonium unumquidque collo longo stricto. Sporae ± 70 /μ latae 3–5 /μ late crenulata; superficies distalis et proximalis distincte reticulata areolis 6–9 /μ latis in utraque.

**GAMETOPHYTE** thallus 5–10mm. long, more or less 0.7mm. broad; 1.5–2 times as broad as thick in transverse section (Fig. 3.33C, a, b, c). upper surface not marked out into aircell areas (Pl. 3.33C, a), shortly sulcate at apex or almost flat. **BRANCHES** multifurcate, divergent, segment obovate-linear; apex obtuse or rounded, margin obtuse or almost rounded. **SCALES** small, hyaline, 1–2 in a segment (Pl. 3.33C, b). **EPIDERMAL CELLS** tumid; air pore small surrounded by 2–4 hyaline cells (Fig. 3.33C, d); aircambers 8–9 across the width of the thallus. **ANTHERIDIA** single, neck not prominent. **ARCHEGONIA** single, neck slightly protruding above the thallus surface. **CAPSULE** single, bulging out on ventral surface with 162–276 spores per capsule. **SPORES** 65–75 /μ, pale brown or brown, triangular-globular with crenulate wing 3–5 /μ wide (Pl. 3.33C, d); distal face reticulated, forming 6–7 areolae across the diameter, areola 8–9 /μ wide with thin border, papillate at the corners (Pl. 3.33C, b);
FIG. 3.33 C

*R. multifida var. divaricata var. nov.*

a, b. Transverse sections of the thallus x 100

c. Transverse section of the thallus x 200

d. Portion of the epidermis x 400

ep = epidermal cell

p = air pore
PLATE 3.33 C

*R. multifida var. divaricata var. nov.*

a. Plant x 20, dorsal surface

b. Spore, distal face x 730

c. Spore, proximal face x 730

d. Spore, optical section x 730
proximal face reticulate, areola 6-9 μ, ridges high, triradiate mark distinct (Pl. 3.33C, c)

CHROMOSOME NUMBER n=8 Voucher: Northern Territory, Bower Bird Creek, O. Na-Thalang No. 304, 30.1.1969 (SYD); South Alligator River, O. Na-Thalang No. 324, 29.1.1969 (SYD).
RANGE: Northern Territory.
HABITAT: at creek bank.


DISCUSSION: The pale green thallus with tumid epidermal cells and the same size of areolae on both sides of spore separate this plant from others (see Table 3.1 for comparison between varieties).

SPECIMENS EXAMINED: see chromosome voucher.

33D. R. multifida var. torticola, var. nov.
Monoecia. Thallus 0.6-0.8mm. latus pagina dorsalis reticulata ob cavernulam aeriam anguste sulcata. Archoegonium unumquidque collo longo plus minusve tortili. Sporae ± 70 μ diam., fuscae vel ferrugines ala 3-4 μ lata plerumque interrupta ad angulum: superficies distalis et proximalis obscurae reticulatae: crista tenuis irregularis.

GAMETOPHYTE thallus 5-10mm. long, 0.6-0.8mm. broad, 1.5-2 times as broad as thick in transverse sections (Fig. 3.33D, a, b, c); upper surface marked with air-chamber areas; narrowly sulcate throughout (Pl. 3.33D, a).
BRANCHES multifurcate, divergent; segment linear, broadened at the place where developing capsule present;
apex truncate or rounded; margin obtuse, uneven.

**SCALES** small, hyaline, persistent, 1-2 in a segment.

**EPIODERM** slightly raised up over air chamber; air pore rather large (Fig. 3.33D, d); air chambers small, 7-10 across the width of the thallus (Fig. 3.33D, a, b, c).

**ANTHERIDIA** single, neck not prominent. **ARCHEGONIA** single, neck long and twisted, persistent (Pl. 3.33D, a).

**CAPSULE** single, bulging out on ventral surface, 44-120 spores per capsule. **SPORES** 60-95 /µ (mostly 70 /µ), dull reddish-brown or brown, sometimes almost opaque; triangular-globular or rather rounded from distal or proximal faces; wing crenulate 3-4 /µ wide, normally incomplete, interrupted at marginal angles (Pl. 3.33D, d); distal face faintly reticulate forming 8-10 incomplete areolae across the diameter, areola 6-8 /µ wide, border of areolae thin and incomplete, ridges low, irregular (Pl. 3.33D, b); proximal face less distinct than the distal ones with irregular ridges, triradiate mark indistinct (Pl. 3.33D, c).

**CHROMOSOME NUMBER** n=8 Voucher: Western Australia, Poison Creek, 50 miles North of Leonora, R.C. Carolin No. 5834, 8.1966 (SYD).

**RANGE**: Western Australia.

**HABITAT**: on mud, at edge of water hole.

**TYPIFICATION**: *R. multifida var. torticolla*. Holotype: Western Australia. Poison Creek, 50 miles North of Leonora, R.C. Carolin No. 5834, 8.1966 (SYD).

**DISCUSSION**: The prominent archegonial neck and the spore characters of *R. multifida var. torticolla* are different from others of the same group. These varieties do not
seem to vary under different environmental conditions (see Table 3.1 for comparison with others).

SPECIMENS EXAMINED: see Typification.
FIG. 3.33 D

*R. multifida var. torticollis* var. nov.

a, b, c. Transverse sections of the thallus $\times 100$

d. Portion of the epidermis $\times 400$

ep = epidermal cell

p = airpore
PLATE 3.33 D

*R. multifida var. torticollis* var. nov.

a. Plant x 27

b. Spore, distal face x 730

c. Spore, proximal face x 730

d. Spore, optical section x 730
### Comparative morphological characters in *Rhamnus-communis*

<table>
<thead>
<tr>
<th>Species</th>
<th>Segments</th>
<th>Sexuality</th>
<th>Segment</th>
<th>Allcumber area on dorsal surface</th>
<th>Dorsal furrow</th>
<th>No. of zigzagers</th>
<th>Archegonium type</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>Rhamnus</em> L.</td>
<td>5-10 ± 1</td>
<td>monoeious</td>
<td>abutted</td>
<td>without markings or indistinct ones</td>
<td>narrowly sulcate at apex</td>
<td>8-12</td>
<td>not prominent</td>
<td>6 = 10</td>
</tr>
<tr>
<td>2. <em>Rhamnus</em> var. magniflora</td>
<td>5-10-1</td>
<td>monoeious</td>
<td>abutted</td>
<td>without markings or indistinct ones</td>
<td>narrowly sulcate at apex</td>
<td>8-12</td>
<td>not prominent</td>
<td>6 = 10</td>
</tr>
<tr>
<td>3. <em>Rhamnus</em> St.</td>
<td>5-10-1</td>
<td>monoeious</td>
<td>broadly linear or elliptical-linear</td>
<td>with markings &amp; normally distinct</td>
<td>narrowly sulcate at apex</td>
<td>8-12</td>
<td>not prominent</td>
<td>6 = 8</td>
</tr>
<tr>
<td>4. <em>Rhamnus</em> var. tortilis var. nov.</td>
<td>5-10-1</td>
<td>monoeious</td>
<td>abacturnate-linear &amp; broadening at capsule position</td>
<td>with markings and normally distinct</td>
<td>narrowly sulcate throughout</td>
<td>9-10</td>
<td>long &amp; inflated</td>
<td>6 = 8</td>
</tr>
<tr>
<td>5. <em>Rhamnus</em> var. filiform var. nov.</td>
<td>5-10-0.5</td>
<td>monoeious</td>
<td>narrowly linear</td>
<td>without markings or indistinct ones</td>
<td>narrowly sulcate at apex</td>
<td>7-8</td>
<td>slightly projecting above the leaf surface &amp; becoming purple</td>
<td>6 = 8</td>
</tr>
<tr>
<td>6. <em>Rhamnus</em> var. divaricata var. nov.</td>
<td>5-10-0.8</td>
<td>monoeious</td>
<td>abutted tapering or linear</td>
<td>without markings or indistinct ones</td>
<td>narrowly sulcate at apex</td>
<td>8-10</td>
<td>slightly projecting above the leaf surface &amp; becoming purple</td>
<td>6 = 8</td>
</tr>
<tr>
<td>7. <em>Rhamnus</em> sp.</td>
<td>6-12, 1-2</td>
<td>dioecious</td>
<td>abacuminate</td>
<td>with markings</td>
<td>narrowly sulcate in g. plant, flat in f. plant</td>
<td>12-16</td>
<td>© not prominent</td>
<td>6 = 8</td>
</tr>
</tbody>
</table>

### Comparative morphological characters in *Rhamnus-communis*

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of spores</th>
<th>Spore Size (µ)</th>
<th>Form</th>
<th>Wing</th>
<th>Distal Face</th>
<th>Prominent Face</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>Rhamnus</em> L.</td>
<td>100 - 160</td>
<td>0.65</td>
<td>Trigonol-globular</td>
<td>0-7 spines, 10-15</td>
<td>ovate, ovate at the corners</td>
<td>ovate 3-6, Trigonolate much distinct</td>
</tr>
<tr>
<td>2. <em>Rhamnus</em> var. magniflora</td>
<td>60-110</td>
<td>0.100</td>
<td>Almost rounded</td>
<td>0-10 spines, ovate, Incomplete, simple</td>
<td>ovate 0-6, Trigonolate much distinct</td>
<td></td>
</tr>
<tr>
<td>3. <em>Rhamnus</em> St.</td>
<td>50 - 290</td>
<td>0.5 - 100</td>
<td>Trigonol-globular</td>
<td>0-10 spines, ovate, Incomplete, simple</td>
<td>ovate 0-6, Trigonolate much distinct</td>
<td></td>
</tr>
<tr>
<td>4. <em>Rhamnus</em> var. tortilis var. nov.</td>
<td>44 - 120</td>
<td>0.5 - 75</td>
<td>Almost rounded</td>
<td>5-7 spines, ovate, papillose high at the corners</td>
<td>ovate 0-7, Trigonolate much distinct</td>
<td></td>
</tr>
<tr>
<td>5. <em>Rhamnus</em> var. filiform var. nov.</td>
<td>20 - 160</td>
<td>0.5 - 70</td>
<td>Trigonol-globular</td>
<td>5-7 spines, ovate, papillose high</td>
<td>ovate 0-7, Trigonolate much distinct</td>
<td></td>
</tr>
<tr>
<td>6. <em>Rhamnus</em> var. divaricata var. nov.</td>
<td>100 - 270</td>
<td>± 75</td>
<td>Trigonol-globular</td>
<td>5-7 spines, ovate, papillose high</td>
<td>ovate 0-7, Trigonolate much distinct</td>
<td></td>
</tr>
<tr>
<td>7. <em>Rhamnus</em> sp.</td>
<td>170 - 340</td>
<td>0.5 - 85</td>
<td>Almost rounded</td>
<td>0-10 spines, ovate, papillose high</td>
<td>ovate 0-7, Trigonolate much distinct</td>
<td></td>
</tr>
</tbody>
</table>
**INCERTAE SEDIS**

1. *R. cancellata* Tayl. J. of Bot. p. 414 (1846); 


*R. cancellata* Tayl. Holotype: Swan River, W.J.
Drummond 1843 (FH)
Isotype: Swan River, W.J.
Drummond (MEL 19740).

*R. vesicata* Tayl. Holotype: Swan River, W.J.
Drummond 1843 (FH)
Specimens collected by Taylor
(MEL 19772)

The type materials of *R. cancellata* Tayl. and
also of *R. vesicata* Tayl. are in a bad condition and had
no mature spores. From Taylor's description of the
surface "- sprinkled over with pale green minute vesicles
of different sizes" make it seem very closely to
*R. crystallina* L., but this it was not possible to
observe from the type material.

Stephani's description and drawings of
*R. cancellata* Tayl. seems to be quite different
from Taylor's as he suggested that it is similar to
*R. fluitans* while in fact *R. cancellata* is larger than
*R. fluitans* (the width of the thallus of the holotype
is about 2.5-3mm.).

*R. acutisulca* St. Holotype: Australia, Leg. Geobel (G.12726).

*R. acutisulca* St. clearly belongs to the *R. fluitans-complex* group, but the character of scales on lateral side of thallus are quite unusual (Stephani, *Incones Hep.* IV: 369. Unpublished) since all almost of the plants belonging to this group have undivided scales on the ventral side of the thallus (see *R. fluitans-complex* group, Chapter III). As for the spore characters which are the most important for identifying this group, no description is provided by the original author and there are also no mature spores in the type material.
IV.

KEY TO RICCIA SPP. IN AUSTRALIA.

1. Upper part of the thallus with compactly arranged tissue forming narrow vertical air chambers, no special air pore, epidermal cells hyaline — subgen. Riccia.

2. Photosynthetic tissue at ventral part of the thallus and mainly at the scales; upper part of the thallus composed of compact hyaline cells, sometimes arranged in columns. Spores 85-100 μ (150 μ), reticulate.  1. R. caroliniiana

*2. Photosynthetic tissue at dorsal part of the thallus, Photosynthetic tissue with narrow vertical air chambers, sometimes the margin of the thallus with polyhedral air chambers; epidermal cells hyaline.

3. Thallus normally with marginal cilia.

4. Capsule bearing 5-15 cilia above it; marginal cilia in dry state long, up to 1000 μ and crowded, sometimes shorter and less dense in moistened state.

5. Thallus 1-1.5 mm, broad, upper surface narrowly channelled.

6. Spores ± 85 μ, clearly reticulate on both sides with 9-10 areolas on distal face, areola 8-12 μ wide, triradiate mark on proximal face distinct.  2. R. longiciliata

*6. Spores ± 75 μ, faintly reticulate on both sides, areolae on distal face normally incomplete, about 8-9 across the diameter, areola 5-7 μ side, triradiate mark on proximal face indistinct.  3. R. crinita
5. Thallus 1.5-2 mm. broad, upper surface broadly channelled. Spores ± 75 μ, clearly reticulate on both sides, 5-7 areolae on distal face, areola 7-14/μ wide, usually larger in the central part, smaller towards the edge, triradiate mark on proximal face distinct.

4. R. areolata

4. Capsule not bearing cilia; marginal cilia normally 350-500 μ long.

7. Cilia present only near the apex, rare elsewhere.

8. Plants small, 2-5 mm. long, 1-2 mm. broad; branches bi-trifurcate, upper surface narrowly channelled. Capsule not protruding on dorsal surface. Spores ± 75 μ.

5. R. crozalsii

8. Plants larger, 2-5 mm. long, 1.5-2.5 mm. broad; branches single or bifurcate, upper surface broadly channelled. Capsule protruding on dorsal surface. Spores ± 100 μ.

6. R. blackii

7. Cilia normally present throughout the thallus; plants large 4-10 mm. long, 2.5-3.5 mm. broad; upper surface very broadly channelled. Capsules many, slightly protruding on dorsal surface. Spores ± 90 μ.

7. R. asprella

3. Thallus without marginal cilia.

9. Scales normally large and many, usually extending beyond the margin or reaching the margin.

10. Scales purple in dry state, occasionally becoming hyaline when in moistened or shady conditions.

11. Spores more or less globose, reticulation similar on all surfaces.

12. Spores unwinged.

13. Spores 90-150 μ; areolae 8-12 across the diameter, 7-13 μ wide, with prominently and equally high ridges.

8. R. macrospora
*13. Spores 85-135 \( \mu \); arecolae 8-16 across the diameter, 5-8 \( \mu \) wide, ridges very low and coarsely dentate in profile.

9. \textit{R. gangetica}

*12. Spores covering with thin membrane attached to the ridges.

14. Plant monoecious, thallus hardly developing purple colour on dorsal surface in strong light. Spores 85-145 \( \mu \), arecolae 5-8 across the diameter, 12-15 \( \mu \) wide.

10. \textit{R. billardieri}

*14. Plant dioecious, thallus easily developing purple colour on dorsal surface in strong light. Spores 85-155 \( \mu \), arecolae 5-6 across the diameter, 15-20 \( \mu \) wide.

11. \textit{R. discolor}

*11. Spores triangular-globular, proximal face with triradiate mark.

15. Plant large, 7-15mm. long, 2.5-5mm. broad, scales always extending beyond the margins. Spores 85-160 \( \mu \).

12. \textit{R. limbata}

*15. Plant small, 3-6mm. long, 1-1.5mm. broad; scales reaching the margin but never extending beyond it. Spores 70-75 \( \mu \).

13. \textit{R. nigrella}

*10. Scales hyaline, occasionally with few cells becoming purple in dry state.

16. Upper surface clearly reticulate.

17. Plant glaucous-green or pale green, only green under moistened condition; upper surface not shining.

18. Thallus 6-12mm. long, 3-4mm. broad; upper surface broadly channelled; scales large, extending beyond the margins. Spores 100-128 \( \mu \), irregularly reticulate on both sides.

14. \textit{R. lamellosa}
*18. Thallus 3-7mm. long, 1.5-2mm. broad, upper surface narrowly channelled; scales reaching the margins. Spores 70-85 /u, regularly reticulate on distal face, proximal face granulate and with scattered irregular ridges.  
15. R. sorocarpa

*17. Plant deep green, upper surface shining; thallus 7-15mm. long, 3.5-5mm. broad; upper surface narrowly sulcate; scales joined with the hyaline margin. Spores 70-85 /u, regularly reticulate.  
16. R. marginata

*16. Upper surface not clearly reticulate.

19. Plant green; thallus 7-10mm. long, 3-5mm. broad; epidermal cells smooth, 5-6 cells around each air pore. Spores 70-80 /u, faintly reticulate on both sides.  
17. R. olgensis

*19. Plant glaucous-green; thallus 5-10mm. long, 2-3mm. broad; epidermal cells turgid, light-reflecting cells, 4 cells around each air pore. Spores ± 75 /u with irregular ridges hardly forming definite areolae.  
18. R. rorida

*9. Scales small, few, present only under the apex.

20. Plant monoecious; upper surface broadly channelled. Spores 70-85 /u, clearly reticulate on both sides.  
19. R. bifurca

*20. Plant dioecious; upper surface narrowly sulcate. Spores 70-85 /u, smooth all over the surface.  
20. R. albida

*17: Upper part of the thallus with loosely arranged chlorophyll-bearing tissue forming polyhedral or large air chambers; epidermal cells containing chloroplasts except those around the air pores. -- subgen. Ricciella.

21. Capsules not bulging out into spherical structures on ventral surface; thallus not strap-like, broader than 1.5mm.

22. Plants annual; on mud or growing in a place which is occasionally flooded; tending to form almost circular compact patches of 5-25mm. diameter.
23. Plant glaucous-green, never with red or purple colour; upper surface without distinct air chamber areas; epidermal cells turgid and light-reflecting cells, cavernous only in older parts. Spores 70-85 \( \mu \), finely reticulate on both sides.  
\[21. \text{R. crystallina}\]

*23. Plant bright-green, usually tinged with red or purple-red at the edge and the tip of the thallus; upper surface cavernous; epidermis disintegrating even in young part of the thallus. Spores 70-100 \( \mu \) with di- or trichotomous branching ridges on both sides.  
\[22. \text{R. cavernosa}\]

*22. Plants neither strictly annual nor always mud dwellings; forming a rosette only in young stages, soon scattered.


25. Thalli large, 7-15mm. long, 3-6mm. broad.  
Spores about 100 \( \mu \).

26. Upper surface of the thalli either marked out with small air chamber areas or indistinct.

27. Thallus 4-6mm. broad; segment oblong.  
Capsules embedded in the thallus. Spores \( \pm 120 \mu \), areoles 12-15 across the distal face; proximal face faintly reticulate; triradiate mark indistinct.  
\[23A. \text{R. papulosa var. papulosa}\]

*27. Thallus 2.5-3.5mm. broad; segment elliptical-oblong or oblong. Capsules prominent on ventral surface. Spores \( \pm 100 \mu \); distal face similar to above; proximal face with thick and low ridges; triradiate mark rather distinct.  
\[23B. \text{R. papulosa var. variabilis}\]

*26. Upper surface of the thalli clearly marked out with large air chamber areas. Thallus 3-6mm. broad; segment obtuse-oblong. Spores \( \pm 120 \mu \); distal face with 6-8 areoles across the diameter; proximal face faintly reticulate.  
\[24. \text{R. spongiosa}\]
25. Thalli and spores normally smaller than above, 5-10 mm. long, 2-4 mm. broad. Spores 75-85 μ.

28. Upper surface of the thallus clearly marked out with rather large air chamber areas. Plant bright green, occasionally developing purple colour in older parts. Spore + 85 μ, areolae 7-9 across the distal face, 10-12 μ wide; proximal face faintly reticulate, sometimes with thick ridges. 25. R. musicola

28. Upper surface of the thalli either marked out with small air chamber areas or indistinct.

29. Plant glaucous-green or pale green; upper surface broadly channelled. Spores + 75 μ, wing crenulate; distal face with 6-7 areolae across the diameter, ridges thin slightly raised up at the corners; proximal face faintly reticulate; triradiate mark indistinct. 26. R. diserticola

29. Plant green or bright-green, upper surface narrowly sulcate at apex, the rest almost flat.

30. Capsules not prominent on ventral surface.

31. Upper surface finely cavernous behind the apex. Spores + 85 μ, wing rather smooth with 3 marginal poles; distal face with 6-8 incomplete areolae, the ridges irregular and prominent; proximal face faintly marked out or sometimes with indistinct ridges, triradiate mark not prominent. 27. R. crassa

*31. Upper surface rarely cavernous. Spores + 75 μ, wing narrow and crenulate with 3 marginal poles, distal face with 7-8 areolae, ridges slightly raised up at the corners; proximal face finely reticulate. 28. R. vesiculosa

*30. Capsules prominent on ventral surface. Spores + 75 μ, wing broad and crenate; distal face with 6-7 areolae; proximal face clearly reticulate, areolae almost the same size as the distal ones. 29. R. junghuhniana
212.

*24. Plant dioecious; thallus 3–8mm. long, 1.5–4mm. broad; scales small and many; male plant with prominent antheridial necks, female plant shortly sulcate at apex. Spores 70–85 µ; distal face with 7–8 areolae across the diameter; proximal face faintly reticulate. 30. R. collata

*21. Capsules bulging out into spherical structures on ventral surface; thallus strap-like, scarcely broader than 1.5mm.

32. Plant dioecious; thallus sometimes up to 2mm. broad, male plant pitted by antheridial ostioles along the middle part of the thallus; female plant slightly broadened where a capsule is developing. Spores ± 70 µ, wing crenulate; reticulate on both sides; triradiate mark rather distinct. 31. R. limicola

*32. Plant monoecious; thallus not up to 1.5mm. broad.

33. Upper surface not marked out by aircambrum areas.

34. Thallus ± 1mm. broad, apex obtuse or rounded.

35. Spores ± 85 µ, triangular-globular; distal face with 6/7 areolae, areola 10–15 µ wide; proximal face clearly reticulate, areola 6–7 µ wide. 32. R. duplex var. duplex

*35. Spores ± 100 µ, almost rounded from distal face; areola 9–10 across the distal face, 6–9 µ wide; proximal face clearly reticulate, areola 6–7 µ wide. R. duplex var. megaspore

*34. Thallus ± 0.5mm. broad, apex truncate or rounded. Spores ± 70 µ, wing smooth with 3 marginal poles; distal and proximal faces faintly reticulate. 33. R. multifida var. filiforma

*33. Upper surface almost marked out by aircambrum areas.
36. Archegonial necks short, slightly projecting above the thallus surface. Spores ± 80 μ; areolae 7-8 μ across the distal face, areola 7-8 μ wide, papillate at the corners; proximal face with distinct triradiate mark, areola 6-7 μ wide.

33. *R. multifida var. multifida*

*36. Archegonial necks long, prominently projecting above the thallus.*

37. Archegonial neck straight. Spores ± 75 μ, wing cremulate with 1-2 marginal poles; areolae 6-7 μ across the distal face, areola 6-9 μ wide; proximal face with distinct triradiate mark, areola 6-8 μ wide.

33. *R. multifida var. divaricata*

*37. Archegonial neck long, twisted. Spores ± 75 μ, wing cremulate and incomplete; indistinctly reticulate on both sides. 33. *R. multifida var. torticolla***
V.

CHROMOSOME NUMBERS OF RICCIA SPECIES IN AUSTRALIA.

The first reports on the cytology of Riccia are Lewis (1902) and Beer (1906). The former worked on R. crystallina L. and reported only 4 chromosomes in the gametophyte, the latter gave 7 or 8 as the haploid number in R. glauca L. Observations were subsequently made in some others, but only about 40 species from more than 200, have been described cytologically (Table 1). Lorbeer (1934) and Müller (1940, 1941), especially working on the R. fluitans-complex, point out that this group could be segregated into four distinct species viz. R. fluitans L. (n=8), R. rhenana Lorb. (n=16), R. duplex Lorb. (n=16) and R. canaliculata Hoffm. (n=8). Berrie (1964) experimented with R. fluitans-complex and suggested that R. rhenana could be the diploid form of R. fluitans and R. duplex probably the diploid form of R. canaliculata. Other works by various authors in the genus Riccia show that further studies of the chromosome numbers have greatly facilitated the solution of some of the taxonomic confusion. Hence the examination of the chromosome numbers of various Riccia species in Australia was undertaken.
<table>
<thead>
<tr>
<th>Name of Plant</th>
<th>Gametophyte chromosomes</th>
<th>Authority</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Riccia arvensis Aust.</td>
<td>8 = 7 + m</td>
<td>Siler (1934)</td>
</tr>
<tr>
<td>2. R. austini. St.</td>
<td>9 = 8 + m</td>
<td>&quot;</td>
</tr>
<tr>
<td>3. R. bischoffii Huben.</td>
<td>8 = 7 + x/y</td>
<td>Lorbeer (1927, 1934)</td>
</tr>
<tr>
<td>4. R. bifurca Hoffm.</td>
<td>8</td>
<td>Vanden Berghen (1955)</td>
</tr>
<tr>
<td>5. R. beyerichiana Hampe</td>
<td>8</td>
<td>&quot;</td>
</tr>
<tr>
<td>6. R. billardieri Mont. et N.</td>
<td>8</td>
<td>Udar and Chopra (1957)</td>
</tr>
<tr>
<td>7. R. californica Aust.</td>
<td>9 = 8 + m (7+2m)</td>
<td>Siler (1934)</td>
</tr>
<tr>
<td>8. R. campbelliana Howe</td>
<td>8 = 7 + m</td>
<td>Siler (1934)</td>
</tr>
<tr>
<td>9. R. canaliculata Hoffm.</td>
<td>8</td>
<td>Lorbeer (1934), Müller (1941)</td>
</tr>
<tr>
<td>10. R. ciliata Link.</td>
<td>8</td>
<td>Lorbeer (1934), Müller (1951)</td>
</tr>
<tr>
<td>11. R. ciliata Hoffm.</td>
<td>8</td>
<td>Vanden Berghen (1955)</td>
</tr>
<tr>
<td>12. R. cruciata Kash.</td>
<td>16 = 14+2m</td>
<td>Kachroo (1955)</td>
</tr>
<tr>
<td></td>
<td>8 = 7 + m</td>
<td>Kachroo (1955) from Berrie (1960)</td>
</tr>
<tr>
<td>13. R. crystallina L.¹</td>
<td>4</td>
<td>Lewis (1906)</td>
</tr>
<tr>
<td></td>
<td>8 = 7 + m</td>
<td>Siler (1934), Kachroo (1955)</td>
</tr>
<tr>
<td></td>
<td>8 = 7 + h</td>
<td>Lorbeer (1934)</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>Vanden Berghen (1955)</td>
</tr>
<tr>
<td>14. R. curtisii Jameson¹</td>
<td>8</td>
<td>McAlister (1928)</td>
</tr>
<tr>
<td></td>
<td>8 = 7 + m</td>
<td>Siler (1934)</td>
</tr>
<tr>
<td></td>
<td>8 = 9 + x/y</td>
<td>Lorbeer (1934)</td>
</tr>
<tr>
<td>15. R. discolor L. et L.</td>
<td>8</td>
<td>Mahabale &amp; Gorgi (1947)</td>
</tr>
<tr>
<td></td>
<td>8 = 7 + m</td>
<td>Kachroo (1955)</td>
</tr>
<tr>
<td>Name of Plant</td>
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<tr>
<td><em>R. himalayensis</em> St. (Syn. of <em>R. discolor</em> L. et L.)</td>
<td>8</td>
<td>Mahabale and Gorgi (1941)</td>
</tr>
<tr>
<td>16. <em>R. donnelllii</em> Aust.</td>
<td>8 = 7 + m</td>
<td>Siler (1934)</td>
</tr>
<tr>
<td></td>
<td>16 = 14 + 2m</td>
<td>Siler (1934)</td>
</tr>
<tr>
<td>17. <em>R. duplex</em> Lorb.¹</td>
<td>16 = 14 + m₁ + m₂</td>
<td>Lorbeer (1934), Müller (1941)</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>Vanden Berghen &amp; Meijer (1951)</td>
</tr>
<tr>
<td>18. <em>R. fluitans</em> L.¹</td>
<td>14/15</td>
<td>Heitz (1927a)</td>
</tr>
<tr>
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<td>16 = 14 + 2m</td>
<td>Lorbeer (1934)</td>
</tr>
<tr>
<td></td>
<td>8 = 7 + m</td>
<td>Tatuno (1941)</td>
</tr>
<tr>
<td></td>
<td>8 = 7 + h</td>
<td>Berrie (1956)</td>
</tr>
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<td></td>
<td>8</td>
<td>Tatuno (1956)</td>
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<tr>
<td>20. <em>R. glauca</em> L.</td>
<td>7/8</td>
<td>Black (1913), Mahabale and Gorgi (1947)</td>
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<tr>
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<td>9 = 8 + m</td>
<td>Beer (1906)</td>
</tr>
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<td></td>
<td>8</td>
<td>Heitz (1927a), Siler (1934), Tatuno (1941)</td>
</tr>
<tr>
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<td>9 = 8 + h</td>
<td>Wentzel (1929)</td>
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<td>R. glauca var. subinermis (Lindb.) Warnst.</td>
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<td>Lorbeer (1934)</td>
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<td>8</td>
<td>Siler (1934)</td>
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<tr>
<td>22. <em>R. gaugetiana</em> Mont.</td>
<td>8 = 7 + x/y</td>
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<td>Siler (1934)</td>
</tr>
<tr>
<td></td>
<td>10 = 8 + 2m</td>
<td>Siler (1934) from Berrie (1960)</td>
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<td>23. <em>R. huebeneriana</em> Lindb.</td>
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<tr>
<td>24. <em>R. intermedia</em> Jones¹</td>
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<td>Berrie (unpubl.)</td>
</tr>
<tr>
<td>25. <em>R. intumescens</em></td>
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<td>Lorbeer (1934)</td>
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<td>16</td>
<td>Berrie (unpubl.)</td>
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Table 5.1 (cont.)

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<th>Name of plant</th>
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<th>Authority</th>
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<tr>
<td>26. <em>R. lesquereuxii</em> Aust</td>
<td>9 = 8 + m</td>
<td>Heitz (1927)a</td>
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<td>27. <em>R. japonica</em> St.</td>
<td>8 = 7 + h</td>
<td>Tatuno (1956)</td>
</tr>
<tr>
<td>28. <em>R. melanospora</em> Kash</td>
<td>16 = 14+2m</td>
<td>Kachroo (1955)</td>
</tr>
<tr>
<td>29. <em>R. membranacea</em> St.</td>
<td>8 = 6+ R^2 + h</td>
<td>Berrie (1958a, o)</td>
</tr>
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<td>30. <em>R. michelii</em> Raddi.</td>
<td>10 = 7 + 2h + m</td>
<td>Lorbeer (1934)</td>
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<tr>
<td>31. <em>R. miyakeana</em> Schiffn.</td>
<td>16 = 14+2h</td>
<td>Tatuno (1956)</td>
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<td>32. <em>R. nigerica</em> Jones</td>
<td>8 = 7 + h</td>
<td>Berrie (1958o)</td>
</tr>
<tr>
<td>33. <em>R. nipponica</em> Hatt.</td>
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<td>Tatuno (1956)</td>
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<td>34. <em>R. rhenana</em> Lorb.</td>
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<td>35. <em>R. sanguinea</em> Kash.</td>
<td>8</td>
<td>Mahabale &amp; Gorgi (1947)</td>
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<td>36. <em>R. sorocarpa</em> Bisch.</td>
<td>9 = 8 + m</td>
<td>Heitz (1927a), Lorbeer (1934), Tatuno (1956)</td>
</tr>
<tr>
<td></td>
<td>8 = 7 + h</td>
<td>Siler (1934), Vanden Berghen (1955)</td>
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<tr>
<td></td>
<td>8 = 7 + m</td>
<td>Siler (1934)</td>
</tr>
<tr>
<td>37. <em>R. sullivantii</em> Aust.</td>
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<td>Siler (1934)</td>
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<tr>
<td>38. <em>R. trichocarpa</em> Howe</td>
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<tr>
<td>39. <em>R. zachariae</em> Lorbeer</td>
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<td>Lorbeer (1934), Müller (1941)</td>
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<td>40. <em>R.</em> sp. 'Algier'</td>
<td>8 = 7 + m</td>
<td>Heitz (1927a)</td>
</tr>
<tr>
<td>41. <em>R.</em> sp. 'Panape'</td>
<td>16 = 14+2m</td>
<td>Tatuno (1949)</td>
</tr>
</tbody>
</table>

N.B. 1 = subg. *Ricciella.*
Material and Method.

Material used for counting the chromosome numbers was fixed in aceto-alcohol (1:3) or propionic-alcohol (1:2). Squash preparations were used exclusively in this study. Most of the chromosomes available for counting were obtained from the antheridia, less frequently from young capsules. Aceto-orcein was used for staining. The examination and drawing were made from temporary squashes and photographs were taken from permanent preparations made in the usual way. All of the figures of chromosomes were redrawn on photographs.

The best time to fix for cytological investigations in most of these Riccia spp. is between 10 a.m. and 12 noon, except for species such as R. macrospora, R. limbata and R. cavernosa in which the best time for fixation is in the late afternoon between 4.00 p.m. to 6.00 p.m.

Some pretreatments were used with R. limbata and R. macrospora which have large numbers of chromosomes and clear figures are rare. The treatment of these two plants with paradichloro-benzene for 6-8 hours gave a clear separation of the chromosomes at metaphase.

The purpose of this cytological investigation of Riccia spp. is mainly to provide chromosome numbers, hence the special staining method to distinguish heterochromatin has not been carried out in this study.

Observation.

All of the counts were made from equatorial plates, some were in early metaphase from mitotic division of antheridia; only two species were counted from metaphase of meiotic division in young capsules.
The comparison of the absolute length of chromosomes between each species has not been made, since the length of the chromosomes in any one species differs in different organs and in the same organ at different stages, e.g. in younger antheridia the size of chromosomes is usually larger than in an older one. The term long, medium and small apply to the comparative length of the chromosomes in each karyotype only. Unfortunately, it was not found possible to use one organ at a given age in all the species.

1. "Ciliata" group.

(1) Ciliata group - long cilia: The comparative karyotypes of the three species in this group are really rather different. The diploid species *R. longiciliata* has 11 long and 5 short chromosomes (Fig. 5.3, 3) indicating a possible allopolyplodont origin. The haploid species: *R. crinita* has rather small chromosomes and are almost of the same size except one which is somewhat smaller than the others (Fig. 5.2, 1) for *R. areolata* 3 of the eight chromosomes are small, 2 of medium length and 3 rather long (Fig. 5.2, 2). None of the species in this group has a very small chromosome.

(2) Ciliata group - short cilia: *R. blackii* (Fig. 5.3, 2) and *R. asprella* (Fig. 5.3, 3) have a very small chromosome, the presence of only one very small chromosome in the diploid *R. blackii* may again indicate an allopolyplodont origin; *R. crozalsii* has 3 long and 5 medium length chromosomes (Fig. 5.3, 1) all of which are rather large compared to those of *R. blackii* and *R. asprella*. 
<table>
<thead>
<tr>
<th>Species (Riccia)</th>
<th>chromosome numbers</th>
<th>very small chromosomes or microchromosomes</th>
<th>Voucher specimens</th>
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<tr>
<td>1. R. longiciliata sp. nov.</td>
<td>16</td>
<td>-</td>
<td>Northern Territory. Palm Valley. O. Na-Thalang No. 100A</td>
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<tr>
<td>2. R. crinita Tayl.</td>
<td>8</td>
<td>-</td>
<td>Alice Springs. R.C.Carolin No. 5393</td>
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<tr>
<td>3. R. areolata sp. nov.</td>
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<td>New South Wales. Prospect Reservoir. O. Na-Thalang No. 244</td>
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<td>5. R. blackii sp. nov.</td>
<td>16</td>
<td>1</td>
<td>Cent. Australia, Mt. Olgia. D. Black (O. Na-Thalang No. 67)</td>
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<tr>
<td>6. R. asprella Carr. et P.</td>
<td>8</td>
<td>1</td>
<td>New South Wales, Coonabarabran. O. Na-Thalang No. 210</td>
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<td>7. R. macrospora St.</td>
<td>40</td>
<td>-</td>
<td>Alice Springs, R.C.Carolin No. 5031</td>
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<td>8. R. gangetica Ahmad</td>
<td>16</td>
<td>1</td>
<td>Northern Territory, Mt. Bundey. O. Na-Thalang No. 208</td>
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<td>9. R. billardieri Mont. et N.</td>
<td>16</td>
<td>1</td>
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<tr>
<td>R. billardieri Mont. et N.</td>
<td>8</td>
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<td>Northern Territory, West El Sharana. O. Na-Thalang No. 293</td>
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<tr>
<td>10. R. discolor L.</td>
<td>8</td>
<td>1</td>
<td>Northern Territory. Coomalie Creek. O. Na-Thalang No. 259</td>
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<td>11. R. limbata Bisch.</td>
<td>16</td>
<td>-</td>
<td>South Australia, Wilpenna. O. Na-Thalang No. 122</td>
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<td>12. R. nigrella DC.</td>
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<td>1</td>
<td>New South Wales, Prospect Reservoir. O. Na-Thalang No. 240</td>
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<td>13. R. lamellosa Raddi.</td>
<td>16</td>
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<td>14. R. sorocarpa Bisch.</td>
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<td>15. R. marginata Carr. et P.</td>
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<td>16. R. oligensis sp. nov.</td>
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<td>18. R. bifurca Hoffm.</td>
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<td>19. R. albida Sull.</td>
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<td>Northern Territory, Palm Valley. O. Na-Thalang No. 100</td>
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<td>20. R. carolinii sp. nov.</td>
<td>10</td>
<td>3</td>
<td>Northern Territory. Robin Water Fall. O. Na-Thalang No. 298</td>
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</table>

*10. R. discolor L. |
<table>
<thead>
<tr>
<th>No.</th>
<th>Species</th>
<th>Genotype</th>
<th>Notes</th>
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<tbody>
<tr>
<td>21</td>
<td>R. crystallina L.</td>
<td>8</td>
<td>Victoria, Barjarg. H. Newson</td>
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<td>(0, Na-Thalang No. 257)</td>
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<td>22</td>
<td>R. cavernosa Hoffm.</td>
<td>8</td>
<td>Western Australia, Glen Cummings</td>
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<td>R.C. Carolin No. 6154</td>
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<td>23</td>
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<td>0, Na-Thalang No. 220</td>
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<td>24</td>
<td>R. spongiosa St.</td>
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<td>25</td>
<td>R. muscicola St.</td>
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<td>26</td>
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<td>27</td>
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<td>var. nov.</td>
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<td>30</td>
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<td>New South Wales, Parramatta Lake</td>
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<td>31</td>
<td>R. junghuhniana Nees &amp; L.</td>
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<td>32</td>
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<td>33</td>
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<td>34</td>
<td>R. duplex var. magispora</td>
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<td>divaricata</td>
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<td>38</td>
<td>R. multifida var.</td>
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<td>Western Aust., Poison Creek</td>
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</tbody>
</table>

*dioecious species

Karyotype analyses are given in Figs. 5.1A, 5.1B, 5.1C, 5.1D & 5.1E.
2. "Squamata" group.

(1) "R. macrospora": *R. macrospora* St. is a hexaploid species with the chromosome number 48. From the plate counting at metaphase, most of the chromosomes do not show much difference in length (Fig. 5.4, 1) which is similar to other polyploid species. For its closely related species *R. gangetica*, the chromosome number seems to be unstable as it was reported to be 24 (Udar & Chopra, 1957) but was found only 16 from the present study (Fig. 5.6, 3). If this triploid species occur as well as the diploid species, there is the possibility that *R. macrospora* had arisen from the triploid *R. gangetica*, since these two species show a great deal of similarity including spore wall characters (see Chapter VII). *R. discolor* has 7 large and 1 small chromosomes, both in male and female plants (Fig. 5.5, 1 & 2). This species is closely related to *R. bilabedri*, but the latter is monocious and is an unstable cytological having two chromosome races, n=16 and n=8 (Fig. 5.5, 3 & 4). The similarity of the spore characters indicates that these two plants have a very close relationship and one of these may have evolved from the other.

(2) "R. limbata": It is very interesting that there seems to be close similarities in morphology between *R. limbata* and *R. nigrella* which are diploid and haploid species respectively. *R. limbata* (Fig. 5.4, 2) has 16 chromosomes of almost the same length while in *R. nigrella* one is very small, 7 are not much different in size (Fig. 5.9, 3). These two species have dark purple scales half of the scale being hyaline the other half almost opaque. They show some similarity in spore characters as well as vegetative characters and drought resistance
habit, but the latter seems to be more limited than the former. The wide range of distribution of *R. limbata* may then be explained by a more successful adaptation at the diploid level.

"*R. sorocarpa*: *R. lamellosa* and *R. rorida* have the chromosome number of 16. The latter is slightly different from the former in having 1 very small chromosome (Fig. 5.7, 3) while the difference in size is not very distinct in *R. lamellosa* (Fig. 5.7, 2). *R. sorocarpa* has 1 small chromosome of the eight (Fig. 5.7, 1). This species is rather closely related to *R. lamellosa* and *R. rorida* in the habit of growing and in some morphological characters. The possibility that the diploid *R. lamellosa* and *R. rorida* are evolved from *R. sorocarpa* seems to be possible. There is 1 very small chromosome, 7 large in *R. olgensis* (Fig. 5.8, 1) while in *R. marginata* which is the diploid species has one very small, 1 small and the rest of nearly the same length (Fig. 5.8, 2). From the morphological evidence, there seems to be some relationship between these two species, but they are quite different in karyotype.

(3) "Laevigata": *R. bifurca* (Fig. 5.9, 1) has 8 rather small chromosomes, they are not very much different in size. This species seems to be closely related to the "ciliata" group in many aspects including chromosome characters, and it may be the origin of the latter group. *R. elbida* which seems to be evolved in a different direction in spore characters does not show the difference in its karyotype. The counts from the male plant show 1 long chromosome, 5 of medium size and 2 are small (Fig. 5.9, 2). It was unfortunate that the karyotype from the female plant was not available because a clear plate was unobtainable.
and the plant was rare.

For R. caroliniana, it is not only different from others in its vegetative features, but also by its chromosome number. There are 10 chromosomes in both male and female plants. The male plant has 3 small and 7 large chromosomes of almost equal length (Fig. 5.6, 1) while in female plant the 3 chromosomes are larger than the male ones and the other 7 are not very much different from the 7 chromosomes in male plant (Fig. 5.6, 2). These 3 chromosomes are possibly the sex-chromosomes.

"R. fluitans-complex": There are 3 species and 4 varieties collected, all except R. limicola are monoecious. R. duplex is a diploid species having 1 very small chromosome and the other 15 of nearly the same length (Fig. 5.10, 1) which is rather different from R. duplex var. megaspora that there are 3 groups of chromosomes, 6 rather long and one of it with sattelite, 9 of medium length and 1 small chromosome (Fig. 5.10, 2). Among the haploid group: R. multifida var. multifida, R. multifida var. filiforme, R. multifida var. divaricata and R. multifida var. torticollis all are haploid species having 1 small chromosome, 1 rather long and 6 of almost equal length (Fig. 5.11, 1, 2, 3 & 4). For R. limicola which is a dioecious species, both male and female plants having 1 small chromosome, but the small one in the female plant is larger than the one found in the male plant (Fig. 5.15, 1 & 2). The small chromosome in each plant may be the sex-chromosome, since the other 7 chromosomes in both plants are comparatively similar in length.

"R. crystallina": R. crystallina has small chromosomes, one is a dot-like, 1 small and the rest of nearly the same length (Fig. 5.14, 1), not like those of R. cavernosa which has 1 very long, 5 of medium and 2 small
chromosomes (Fig. 5.14, 2).

"R. papulosa": R. papulosa (Fig. 5.13, 2), a diploid species having 1 very small chromosome, 1 small chromosome and 14 of almost equal length is probable may have arisen from R. papulosa var. variabilis a haploid species (Fig. 5.13, 3). R. spongiosa has 1 very small chromosome and 7 of almost the same length (Fig. 5.12, 1) which its karyotype is similar to some of those of "R. vesiculosa" group.

"R. vesiculosa": R. muscicola (Fig. 5.12, 2), R. deserticola (Fig. 5.12, 3) and R. crassa (Fig. 5.12, 4) all have the chromosome number 8 including 1 very small, 1 longest and 6 are not so noticeably different in length. R. junghuhmiana is slightly different from the above group that the chromosomes are in 4 categories, 4 rather long, 2 medium, 1 rather small and 1 very small or dot-like chromosomes (Fig. 5.15, 3). In R. vesiculosa (Fig. 5.13, 1), the smallest chromosome is not as small as the dot-like which occur in others (e.g. R. deserticola); there are 2 rather long, 4 of medium length, 1 rather small and 2 small chromosomes. For R. collata which is a dioecious species, the karyotypes of male and female plants are slightly different. There are 2 chromosomes which are smaller than the other 6 in male plant (Fig. 5.13, 3), but in the female plant the 6 chromosomes are of medium length and the 2 are long (Fig. 5.14, 4) instead of 2 small chromosomes as is present in the male plant.
Discussion

Apparently, no exact duplication of each chromosome set can be traced between haploid and diploid or polyploid species e.g. *R. papulosa var. papulosa* and *R. papulosa var. variabilis, R. billardieri* the diploid and the haploid form. It is probable that the diploid species may have evolved from the haploid one, but consequent translocation mutation occur in the diploid species as well as in the haploid. This may explain why the two microchromosomes or very small chromosomes do not occur in the diploid species which is morphologically similar to the haploid one e.g. *R. billardieri*.

It is uncertain that the longest and the shortest chromosomes of some karyotypes are concerned with sex determination in *Riccia* spp., since this character does not occur in all species examined (Fig. 5.1a, 5.1b, 5.1c & 5.1d; Table 3.3). The small chromosomes occur 73.53% in all monoecious species observed, but only 50% in the subgenus *Riccia* while in subgenus Ricciella is 87.5%. For the longest chromosome, it does not occur corresponding with the small chromosome viz. subgenus *Riccia* 77.77%, but appears 93.75% in monoecious *Ricciella*. This may indicate that in the subgenus *Ricciella* the longest and the shortest chromosomes are sex-chromosomes, but for subgenus *Riccia* this still seems to be rather doubtful.

The dioecious species presents 12.82% in all species observed, 14.28% in subgenus Riccia, 11.11% in subgenus Ricciella. *R. discolor* and *R. albida* of
TABLE 3.3

Showing the distributions of sexualities and chromosome numbers of the two subgenus.

<table>
<thead>
<tr>
<th></th>
<th>Riccia</th>
<th>Ricciella</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of species</td>
<td>20 species</td>
<td>13 species,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5 varieties</td>
</tr>
<tr>
<td>No. of dioecism</td>
<td>3 spp.</td>
<td>2 spp.</td>
</tr>
<tr>
<td>No. of monoecism</td>
<td>17 spp.</td>
<td>11 spp. + 5 var.</td>
</tr>
<tr>
<td>n = 48</td>
<td>1 spp (monoecious)</td>
<td>-</td>
</tr>
<tr>
<td>n = 16</td>
<td>8 spp (monoecious)</td>
<td>2 spp. + 1 var.</td>
</tr>
<tr>
<td>n = 10</td>
<td>1 spp (dioecious)</td>
<td>-</td>
</tr>
<tr>
<td>n = 8</td>
<td>8 spp (monoecious)</td>
<td>8 spp. + 5 var.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(monoecious)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2 spp (dioecious)</td>
</tr>
<tr>
<td>monoeccious with m</td>
<td>5 spp (diploid)</td>
<td>2 spp. + 1 var.</td>
</tr>
<tr>
<td>chromosome</td>
<td></td>
<td>(diploid)</td>
</tr>
<tr>
<td>monoecious without</td>
<td>4 spp (haploid)</td>
<td>7 spp. + 4 var.</td>
</tr>
<tr>
<td>m chromosome</td>
<td></td>
<td>(haploid)</td>
</tr>
<tr>
<td>monoecious without</td>
<td>3 spp (diploid)</td>
<td>2 spp (haploid)</td>
</tr>
<tr>
<td>m chromosome</td>
<td>5 spp (haploid)</td>
<td></td>
</tr>
</tbody>
</table>

the former subgenus have haploid chromosome number 8.
There is only slight difference between the karyotype of male and female plants (Fig. 5.5, 1 & 2), this is probable that the x and y chromosomes do not differ in size like those of *R. curtisii* (Lewis, 1961). For *R. albida* the karyotype from female plant was unobtainable.
*R. caroliniana* of the same subgenus has the basic number 10. Male and female karyotypes have 7 similar chromosomes and
3 are of different sizes which possibly are involved in sex determination.

*R. limicola*, R. *collata*, the dioecious species of subgenus Ricciella show the same karyotype in both male and female plants which is the same as *R. discolor*.

Within the groups demarcated by morphological features, there is not always agreement in karyotype, i.e. *R. cavernosa* and *R. crystallina*, the former with uneven sizes of chromosome while in the latter there appears to have been little change in chromosome from which might imply few translocations, inversion etc. during the evolution of this species. Similar situations occur in the "ciliata" group, e.g. *R. crinita* and *R. areolata*, however, which have similar macroscopic characters, there is considerable difference in chromosome form, indicating that translocations etc., probably have been important. At the cytological level, then, one can distinguish 3 types of change accompanying morphological evolution.

1. Mutation and recombination.
2. Translocations, deletions etc.
3. Polyploidization.

It is possible that in some cases all three may be involved in the evolution of a group (see Chapter VIII on phylogeny).

The haploid number of 8 is found in 24 species, 13 are in subgenus Ricciella, 11 are in subgenus Riccia.

Eleven species have haploid chromosome numbers of 16, 8 are Riccia and 3 are Ricciella.

*R. macrosperma* in subgenus Riccia is a hexaploid species with chromosome number 48. *R. caroliniana* has haploid number of 10 (anuploid?)
Polyploidy occur 30.76% of all species examined, 28.20% are diploid and 2.56% are hexaploid. The polyploidy series are multiple of the basic chromosome number 8 and all are monoecious.

There appears to be some related haploid-diploid species pairs and diploid-higher polyploid pairs. The experimental production of artificial polyploids from natural haploids and vice versa would provide further interesting systematic and phylogenetic information on the genus.

The distribution of the diploid and polyploid species indicate that they are better adapted to drier conditions than their haploid "pairs".
FIG. 5.1 A

Drawing of mitosis (at metaphase) in antheridial cells, ca. x 2,200

1. R. areolata sp. nov.
2. R. crinita Tayl.
3. R. crozalsii Levier
4. R. longiciliata sp. nov.
5. R. blackii sp. nov.
6. R. asprella Carr. et P.
7. R. bifurca Hoffm.
8. R. albida Sull.
9. R. nigrella DC.
10. R. algensis sp. nov.
11. R. marginata Carr et P.
12. R. sorocarpa Bisch.
FIG 5.1 B

13. _R. lamellosa_ Raddi — mitosis in antheridial cell
14. _R. limbata_ Bisch — meiosis in spore mother cell
15. _R. macrospora_ St. — meiosis in spore mother cell

(all figures ca x 2.200)
FIG. 5.1 C


16.b. *R. discolor* L. et L. mitosis in antheridial cell

17. *R. rorida* sp. nov – mitosis in antheridial cell

18.a. *R. billardieri* Mont et N. – mitosis in antheridial cell

18.b. *R. billardieri* Mont et N. mitosis in antheridial cell

19. *R. gangetica* Ahmed – mitosis in antheridial cell

20 a. *R. caroliniana* sp. nov. – mitosis in apical cell in female plant.

20.b. *R. caroliniana* sp. nov. – mitosis in antheridial cell

(all figures ca. x 2,200)
FIG. 5.1 D.

Drawings of mitosis (21-29) in antheridial cells ca x 2,200.

21. R. crystallina L.
22. R. cavernosa Hoffm.
23. R. spongiosa St.
24. R. muscicola St.
25.a. R. papulosa St var. papulosa
25.b. R. papulosa var. variabilis
26. R. deserticola St.
27. R. crassa St.
28. R. vesiculosa Carr et P.
29. R. junghuhniana Nees et Lindlb.
30.a. R. collata sp. nov. - mitosis in antheridial cell
30.b. R. collata sp. nov. - mitosis in apical cell in female plant.
Fig. 5.1D

21. 22. 23.

24. 25a. 25b.

26. 27. 28.

29. 30a. 30b.
FIG. 5.1 E.

Drawings of mitosis (32a – 33d) in antheridial cells, ca. x 2,200.

31 a. *R. limicola* sp. nov. – *mitosis* in apical cell in female plant.
31 b. *R. limicola* sp. nov. – *mitosis* in antheridial cell
32 a. *R. duplex* Lorb var. *duplex*
32 b. *R. duplex* var. *megaspora* var. nov.
33 a. *R. multifida* var. *multifida* var. nov.
33 b. *R. multifida* var. *filiforme* var. nov.
33 c. *R. multifida* var. *divaricata* var. nov.
33 d. *R. multifida* var. *torticolla* var. nov.
FIG. 5.2

Karyotypes and idiograms ca x 2,200


2. *R. areolata* sp. nov.

3. *R. longiciliata* sp. nov.
FIG. 5.3

Karyotypes and idiograms ca x 2,200

2. *R. blackii* sp. nov.
3. *R. asprella* Carr. et P.
FIG. 5.4

Karyotypes & idiograms ca x 2,200

1. *R. macrospera* St.

Fig. 5.4
FIG. 5.5

Karyotypes & idiograms ca x 2,200

1. *R. discolor* L. et L. (from female plant)

2. *R. discolor* L. et L. (from male plant)

3. *R. billardieri* Mont. et N.

4. *R. billardieri* Mont. et N.
Fig. 5.5

1.

2.

3.

4.
FIG. 5.6

Karyotypes & idiograms  ca x 2,200

1. *R. caroliniana* sp. nov (from the apical cell of the female plant).

2. *R. caroliniana* sp. nov. (from antheridium)

3. *R. gangetica*. Ahmed
Fig. 5.6

1. 

2. 

3. 
240.
FIG. 5.7

Karyotypes & idiograms ca x 2,200

1. *R. sorocarpa* Bisch

2. *R. lamellosa* Raddi

3. *R. rorida* sp. nov.
FIG. 5.8

Karyotypes & idiograms  ca x 2200

1. *R. olgensis* sp. nov.

2. *R. marginata* Carr et P.
FIG. 5.9.

Karyotypes and idiograms ca x 2,200


2. *R. albida* Sull.

3. *R. nigrella* DC.
FIG. 5.10

Karyotypes & idiograms ca x 2,200

1. *R. duplex* var. *duplex.*

FIG. 5.11.

Karyotypes & idiograms ca x 2,200

1. R. multifida var. multifida
2. R. multifida var. filiforme var. nov.
3. R. multifida var. divaricata var. nov.
4. R. multifida var. torticollis var. nov.
Fig. 5.11

1.

2.

3.

4.
FIG. 5.12.

Karyotypes & idiograms ca x 2,200

1. *R. spongiosa* St.

2. *R. muscicola* St.

3. *R. deserticola* St.

4. *R. crassa* St.
Fig. 5.12

1.  

2.  

3.  

4.  

(117,31)
FIG. 5.13.

Karyotypes & idiograms ca x 2,200

1. *R. vesiculosa* Carr. et P.

2. *R. papulosa* St. var. *papulosa*

3. *R. papulosa* var. *variabilis* var. nov.
Fig. 5.13

1.

2.

3.
FIG. 5.14.

Karyotypes & idiograms ca x 2,200

1. **R. crystallina** L.

2. **R. cavernosa** Hoffm.

3. **R. collata** sp. nov. (from antheridium)

4. Ricollata sp. nov. (from the apical cell of the female plant).
FIG. 5.15.

Karyotypes & idiograms ca x 2,200

1. *R. limicola* sp. nov. (from antheridium)

2. *R. limicola* sp. nov. (from the apical cell of the female plant)

VI.

POLYPLOIDY IN "R. FLUITANS-COMPLEX".

"R. fluitans-complex" is a species-complex of aquatic and terrestrial form having narrow multifurcate strap-like thalli and comprising sterile as well as fertile species. The plants belonging to this group have extremely variable vegetative characters which react to slight environmental differences.

Previously, the name *R. fluitans* was applied to various taxa of this group (Donaghy, 1916; Familler, 1920; Gaisberg, 1921; Evans, 1922) and sometimes to *R. hubineriana* Lindb., a closely related species. Experimental work on the two aquatic forms of *Riccia* by Carter (1935) did not provide definite distinctions between these plants. She only concludes that the "broad terrestrial form" is sterile and possibly *R. fluitans* L., and the "narrow thalli" which are fertile possibly *R. canaliculata* Hoffm.

The work on cytology (Lorbeer, 1934) and cultural experiments (Müller, 1940, 1941) of "R. fluitans-complex" in Europe shows that there are 4 species belonging to this group: *R. rhenana* (n=16), sterile; *R. fluitans* (n=8), sterile; *R. duplex* (n=16), fertile (monoeccious); *R. canaliculata* (n=8), fertile and probably dioecious. Müller's contributions have been generally accepted and these 4 species are now usually recognized. There are, however, a few species which were described earlier and despite Müller's contribution, still remained uncertain in their taxonomic status. They are: *R. acutisulca* St., *R. multifida* St., *R. burnettensis* St., *R. cancellata* Tayl.
(?) R. linearis Schiffn., R. hasskarliana St., R. stricta Arnell and R. abuensis Bapna. All of these plants need a careful investigation. The first four species were reported from Australia, R. acutisulca and R. cancellata are still unknown, R. burnettensis is established as a synonym of R. multifida (see Chapter III; R. multifida St.)

Recently, Berrie (1964) suggested that R. rhenana is possibly a diploid R. fluitans and R. duplex is probably a diploid R. caeniculata. Since living authentic material of R. duplex was not available to him, he was unable to make a true comparison between the latter pair.

The collections of the "R. fluitans-complex" from various places in Australia, there are both haploid and diploid taxa which are mainly monoecious. Among the monoecious taxa, 4 are haploid and 2 are diploid. It was found that one of the diploid species is similar to R. duplex Lorb. in every aspect and the other is slightly different (R. duplex var. magaspura nov.). For the monoecious haploid taxa viz. R. multifida St., R. multifida var. filiforma var. nov., R. multifida var. divaricata var. nov., and R. multifida var. torticolla var. nov., they seem to share similar characters as well as habitat with R. duplex, e.g. spore characters and semiterrestrial habit. There is, then, a possibility that R. duplex may have evolved from either of these species.

The present studies then had been carried out with the same procedure as that of Berrie (1964), in an attempt to find out the relationship between the haploid species with the diploid one.
Observation.

The treated thalli of *R. multifida* St., *R. multifida* var. *filiform* and *R. multifida* var. *torticollis* show different reactions to colchicine treatment (Table 5.1). For *R. multifida* var. *divaricata* which was collected in the beginning of 1969 has not been treated with colchicine, but a natural diploid arose from the haploid clone after growing under the same condition as the others for 7 months.

Among the three varieties treated, the diploidized *R. multifida* was the only one that showed normal growth and produced spores. The vegetative and spore sizes increase almost 1/3 the size of the haploid plant. The diploid thalli show less frequent branching, but maintains all other characters (Pl. 6.1, 2). The diploid spores are larger (Pl. 6.2, a & b) and the number of areolae increased from 7-8 to 10-14, the wing and the papillae are the same as those of the haploid species (Pl. 6.2, e,b,c & d). For the karyotype, the chromosome set of the induced diploid *R. multifida* is the duplicate set of the haploid *R. multifida* and each chromosome seems to correspond to each other with the haploid set (Fig. 6.1, 1 & 2).

For *R. multifida* var. *filiforme*, the induced diploid plant behaved in the same way as the above species (Pl. 6.1, 3, Table 6.1), except its spores are abnormal. The spore mother-cells fail to divide into normal tetrads. According to the induced diploid *R. multifida* var. *filiforme* hardly produced capsule, this prohibits the further observation of meiosis. The karyotype from the vegetative thalli seems to be the
normal duplicated set of the haploid one.

In R. multifida var. torticolla, the treatment resulted in abnormal growth of the thalli (Pl. 6.1, 4), but the plant still remained haploid. The affected thalli produced larger cells at the margin and develop tuber-like structures instead of capsules. No capsules were observed even after growing for nearly two years.

The natural diploid R. multifida var. divaricata is also simply a large form of the haploid one (Pl. 6.1, 5; Table 6.1), but not forming capsule.

The morphological features of the induced diploids and natural diploid are compared with the parent haploids in Table 6.1.

Discussion.

The abnormality found in the treated thalli of R. multifida var. filiforme and R. multifida var. torticolla may have arisen by the different sensitivity of these two plants to colchicine treatments. The different concentrations of colchicine and different periods of treatments had been tried and it was found that: if the concentration is less than 0.3%, no matter the period of treatment is 6 or 8 hours the plants still remain in its haploid stage, but if the concentration is higher than 0.5% or 0.5% with longer period the plants produce callus-like tissue and soon die. The latter effect also occurred in attempts to induce diploid plants of R. muscicola, R. crinita and R. nigrella.

For the diploid R. multifida and R. multifida var. divaricata it has not been possible to show that
TABLE 6.1

Comparing the haploid species with the induced diploids.

<table>
<thead>
<tr>
<th>Species</th>
<th>width of thallus</th>
<th>No. of air chambers</th>
<th>size of spores</th>
<th>no. of areolae</th>
<th>size of areolae</th>
</tr>
</thead>
<tbody>
<tr>
<td>R. multifida (haploid)</td>
<td>0.5-1</td>
<td>8-10</td>
<td>±80</td>
<td>7-8</td>
<td>7-8</td>
</tr>
<tr>
<td>R. multifida diploid</td>
<td>1-1.2</td>
<td>12-14</td>
<td>±100</td>
<td>10-14</td>
<td>8-10</td>
</tr>
<tr>
<td>2. R. multifida var. filiforme (haploid)</td>
<td>±0.5</td>
<td>6-7</td>
<td>±70</td>
<td>5-7</td>
<td>6-8</td>
</tr>
<tr>
<td>induced diploid</td>
<td>±0.7</td>
<td>10-12</td>
<td>abnormal spores</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. R. multifida var. torticollis (haploid)</td>
<td>±0.6</td>
<td>7-10</td>
<td>±70</td>
<td>9-10</td>
<td>6-3</td>
</tr>
<tr>
<td>treated haploid</td>
<td>±0.8</td>
<td>8-10</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. R. multifida var. divaricate (haploid)</td>
<td>±0.8</td>
<td>8-10</td>
<td>±75</td>
<td>6-7</td>
<td>6-8</td>
</tr>
<tr>
<td>natural diploid</td>
<td>1-1.2</td>
<td>10-12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R. duplex</td>
<td>±1</td>
<td>8-12</td>
<td>±85</td>
<td>6-7</td>
<td>10-15</td>
</tr>
</tbody>
</table>
either of these diploid plants is similar to *R. duplex* (Pl. 6: 1, 2, 3, 4 & 5). Since the induced diploid and the natural diploid seem to maintain their characters closely to the haploid form, it is suggested that *R. duplex* may not have directly arisen from any of the haploid species. The diploidization may possibly originate from the haploid species; but the gradual process of further differentiation i.e. mutation, translocation and selection under different circumstances in either or both haploid and diploid plants may be a separating mechanism; or they are allopolyploid. This may explain why *R. duplex* has two different sizes of microchromosome and the induced diploid species has 2 identical microchromosomes.

These observations, together with the comparative karyotypes (Chapter 5) indicate that it is improbable that any of the diploid species have arisen recently as simple polyploidization of existing haploid species.
FIG. 6.1

Drawings of karyotypes & idiograms  ca x 2,200

1. *R. multifida* St. var. *multifida*

2. The induced diploid *R. multifida* St.
   var. *multifida*. 
Plate 6.1

Photographs of plants, x10, showing R. duplex, and the haploid with the induced diploid in R. fluitans-complex.

1. R. duplex.

2. R. multifida var. multifida - left, haploid; right, diploid.

3. R. multifida var. filiform - left, diploid; right, haploid.

4. R. multifida var. torticollis - left, treated thallus.

5. R. multifida var. divaricata - left, diploid; right, haploid.
PLATE 6.2

a & b. - spores of the induced diploid

*R. multifida* var. *multifida* x 730

c & d. - spores of *R. multifida* var.

*multifida* (haploid) x 730
VII.

FINE STRUCTURE OF SPORE WALL.

Introduction

Since the last two decades of the 19th century, many investigators have examined sporogenesis and spore wall stratification in bryophytes (Davis, 1889; Farmer and Moore, 1905; Beer, 1906; Humphrey, 1906; Clapp, 1912; Black, 1913; Blair, 1926; Siler, 1934; Jovel-Ast, 1966, 1967). Beer was the first who examined the spore development of the genus Riccia, showing the fundamental characteristics of the wall stratification (see fig. 7.1, 1, 2, 3, 4 & 5 for diagrametic of spore wall of Riccia) and its chemical constitution. He observed that the spore wall is formed within the "special cell wall" or "the special-mother-cell wall". Three layers can be distinguished in the mature spore wall; 1) The thin laminated first spore wall, 2) The outer loosely arranged lamellar secondary spore wall, and 3) The inner homogenous layer. He also mentioned the "mucilage plug" that formed at the equatorial rim. A few years later, Black (1913) investigated the development of the spore coat in Riccia frostii. Her observation agrees with those of Beer, except that the "mucilage plug" was not observed. After Beer and Black, the study of the spore wall character did not receive any attention until Jovel-Ast (1966) made an attempt to compare the wall structures of R. crystallina and R. cavernosa, and again in 1967 when she studied the tetrad spore of R. perssonii. So great is the variation of spore wall form and ornamentation within this genus, such features are of considerable use in Taxonomic studies.
Since the light microscope observations are limited by the resolving power of the microscope, by the use of electron microscopy, it should be possible to obtain a better understanding of the spore features which give rise to the ornamentations and the opacity.

Since the following investigation was undertaken to clarify our knowledge of Taxonomic characters of the mature spore, it has concentrated upon the stratification and sculpturing of the wall.

**Materials and Methods.**

Spore material of 14 selected species representing 8 groups were freshly fixed from the living material. Mature tetrads with pigmentation and sculpturing were chosen as, at this stage, the spore has developed all the principal characters of the fully mature stage except that they are still loosely held in tetrads. It was found that at this stage it was easier to fix and section the material.

Fixation and embedding methods were used as follow:

1. Prefix with 3% glutaraldehyde in 0.025 M phosphate buffer pH 6.8 for 24 hours at 5°C.
2. Wash in same buffer (+ sucrose), two changes about 30 minutes at room temperature.
3. Post-fixation in 2% O₃O₄ in same buffer for 2 hours at r.t.
4. Wash in distilled water 4 minutes, two changes.
5. Dehydrate through ethanol series: 30%, 50%, 70%, 80%, 90%, 15 minutes of each and follow by 2 changes of absolute alcohol for 2 hours.
6. Infiltration with mixture of propylene oxide
and absolute alcohol (equal part) for 30 minutes, then
change to pure propylene oxide for 30 minutes.

7. Transfer to 50:50 propylene oxide and araldite
mixture, leave overnight or few days.

8. Change to fresh araldite mixture and leave for
24-48 hours at room temperature.

9. Embedding in fresh araldite mixture in gelatin
capsule and leave in oven at 60–65°C for 2 days.

Sections for electron microscopy were cut
using a glass knife with the Porter–Blum ultramicrotome.
The sections were about 600–700 Å thick.

Electron microscopic observations and electron
micrographs were made using Simms Elmiskop I at the
Electron Microscope Unit, Sydney University.

Observations.

Morphologically, the spores of Riccia spp. are
of many types (Fig. 2.4) as those described by using light
microscope and can be grouped by its form (shape) or
sculptured or colour. The EMGs (electron micrographs)
of spore wall of 14 species observed, shows the basic
similarity of the intine layer, but variations in the
exine such as the thickness of the layers, the size of
granules and their density, and the gaps between
laminae are quite evident.

References to the EMGs of the spores of
Bryophytes (Afzelius, 1957; Gunther, 1960; McClymont
& Larson, 1964; Horner et al, 1966) shows that the
stratification in Riccia is similar to that of Riccardia
pinguis which also shares the lamellated exine structure
with Lycopodium (Afzelius et al, 1954). The terminology
used in this present description follows that used by
Horner (1965) who described the spore wall layers of *Riccardia pinguis* as follow:

- **exine**
  - sexine — sculptured outer layer
  - projecting laminae
  - nexine — contiguous inner layer of laminae

- **spore wall**
  - intine — homogenous inner layer

The term "lamina" means an electron translucent band (E.T.B.) limited by electron dense (opaque) bands (E.D.B.) (Fig. 7.1, 6).

The spore wall layers observed in *Riccia* spp. are of two types: 1) with three distinct layers, i.e. sexine, nexine and intine (Fig. 7.1, 8, 10, 11), 2) consisting of two layers, exine and intine (Fig. 7.1, 7 & 9). The sculpturing of spores of all species is mainly formed by the exine, the intine is involved only at the basal part of the sculpturings or not entering into their constitution at all. The laminated exine appears as composed of many laminae. These laminae seem to have a concentric- reticulate structure since in the sections (Pl. 7.5) they branch and join in several places, with the gaps in between. These gaps are normally occupied by granules differing in size between species. The inner part of exine or "nexine" was not observed in every species. In those species with a distinct nexine, it is commonly composed of a few broad laminae with rather dense granules in the gap (Pl. 7.8), but those with indistinct nexine this layer normally clearly separated from sexine at the base of each papilla (Pl. 7.12 & 7.13). The space between sexine and nexine
usually appears only on the distal face of the spore and normally has a large number of granules but does not appear on the proximal face (Pl. 7.17). The size and density of granules in different parts of the exine seem to take part in the colouration of the spore, i.e. its opacity. The dark or opaque spore shows a greater number and density of granules (Pl. 7.3, 7.5) than the light coloured spore (Pl. 7.6). The primexine does not appear as a distinct layer from the exine, except in certain species e.g. *R. limbata* in which a few laminae on the outer side (periphery) seem to loosely arranged (Pl. 7.4). The thin, electron opaque layer which separates the exine from the intine in *Museci* (McClymont & Larson, 1964) is not apparent in *Riccia*.

The intine is homogenous. It shows fibrillar structure and in some species one can trace back the origin of this fibril to its formation by a layer of fine granules (Pl. 7.13). Sometimes, this layer shows a different density, but this might be caused by slight local variations in the fixation or sectioning.

The "perine" appears as an electron translucent layer in some species at the nearly mature stage. (Fig. 7.1, 4 & 5; Pl. 7.6, 7.14). This layer is possibly the persistent special-mother-cell wall which normally disintegrates during the development of the spore in some species, but remains attached to the boundary of the spore at equatorial rim in others. This feature is known as the "wing" ("a "wing" an equatorial narrow fringe", Bratman, 1965) of the spore (Fig. 7.1, 4).
### Table 7.1

**Measurement of spore wall stratification.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Exine</th>
<th>Papilla height from the base of exine, 4</th>
<th>Intine thickness (μ)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Thickness</td>
<td>Lamina thickness</td>
<td></td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>no.</td>
<td>EMB A°</td>
</tr>
<tr>
<td>1. R. bulbosum</td>
<td>3-3.5</td>
<td>12-15</td>
<td>600-1300</td>
</tr>
<tr>
<td>2. R. granitica</td>
<td>3.2-4.6</td>
<td>12-12</td>
<td>600-2000</td>
</tr>
<tr>
<td>3. R. microspora</td>
<td>4.3-4.6</td>
<td>12-15</td>
<td>600-2000</td>
</tr>
<tr>
<td>4. R. limicola</td>
<td>3-4</td>
<td>60-65</td>
<td>600-2000</td>
</tr>
<tr>
<td>5. R. albida</td>
<td>10-12</td>
<td>35-40</td>
<td>300-1000</td>
</tr>
<tr>
<td>6. R. marginita</td>
<td>0.6-0.8</td>
<td>10-12</td>
<td>1000-1300</td>
</tr>
<tr>
<td>7. R. corymbosum</td>
<td>0.8-1</td>
<td>15-16</td>
<td>600-2000</td>
</tr>
<tr>
<td>8. R. crassula</td>
<td>1-1.3</td>
<td>30 forming distinct lamina</td>
<td>27-30</td>
</tr>
<tr>
<td>9. R. bulbosa</td>
<td>1.0-1.1</td>
<td>10-11</td>
<td>1000-2000</td>
</tr>
<tr>
<td>10. R. papusa</td>
<td>2.2-2.5</td>
<td>40-50</td>
<td>600-1300</td>
</tr>
<tr>
<td>11. R. corymbosum</td>
<td>0.8-1</td>
<td>12-15</td>
<td>600-1300</td>
</tr>
<tr>
<td>12. R. corymbosum</td>
<td>1.5-1.6</td>
<td>20-22</td>
<td>800-1300</td>
</tr>
<tr>
<td>13. R. crassula</td>
<td>1.3-1.5</td>
<td>13-15</td>
<td>600-1300</td>
</tr>
<tr>
<td>14. R. limicola</td>
<td>0.8-1</td>
<td>10-12</td>
<td>600-1300</td>
</tr>
</tbody>
</table>
Discussion

The previous light microscope observations of the sporogenesis and spore wall formation of *Riccia* spp. (Beer, 1906; Black, 1913; Jovet-Ast, 1966 & 1967) provide a good foundation for understanding the character of the wall stratification and its composition. Beer (1906) gives an excellent description and illustrations of spore development and the spore wall layers. His interpretation of the spore wall of *Riccia glauca* is that it is developed and deposited internally by the individual spore protoplast and, at maturity, consists of three layers. The first spore wall is a rather densely laminated structure and becomes deeply stained with aniline blue, generally regarded as indicative of callose. It has an uneven outline forming papillose projections. The secondary spore wall is divided into two layers: the outer laminated layer and the inner homogenous layer. The outer layer consists of loosely arranged lamellae which sometimes lie closely against the first spore wall and separated widely at the equatorial rim from the first spore wall, which he calls the "mucilage plug" (Erdtman, 1965, "pore-like marginal depression"). This second outer layer probably consists of pectose-cellulose substances. The inner zone is generally separated from the loose lamellae by a gap; it has a homogenous appearance which he believed is really built up of successive lamella. This layer gives the cellulose reaction when stained with iodine.

Comparing Beer's classification of spore wall by light microscope with the present EMGs, it seems likely that what he called first spore wall and outer
part of the secondary spore wall correspond to the "exine" and the inner part of the secondary spore wall is what is here regarded as intine. The dark layer between the outer and inner secondary spore wall (his fig. 26; Pl. 27) is probably the layer of nexine. There is one feature which does not quite agree with his drawing (his fig. 21, 23; Pl. 21) of the section of spore at the equatorial rim. From the EMGs (Fig. 7.15), it shows clearly that the "mucilage plug" is limited by the sexine on the outer face and by the nexine on the inner surface but it was probably beyond the resolving power of his light microscope to differentiate the detailed construction of the exine layer.

Black (1913) confirms Beer's observations in her study of the development of the spore coat in Riccia frostii. After these two works, there was no other report until in 1957. Erdtman (1957) including some observations of the spore characters of Riccia in his general description of the spore of bryophytes. The detail of the wall constitution as far as he describes the spore of Riccia beyrichiana is "sclerine" is comparatively thick, consisting of an inner, possibly laminated "nexinous" and an outer more or less undulating or reticulate "sexinous" layer, the latter is often provided with spina or spinular-like process, the inner, central part of which indicating that the processes are provided with a central hollow communicating with void space between the "sexinous" and the "nexinous" layers. This also agrees with the present observation, except for the detail characters of each layer which he did not mention.

The recent studies of Riccia crystallina,
R. cavernosa and R. personii with particular reference to the spore wall by Jovet-Ast (1966, 1967) are based on light microscopy. Therefore it was impossible for her to observe the fine structure of the wall. In fact, she only found it possible to distinguish the number of layers and a little information about their composition.

The 14 species observed show a great deal of variation in the exine stratification from subgenus to subgenus, group to group and even from species to species.

In the subgenus Ricciella, there is the basic similarity in the number of layers, i.e. in all of the species observed, their spore wall is composed of sexine, nexine and intine, large and dense granules are not apparent, (Fig. 7, 1, 10) but they differ in the thickness and density of laminae in the exine layer. R. papulosa (Pl. 7, 10) which represents the group with a large thallus and large spore has the thickest exine and intine. (Table 7, 1) of all the subgenus Ricciella. It also shows the compact laminae in the sexine layer, papilla without a central hollow, the nexine separated from the sexine by a narrow gap with denser granules than the sexine.

For others viz. R. crassa (''R. vesiculosa'' group), R. crystallina and R. oeovernos (''R. crystallina'' group) and R. limicola (R. fluitans-complex group), they are not distinctly different in the thickness of exine and intine (Table 7, 1, Pl. 7, 11 - 7, 14). The EDB of all species are comparatively thin as well as the ETB. R. cavernosa which has rather dark and opaque mature spores shows the largest size of granules 300-500 A° while in others they are only 50-150 A°. It shares the indistinct nexine layer with R. crystallina (Pl. 7, 12, 7, 13), its closest species, and the difference between these 2 species are the
density of laminae and the size of granules (Table 7.1) not in the number of layers as suggested by Jovet-Ast (1966). *R. crassa* (Pl. 7.11) has a distinct sexine and nexine. The sexine character is similar to the "*R. crystallina*" group in the number of laminae. In the features of the nexine it is closer to those of *R. papulosa* in having rather dense granules but this layer in *R. crassa* is separated from the sexine by a wider gap. For *R. limicola*, the character of the sexine resembles that of *R. papulosa* (Pl. 7.14 & 7.10) in the size and characters of laminae (Table 7.1) as well as the granules, except the latter has a thicker and more compact sexine. The nexine of *R. limicola* is similar to its sexine and broadly separated from the latter.

In this subgenus, there seems to have been some relationship between each species as well as between each group. The exine structure is less differentiated and the size of granules is almost the same as the EDB. This character shows that the EDB is possibly formed by a simple line-up of the granules and the formation of the laminae is of regularly centripetal type which results in rather uniform exine features. The small size of the granules which rarely appear in the sexine but sometimes are present sparsely in the gap or in the nexine appears to be a characteristic of this subgenus although more species need to be examined.

In subgenus *Riccia*, the variation among species and groups is clearer. The group which normally possesses large purple scales and is drought resistant produces rather opaque spores, the spore wall characters are different among sub group such as the structure of laminae between the sub group with globose spore ("*R. macrospora*"
group) and with triangular-globular spore ("R. limbata" group). *R. billardieri*, *R. gangetica* and *R. macrosperma* belong to the former subgroup have broad and irregularly arranged laminae with numerous granules in between (Fig. 7.1, 7, Pl. 7.1, 7.2 & 7.3); while in *R. limbata* of the latter subgroup has narrower and more uniform laminae with fewer granules than the former (Fig. 7.1, 7 & Pl. 7.4). This may indicate the different line in their evolution or possibly each subgroup had not arisen from the same origin. *R. billardieri*, *R. gangetica* and *R. macrosperma* show their closely related spore characters especially between the first two species, they only differ in the density of granules which seems to be rather dense and uniformly scattered in *R. gangetica* but less dense in *R. billardieri*; and the exine and intine of the former are thicker than the latter (Pl. 7.1 & 7.2, Table 7.1). *R. macrosperma* (Pl. 7.3) shares all spore wall stratification characters with its closely related species, except in this species every character is of the larger size (Table 7.1) and exine layer is compact with large granules.

*R. albida* which is a distinct species in having smooth and globose spore also shows distinct characters of the spore wall (Fig. 7.1, 8 & Pl. 7.5, a & b). It has the thickest exine (10-12 μ) which is composed of thick EDB and large granules. The laminae of this species differ from those of other species in having thick EDB and very thin ETE (Table 7.1, 5) in showing a very clearly reticulate net work, and in not forming papillate sculpture. The nexine is composed of thin laminae without granules.

*R. marginata* which represents the group of plants
with hyaline scales, has spore wall characters resembling those of subgenus Ricciella (Fig. 7.1, 10 & Pl. 7.6, a & b) in almost every aspect (Table 7.1).

Throughout the "ciliata" group *R. crozalsii*, *R. areolata* and *R. blackii*, the wall structure is very similar to each other (Fig. 7.1, 11 & Pl. 7.7, 7.8, 7.9), but different from other groups. It appears that the exine of this group is not composed of distinctly layers of EDB and ETB especially in *R. areolata*. The irregularly arranged laminae seem to cause by the deposition of 2 types of granules, the fine and less electron dense granules forming the electron translucent part of the exine, while the coarser and electron dense granules form the scattered EDB. In this group, some species like *R. blackii* and *R. areolata* has a deposition of various size of granules on its outer surface (Pl. 7.8 & 7.9) which is rather unusual among *Riccia* spp. The origin, formation and function of these granules need a further study of the development of the spore. The nexine is separated from sexine by a narrow gap usually with scattered granules.

For this subgenus, it appears that each group has rather distinct features of the exine which distinguish between the groups. The laminate-granulate exine type of the subgroup *R. macrospora* - group (Fig. 7.1, 7) is quite different from that of *R. albida* (Fig. 7.1, 8) in the sculpturing formation, the laminae and the granules. *R. marginate* of the *R. sorocarpa* - group is very similar to *R. crassa* of the "*R. vesiculosa*" group in subgenus Ricciella, the same as *R. limbata* of the "*R. limbata*" group with "*R. papulosa*" group has an exine resembling *R. papulosa* (Fig. 7.1, 9). The "*R. ciliata*" group has a
different formation of exine (Fig. 7.1, 11) and is not related to other groups.

Between subgenus Riccia and Ricciella, some species of each subgenus share the exine structure with each other as mentioned above. This shows the possibility that some species in the former subgenus have evolved from the latter subgenus or vice versa.

This would appear to be the first E.M. survey of the wall construction in Riccia. It raises many interesting points for present and further studies. There are 4 major types of exine composition in the 14 species examined: 1) The laminate-granulate type of the subgroup "R. macrosperma" (Fig. 7.1, 7), 2) The laminate-granulate type of R. albida (Fig. 7.1, 8), 3) The laminate with small and few granules type of most Ricciella (Fig. 7.1, 10) and 4) The granulate-laminate type of the "ciliata" group (Fig. 7.1, 11). Regarding the papillae, there are two types: one with a central hollow (Fig. 7.1, 7, 10 & 11) and the other with a solid structure (Fig. 7.1, 9).

The presence of granules on the outer surface of the exine of R. areolata (Pl. 7.8) and R. blackii (Pl. 7.9) would be of particular interest in the study of its sporogenesis and chemical constinctions. Since in others, there is no evidence of external disposition on the exine. This might suggest that there is more than one type of spore wall development among Riccia. Furthermore, the appearance of various sizes of granules in the developing spore may indicate a different function in forming certain parts of the spore wall. The large granules seem to form from group of small granules (Pl. 7.8), and in most species the size of granules between laminae is
almost the same as EDB (Pl. 7.5). The newly formed EDB already shows the line-up of small granules (Pl. 7.16), this confirms Sitte's hypothesis of layer formation (1959, 1960) which he suggested that the lamellar (= EDB, using here) may have formed from the hold together of the thin sheets (thin sheets = 1 granule layer in thickness) forming thicker layers. In Riccia case the EDB may form from two types: one from a single layer of granules which equal to Sitte's "thin sheet", and another from a combined "thin sheets" which resulted in a thick laminae.

The present study indicates difference in exine stratification from the flowering plants, gymnosperms, pteridophytes (except Lycopodium) and most of the bryophytes (Heslop-Harrison, 1962; Erdtman, 1957, 1965; Larson et al, 1962; McClymont & Larson, 1964; Gunther, 1960). The most closely related groups appear to be Lycopodium (Afzelius et al, 1954) and Riccardia pinguis (Horner et al, 1966). Riccia shares most of the general characters with the latter, except that in Riccardia pinguis the papillae are composed of loosely arranged laminae which are not continuous and without granules (Horner et al, 1966; Fig. 34-39). The spore wall of the Musci appear to be quite different from those of Riccia.

It is very interesting that the spore wall stratification among the Musci is comparable with those layers described for pollen (McClymont & Larson, 1964). The exine layer is non-stratified and is an electron opacity structure. The intine is quite thick and multi-layered. This difference between mosses and hepatics spore wall may support Chopra's conclusion that neither of the two taxa has been derived from the other (Chopra, 1969).
Conclusion

The results of this investigation show the following: (1) the similarity of the intine layer in all species observed; (2) the variation of exine composition among groups and between closely related species, there are such variations as the thickness of layers, the size of granules, the formation of papillae and the separation into sexine and nexine, these should prove to be of taxonomic value; (3) the strongly resemblance of spore wall stratifications of *R. macrospera* St., *R. gangelo* Ahmad and *R. billardieri* as well as the "ciliate" group which has the deposition of granules on its outer surface; (4) the completely different spore wall stratification between mosses and hepatics (*Riccariad* & *Riccia*) which is another character indicates the different evolution of these two groups.
273.
1,2,3,4, & 5 - diagrams showing the development of the spore wall; 1, spore mother cell; 2 & 3, spores in tetrad; 4, spore at nearly mature stage; 5, mature spore.
6, diagram showing the exine structure.
7,8,9,10 & 11 - types of spore wall stradifications in Riccia spp.

**SMW** = spore mother-cell wall

**SMCW** = special mother-cell wall

**SW** = spore wall

**M,m** = mucilage plug, or enlarged marginal angle

**W** = wing

**p** = papilla

**pe** = perine, parin

**ex** = exine, se = sexine, ne = nexine

**in** = intine

**EDB** = electron dense band

**ETB** = electron translucent band

**L** = lamina

**g** = granules

(in all figures)
PLATE 7.1

*R. billardieri* Mont et N.

a. Part of the spore wall  x 5,000

b. Portion of the exine  x 30,000

In all figures:

- p = papilla
- e = exine
- s = sexine
- n = nexine
- i = intine

EDB = electron dense band
ETB = electron translucent band
G = granule
275.
PLATE 7.2

*R. gangelica* Ahmad

a. Part of the spore wall $\times$ 5,000

b. Portion of the exine $\times$ 30,000
PLATE 7.3

*R. macrosperma* St.

a. Part of the spore wall  \(\times\) 5,000

b. Portion of the exine  \(\times\) 30,000
PLATE 7.4

*R. limbata* Bisch

a. Part of the papilla x 5,000

b. Portion of the exine x 30,000

c. Portion of the intine x 30,000
PLATE 7.5

R. albida Sull.

a. Part of the exine x 5,000
b. Portion of the exine x 30,000
c. Part of the intine and nexine x 30,000
PLATE 7.6

*R. marginata* Carr. et P.

a. Part of the spore wall x 15,000

b. Portion of the spore wall x 30,000
PLATE 7.7

*R. crozalsii* Lev.

a. Part of the spore wall  × 5,000

b. Portion of the spore wall  × 30,000
PLATE 7.8

*R. areolata* sp. nov.

a. *Part of the spore wall* × 15,000

b. *Portion of the spore wall* × 30,000
PLATE 7.9

*R. blackii* sp. nov.

a. Part of the spore wall \(\times 10,000\)

b. Portion of the spore wall \(\times 30,000\)
PLATE 7.10

*R. papulosa* St.

a. Part of the spore wall x 5,000

b. Portion of the exine x 30,000

c. Portion of the exine x 30,000
PLATE 7.11

*R. crassa* St.

a. Part of the spore wall $\times 10,000$

b. Portion of the exine $\times 30,000$
PLATE 7.12

*R. cavernosa* Hoffm

a. Part of the spore wall  x 5,000

b. Portion of the sexine  x 30,000
PLATE 7.13

*R. crystallina* L.

a. Part of the spore wall x 10,000

b. Portion of the spore wall x 30,000
PLATE 7.14

*R. limicola* _sp. nov._

a. Part of the spore wall x 10,000

b. Portion of the spore wall x 30,000
R. crozalsii Lov

Part of the spore wall at the marginal angle showing the mucilage plug.
PLATE 7.16

R. cavernosa Hoffm.

Part of the developing spore wall, showing the EDB formed by the layers of granules.
290.
PLATE 7.17

*R. aveolata* sp. nov.

Part of the spore wall from proximal face x 20,000
DISCUSSION

The earliest occurrence of the Marchantiales is from the Rhaetic-liasic of Sweden (Lundblad, 1954). The possession of chambered thallus bearing definite pores of the Marchantiacolites Lund. and of the spore tetrads of Ricciisporites Lund. closely resembles the extant genus Riccia and probably they were the ancestral stocks of the present Marchantiales. Lundblad (1954) also points out that the spore tetrads of the Ricciisporites Lund. are comparable with those of the living Riccia curtisii Jam., and "Ricciisporites is most probably the spore of Ricciopsis; both genera may correspond to plants habitually similar to the modern Riccia". This may indicate that chambered thallus and the synspora forms are more primitive than the solid thallus and separated spore forms. If so, then the "semiterrestrial" group which including R. curtisii Jam. R. perssonii Khan etc. are probably the sources of derivations among Riccia spp. and possibly from this group the evolution within the genus has been largely determined by adaptation to aquatic and terrestrial habitats. In the first case a few species have a free-floating aquatic form which occasionally becomes terrestrial, while in the latter case many species are still hygrophilous plants and the others are xerophilous species which show different ways of becoming adapted to the same habitat.
ADAPTATION TO AN AQUATIC HABITAT

The "R. fluitans-complex" seems to migrate from terrestrial form to an aquatic form as most of the species except R. fluitans L. and R. rhenana Lorb. are still showing the main part of their life-cycle on land and only occasionally become floating forms. The adaptations to an aquatic habitat of this group are simply by the reduction of the size of the thallua (which is thin and narrow), rhizoids, scales and airpores whilst the thallus develops a loosely arranged tissue with large airspaces.

ADAPTATION TO A DRYER HABITAT

The apparent morphological adaptations to the dryness found in this genus are as follows.

1. The resistance of the protoplast to drying out, and the power to become air-dry yet still viable similar to those of terrestrial algae (Jeffrey, 1962). This occurs in a few species of the subgenus Ricciella, i.e. R. spongiosa, R. papulosa, but in almost all species of the subgenus Riccia this is accompanied by other adaptive characters.

2. The development of outer, spongy, dead cells protecting the inner living part, e.g. R. albida sull.

3. The possession of large scales at lateral-ventral side which, in dry situations, will curve inwards and cover the upper surface of the thallus.
This is found in almost all *Riccia* spp. with large scales, e.g. *R. limbata* Bisch, *R. macrospora* St., *R. lamellosa* Raddi etc.

4. The presence of cilia at the margins and sometimes on the dorsal surface of the thallus of the "Ciliata" group which behave the same way as the scales protecting the thallus in the previous cases and may serve to trap what little water there is.

5. The forming of tuber-like structures which frequently occur in the species belonging to the tropical monsoon climate, i.e. *R. billardieri* Mant et N., *R. discolor* L. et L. etc. The tuber behaves like a dormant part of the thallus which will give rise to a new thallus under a favourable conditions.

6. Having photosynthetic part on ventral side of the thallus especially at the scales which is protected by the upper hyaline tissue, e.g. *R. caroliniana*. Parihar (1965) suggests that the possession of chloroplasts in the scales of the hepatic is an adaptation to moist conditions as Mehra (1957) reports such the scales of *Asterella blumeance*, *A. reticulata* etc., but those are quite different from the case in *R. caroliniana* in which other parts of the thallus are devoid of chloroplasts and the plants are found growing in a dry situations.
7. The duration of spore viability, for which infact no experimental data has been recorded, will probably show a correlation between the taxon and its ecology (Schuster, 1966). Schuster (1959) also mentions that in R. atromarginata its spores will be at least as highly resistant to desiccation as the vegetative thalli. For the annual species, i.e. R. crystallina L., the spores are the only surviving part from one growing season to another and retain their viability for a rather long period, at least almost one year. This duration period is probably longer in xerophilous Riccia which shows a thicker spore wall layer than those of the hygrophilous forms (see chapter VII). Those species which are highly resistance to drought conditions appear to have a large number of granules associated with a thick exine layer, i.e. R. albida, R. macrospora, R. areolata etc. which probably assist in resistance of the spore wall to extreme environmental changes.

From the cytological point of view evolutions appears to have occurred at two levels:

1. Adaptation at the haploid level which has been accompanied by chromosomal changes such as translocations, deletions and probably mutations etc., as indicated by the differences in the relative sizes of chromosomes within
sets (see chapter V, Cytology) or even without altering visibly the external appearance of the chromosome. The changes in sequence of genes by translocations, crossing over etc. which will gradually bring about altered karyotypes (Swanson, 1957). These together with other changes in basic number involving loss or gain of "dot" or microchromosomes, appear to be the cause of evolution among the haploid Riccia. This type of evolution can be seen in R. areolata, R. asprella which produce cilia, R. albida forming spongy dead cells in the outer part of the thallus, R. sorocarpa having a thick secondary epidermal cells, and etc.

2. By diploidisation and polyploidisation which is often found in species of plants adapted to extreme or new habitats (Stebbins, 1950) which also occurs in the genus Riccia, and mainly at the diploid level. Many of the diploid Riccia have features resembling those of their haploid allies, i.e. R. limbata Bisch. and R. nigrella DC., R. duplex Lorb. an and other "R. fluitans-complex", R. longieiliata and R. crinita. This type of diploid is probably an intersubspecies or intervarietal autopolyplloid which is the result of adaption to a new habitat and follows translocations and recombinations of the karyotypes. Other diploid species like
R. marginata, R. blackii, R. gangetica and R. lamellasa may have arisen from hybridization between two closely related species and becoming allopolyploid as they all show less similarity with the related haploid species. Two of the diploid taxa viz. R. billardieri and R. papulosa are possibly only lately derived from their haploid forms by simple doubling of the chromosome sets (see chapter V, cytology). R. macrospora is the only hexaploid species and shares most of the spore characters with R. gangetica a diploid species which was reported to be triploid from India. It seems very likely that R. macrospora is an allopolyploid which is derived from hybridization between two or more distantly related species. This hexaploid species occupies a different habitat from the related diploids and possesses a wider range of drought resistance which has probably resulted from a successful adaptation to the dry habitat since this species is widespread in Central Australia.

The distribution of Riccia spp. in Australia is still rather incompletely known as collections are limited from Western Australia and Queensland. From 33 species collected, 14 could possibly be introduce: R. crozaleii, R. lamellosa, R. nigrella, R. bifurea, R. sorocarpa, R. crystallina, R. cavernosa and R. duplex all are widely distributed throughout the world, especially the last four; R. gangetica, R. billardieri and R. discolor belong to the tropical monsoon countries
i.e. India, Indonesia and probably Southeast Asia, 
*R. junghuhnniana* is only reported from Indonesia, 
*R. limbata* is a South Africa species and *R. albida* is 
only reported from Texas, U.S.A. How and when or by 
what means they arrived in Australia is unknown, and 
likely to remain so. The migrations however must have 
happened.

The evolution of *Riccia* spp. in Australia, 
then, probably occurred in two ways: (1) The adaptation 
of the migrating species to the new environments by 
polyploidisation thus migrating more successfully than 
the unadapted species e.g., *R. macropora*. (2) Evolution 
among the endemic species themselves by hybridizing 
between a closely related species and possibly with the 
migrating species, polyploidisation, translocation, 
recombination, mutation etc.

Among the subgenus *Ricciella*, the relationships 
between species and species connect the groups by group 
and group are very evident and many species showing 
intermediate vegetative and spore characters. For the 
vegetative features, there seems to be an adaptation in 
the formation of aircambers and airpores to various 
habitats which is only slightly different between each 
species and each group. The comparative study of the 
spore walls from the representative of four groups shows 
the similarity of the stratification (see chapter VII). 
Only in *R. papulosa* does the spore wall appear to be very 
thick and rather similar to that of *R. limbata* in the 
subgenus *Riccia*. The diploidisation seems less evident 
and only 2 species are diploid, viz. *R. papulosa* and 
*R. duplex*. Their adaptation to dryer habitat appears 
to be less advanced than those in the subgenus *Riccia*. 

The possible relationship and evolution in the subgenus *Ricciella* is shown in Fig. 8.1.

In the subgenus *Riccia*, each group seems to be demarcated by both vegetative and spore characters, and the relationships between the groups is not so noticeable (Fig. 8.2). The "Ciliata" group shows a great advance in adaptation to dry habitat and such adaptation not only occurs at the haploid level, but also at the diploid level (*R. longiciliata, R. biackii*) which is similar as in the "Squamata" group. The former group is closely related to the "Leavigata" group, but more resistant to dryer habitat. From the vegetative features, it seems very likely that the "ciliata" group is probably derived from the species close to the "Leavigata" group. *R. macrospora* and *R. limbata* are both well adapted to xerophytic habitat, but the formation of the spore stratification shows a great deal of difference (see chapter VII). Subgroup "*R. sorocarpa*" i.e., *R. marginata* which belong to the "Squamata" group does not share the spore characters with "*R. macrospora*" or "*R. limbata*". *R. albida* is a distinct species in having smooth spore wall. The comparative study of the spore wall structures from the representatives of groups and subgroups combined with the vegetative features shows that the evolution among this subgenus is more advanced and more complicated than in the subgenus *Ricciella*. Cytologically, there must have been great changes in the karyotype of each group and even among the same group which probably can be summarized as follows:
1) Environmental conditions promoting evolution.
2) Gradual mutation.
3) Translocations, deletions.
4) Hybridization to form allopolyploid.
5) Aneuploidy (only one species, *R. caroliniana*).

*R. caroliniana* is probably endemic to Australia and has developed a different adaptation to dryness and is not closely related to any other *Riccia* spp. The possession of chlorophyll bearing scales, the hyaline upper surface and the haploid chromosome number of 10 in *R. caroliniana* separate it completely. Possibly this species has only recently evolved and thus has not had the time to achieve a wider distribution.

The investigation of vegetative and spore characters in subgenus *Riccia* and subgenus *Ricciella* shows that there is some relationship between these two subgenera, i.e. *R. marginata* of the former subgenus shares most of the spore characters with *R. crassa* in the latter subgenus and also between *R. limbata* and *R. papulosa*. This may indicate that either species of each subgenus were derives from others.

From the present investigation, the classification of groups and subgroups is still indefinite owing to the number of *Riccia* spp. occurring in Australia being only a few representatives of the whole genus. The division of the subgenera into groups and subgroups here is to provide a better understanding among the Australian *Riccia* and to use as a shorter term when referring to their possible phylogeny. However, it is
expected that a complete investigation of the whole genus alone will give a satisfactory delimitation of the groups and subgroups. The writer also hope that the basic problems of the identification of *Riccia.* in Australia have been reduced and the further investigation of the geographical distribution of this genus, especially in the Tropical zone to the north, should provide a better and clearer understanding of this genus in Australia.
Fig. 8.1

POSSIBLE RELATIONSHIP IN THE SUBGENUS RICCIELLA

TERRESTRIAL

Monocious

R. muscicola
R. grasse
R. deserticola
R. vasculosa
R. junphuthiana

R. collata n.s

Dioecious

R. sppulosa
var. vasculosa n.s
var. variable n.s

R. spongiosa n.s

SEMITERRESTRIAL

Monocious

n.s

R. crystallina
R. cavernosa

Monocious

n.s

R. fluitans-complex

Monocious

n.s

R. duplex var. duplex var. megaspore

Dioecious

R. limicola n.s

R. multiflora var. multiflora

var. filiforme

var. torticolla var. divaricata
Fig. 2.2

POSSIBLE RELATIONSHIP IN THE SUBGENUS BICOA

CILIATA
- R. blanchii
  - R. ciliata
    - R. crozatii

LAEVIGATA
- R. albida
- R. bifera

SQUAMATA
- R. macronema
- R. pampinosa
- R. salicola
- R. discolor
- R. arcata
- R. luteola

SQUAMATA (Scales purple)

VIRIDISQUAMATA
- R. caroliniana

[Diagram showing relationships between the genera and species mentioned above]
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N.B. * not seen in original.

Appendix.


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