

# Spore morphology of Hepaticae in Japan\*

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## Introduction

The spores of Hepaticae have a protective outer coat which is often ornamented with sculptures such as spines, verrucae, granules, and reticula. Therefore, the spore structure is an important taxonomical character in certain Hepaticae, especially in Anthocerotales, Marchantiales and Sphaerocarpaceae, and has usually been illustrated in taxonomical works. External characters of the spores are also often treated in the studies of spore germination. But the studies, which laid stress on the spore morphology and its phylogenetic value, have been neglected. Some characters of the spores such as cell stage, polarity and tetrad scar, are specific and constant in a family or a genus of Hepaticae, and seem to comprise phylogenetic significance in themselves as in the case of Pteridophyta, where for example, tetrahedral triradiate spores are considered more primitive than bilateral monolete spores (Harris

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1955).

Recently in palynology, the spore morphology of Bryophyta has become the object of the palynologist's attention along with pollens and spores of Tracheophyta. My teacher, Prof. Horikawa, who had made a practice of illustrating spores in his taxonomic works (1928, 1929a, b, 1930, 1934), suggested that I undertake this subject for my special study and since 1960 I have been engaged in this project.

The main purpose of this work is to describe and illustrate the spore structure of Japanese Hepaticae, to ascertain the possibility of grouping spores by their characters into family, generic and even specific groups as to their several types and to relate them to their possible phylogenetic significance.

Knox (1939) studied the spores of Bryophyta based upon the materials of various species from Britain and other countries, illustrating the spores of some species of Bryophyta, but did not group them in any way. McClymont (1955), Terasmae (1955), Erdtman (1957, 1965), Tallis (1962), and Miyoshi (1962) described and illustrated the spores of several species of Musci, while Shin (1963), McClymont & Larson (1964), Shin & Muroya (1965) reported an electron microscopical structure of spore walls. Spores of various species of Hepaticae from Sweden and other countries were illustrated and described by Erdtman (1957, 1965). Inoue (1960) pointed out the important relation between germination and the structure of spores, especially the polarity of spores in Marchantiales. Horikawa & Miyoshi (1963) reported from a palynological point of view on the spores of six species representing all generic members of Anthocerotaceae. Ono (1966a, b) also described and illustrated the spores of Jungermanniales. Müller (1948, 1951) measured the ratio of equatorial diameter of spore to width of elater in numerous species of Hepaticae and emphasized its value as a taxonomically important character. Furthermore, Horikawa & Miyoshi (1965) suggested some morphological relationships between spores and elaters.

I wish to express my thanks to Prof. Emer. Y. Horikawa of Hiroshima University for his constant encouragement and for stimulating my interest in the study of Bryophyta. Sincere thanks are also due to Dr. H. Suzuki and Dr. H. Ando of the same institution, for their very helpful suggestions and criticism during the course of the investigation. I must express my gratitude to Prof. Dr. J. Nakamura of Kohchi University and Dr. K. Sasaki of Hiroshima University for their advice on many matters. I also express my thanks to Dr. T. Seki and Dr. K. Nehira for their kind help in collecting and determining the materials. Deep gratitude is also due to many colleagues for their kind help for the materials which they made available to me. Last, but not least, I express my thanks to Mr. L. A. Charette of Burlington for his kind help in editing the manuscript.

## Methods

### Preparations

There are usually two methods to apply for chemical treatment of spores: acetolysis (Erdtman method) and KOH method. The acetolysis method seems to be too intense for spores of Hepaticae and sometimes destroys the spore coat, especially the delicate perine. Therefore, the preparations of the large, unicellular spores with well-developed sculptures were treated by boiling an entire capsule with 10% KOH in a centrifuge tube for a few minutes, and then centrifuged and washed with water. But the unicellular spores, smaller than about  $25\mu$  in equatorial diameter, which have poor ornamentation and can hardly be distinguished into genera or even families from their external sculpture, were not treated with 10% KOH. They were directly mounted in glycerine-jelly under natural dry condition. The multicellular spores also were not treated with 10% KOH because of the exine being

stretched, thin and brittle, and the dry spores were directly mounted in glycerine-jelly under a cover glass sealed with Canada-balsam. However, the multicellular spores of *Conocephalum* and *Pellia*, when mounted in glycerine-jelly, became very irregular in shape and bullate and it was difficult to distinguish each cell stage. On the other hand, the spores mounted in water were swollen and comparatively regular in shape, sometimes showing each cell stage.

### Measurements

Measurements shown in Fig. 1 were made with  $15\times 40$  magnification excluding the sculptural projection. The range of the equatorial diameter based on 50 spores per species is shown in microns with the mean in parenthesis, and in addition, there is given  $m. \pm s.d.$ , namely the mean plus and minus the standard deviation. The KOH method is apt to make the spores change in size, and the spores treated by this method showed some expansion in size as compared with non-treated spores. Other measurements such as thickness of exine, length of polar axis, and sculptures, were shown on the average of 5-10 spores per species. Detailed structures of the ornamentation were observed with  $10\times 100$  magnification.

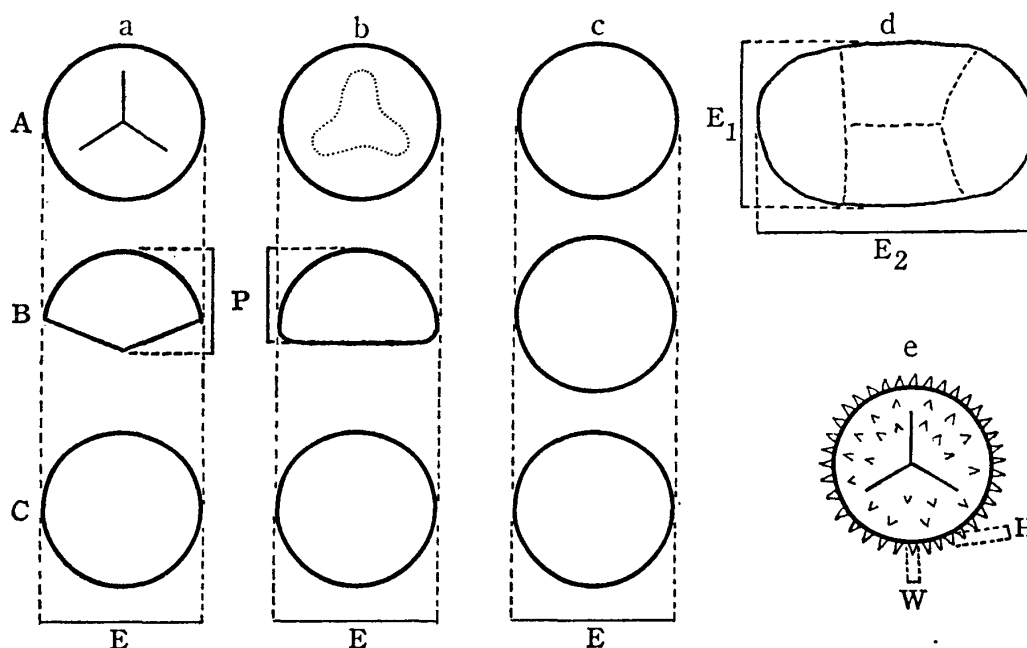


Fig. 1. a-d. Method to calibrate the spores. A: Proximal polar view. B: Equatorial view (Profile). C: Distal polar view. E: Equatorial diameter ( $E_1$ : minor axis,  $E_2$ : major axis). P: Polar axis. e. Method to calibrate the sculptures of spores. H: Height of sculpture. W: Width of sculpture at base.

### Microtome technique

Material was dehydrated in ethyl alcohol and imbedded in paraffin with melting point  $52-54^{\circ}\text{C}$ . The spores or the sporophytes were left in the melted wax in the oven for about 10 days to obtain proper infiltration. Sections were prepared to a thickness of  $5-10\mu$ , those cut  $5-7\mu$  thick being the most satisfactory. The sections were stained by haematoxylin-eosin method (Böhmer's haematoxylin). The ribbons of some sections were mounted in Canada-balsam for permanent preparation.

### Explanation of figures

Figures 2-10 were illustrated at a magnification  $\times 900$  except Figs. 4-d, 5-b, e, 6-d, 7-h, i, 8-q, the magnifications of which are given in the legend for each figure. The following

abbreviations are used in the explanation of figures :

P. p. v. = Proximal polar view. D. p. v. = Distal polar view. E. v. = Equatorial view. P. v. = Polar view. (This abbreviation was used for cryptopolar spores, in which it is difficult to distinguish the proximal from the distal side.) A. = Apolar spore. M. = Multicellular spore.

### Materials

Materials used in this study were collected in Japan either by myself or by my colleagues. These materials represent 3 orders, 28 families, 52 genera and 70 species. Table 1 shows the materials with their localities and dates of collection.

Table 1. Materials and their localities.

Species	Locality	Date	
Anthocerotales			
<i>Phaeoceros laevis</i> .....	Nangoku city, Kohchi Pref.	Apr.	1962
	Taishaku-kyo, Hiroshima Pref.	Sept.	1962
	Onoaida, Isl. Yakushima	Mar.	1963
	Naon, Isl. Amamiohshima	Mar.	1964
	Mt. Yuwan, Isl. Amamiohshima	Mar.	1964
<i>P. miyakeanus</i> .....	Nichinan city, Miyazaki Pref.	May	1946
<i>Anthoceros formosae</i> (f. <i>gemmulosus</i> ) .....	Nichinan city, Miyazaki Pref.	May	1946
<i>A. nagasakiensis</i> .....	Uwami-cho, Ehime Pref.	Mar.	1959
	Nichinan city, Miyazaki Pref.	June	1946
<i>Aspiromitus miyabeanus</i> .....	Hatsukaichi-cho, Hiroshima Pref.	Dec.	1962
		Jan.	1963
<i>Dendroceros japonicus</i> .....	Toyo-cho, Kohchi Pref.	Apr.	1962
<i>Megaceros tosanus</i> .....	Mt. Futamata, Kagoshima Pref.	Apr.	1962
	Taniyama city, Kagoshima Pref.	Mar.	1963
	Kurio, Isl. Yakushima	Mar.	1963
	Anbo, Isl. Yakushima	Mar.	1963
	Hiroshima city, Hiroshima Pref.	Apr.	1964
	Tosa-Yamada-cho, Kohchi Pref.	May	1964
<i>Notothylas japonica</i> .....	Fuchu-cho, Hiroshima Pref.	Nov.	1962
		Nov.	1964
Marchantiales			
<i>Targionia hypophylla</i> .....	Ohtaki-mura, Saitama Pref.	Aug.	1962
<i>Plagiochasma intermedium</i> .....	Mt. Chichibu, Saitama Pref.	Aug.	1962
	Taishaku-kyo, Hiroshima Pref.	Sept.	1962
		Sept.	1964
<i>P. japonicum</i> .....	Taishaku-kyo, Hiroshima Pref.	Sept.	1962
<i>Reboulia hemisphaerica</i> .....	Hiroshima city, Hiroshima Pref.	May	1962
	Taniyama city, Kagoshima Pref.	Mar.	1963
	Higashinakama, Isl. Amamiohshima	Mar.	1964
	Tosa city, Kohchi Pref.	May	1965
<i>Asterella odora</i> .....	Mt. Chichibu, Saitama Pref.	Aug.	1962
<i>A. pusilla</i> .....	Mt. Chichibu, Saitama Pref.	Aug.	1962
<i>Mannia levigata</i> .....	Ohtaki-mura, Saitama Pref.	Sept.	1952

<i>Conocephalum conicum</i> .....	Hiroshima city, Hiroshima Pref.	Apr.	1962
	Mt. Daisen, Tottori Pref.	Apr.	1965
<i>C. supradecompositum</i> .....	Mt. Futamata, Kagoshima Pref.	Apr.	1962
	Mt. Kaimon, Kagoshima Pref.	Mar.	1964
	Mt. Daisen, Tottori Pref.	Apr.	1965
<i>Sauteria alpina</i> .....	Mt. Rishiri, Hokkaido	July	1954
<i>Peltolepis quadrata</i> .....	Mt. Rishiri, Hokkaido	Aug.	1963
<i>Preissia quadrata</i> .....	Mt. Rishiri, Hokkaido	Aug.	1963
<i>Marchantia cuneiloba</i> .....	Taishaku-kyo, Hiroshima Pref.	Sept.	1962
<i>M. diptera</i> .....	Fuchu-cho, Hiroshima Pref.	June	1964
<i>M. tosana</i> .....	Fuchu-cho, Hiroshima Pref.	July	1962
		June	1964
<i>Dumortiera hirsuta</i> .....	Senogawa-cho, Hiroshima Pref.	May	1962
	Mt. Eboshi, Kagoshima Pref.	Mar.	1964
	Kurio, Isl. Yakushima	Mar.	1963
	Anbo, Isl. Yakushima	Mar.	1963
	Mt. Yuwan, Isl. Amamiohshima	Mar.	1964
	Tosa city, Kohchi Pref.	May	1965
<i>Wiesnerella denudata</i> .....	Nangoku city, Kohchi Pref.	Apr.	1962
	Mikawa-cho, Yamaguchi Pref.	May	1963
<i>Riccia crystallina</i> .....	Hiroshima city, Hiroshima Pref.	Sept.	1963
<i>R. glauca</i> .....	Fuchu-cho, Hiroshima Pref.	Nov.	1964
<i>R. huebeneriana</i> .....	Fuchu-cho, Hiroshima Pref.	Nov.	1964
<i>Ricciocarpus natans</i> .....	Fuchu-city, Hiroshima Pref.	Oct.	1965
Jungermanniales			
Anacrogynae			
<i>Metzgeria conjugata</i> ssp. <i>japonica</i>	Anbo, Isl. Yakushima	Mar.	1963
<i>Riccardia miyakeana</i> .....	Ohno-cho, Hiroshima Pref.	Apr.	1962
<i>R. nana</i> .....	Mt. Eboshidake, Kagoshima Pref.	Mar.	1963
<i>R. pinguis</i> .....	Taniyama city, Kagoshima Pref.	Mar.	1963
	Tainoko, Isl. Yakushima	Apr.	1963
	Mt. Daisen, Tottori Pref.	Apr.	1963
<i>Pellia fabbroniana</i> .....	Mt. Futamata, Kagoshima Pref.	Apr.	1962
	Mt. Daisen, Tottori Pref.	Apr.	1965
<i>P. neesiana</i> .....	Mt. Daisen, Tottori Pref.	Apr.	1965
<i>Makinoa crispata</i> .....	Mt. Futamata, Kagoshima Pref.	Apr.	1962
	Hiroshima city, Hiroshima Pref.	Apr.	1962
<i>Pallavicinia lyellii</i> .....	Suzukawa, Isl. Yakushima	Mar.	1963
	Kurio, Isl. Yakushima	Apr.	1965
<i>Cavicularia densa</i> .....	Mt. Daisen, Tottori Pref.	Apr.	1965
<i>Fossombronina japonica</i> .....	Kaitaichi-cho, Hiroshima Pref.	Dec.	1962
	Ohgachi, Isl. Amamiohshima	Mar.	1964
Calobryineae			
<i>Calobryum rotundifolium</i> .....	Hiroshima city, Hiroshima Pref.	Apr.	1962
Acrogynae			
<i>Trichocolea tomentella</i> .....	Mt. Futamata, Kagoshima Pref.	Apr.	1962
<i>Trichocoleopsis sacculata</i> .....	Mt. Saragamine, Ehime Pref.	May	1962
<i>Chiloscyphus polyanthus</i> .....	Hiroshima city, Hiroshima Pref.	Apr.	1962
	Tainoko, Isl. Yakushima	Mar.	1963

<i>Heteroscyphus bescherellei</i> .....	Mikawa-cho, Yamaguchi Pref.	May	1963
<i>H. planus</i> .....	Hatsukaichi-cho, Hiroshima Pref.	Apr.	1962
<i>Lophocolea heterophylla</i> .....	Hiroshima city, Hiroshima Pref.	May	1962
<i>L. horikawana</i> .....	Ino-cho, Kohchi Pref.	May	1962
<i>Jungermannia infusca</i> .....	Mt. Eboshi, Kagoshima Pref.	Mar.	1963
	Nagao-cho, Kagawa Pref.	Apr.	1963
<i>J. radiculosa</i> .....	Hiroshima city, Hiroshima Pref.	Dec.	1962
<i>Plagiochila ovalifolia</i> .....	Mt. Kuroson, Kohchi Pref.	May	1962
<i>Mylia verrucosa</i> .....	Mt. Yatsugatake, Nagano Pref.	Aug.	1962
<i>Scapania spinosa</i> .....	Hiroshima city, Hiroshima Pref.	Apr.	1962
	Tainoko, Isl. Yakushima	Mar.	1963
<i>S. stephanii</i> .....	Nabara-kyo, Hiroshima Pref.	Apr.	1962
<i>Cephalozia otaruensis</i> .....	Kurio, Isl. Yakushima	Mar.	1963
	Anbo, Isl. Yakushima	Mar.	1963
	Mt. Futamata, Kagoshima Pref.	Apr.	1962
<i>Nowellia curvifolia</i> .....	Mt. Futamata, Kagoshima Pref.	Apr.	1962
<i>Schiffneria hyalina</i> .....	Mt. Futamata, Kagoshima Pref.	Apr.	1962
<i>Jackiella brunnea</i> .....	Mt. Gokurakuji, Hiroshima Pref.	Dec.	1962
<i>Odontoschisma denudatum</i> .....	Ino-cho, Kohchi Pref.	May	1962
<i>Bazzania albicans</i> .....	Ino-cho, Kohchi Pref.	May	1962
<i>Lepidozia vitrea</i> .....	Kurio, Isl. Yakushima	Mar.	1963
<i>Calypogeia tosana</i> .....	Kurio, Isl. Yakushima	Mar.	1963
	Anbo, Isl. Yakushima	Mar.	1963
<i>Radula oyamensis</i> .....	Anbo, Isl. Yakushima	Mar.	1963
<i>Porella ulophylla</i> .....	Nagao-cho, Kagawa Pref.	Apr.	1963
<i>Frullania muscicola</i> .....	Nagao-cho, Kagawa Pref.	Apr.	1963
<i>F. kagoshimensis</i> .....	Toyo-cho, Kohchi Pref.	May	1962
<i>Jubula hutchinsiae</i> ssp. <i>javanica</i> ...	Mt. Futamata, Kagoshima Pref.	Mar.	1962
<i>Brachiolejeunea sandvicensis</i> .....	Toyo-cho, Kohchi Pref.	May	1962
	Nagao-cho, Kagawa Pref.	Apr.	1963
<i>Leptolejeunea subacuta</i> .....	Ino-cho, Kohchi Pref.	May	1962
<i>Ptychanthus striatus</i> .....	Mt. Kuroson, Kohchi Pref.	May	1962
<i>Spruceanthus polymorphus</i> .....	Anbo, Isl. Yakushima	Mar.	1963

### Spore characters

#### Aggregation

Permanently adherent tetrad spores have been observed in mature sporangia among some Hepaticae, such as *Sphaerocarpos*, *Riccia curtisii*, and *R. compacta*. But the phenomenon of spore compound grains was not encountered in any species treated in this work, all species having the spores of single separate type. Aggregation, as seen in pollen with dyad, polyad or pollinium, was not found in mature spores of Hepaticae.

Separation of the spores may occur before, or after, the wall receives its final pattern. The pattern appears in general to be formed at a late stage of development. Sometimes the characteristic sculpture is absent or more poorly defined on the proximal portion (the contact areas) than on the distal side of the spores as in *Anthoceros*, *Reboulia*, *Peltolepis*, etc. It may be true that the separation of spores from the tetrads is late in these genera.

The spores of many species of Hepaticae are uniformly unicellular, but some genera

such as *Dendroceros*, *Conocephalum*, and *Pellia*, have spores which are already multicellular when they are liberated from the capsule.

### Symmetry and external shape

The spores of Hepaticae are seldom quite spherical owing to the fact that they develop in close proximity to one another in tetrad. Divergence from the tetrad spores is either toward tetrahedral trilete spores with three contact faces which are flattened, and a free surface which is rounded, or toward nearly bilateral, deformed trilete spores. Thus the symmetry may be radial except the apolar and multicellular spores. The surface which is in contact with the adjacent members of the spore tetrad is called the proximal surface and the free surface is the distal surface.

The polarity of the spore is based on an axis, which is directed toward the center of tetrad during spore formation. The polar axis passes through the center of the spore and of the proximal and distal surfaces, and it is customary to refer to the proximal pole and the distal pole respectively. The equator, generally the outline or limb of the spores seen in polar view, divides the spores into two hemispheres (proximal and distal, or apical and abapical), which seem to be somewhat unequally developed according to the size and flattening of the contact area. Owing to this unequal development and to the presence of the tetrad scar on the proximal surface, spores of Hepaticae are generally anisopolar, though cryptopolar spores are also seen, which lack the typical tetrad scar, for example, in *Targionia hypophylla* the spores are very similar to tetrahedral trilete spores showing a clear polar axis, but there is no triradiate mark on it.

Anisopolar spores with trilete mark and cryptopolar spores are tetrahedral in shape, and the outline is triangular in polar view, and fan-shaped or semicircular in profile. The proximal portion is pyramidal or subpyramidal (more flattened) and the distal portion hemispherical. Deformed trilete spores are almost circular in polar view, with the profile semicircular or kidney-shaped. The proximal portion is flat or hollow, and the distal one is hemispherical. Apolar spores are generally globose in outline, lacking a distinct polar axis and it is difficult to exactly distinguish between the equatorial diameter and polar axis. Multicellular spores are usually irregular-globose or ovoid.

### Aperture

Apertures of spores in Hepaticae are less complex and less varied than those of pollen grains in flowering plants, and consist of dehiscent fissures which are trilete or deformed trilete, and termed laesura. Trilete laesura may consist of simple commissure or may also include lips which are thickened or ornamented areas, giving a rimmed appearance. Deformed-trilete laesura or circular laesura is composed of simply opened areas without ornamentation.

In this description the laesurae are long if they reach, or nearly reach, to the equator, and short if they conspicuously fail to do so.

### Size of spores

As a result of studying Hepaticae spores in 70 species belonging to 28 families, I have been able to group them into two types based on the size. The first type includes spores which are smaller than  $25\mu$  in diameter and morphologically almost similar to each other even among different families. Therefore such spores are very difficult to identify exactly. Spores of the second type are larger than  $25\mu$ , and in this the characters such as cell stages, polarity, shape, sculpture and color are remarkably diversified. It is relatively easy to distinguish the spores of this type as to their families, genera or even as to species. In this paper the spores of the first type are measured only as to the diameter and the description is

omitted, especially in Jungermanniales acrogynae, whereas the spores of Anthocerotales, Marchantiales, Jungermanniales anacrogynae and some species of Jungermanniales acrogynae, which almost all fall into the second type, are described and illustrated.

The size of Hepaticae spores varies from about  $9\mu$  to over  $90\mu$  in unicellular spores, from  $30\mu$  to over  $130\mu$  in multicellular spores. Only a few species exhibit some extremes from these ranges, and this is particularly so in the large size class. Generally speaking, trilete spores and multicellular spores belong to the large size class, and deformed trilete spores belong to the small size class.

Erdtman (1945) has proposed a series of size classes, following which the size of spores was analysed here with respect to Japanese Hepaticae and Musci, and New Zealand Pteridophyta, the last being given for comparison. On the whole the spores of Bryophyta are

Table 2. Size classes of spores in Hepaticae, Musci and Pteridophyta.

Size class (Erdtman 1945)	Size ( $\mu$ )	Japanese Hepaticae	Japanese Musci*	New Zealand Pteridophyta**
Very small	$<10$	1.4% (1)	9.5% (16)	
Small	10—25	41.4 (29)	57.9 (98)	9%
Medium	25—50	30.0 (21)	31.4 (53)	67
Large	50—100	27.2 (19)	1.2 (2)	24
Very large	100—200			1
Gigantic	$200<$			

( ) = Number of species. \*Miyoshi (unpublished). \*\*Harris (1955).

smaller than those of Pteridophyta: size range of the former exhibits a peak in the "small" size class as compared with the latter whose peak is in the "medium" size class.

The size range of the spores in each species is mostly expressed by more or less normal curve in Hepaticae, though Musci includes some species of *Macromitrium*, *Miyabea*, *Mnium*, etc. with dimorphic spores showing a bimodal curve.

Difference in the size range of spores associated with polyploidy of *Dumortiera hirsuta* was reported by Tatuno (1952), in which the major axis of spores was measured as  $22.78\mu$  in monoploid,  $26.56\mu$  in diploid and  $29.86\mu$  in triploid. Some materials of this species collected from various localities were measured and tabled together with Tatuno's results (Table 3), which indicates that they seem to belong to the diploid or triploid.

### Spore wall

Leitgeb (1883) studied the structure and development of the spores of Hepaticae, and he recognized a 3-layered structure of the spore coat: intine, exine and perinium from inner to outer layer. Haupt (1921) studied sporogenesis in *Reboulia hemisphaerica*, and he described that "The exine and intine are differentiated in the tetrad stage, and the epispore has begun to develop." Erdtman (1952) described sporoderm stratification as follow: "The spore wall (sporoderm) usually consists of two main strata, an inner, soft (malacodermatous) layer, intine, and an outer, hard (sclerodermatous) layer, sclerine. Sclerine is usually synonymous with exine. In the spores of certain plants (certain mosses, ferns, etc.), however, it also comprises as outer layer, perine. The presence of this layer seems to be due to the activity of a periplasmodium with perinogeous properties."

The inner layer, intine is not preserved in fossil spores, which is also the case in fresh spores when certain methods of preparation are used, and hence the differences in thickness are not taken into account in providing criteria for identification. The outer layer,



Table 8. Difference of the size range of spores in *Dumortiera hirsuta* associated with polyploidy.

Ploidy	Major axis	Minor axis	Locality
	s. (m. ) l. *	s. (m. ) l.	
Monoploid	(22.78)**	(15.00)**	Mt. Kaharudake, Fukuoka Pref.
Diploid	(26.56)**	(18.11)**	Mt. Kaharudake, Fukuoka Pref.
	23 (26.0) 30	15 (17.9) 21	Mt. Eboshidake, Kagoshima Pref.
	24 (26.0) 30	16 (17.9) 21	Kurio, Isl. Yakushima
	23 (25.5) 29	15 (17.7) 21	Anbo, Isl. Yakushima
	24 (27.3) 30	16 (18.5) 21	Mt. Yuwandake, Isl. Amamiohshima
	24 (27.0) 33	16 (18.5) 21	Tosa city, Kochi Pref.
Triploid	(29.86)**	(20.15)**	Mt. Kaharudake, Fukuoka Pref.
	27 (29.9) 34	18 (21.6) 24	Senogawa-cho, Hiroshima Pref.
	27 (30.1) 35	18 (19.9) 24	Anbo, Isl. Yakushima

\*s. (m. ) l. =shortest diameter (mean diameter) longest diameter. \*\*Tatuno (1952).

exine is a strong layer and is preserved in fossil spores and fresh spores regardless of the methods of preparation and may be divided into two layers, namely, the inner, nonsculptured part known as nexine and the outer, sculptured part, sexine. The carving patterns of the sexine, often referred to as the sculpture, are the most important diagnostic character of the spores without perine.

The outermost layer, perine is marked by characteristic sculptures which give an important factor for systematic comparison of the spores, especially in many species of Marchantiales and some species of Jungermanniales.

### Sculpture

Differences in sculptures are the most important factor in making an exact identification of the spores. The main sculptural patterns cited are as follows:

Sculptural patterns	Examples
psilate.....	Fig. 2-b, c.
baculate.....	Fig. 6-g, h, i.
bullate .....	Fig. 7-a, b, c.
granulate .....	Fig. 8-i, j, k, m, n.
echinate.....	Fig. 2-a, e, f.
echinulate.....	Fig. 2-d, g, h, i.
polyforate.....	Fig. 9-v <sub>1</sub> , v <sub>2</sub> ; 10-a, b.
reticulate .....	Fig. 3-a, b, c, d, f.
saccate .....	Fig. 6-c, e, f.
verrucate .....	Fig. 2-j; 5-d.

These sculptures are divided into two groups. One is composed of patternless, smooth or minutely sculptured spores (psilate). The other consists of spores with cavities or projections such as reticulate, echinate, and verrucate.

### Color

Color is of no great importance in distinguishing the spores in many species of Hepaticae, because there is scarcely any difference in the spores of different families or genera. The color is dissimilar, even in the same species, between fresh spores with some chloroplasts and the dry spores. Furthermore, the color may be changed by chemical treatment. The spores treated with 10% KOH are usually made darker in color. Almost all species have

yellowish-brown spores and it is difficult to place the spore into families or genera by their color. However dark-brown or black spores are characteristic of some genera, such as *Asterella*, *Targionia*, and *Ricciocarpus*. According to Proskauer (1958), *Anthoceros* has dark brown spores and those of *Phaeoceros* are golden yellow in color, color being one of the important diagnostic characters in distinguishing these two genera.

### Spore and elater

Müller (1948) showed the ratio of equatorial diameter of spore to width of elater in numerous species of Jungermanniales and emphasized that this value is often a taxonomically important character for identification of each species and sometimes also for genus and family. The ratio of equatorial diameter of spores to width of elater has been calculated (Horikawa & Miyoshi, 1965) and is shown in Table 4.

Table 4. The ratio of equatorial diameter of spore to width of elater.

Species	Spore* ( $\mu$ )	Elater** ( $\mu$ )	Ratio
<b>Anthocerotales</b>			
<i>Phaeoceros laevis</i> .....	40	14	2.9 : 1
<i>Dendroceros japonicus</i> .....	76×96	11	6.9-8.7 : 1
<i>Megaceros tosanus</i> .....	34	9	3.8 : 1
<b>Marchantiales</b>			
<i>Reboulia hemisphaerica</i> .....	47	13	3.6 : 1
<i>Asterella pusilla</i> .....	54	9	6.0 : 1
<i>Conocephalum conicum</i> .....	84×95	21	4.0-4.5 : 1
<i>Marchantia cuneiloba</i> .....	26	9	2.9 : 1
<i>M. diptera</i> .....	22	6	3.8 : 1
<i>M. tosanana</i> .....	28	9	3.1 : 1
<i>Wiesnerella denudata</i> .....	32	7	4.6 : 1
<b>Jungermanniales</b>			
<i>Riccardia miyakeana</i> .....	14	11	1.3 : 1
<i>Pellia fabbronia</i> .....	56×72	12	4.7-6.0 : 1
<i>Makinoa crispata</i> .....	24	17	1.4 : 1
<i>Cavicularia densa</i> .....	49×58	13	3.8-4.5 : 1
<i>Calobryum rotundifolium</i> .....	20	7	2.9 : 1
<i>Trichocolea tomentella</i> .....	13	12	1.1 : 1
<i>Trichocoleopsis sacculata</i> .....	52	8	6.5 : 1
<i>Lophocolea heterophylla</i> .....	12	10	1.2 : 1
<i>L. horikawana</i> .....	12	9	1.3 : 1
<i>Mylia verrucosa</i> .....	16	11	1.5 : 1
<i>Scapania spinosa</i> .....	11	10	1.1 : 1
<i>S. stephanii</i> .....	12	8	1.5 : 1
<i>Jackiella brunnea</i> .....	13	8	1.6 : 1
<i>Radula oyamensis</i> .....	21	6	3.5 : 1
<i>Porella ulophylla</i> .....	42×47	17	2.5-2.8 : 1
<i>Jubula hutchinsiae</i> ssp. <i>javanica</i> .....	10	9	1.1 : 1
<i>Ptychanthus striatus</i> .....	36×46	14	2.6-3.3 : 1

\* The mean of equatorial diameter in the spore description. \*\* The mean of width on central part of elater.

## Spore descriptions

### I. Anthocerotales

The spore structures of Anthocerotales have been described and illustrated by many taxonomists as one of the important diagnostic characters. Because these spores are comparatively large in size and show great diversity in sculpture, it is relatively easy to distinguish the spores of this family into genera or even species. They may be also worthy of attention in work of palynology. Knox (1939) has studied the general spore structure of Anthocerotaceae. Proskauer (1957, 1958) studied many specimens of *Anthoceros* from various localities throughout the world and established a new genus, *Phaeoceros*. According to his studies, spores are dark brown in *Anthoceros* and golden yellow in *Phaeoceros*. Horikawa & Miyoshi (1963) examined and illustrated the spore structures of six species including all generic members of Anthocerotaceae.

#### Key to the species treated based on spore morphology

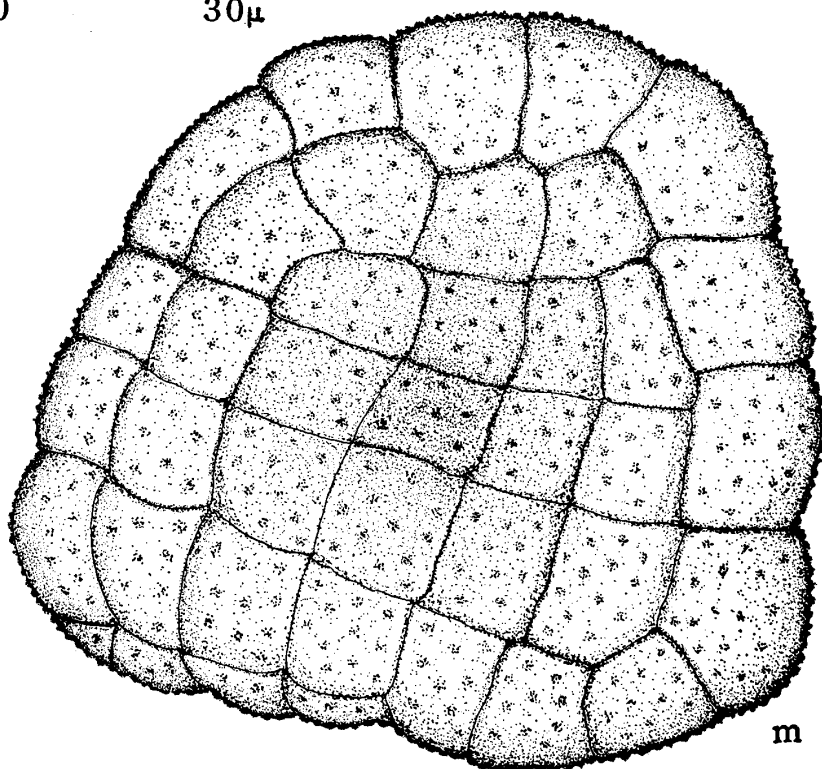
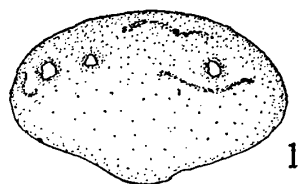
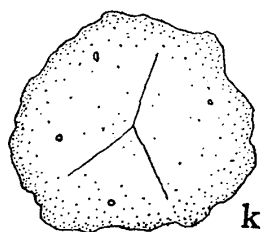
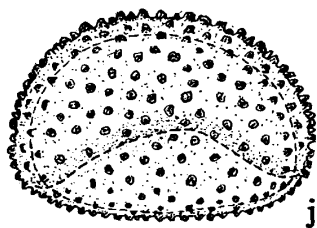
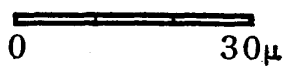
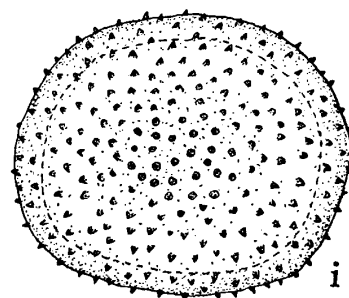
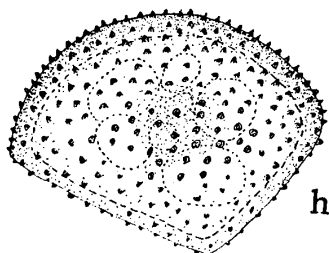
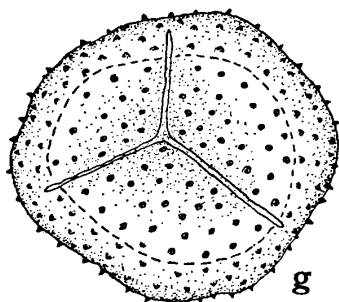
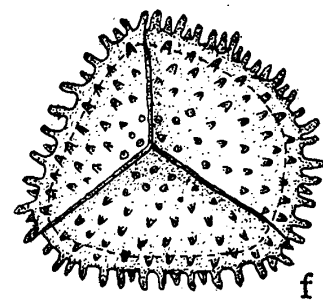
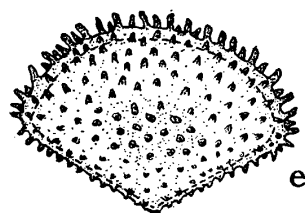
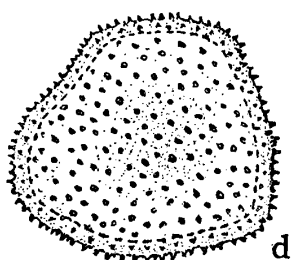
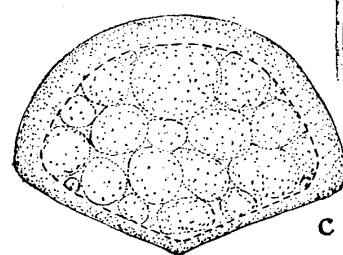
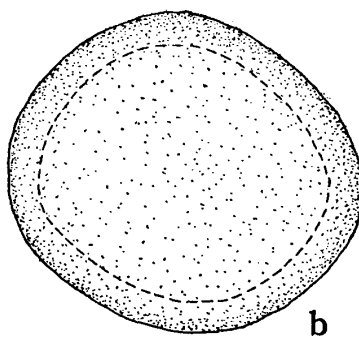
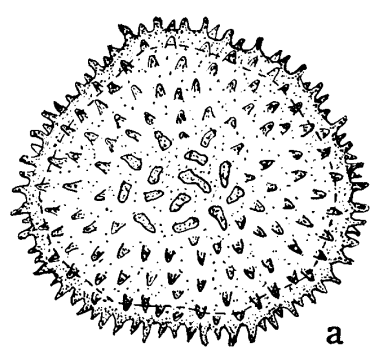
- A. Spores unicellular ; polarity anisopolar
  - B. Tetrad scar trilete
    - C. Sculpture echinate
      - D. Exine 1-1.5  $\mu$ ; equatorial diameter 26 (29) 33  $\mu$   
 ..... *Anthoceros formosae* f. *gemmulosus*
      - D. Exine 1.5-2.5  $\mu$ ; equatorial diameter 34 (38) 54  $\mu$   
 ..... *Anthoceros nagasakiensis*
    - C. Sculpture echinulate
      - D. Exine about 2  $\mu$ ; equatorial diameter 28 (31) 36  $\mu$ .....*Phaeoceros miyakeanus*
      - D. Exine 3-4  $\mu$ ; equatorial diameter 30 (40) 45  $\mu$  .....*Phaeoceros laevis*
    - C. Sculpture granulate; exine 0.5-1  $\mu$ ; equatorial diameter 27 (34) 39  $\mu$   
 ..... *Megaceros tosanus*
    - C. Sculpture psilate; exine 2.5-3.5  $\mu$ ; equatorial diameter 40 (46) 55  $\mu$   
 ..... *Notothylas japonica*
  - B. Tetrad scar deformed trilete; sculpture verrucate; exine 1.5-2  $\mu$ ; equatorial diameter 30 (37) 45  $\mu$  .....*Aspiromitus miyabeanus*
- A. Spores multicellular; polarity missing; tetrad scar lacking; sculpture granulate; exine about 1  $\mu$ ; equatorial diameter 60 (76) 95  $\times$  70 (96) 135  $\mu$   
 ..... *Dendroceros japonicus*

#### 1. *Phaeoceros laevis* (L.) Proskauer (Fig. 2-g, h, i) (Pl. 1-d, e)

Unicellular, anisopolar, tetrahedral, trilete; laesura long, usually reaching to the equator; commissure rarely bordered by the ridges of sexine; shape rounded-triangular in polar view; profile fan-shaped; proximal portion subpyramidal; distal side dome-shaped; equatorial diameter 30 (40) 45  $\mu$ , m.  $\pm$  s. d. 38-42  $\mu$ ; polar axis 27-30  $\mu$ . Exine 3-4  $\mu$ , echinulate; the spinules about 1  $\mu$ , sparsely scattered on proximal and dense on distal side. Color yellowish-green containing many chloroplasts in fresh condition, but yellowish-brown after KOH treatment.

Specimen studied: Takimoto, Nangoku city, Kohchi Pref., Apr. 28, 1962, N. Miyoshi.

Illustrations: Proskauer (1957), Magohuku & Yamada (1964). *Anthoceros laevis*: Macvicar (1926), Horikawa (1939), Frye & Clark (1947), Müller (1954), Makino (1957), Horikawa & Miyoshi (1963).



2. **Phaeoceros miyakeanus** (Schiffn.) Hatt. (Fig. 2-d)

Equatorial diameter 28(31)36  $\mu$ , m.  $\pm$ s. d. 29-33  $\mu$ ; polar axis 21-24  $\mu$ . Exine about 2  $\mu$ , echinulate; the spinules 1-2  $\mu$  long and 0.5-1  $\mu$  wide at base, scattered all over the surface, except on laesura. Color yellowish-brown.

Specimen studied: Obi, Nichinan city, Miyazaki Pref., May 1946, S. Hattori. (Hep. Jap. Exsic. Ser. 2, No. 53)

3. **Anthoceros formosae** St. f. **gemmulosus** Hatt. (Fig. 2-e, f)

Unicellular, anisopolar, tetrahedral, trilete; laesura long, reaching to the equator; commissure rarely bordered by the ridges of sexine; shape irregularly rounded-triangular in polar view; profile fan-shaped; proximal portion subpyramidal; distal side dome-shaped; equatorial diameter 26(29)33  $\mu$ , m.  $\pm$ s. d. 27-31  $\mu$ ; polar axis 21-24  $\mu$ . Exine about 1-2  $\mu$ , echinate; the spines about 3  $\mu$  long and about 1-1.5  $\mu$  wide at base, scattered all over the surface except on laesura, especially dense on the distal side. Color brown or dark-brown.

Specimen studied: Obi, Nichinan city, Miyazaki Pref., May 1946, S. Hattori. (Hep. Jap. Exsic. Ser. 2, No. 51)

Illustration: Hattori (1944).

4. **Anthoceros nagasakiensis** St. (Fig. 2-a) (Pl. 1-a, b, c, g)

External shape and laesura as in *A. formosae* f. *gemmulosus*; equatorial diameter 34(38)45  $\mu$ , m.  $\pm$ s. d. 36-40  $\mu$ ; polar axis 26-31  $\mu$ . Exine 1.5-2.5  $\mu$ , echinate; the spines 3-3.5  $\mu$  long and about 2  $\mu$  wide at base, scattered all over the surface except on laesura. Color dark-brown.

Specimen studied: Obi, Nichinan city, Miyazaki Pref., June, 1946, S. Hattori. (Hep. Jap. Exsic. Ser. 2, No. 54)

Illustration: Horikawa & Miyoshi (1963).

5. **Aspiromitus miyabeanus** St. (Fig. 2-j) (Pl. 1-f; 4-e, f)

Unicellular, anisopolar, vague tetrahedral, deformed-trilete; laesura short, expanded broadly, not tapering at the end and concave; margo smooth or sometimes crumpled; shape round in polar view; profile kidney-shaped; proximal portion concave; distal side hemispherical; equatorial diameter 30(37)45  $\mu$ , m.  $\pm$ s. d. 34-40  $\mu$ ; polar axis 20-25  $\mu$ . Exine 1.5-2  $\mu$ , verrucate; the verrucae 1-2  $\mu$  in diameter and about 2  $\mu$  in height, denser and larger on distal side than on proximal part. Color yellowish-brown.

Specimen studied: Hayatani Shrine, Hatsukaichi-cho, Saeki-gun, Hiroshima Pref., Jan. 6, 1963, N. Miyoshi.

Illustration: Horikawa & Miyoshi (1963)

6. **Dendroceros japonicus** St. (Fig. 2-m) (Pl. 1-j)

Multicellular with 30-60 celled stage in mature capsule, polarity missing; laesura unconfirmed apparently due to the disappearance of laesura by the endogenous germination within the stretched exine; external shape irregular-spheroidal or ovoid, difficult to distinguish the equatorial diameter and polar axis; diameter 60(76)96  $\times$  70(96)135  $\mu$ . Exine about 1  $\mu$ , granulate; the granules about 1  $\mu$ , scattered all over the surface. Color yellowish-green with one chloroplast per cell in fresh spores, but yellow or yellowish-brown in dry condition.

Specimen studied: None, None-cho, Aki-gun, Kohchi Pref., May 2, 1962, K. Nehira.

Fig. 2. a. *Anthoceros nagasakiensis* (D. p. v.). b. *Notothylas japonica* (D. p. v.). c. ditto (E. v.). d. *Phaeoceros miyakeanus* (D. p. v.). e. *Anthoceros formosae* f. *gemmulosus* (E. v.). f. ditto (P. p. v.). g. *Phaeoceros laevis* (P. p. v.). h. ditto (E. v.). i. ditto (D. p. v.). j. *Aspiromitus miyabeanus* (E. v.). k. *Megaceros tosanus* (P. p. v.). l. ditto (E. v.). m. *Dendroceros japonicus* (M.).

Illustrations: Hattori (1944), Nehira (1963), Horikawa & Miyoshi (1963).

7. **Megaceros tosanus** St. (Fig. 2-k, 1) (Pl. 1-h)

Unicellular, tetrahedral, trilete; laesura rarely observed, short, not reaching to the equator; shape rounded-triangular or circular in polar view; profile plano-convex, proximal portion flat, sometimes concave; distal side dome-shaped; equatorial diameter 27(34)39  $\mu$ , m.  $\pm$ s. d. 31-37  $\mu$ ; polar axis 14-18  $\mu$ . Exine 0.5-1  $\mu$ , granulate; the granules irregular, about 1  $\mu$  in diameter, scattered on both sides; the surface uneven, sporadically pitted; the hollow irregular, about 1-2  $\mu$  in diameter and 0.5-1  $\mu$  in depth. Color yellowish-green in fresh spores, but yellow after KOH treatment.

Specimen studied: Futamata, Kohyama-cho, Kimotsuki-gun, Kagoshima Pref., Apr. 1, 1962, N. Miyoshi.

Illustrations: Horikawa (1939), Nehira (1963), Horikawa & Miyoshi (1963), Magohuku & Yamada (1964).

8. **Notothyas japonica** Horik. (Fig. 2-b, c) (Pl. 1-i)

Unicellular, tetrahedral, trilete; laesura generally reaching to the equator; shape rounded-triangular or round in polar view; profile fan-shaped; proximal portion subpyramidal; distal side hemispherical; equatorial diameter 40(46)55  $\mu$ , m.  $\pm$ s. d. 43-49  $\mu$ ; polar axis 30-36  $\mu$ . Exine 2.5-3.5  $\mu$ , psilate, almost smooth all over the surface. Color dark-brown.

Specimen studied: Yahata, Fuchu-cho, Aki-gun, Hiroshima Pref., Nov. 19, 1962, N. Miyoshi.

Illustrations: Horikawa (1929b, 1939), Horikawa & Miyoshi (1963).

## II. Marchantiales

In Marchantiales the spores show a greater variations in size and sculpture than in any other groups of Hepaticae. Therefore the spore morphology of this order has been studied by many bryologists as one of the important characters in taxonomy and in study of spore germination. Knox (1939) studied general spore structures of the order, and compared the spores of *Riccia crystallina*, *R. beyrichiana*, *R. fluitans* and *Plagiochasma subplanum* with fossil spores in coal of the Carboniferous age in Scotland. Erdtman (1957) also illustrated diagnostic characters of spores in Marchantiales. Recently Inoue (1960) studied the spore structures and the spore germination in Marchantiales, and found a close relation of the spore germination to the spore morphology, especially to the polarity of spore.

### Key to the species treated based on spore morphology

- A. Spores unicellular
  - B. Polarity anisopolar; tetrad scar trilete
    - C. Sculpture double reticulate
      - D. Exine about 2-3  $\mu$ ; equatorial diameter 48(57)66  $\mu$ .....*Asterella odora*
      - D. Exine difficult to measure; equatorial diameter 45(54)60  $\mu$   
.....*Asterella pusilla*
    - C. Sculpture double-reticulate and echinulate, exine about 1-2  $\mu$ 
      - D. Equatorial diameter 54(62)70  $\mu$  .....*Plagiochasma japonicum*
      - D. Equatorial diameter 42(47)54  $\mu$  .....*Plagiochasma intermedium*
    - C. Sculpture reticulate
      - D. Exine measurable

- E. Exine 2-3 $\mu$ ; equatorial diameter 42(47)54  $\mu$ .....*Reboulia hemisphaerica*
- E. Exine about 3  $\mu$ ; equatorial diameter 48(53)57  $\mu$   
..... *Riccia huebeneriana*
- E. Exine 3-5  $\mu$ ; equatorial diameter 60(68)80  $\mu$ .....*Riccia crystallina*
- D. Exine difficult to measure
  - E. Equatorial diameter 57(66)75  $\mu$ .....*Riccia glauca*
  - E. Equatorial diameter 54(59)66  $\mu$ .....*Ricciocarpus natans*
- C. Sculpture saccate; exine about 2  $\mu$ , equatorial diameter 40(48)54  $\mu$   
..... *Mannia levigata*
- B. Polarity cryptopolar; tetrad scar lacking or alete
  - C. Sculpture baculate; exine 0.5-1  $\mu$ ; equatorial diameter 27(30)34  $\mu$   
..... *Dumortiera hirsuta*
  - C. Sculpture double-reticulate; exine 2-3  $\mu$ ; equatorial diameter 40(47)51  $\mu$   
..... *Targionia hypophylla*
  - C. Sculpture bullate or reticulate
    - D. Exine 3-4 $\mu$ ; equatorial diameter 40(47)51  $\mu$ .....*Preissia quadrata*
    - D. Exine about 0.5  $\mu$ 
      - E. Equatorial diameter 24(26)30  $\mu$ .....*Marchantia cuneiloba*
      - E. Equatorial diameter 18(22)24  $\mu$ .....*Marchantia diptera*
      - E. Equatorial diameter 24(28)31  $\mu$ .....*Marchantia tosona*
  - C. Sculpture saccate
    - D. Exine about 1  $\mu$ ; equatorial diameter 50(62)75  $\mu$ .....*Peltolepis quadrata*
    - D. Exine 0.5-1  $\mu$ ; equatorial diameter 27(32)37  $\mu$ .....*Wiesnerella denudata*
    - D. Exine difficult to measure; equatorial diameter about 40-60  $\mu$   
..... *Sauteria alpina*
- A. Multicellular; polarity missing; tetrad scar lacking; exine about 0.5  $\mu$
- B. Sculpture verrucate and granulate; diameter 70(84)96  $\times$  81(95)114  $\mu$ , 70(87)105  $\mu$   
..... *Conocephalum conicum*
- B. Sculpture granulate; diameter 45(63)81  $\times$  54(70)87  $\mu$ , 57(69)87  $\mu$   
..... *Conocephalum supradecompositum*

### 1. *Targionia hypophylla* L. (Fig. 3-f)

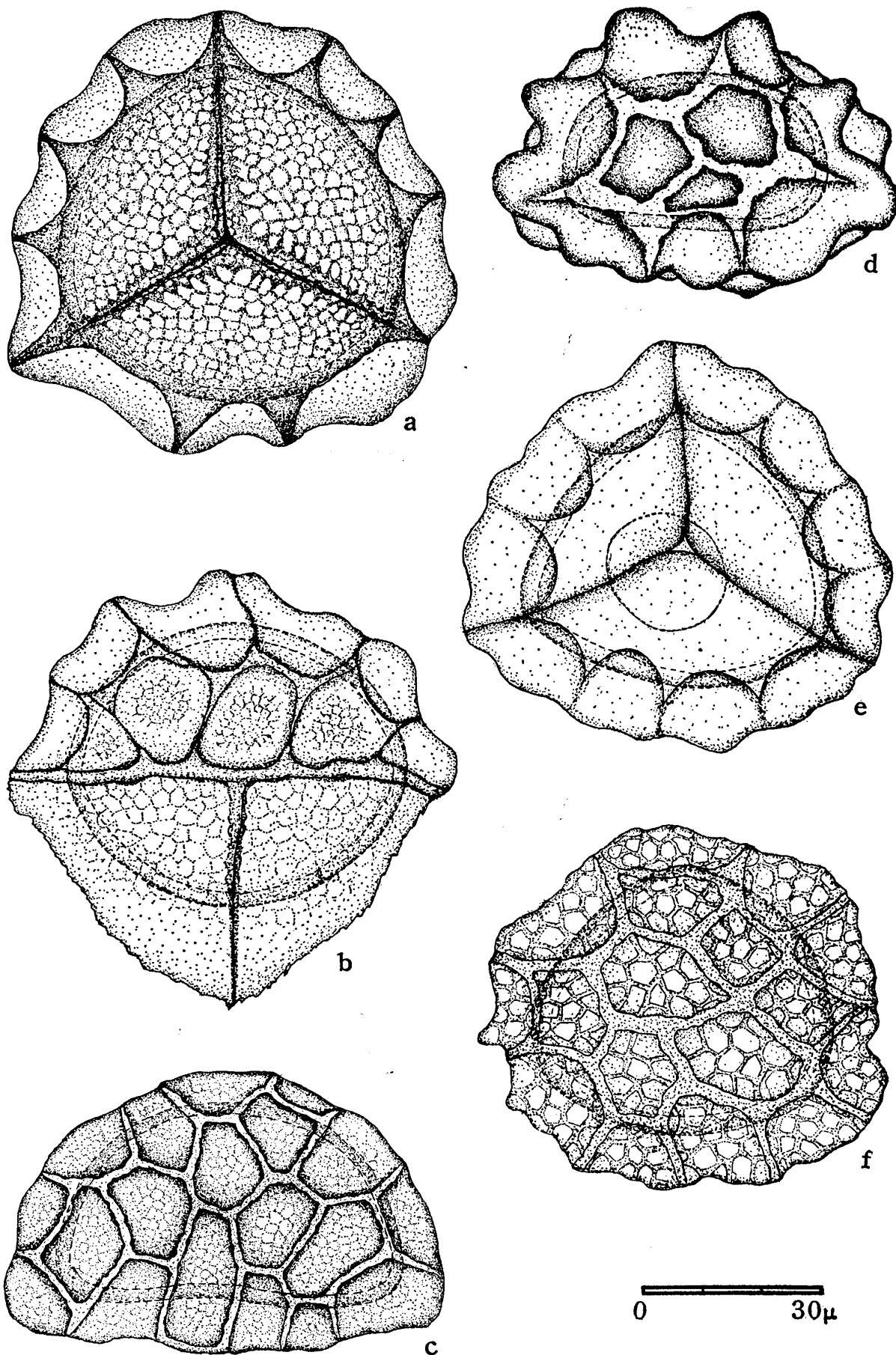
Unicellular, cryptopolar, indistinctly tetrahedral, generally alete; laesura usually lacking; shape round or rounded-triangular in polar view; profile hemispherical; proximal portion flat; equatorial diameter 36(41)45  $\mu$ , m.  $\pm$ s.d. 39-43  $\mu$ ; polar axis 27-30  $\mu$ . Exine 2-3  $\mu$ . Outermost layer perinous; the perine doubly reticulate on the distal side, the large lumina hexagonal or pentagonal in double network, 6-15  $\mu$  in size and 3-4 meshes through a diameter of one large lumina; on the proximal face the perine reticulate, lumina very irregular and similar to the ornamentation of the distal face of *Preissia quadrata*; width of perine 6-10  $\mu$  at the equator. Color dark-brown.

Specimen studied: Kaminakao, Ohtaki-mura, Chichibu-gun, Saitama Pref., Aug. 26, 1962, N. Miyoshi.

Illustrations: Horikawa (1939), Müller (1954), Kachroo (1955), Erdtman (1957).

### 2. *Plagiochasma japonicum* St. (Fig. 4-e; 5-a)

Unicellular, anisopolar, tetrahedral, trilete; laesura long, reaching to the equator; commissure covered with perine, the perine of two parts of proximal three faces united on the commissure and projected about 2-3  $\mu$  in height as wing; shape, excluding perine, rounded-triangular in polar view; profile plano-convex; proximal portion flat; equatorial diameter 54(62)70  $\mu$ , m.  $\pm$ s.d. 59-65  $\mu$ ; polar axis 42-51  $\mu$ . Exine thin, about 1-2  $\mu$ , but difficult to measure exactly. Outermost layer perinous; the perine doubly reticulate and





echinulate, well developed on the distal side and reduced or devoid on the proximal face, the large lumina irregular-pentagonal or hexagonal in shape and 4-5 meshes through a diameter on distal side, the small lumina vaguely observed, the spinules sparsely scattered; width of winged perine 12-15  $\mu$  at the equator. Color yellowish-brown.

Specimen studied: Taishaku-kyo, Hiroshima Pref., Sept. 22, 1962, K. Nohira.

3. **Plagiochasma intermedium** Lindenb. & Gott. (Fig. 4-c, d) (Pl. 4-a, b, c, d)

External shape and laesura as in *P. japonicum*. Equatorial diameter 42(47)54  $\mu$ , m.  $\pm$  s. d. 44-50  $\mu$ ; polar axis 27-36  $\mu$ . Exine thin, about 1-2  $\mu$ .

Specimen studied: Taishaku-kyo, Hiroshima Pref., Sept. 30, 1964, N. Miyoshi.

Illustrations: Erdtman (1957), Inoue (1960), Jovet-Ast (1965).

4. **Reboulia hemisphaerica** (L.) Raddi (Fig. 3-d, e) (Pl. 2-a, b, c)

Unicellular, anisopolar, tetrahedral, trilete; laesura long, usually reaching to the equator; commissure covered with the narrow ridges of perine; shape, excluding perine, rounded-triangular in polar view; profile plano-convex; proximal portion flat; equatorial diameter 42(47)54  $\mu$ , m.  $\pm$  s. d. 44-50  $\mu$ ; polar axis 33-39  $\mu$ . Exine 2-3  $\mu$ . Outermost layer perinous; the perine reticulate on the distal face, the lumina irregular in shape and 4-5 meshes through a diameter; the proximal face reticulate only on the equator or devoid of sculpture; width of the winged perine about 6-12  $\mu$  at the equator; sometimes an oil drop is present in a spore. Color yellowish-brown or brown.

Specimen studied: Botanical garden in Hiroshima Univ., Hiroshima city, May 2, 1962, N. Miyoshi.

Illustrations: Horikawa (1929a, 1939), Inoue (1960), Cavers (1964).

5. **Asterella odora** Hatt. (Fig. 3-a, b)

Unicellular, anisopolar, tetrahedral, trilete; laesura long, reaching to the equator; commissure covered with narrow ridges of perine; shape, excluding perine, rounded-triangular in polar view; profile elliptical or spherical and rarely plano-convex; proximal portion dome-shaped or flat; equatorial diameter 48(57)66  $\mu$ , m.  $\pm$  s. d. 53-61  $\mu$ ; polar axis 40-50  $\mu$ . Exine about 2-3  $\mu$ , but difficult to measure exactly. Outermost layer perinous; the perine double-reticulate all over the surface except laesura, the large lumina irregular, 10-15  $\mu$  in diameter and 5-6 meshes through a diameter on the distal face, furthermore, the small lumina observed in the large lumina; the proximal face covered with small and irregular lumina or sometimes devoid of it; width of winged perine 6-10  $\mu$  at the equator. Color brown or dark-brown.

Specimen studied: Mitsumine, Mt. Chichibu, Saitama Pref., Aug. 27, 1962, N. Miyoshi.

Illustrations: Hattori (1944), Inoue (1960).

6. **Asterella pusilla** Shimizu et Hatt. (Fig. 3-c)

Main characters of this spore same as in the preceding species; equatorial diameter 45(54)60  $\mu$ , m.  $\pm$  s. d. 50-58  $\mu$ ; polar axis 35-40  $\mu$ . Width of wavy perine 6-12  $\mu$  at equator.

Specimen studied: Jumonji pass, Mt. Chichibu, Saitama Pref., Aug. 27, 1962, N. Miyoshi.

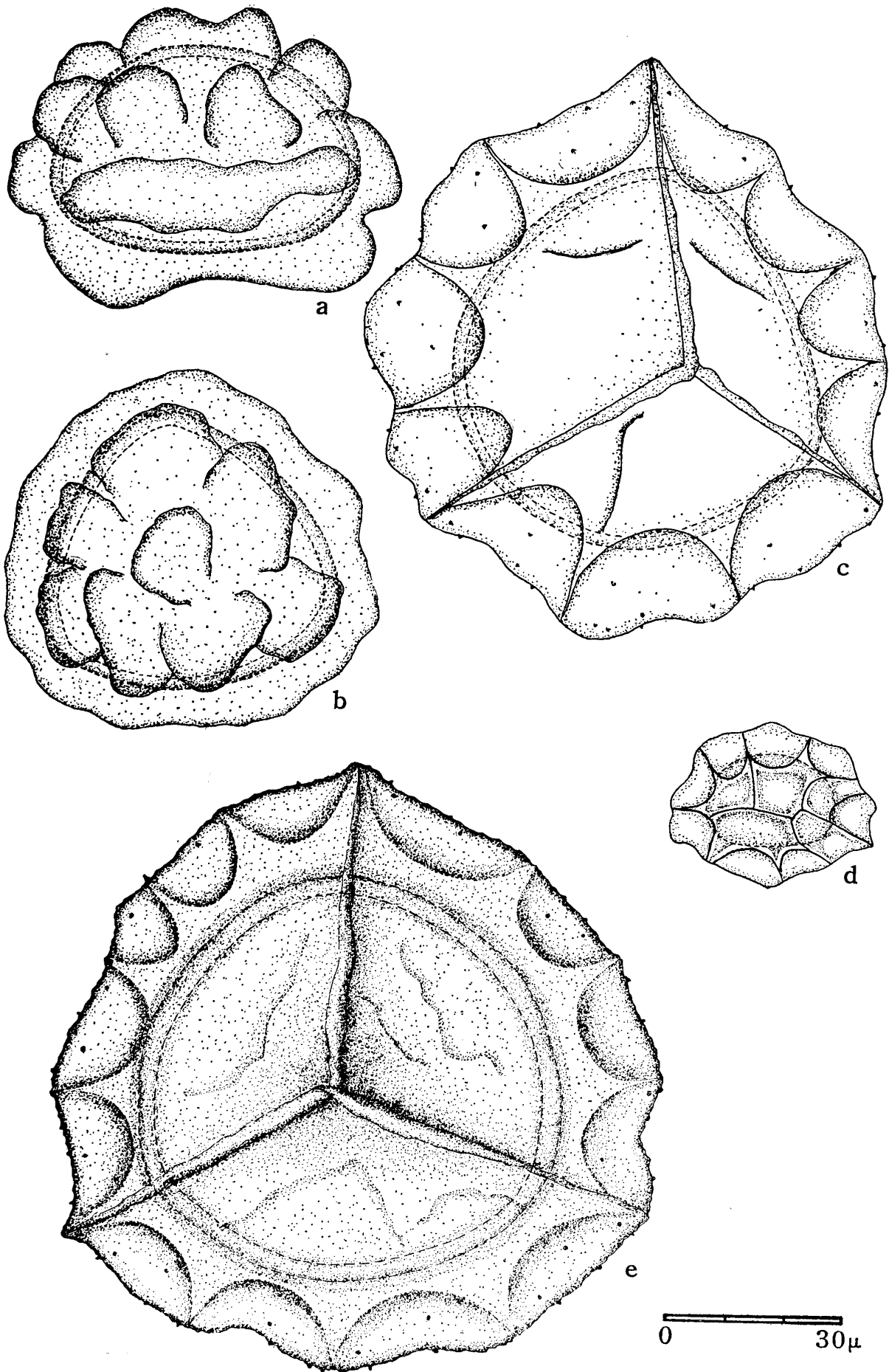
Illustration: Shimizu & Hattori (1952).

7. **Mannia levigata** Shimizu et Hatt. (Fig. 4-a, b)

Unicellular, anisopolar, tetrahedral, trilete; laesura long, reaching to the equator;

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Fig. 3. a. *Asterella odora* (P. p. v.). b. ditto (E. v.). c. *A. pusilla* (E. v.). d. *Reboulia hemisphaerica* (E. v.). e. ditto (P. p. v.). f. *Targionia hypophylla* (D. p. v.).



shape, excluding perine, rounded-triangular in polar view; profile plano-convex or elliptical; proximal portion flat or dome-shaped; equatorial diameter  $40(48)54\mu$ , m.  $\pm$  s. d.  $45-51\mu$ ; polar axis  $30-39\mu$ . Exine about  $2\mu$ . Outermost layer perinous; the perine winged on the distal face, the fin irregular, flaccid, projected about  $3-10\mu$  and sometimes appearing as being a great sack in equatorial view; central part of proximal face reticulate, the lumina irregular, about  $5-10\mu$  in diameter, the edge psilate and smooth; width of double-winged perine  $6-10\mu$  at the equator. Color brown.

Specimen studied: Kami-Nakao, Ohtaki-mura, Chichibu-gun, Saitama Pref., Sept. 2, 1952, D. Shimizu (no. 52817).

Illustration: Shimizu & Hattori (1953).

#### 8. *Conocephalum conicum* (L.) Dum. (Fig. 5-d, e)

Multicellular in mature capsule, polarity missing; laesura unconfirmed, apparently due to the disappearance of tetrad scar by the endogenous germination within the stretched exine, but traces of laesura often observed as one or two recurved ridges densely covered with projections; external shape irregular-spheroidal or globular, difficult to distinguish the equatorial diameter and polar axis; diameter  $70(84)96 \times 81(95)114\mu$ ,  $70(87)105\mu$ . Exine very thin, about  $0.5\mu$ , verrucate and granulate; the verrucae irregular,  $2-3\mu$  in diameter and about  $2\mu$  in height; the granules smaller than  $1\mu$ , both projections mixed and scattered all over the surface. Color brown or dark-brown.

The multicellular stage of these spores is difficult to observe in the preparations which are mounted in glycerine-jelly, but are rarely observable when the fresh spores are mounted in water.

Specimen studied: Mitaki cho, Hiroshima city, Apr. 5, 1964, N. Miyoshi.

Illustrations: Horikawa (1929b, 1939), Erdtman (1957), Inoue (1960).

#### 9. *Conocephalum supradecompositum* (Lindb.) St. (Fig. 5-b, c)

External shape, laesura and color identical with the preceding species, but size range and projection of the spores different from those of the preceding species; diameter of spheroidal spore  $45(63)81 \times 54(70)87\mu$ ,  $57(69)87\mu$ . Exine very thin, about  $0.5\mu$ , granulate; the granules about  $0.5\mu$ , densely scattered all over the surface and frequently some granules adhering.

Specimen studied: Mt. Kaimon, Kagoshima Pref., Mar. 14, 1964, N. Miyoshi.

Illustrations: Horikawa (1929b, 1939), Inoue (1960).

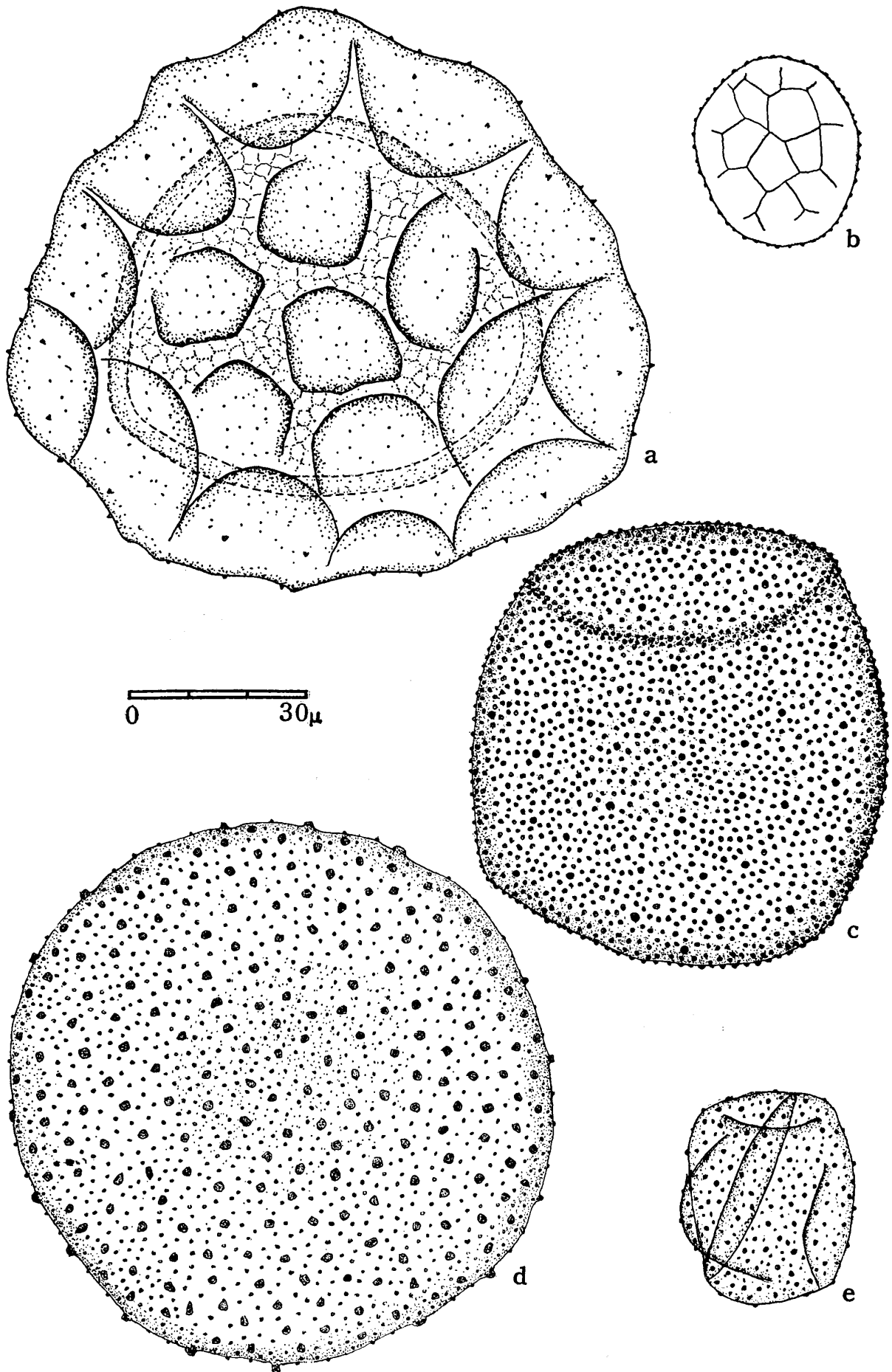
#### 10. *Peltolepis quadrata* (Sauter) K. Muell. (Fig. 6-c, d)

Unicellular, cryptopolar, indistinctly tetrahedral, generally alete; laesura lacking or vaguely observed as to form very rough wrinkles; shape, excluding perine, rounded-triangular in polar view; profile elliptical or fan-shaped; equatorial diameter  $50(62)75\mu$ , m.  $\pm$  s. d.  $56-68\mu$ ; polar axis  $40-45\mu$ . Exine about  $1\mu$ . Outermost layer perinous; the perine saccate on the distal side, the sacks  $6-9\mu$  in diameter,  $3-5\mu$  in height and 9-11 in number through equatorial diameter, the sacks like a wart at external shape but the inside empty and observed as ring in polar view; on the proximal side the sacks reduced and irregular wrinkles observable. Color brown or dark-brown.

Specimen studied: Mt. Rishiri, Hokkaido, Aug. 13, 1963, N. Miyoshi.

Illustration: Shimizu & Hattori (1955)

Fig. 4. a. *Mannia levigata* (E. v.). b. ditto (D. p. v.). c. *Plagiochasma intermedium* (P. p. v.). d. ditto (E. v.,  $\times 303$ ). e. *P. japonicum* (P. p. v.).



11. **Sauteria alpina** Nees

Material unsatisfactory. External shape identical with *Peltolepis quadrata*; equatorial diameter about 40-60  $\mu$ .

Specimen studied: Mt. Rishiri, Hokkaido, July 25, 1954, D. Shimizu (no. 53758).

Illustration: Shimizu & Hattori (1955).

12. **Preissia quadrata** (Scop.) Nees (Fig. 6-a, b)

Unicellular, cryptopolar, indistinctly tetrahedral, generally alete; laesura lacking or rarely observed; shape, excluding perine, round or rounded-triangular in polar view; profile elliptical, proximal portion dome-shaped; equatorial diameter 40(47)51  $\mu$ , m.  $\pm$ s.d. 45-49  $\mu$ ; polar axis 33-39  $\mu$ . Exine 3-4  $\mu$ . Outermost layer perinous; the perine reticulate all over the surface, the lumina of the distal wall making very irregular so as to form very rough wrinkles or wings; width of wavy perine 6-12  $\mu$  at the equator. Color brown or dark-brown.

Specimen studied: Mt. Rishiri, Hokkaido, Aug. 13, 1963, N. Miyoshi.

Illustration: Inoue (1960)

13. **Marchantia tosana** St. (Fig. 7-a, b)

Unicellular, cryptopolar, indistinctly tetrahedral, usually alete; laesura poorly observed, sometimes difficult to recognize precisely; shape rounded-triangular in polar view; profile fan-shaped or hemispherical; proximal portion subpyramidal or flat; equatorial diameter 24(28)31  $\mu$ , m.  $\pm$ s.d. 26-30  $\mu$ ; polar axis 18-21  $\mu$ . Exine about 0.5  $\mu$ . Outermost layer perinous; the perine poorly developed, reticulate or bullate all over the surface; the lumina very irregular so as to form wrinkles rather than lumina, especially on the proximal side; width of the wing 2-3  $\mu$  at the equator. Color yellowish-brown.

Specimen studied: Fuchu-cho, Aki-gun, Hiroshima Pref., July 1, 1962, N. Miyoshi.

Illustrations: Horikawa (1939), Makino (1957), Inoue (1960).

14. **Marchantia cuneiloba** St. (Fig. 7-d)

Almost identical with *M. tosana*; equatorial diameter 24(26)30  $\mu$ , m.  $\pm$ s.d. 24-28  $\mu$ ; polar axis 15-21  $\mu$ . Exine about 0.5  $\mu$ . Width of perine about 3  $\mu$  at the equator.

Specimen studied: Taishaku-kyo, Hiroshima Pref., Sept. 23, 1962, K. Nehira.

15. **Marchantia diptera** Mont. (Fig. 7-c)

Equatorial diameter 18(22)24  $\mu$ , m.  $\pm$ s.d. 20-24  $\mu$ ; polar axis 13-15  $\mu$ . Exine about 0.5  $\mu$ . Width of perine about 3  $\mu$  at the equator.

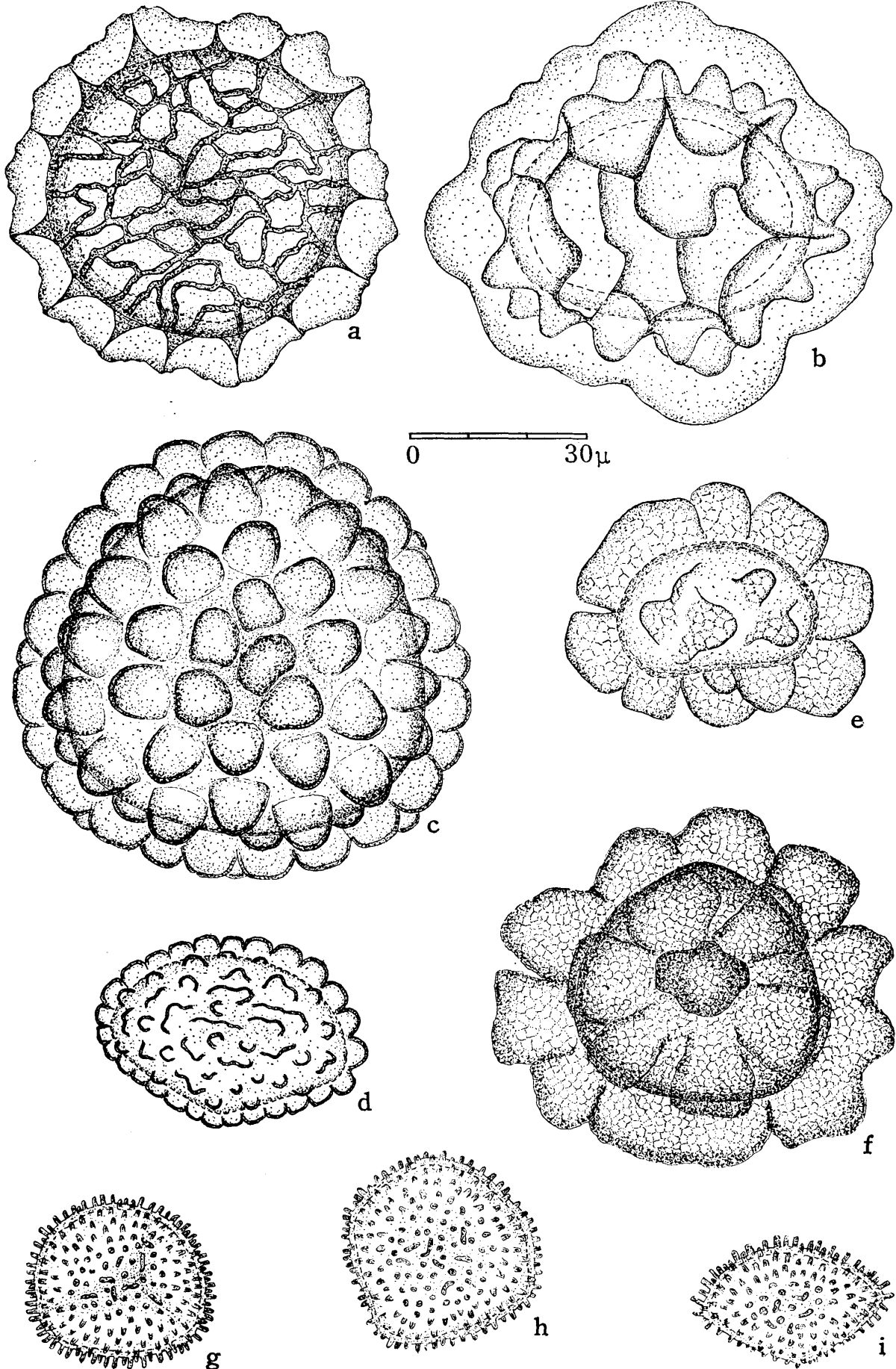
Specimen studied: Fuchu-cho, Aki-gun, Hiroshima Pref., July 1, 1962, N. Miyoshi.

Illustrations: Horikawa (1930), Makino (1957).

16. **Dumortiera hirsuta** (Sw.) Reinw., Bl. et Nees (Fig. 6-g, h, i)(Pl. 2-g)

Unicellular, cryptopolar or rarely apolar, indistinctly tetrahedral or globose, generally alete; laesura usually lacking and rarely observed, shape circular or rounded-triangular in polar view; profile hemispherical or elliptical, showing a clear polar axis, but usually difficult to distinguish two sides in polar view as in *Wiesnerella denudata*; equatorial diameter 27(30)34  $\mu$ , m.  $\pm$ s.d. 28-32  $\mu$ ; polar axis 18-24  $\mu$ . Exine 0.5-1  $\mu$ , baculate; the rod densely distributed all over the surface, about 3  $\mu$  in height and 1-2  $\mu$  in width at the base; perine lacking. Color brown.

Fig. 5. a. *Plagiochasma japonicum* (D. p. v.). b. *Conocephalum supradecompositum* (M., optical section,  $\times 300$ ). c. ditto (M.). d. *C. conicum* (M.). e. ditto (M.,  $\times 300$ ).



Difference of the size range of spores in this species associated with polyploidy was previously mentioned in "Spore characters" (Table 3). The above-described spores seem to be of triploid species judging from comparison with the results of study by Tatuno (1952).

Specimen studied: Nakano, Senogawa-cho, Aki-gun, Hiroshima Pref., May 5, 1962, N. Miyoshi.

Illustrations: Horikawa (1939), Frye & Clark (1937), Erdtman (1957), Inoue (1960).

17. **Wiesnerella denudata** (Mitt.) St. (Fig. 6-e, f) (Pl. 2-d, e, f)

Unicellular, cryptopolar, indistinctly tetrahedral, generally alete; laesura usually lacking; shape, excluding perine, circular or rounded-triangular in polar view; profile elliptical or hemispherical owing to a clear polar axis, but difficult to distinguish proximal side and distal one in polar view, because of laesura lacking and ornamentation similar on both sides; equatorial diameter 27(32)37 $\mu$ , m.  $\pm$  s. d. 30-34 $\mu$ ; polar axis 20-26 $\mu$ . Exine 0.5-1 $\mu$ . Outermost layer perinous; the perine saccate all over the surface; the sacks irregular, large, about 10-15 $\mu$  in diameter and 4-5 in number through a diameter, the sacks covered with reticulate ornamentation all over the surface, the lumina small, about 2-3 $\mu$ ; width of the wing 6-12 $\mu$  at the equator. Color brown.

Specimen studied: Negasa, Mikawa-cho, Kuga-gun, Yamaguchi Pref., May 3, 1963, N. Miyoshi.

Illustrations: Horikawa (1930, 1939), Inoue (1957, 1960).

18. **Riccia crystallina** L. (Fig. 7-g)

Unicellular, anisopolar, tetrahedral, trilete; laesura long, reaching to the equator; commissure covered with narrow ridges of reticulum; shape rounded triangular in polar view; profile fan shaped; proximal portion subpyramidal; equatorial diameter 60(68)80 $\mu$ , m.  $\pm$  s. d. 64-72 $\mu$ ; polar axis 42-45 $\mu$ . Exine 3-5 $\mu$ . Outermost layer perinous; the perine reticulate all over the surface; the lumina comparatively regular, hexagonal or pentagonal in shape, 10-18 $\mu$  in size, 5-6 meshes through a diameter on the distal face and 6-12 $\mu$  in size on the proximal; width of winged perine 6-12 $\mu$  at the equator. Color brown or dark-brown.

Specimen studied: Botanical garden of Hiroshima Univ., Hiroshima city, Sept. 4, 1963, N. Miyoshi.

Illustrations: Macvicar (1926), Frye & Clerk (1937), Müller (1954).

19. **Riccia glauca** L. (Fig. 7-h)

Identical with *R. crystallina* except for the size range. Equatorial diameter 57(66)75 $\mu$ , m.  $\pm$  s. d. 62-70 $\mu$ ; polar axis 45-50 $\mu$ . Exine difficult to measure. Lumina 6-12 $\mu$  in size, 7-8 meshes through a diameter on the distal face and 6-9 $\mu$  in size on the proximal; width of perine about 6 $\mu$  at the equator.

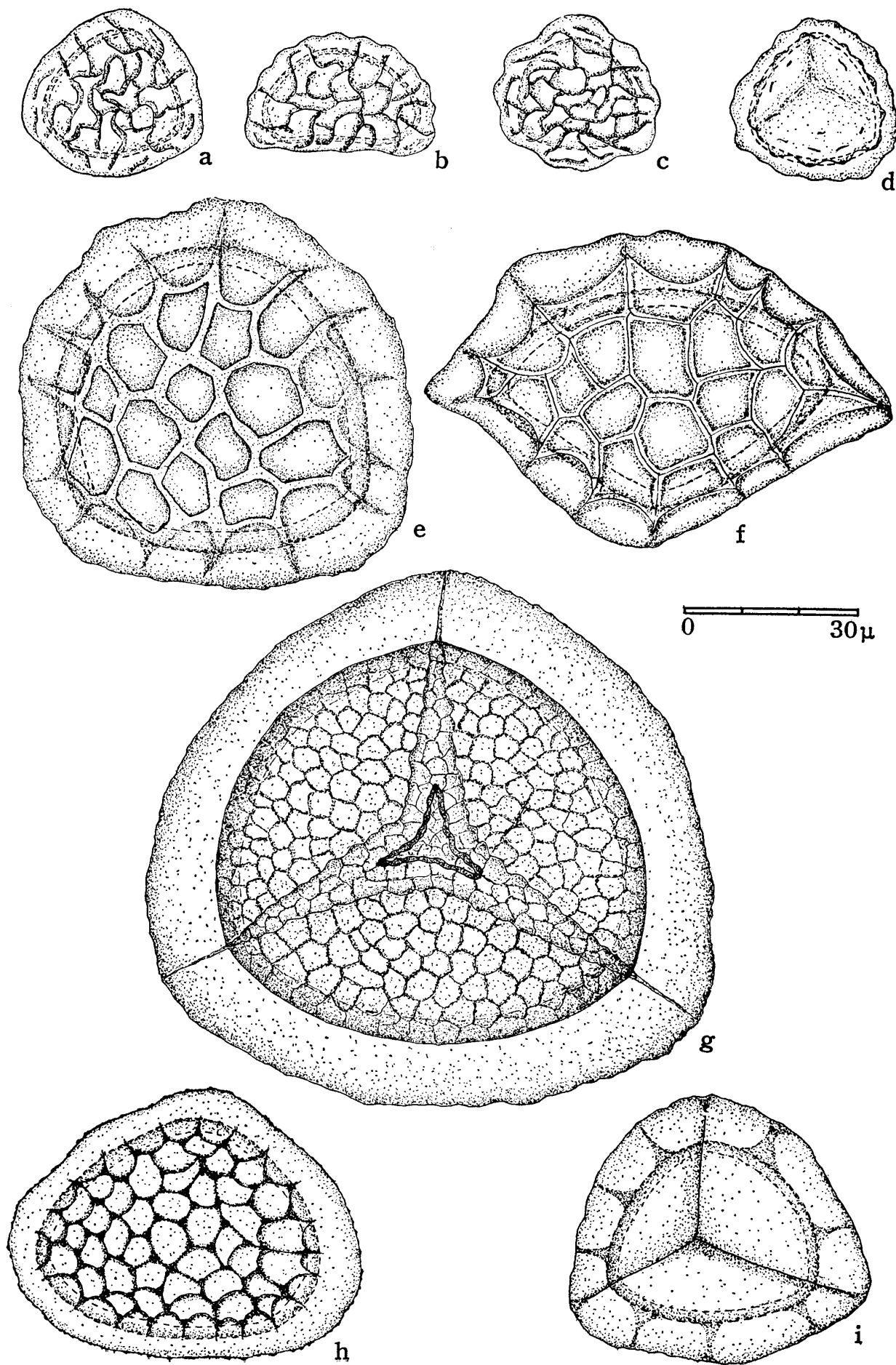
Specimen studied: Yahata, Fuchu-cho, Aki-gun, Hiroshima Pref., Nov. 22, 1964, N. Miyoshi.

Illustrations: Macvicar (1926), Horikawa (1939).

20. **Riccia huebeneriana** Lindb. (Fig. 7-e, f)

Equatorial diameter 48(53)57 $\mu$ , m.  $\pm$  s. d. 50-60 $\mu$ ; polar axis 36-40 $\mu$ . Exine about 3 $\mu$ . Lumina 6-15 $\mu$  in size, 6-7 meshes through a diameter on the distal face and 4-6 $\mu$  in size on the proximal; width of perine 6-10 $\mu$  at the equator.

Fig. 6. a. *Preissia quadrata* (D. p. v.). b. ditto (E. v.). c. *Peltolepis quadrata* (D. p. v.). d. ditto (E. v.,  $\times 600$ ). e. *Wiesnerella denudata* (E. v.). f. ditto (P. v.). g. *Dumortiera hirsuta* (P. p. v. ?). h. ditto (P. v.). i. ditto (E. v.).





Specimen studied: Yahata, Fuchu-cho, Aki-gun, Hiroshima Pref., Nov. 10, 1964, N. Miyoshi.

Illustrations: Macvicar (1926), Müller (1954), Mehra & Kachroo (1961).

21. **Ricciocarpus natans** (L.) Corda (Fig. 7-i)

Unicellular, anisopolar, tetrahedral, trilete; laesura long, reaching to the equator; shape rounded triangular in polar view; profile fan-shaped; proximal portion subpyramidal; equatorial diameter  $54(59)66\mu$ ; polar axis  $42-48\mu$ ; both measurements include the winged perine. Exine difficult to measure. Cutermost layer perinous; the perine seemingly reticulate, but difficult to observe it, because of dark-brown to deep black color of the spore wall.

In the future it is planned to make clear the walls of these spores by a bleaching method and to observe more exactly the ornamentation of the spore.

Specimen studied: Kurio-cho, Fuchu city, Hiroshima Pref., Oct. 31, 1965, H. Suzuki.

Illustrations: Horikawa (1939), Müller (1954).

### III. Jungermanniales

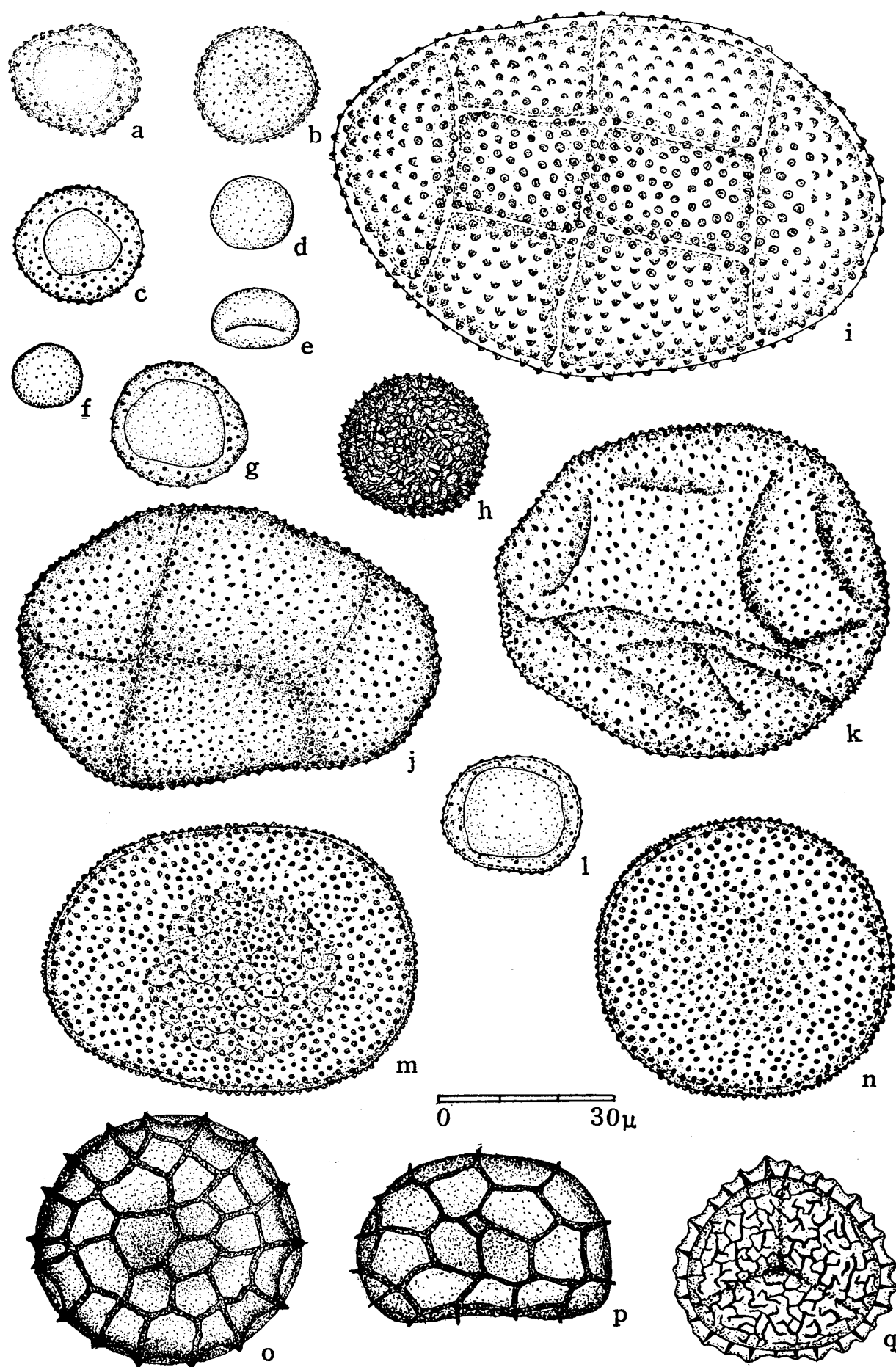
#### A. Jungermanniales anacrogynae

The materials belonging to this group which were studied represent seven families: Metzgeriaceae, Riccardiaceae, Makinoaceae, Pelliaceae, Pallaviciniaceae, Blasiaceae and Fossombroniaceae. Among Metzgeriaceae, Riccardiaceae, Makinoaceae and Pallaviciniaceae, the spores show little divergence in both size and ornamentation. The polarity and tetrad scar have not been studied by previous workers. The spores of these families are anisopolar, and have a deformed-trilete mark on the proximal side according to my observation. Multicellular and deformed spores are observed in Pelliaceae, and the enlargement of the spore in the early stage of the endogenous germination is also recognized in Blasiaceae. In Fossombroniaceae, the spores are sufficiently distinctive to be used for taxonomic purposes, as exemplified by the fact that the subdivision of the genus *Fossombronia* by Stephani (1900) and others has been based upon spore characters.

#### Key to the species treated based on spore morphology

- A. Spores unicellular
  - B. Polarity anisopolar
    - C. Tetrad scar trilete; sculpture reticulate; exine difficult to measure; equatorial diameter  $39(43)48\mu$  ..... *Fossombronia japonica*
    - C. Tetrad scar deformed-trilete
      - D. Sculpture reticulate; exine about  $0.5\mu$ .
        - E. equatorial diameter  $21(24)28\mu$  ..... *Makinoa crispata*
        - E. equatorial diameter  $20(23)25\mu$  ..... *Pallavicinia lyellii*
      - D. Sculpture granulate
        - E. Exine about  $0.5\mu$ 
          - F. Equatorial diameter  $18(20)23\mu$  ..... *Metzgeria conjugata* ssp. *japonica*
          - F. Equatorial diameter  $15(17)19\mu$  ..... *Riccardia pinguis*

Fig. 7. a. *Marchantia tosona* (D. p. v.). b. ditto (E. v.). c. *Marchantia diptera* (D. p. v.). d. *Marchantia cuneiloba* (P. p. v.?). e. *Riccia huebeneriana* (D. p. v.). f. ditto (E. v.). g. *Riccia crystallina* (P. p. v.). h. *Riccia glauca* (D. p. v.,  $\times 600$ ). i. *Ricciocarpus natans* (P. p. v.,  $\times 600$ ).



- E. Exine thinner than  $0.5\mu$ ; equatorial diameter  $12(14)16\mu$   
 ..... *Riccardia miyakeana*
- E. Exine very thin, difficult to exactly measure; equatorial diameter  
 $9(11)12\mu$  ..... *Riccardia nana*
- B. Polaririty apolar; tetrad scar lacking; sculpture granulate; exine about  $1\mu$ ; dia-  
 meter  $40(49)57 \times 51(58)70\mu$ ,  $47(51)60\mu$  ..... *Cavicularia densa*
- A. Spores multicellular; polarity missing; tetrad scar lacking; sculpture granulate; exine  
 about  $0.5\mu$
- B. diameter  $36(56)75 \times 54(72)87\mu$  ..... *Pellia fabbroniana*
- B. diameter  $57(64)81 \times 67(86)105\mu$  ..... *Pellia neesiana*

### 1. *Metzgeria conjugata* Lindb. ssp. *japonica* (Hatt.) Kuwahara (Fig. 8-a, b)

Unicellular, anisopolar, bilateral, deformed-trilete; laesura triangular or rounded; shape circular in polar view; profile hemispherical or kidney-shaped; equatorial diameter  $18(20)23\mu$ , m.  $\pm$ s. d.  $19-21\mu$ ; polar axis  $15-18\mu$ . Exine very thin, about  $0.5\mu$ , granulate; the granules about  $0.5\mu$  in diameter and scattered all over the surface except on laesura. Color yellowish-brown.

Specimen studied: Isl. Yakushima, Kagoshima Pref., Mar. 23, 1963, K. Nehira.

Illustration: Kuwahara (1958).

### 2. *Riccardia pinguis* (L.) Gray (Fig. 8-c)

External shape and laesura identical with *Metzgeria conjugata* ssp. *japonica*; equatorial diameter  $15(17)19\mu$ ; polar axis  $12-13\mu$ . Exine very thin, about  $0.5\mu$ , granulate; the granules about  $0.5\mu$  in diameter and densely distributed all over the surface except on laesura. Color yellowish-brown.

Specimen studied: Isl. Yakushima, Kagoshima Pref., Mar. 20, 1963, N. Miyoshi.

Illustrations: Showalter (1925), Müller (1954), Mizutani & Hattori (1957), Nehira (1962).

### 3. *Riccardia miyakeana* Schiffn. (Fig. 8-d, e)

Equatorial diameter  $12(14)16\mu$ , m.  $\pm$ s. d.  $13-15\mu$ ; polar axis  $9-12\mu$ . Exine thinner than  $0.5\mu$ , granulate; the granules smaller than  $0.5\mu$ , scattered all over the surface except on laesura. Color brown.

Specimen studied: Ohno-cho, Saeki-gun, Hiroshima Pref., Apr. 1, 1962, K. Nehira.

Illustrations: Hattori (1944), Magohuku & Yamada (1964).

### 4. *Riccardia nana* Mizutani et Hatt. (Fig. 8-f)

Equatorial diameter  $9(11)12\mu$ , m.  $\pm$ s. d.  $10-12\mu$ ; polar axis  $6-9\mu$ . Exine very thin and difficult to measure exactly, granulate or psilate; the ornamentation poorly developed and hard to distinguish clearly. Color yellowish-brown.

Specimen studied: Mt. Eboshidake, Kagoshima Pref., Mar. 18, 1963, N. Miyoshi.

Illustration: Mizutani & Hattori (1957).

### 5. *Pellia fabbroniana* Raddi (Fig. 8-j, k)

Multicellular with about 10-celled stage in mature capsule (each cell of a multicellular spore easily observed and counted when fresh, but difficult in dry or old conditions.);

Fig. 8. a. *Metzgeria conjugata* ssp. *japonica* (P. p. v.). b. ditto (D. p. v.). c. *Riccardia pinguis* (P. p. v.). d. *Riccardia miyakeana* (D. p. v.). e. ditto (E. v.). f. *Riccardia nana* (D. p. v.) g. *Makinoa crispata* (P. p. v.). h. ditto (D. p. v.). i. *Pellia neesiana* (M.). j-k. *Pellia fabbroniana* (M.). l. *Pallavicinia lyellii* (P. p. v.). m-n. *Cavicularia densa* (A.). o. *Fossombronia japonica* (D. p. v.). p. ditto (E. v.). q. ditto (P. p. v.,  $\times 600$ ).

polarity missing; laesura unconfirmed apparently due to the disappearance of tetrad scar by the endogenous germination within the stretched exine; external shape spheroidal or ovoid, difficult to distinguish the equatorial diameter and polar axis; diameter  $36(56)75 \times 54(72)87\mu$ . Exine very thin, about  $0.5\mu$ , granulate; the granules smaller than  $1\mu$ , densely distributed all over the surface. Color yellowish-green with chloroplasts in fresh spores, but yellowish-brown in dry condition.

Specimen studied: Mt. Futamata, Kagoshima Pref., Apr. 1, 1962, N. Miyoshi.

Illustration: Showalter (1925).

6. **Pellia neesiana** (Gott.) Limpr. (Fig. 8-i)

Essentially identical with *P. fabbroniana*, but size of spores and granules larger than the preceding. The diameter  $57(64)81 \times 67(86)105\mu$ ; the granules about  $1\mu$

Specimen studied: Mt. Daisen, Tottori Pref., Apr. 27, 1965, K. Nehira.

Illustration: Horikawa (1939).

7. **Makinoa crispata** (St.) Miyake (Fig. 8-g, h) (Pl. 3-a, b)

Unicellular, anisopolar, bilateral, deformed-trilete; laesura rounded or triangular, about  $15-18\mu$  in diameter, bordered by the recurved edges of sexine; shape circular in polar view, profile hemispherical or kidney-shaped; proximal portion flat or hollow; equatorial diameter  $21(24)28\mu$ , m.  $\pm$  s. d.  $23-25\mu$ ; polar axis  $16-18\mu$ . Exine very thin, about  $0.5\mu$ , reticulate on the distal side; the lumina very small, about  $1-2\mu$  in diameter, more than 10 meshes through a diameter; on the proximal side, except on laesura, granulate or reticulate, but difficult to determine accurately because of poor sculpturing. Color yellowish-brown.

Specimen studied: Mitaki-cho, Hiroshima city, Apr. 14, 1962, N. Miyoshi.

Illustrations: Horikawa (1929a, 1939), Inoue (1958), Magohuku & Yamada (1964).

8. **Pallavicinia lyellii** (Hook.) Gray (Fig. 8-1)

External shape identical with *Makinoa crispata*; equatorial diameter  $20(23)25\mu$ , m.  $\pm$  s. d.  $22-24\mu$ ; polar axis  $12-15\mu$ . Exine very thin, about  $0.5\mu$ , reticulate on the distal side, the lumina irregular and very small, about  $1-3\mu$  in diameter, more than 10 meshes through a diameter; on the proximal side granulate except on laesura. Color yellowish-green even in comparatively old and dry condition.

Specimen studied: Isl. Yakushima, Kagoshima Pref., Mar. 20, 1963, N. Miyoshi.

Illustrations: Macvicar (1926), Horikawa (1939).

9. **Cavicularia densa** St. (Fig. 3-m, n)

Unicellular, apolar, tetrahedral shape missing, dehiscence or laesura unconfirmed, apparently due to the enlargement of the spore in early stage of the endogenous germination; external shape irregular-spherical or ovoid, difficult to distinguish the equatorial diameter and polar axis, diameter  $40(49)57 \times 51(58)70\mu$ ,  $47(51)60\mu$ . Exine thin, about  $1\mu$ , granulate; the granules  $1\mu$  or smaller than  $1\mu$ , densely distributed all over the surface. Color yellowish-green with many chloroplasts in fresh spores, but yellow or yellowish-brown in dry condition.

Specimen studied: Mt. Daisen, Tottori Pref., Apr. 27, 1965, K. Nehira.

Illustrations: Horikawa (1928, 1939), Makino (1957).

10. **Fossombronia japonica** Schiffn. (Fig. 8-o, p, q)

Unicellular, anisopolar or cryptopolar, vaguely tetrahedral, trilete or alete; laesura poorly developed with slender ridges and often difficult to observe; shape circular or rounded-triangular; profile hemispherical or fan-shaped, proximal portion flat; equatorial diameter  $39(43)48\mu$ , m.  $\pm$  s. d.  $40-46\mu$ ; polar axis  $30-36\mu$ . Exine difficult to measure,

Outermost layer perinous; the perine reticulate all over the surface; the lumina of distal wall comparatively regular in shape, about  $6-15\mu$  in diameter and 6-7 meshes through a diameter; on the proximal side the lumina indistinct, irregular and small, about  $3-5\mu$  in diameter. Color dark-brown. In this species reticulum of the spores is similar to that of *Riccia*, but the former has an indistinct triradiate mark as opposed to the latter which has the typical one.

Specimen studied: Isl. Amamiyoshima, Kagoshima Pref., Mar. 18, 1964, N. Miyoshi.

Illustration: Inoue (1959).

## B. Calobryineae

*Calobryum rotundifolium* is endemic to Japan, and bears some primitive characters which are important in discussing phylogeny of Hepaticae, however, the spores show little difference in both size and sculpture from those of many species in Jungermanniales.

### 1. *Calobryum rotundifolium* (Mitt.) Schiffn. (Fig. 1-a<sub>1</sub>, a<sub>2</sub>)

Unicellular, anisopolar, bilateral, deformed-trilete; laesura indistinctly observed, usually rounded, about  $15-18\mu$ ; shape circular in polar view, profile hemispherical or kidney-shaped, proximal portion concave; equatorial diameter  $18(20)23\mu$  m.  $\pm$  s. d.  $19-21\mu$ , polar axis  $13-16\mu$ . Exine very thin, about  $0.5\mu$ , granulate, the granules about  $0.5\mu$  in diameter and height, densely distributed all over the surface, except on laesura; color yellowish-brown.

Specimen studied: Mitaki-cho, Hiroshima city, Apr. 14, 1962, N. Miyoshi.

Illustrations: Horikawa (1929b, 1939), Nehira (1961).

## C. Jungermanniales acrogynae

In this group the spore structure of many families exhibits a remarkable degree of uniformity. The spores are small, ranging from  $9\mu$  to  $25\mu$  in diameter, thin-walled and finely granular or smooth, rendering such spores very difficult to be exactly placed into genera or even families. Within the group, however, some exceptions have been observed. In Porellaceae, Frullaniaceae, Lejeuneaceae and *Trichocoleopsis* the spores are large, ranging from  $20\mu$  to  $70\mu$ , and irregular in shape. It is relatively easy to place the spores into families or genera. Endogenous germination within the stretched exine of spore is clearly recognized in *Porella*, and the irregularly spherical or elliptical spores of Lejeuneaceae may also belong to this type (endogenous germination), but I could not observe multicellular feature of the spores, so these are described as "unicellular" for convenience in this work. Description of small spores with poor ornamentation is omitted and only the size range is given in Table 4. Illustrations were made from the spores of some species in ten families. Structure and stratification of the walls of these spores will be a subject to be investigated by electron microscopy in future.

### Key to the species treated based on spore morphology

#### A. Unicellular

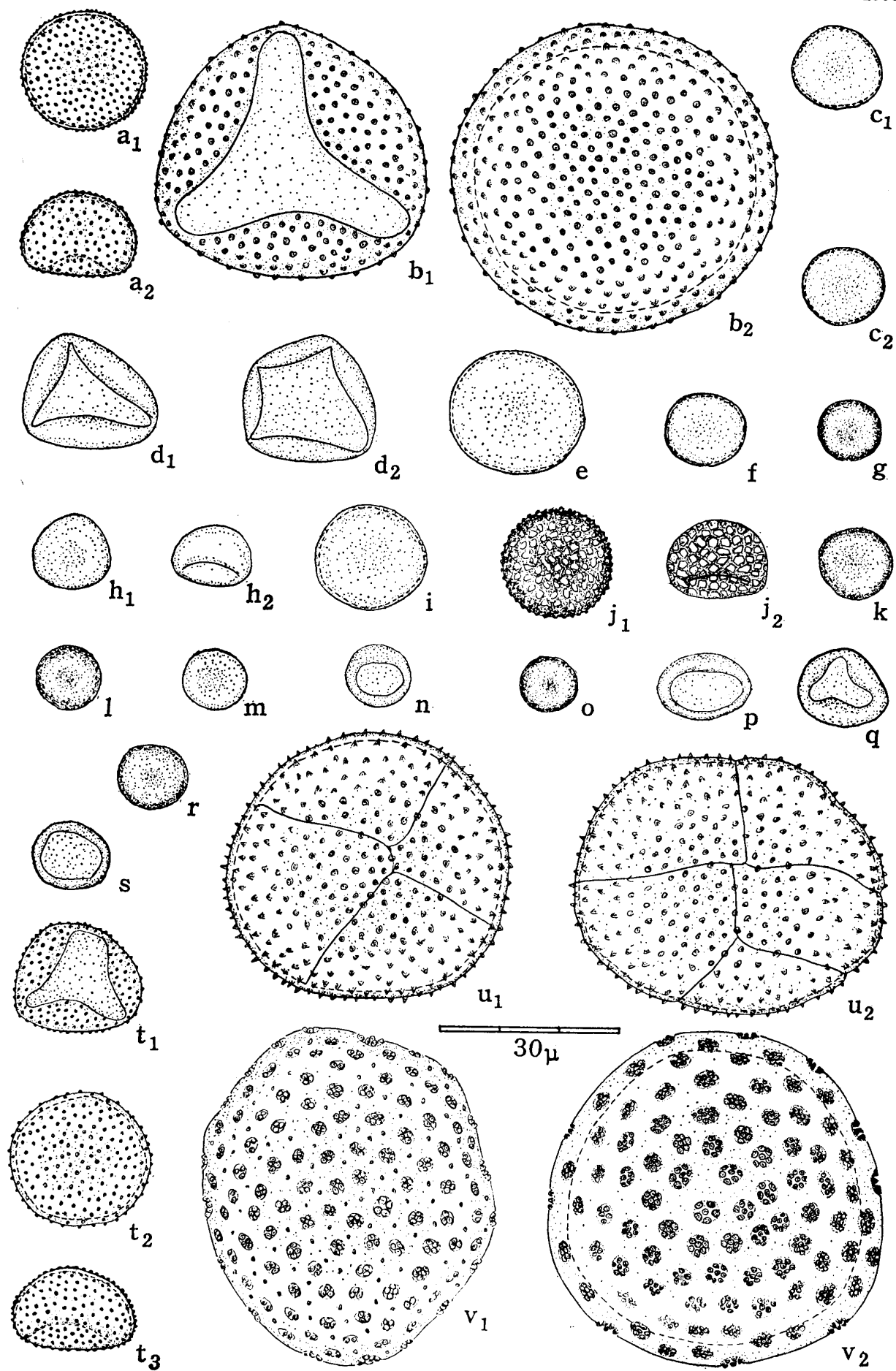
B. Polarity anisopolar; tetrad scar deformed-trilete; sculpture granulate; exine  $0.5-1\mu$ ; equatorial diameter  $18(21)26\mu$  ..... *Radula oyamensis*

B. Polarity apolar; tetrad scar lacking

#### C. Sculpture granulate

D. Exine  $1-3\mu$ ; equatorial diameter  $45(52)60\mu$  ..... *Trichocoleopsis sacculata*

D. Exine  $0.5-1\mu$ ; diameter  $15(20)27 \times 24(40)60\mu$  ..... *Leptolejeunea subacuta*



- C. Sculpture echinulate and echinate; exine about  $1\mu$ ; diameter  $40(52)72 \times 54(70)102\mu$ ,  $51(59)69\mu$ .....*Brachiolejeunea sandvicensis*
- C. Sculpture granulate and echinate; exine about  $3\mu$ ; diameter  $27(36)42 \times 39(46)63\mu$ ,  $36(40)42\mu$  .....*Spruceanthus polymorphus*
- C. Sculpture echinulate; exine  $0.5-1\mu$ ; diameter  $28(36)45 \times 39(46)51\mu$ ,  $34(36)45\mu$  ..... *Ptychanthus striatus*
- A. Multicellular; polarity missing; tetrad scar lacking
- B. Sculpture polyforate and granulate
- C. Exine about  $3\mu$ ; diameter  $30(45)54 \times 40(55)66\mu$ ,  $48(55)63\mu$ ..... *Frullania muscicola*
- C. Exine about  $6\mu$ ; diameter  $27(42)66 \times 33(53)80\mu$ ,  $30(48)63\mu$  ..... *Frullania kagoshimensis*
- B. Sculpture echinulate; exine about  $1\mu$  or thinner than  $1\mu$ ; diameter  $39(42)45 \times 43(47)54\mu$ ,  $38(44)51\mu$ , .....*Porella ulophylla*

### 1. *Trichocoleopsis sacculata* (Mitt.) Sh. Okamura (Fig. 9-b<sub>1</sub>, b<sub>2</sub>) (Pl. 3-g)

Unicellular, apolar; tetrahedral shape and laesura usually missing, and rarely observed; external shape almost spherical, difficult to distinguish the equatorial diameter and polar axis; diameter  $45(52)60\mu$ , m.  $\pm$  s. d.  $48-56\mu$ . Exine  $1-3\mu$ , difficult to measure exactly, granulate; the granules about  $1\mu$ , densely covering all over the surface. Color yellowish-brown.

Specimen studied: Mt. Saragamine, Ehime Pref., May 4, 1962, T. Seki.

### 2. *Radula oyamensis* St (Fig. 9-t<sub>1</sub>, t<sub>2</sub>, t<sub>3</sub>)

Unicellular, apolar; tetrahedral shape and laesura usually unconfirmed, but deformed trilete rarely observed; external shape irregular-spherical, diameter  $18(21)26\mu$ , m.  $\pm$  s. d.  $19-23\mu$ . Exine  $0.5-1\mu$ , granulate, the granules about  $0.5\mu$ , scattered all over the surface.

Specimen studied: Anbo, Isl. Yakushima, Kagoshima Pref., Mar. 23, 1963, K. Nehira.

### 3. *Porella ulophylla* (St.) Hatt. (Fig. 9-u<sub>1</sub>, u<sub>2</sub>)

Multicellular; polarity missing; tetrahedral shape and laesura missing; external shape irregular-spherical or elliptical, difficult to distinguish the proximal face and the distal one; diameter  $39(42)45 \times 43(47)54\mu$ ,  $38(44)51\mu$ . Exine thin, about  $1\mu$  or thinner in thickness, echinulate, the spinules  $1\mu$  long and about  $0.5\mu$  wide at base, covering all over the surface. Color yellowish-brown.

Specimen studied: Ohkubo-ji, Nagao-cho, Ohkawa-gun, Kagawa Pref., Apr. 4, 1963, N. Miyoshi.

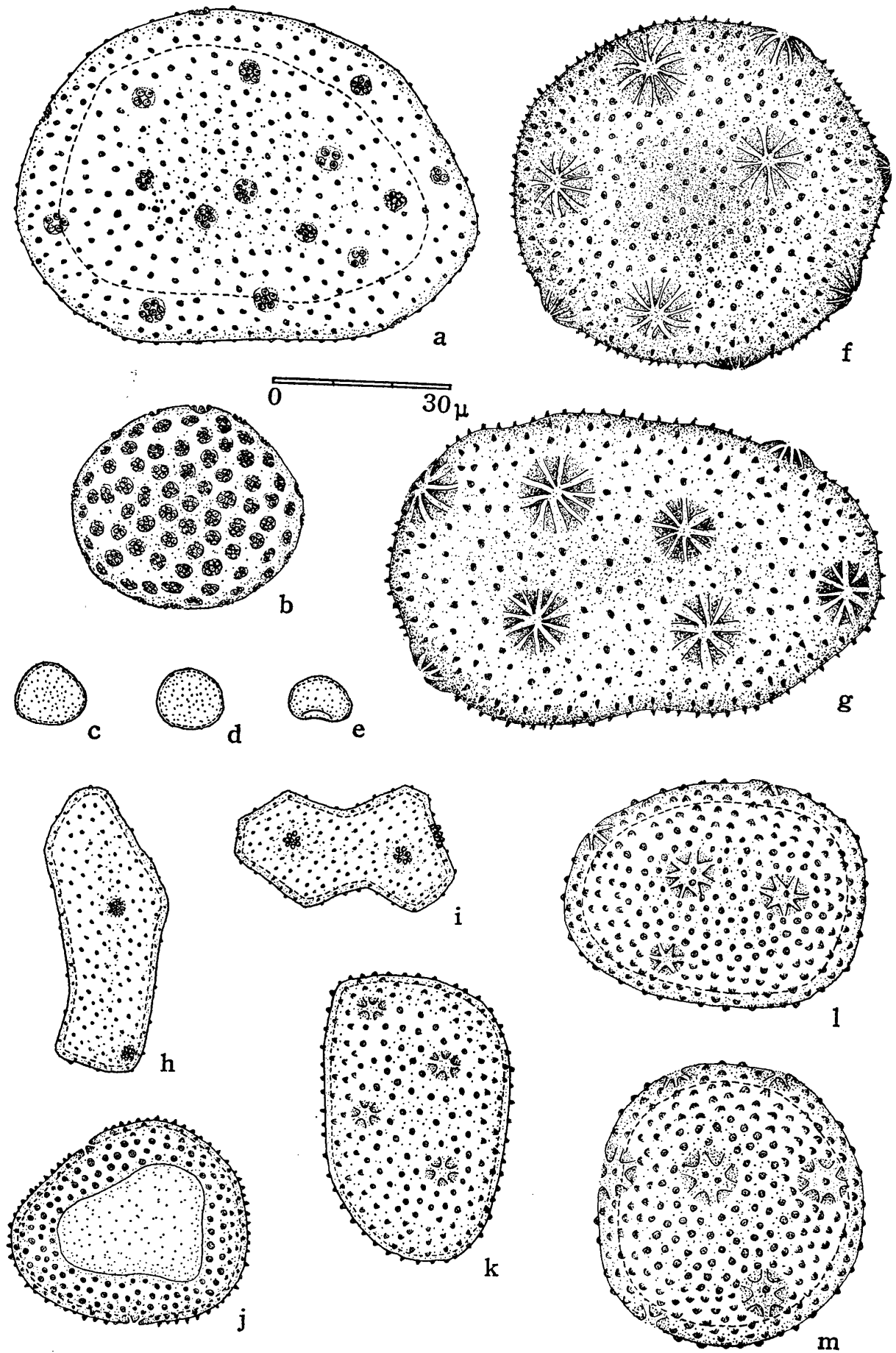
Illustrations: Horikawa (1930, 1939).

### 4. *Frullania muscicola* St. (Fig. 9-v<sub>1</sub>, v<sub>2</sub>) (Pl. 3-e, f)

Multicellular; polarity missing; tetrahedral shape and laesura missing; external shape

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Fig. 9. a<sub>1</sub>. *Calobryum rotundifolium* (D. p. v.). a<sub>2</sub>. ditto (E. v.). b<sub>1</sub>. *Trichocoleopsis sacculata* (P. p. v., rarely observed). b<sub>2</sub>. ditto (A.). c<sub>1</sub>, c<sub>2</sub>. *Trichocolea tomentella* (A., ?). d<sub>1</sub>, d<sub>2</sub>. *Chiloscyphus polyanthus* (P. p. v.). e. ditto (D. p. v.). f. *Heteroscyphus bescherelei* (D. p. v.). g. *Lophocolea heterophylla* (D. p. v.). h<sub>1</sub>. *Jungermannia radiculosa* (D. p. v.). h<sub>2</sub>. ditto (E. v.). i. *Plagiochila ovalifolia* (P. v.). j<sub>1</sub>. *Mylia verrucosa* (D. p. v.). j<sub>2</sub>. ditto (E. v.). k. *Scapania spinosa* (P. v.). l. *Cephalozia otaruensis* (D. p. v.). m. *Nowellia curvifolia* (P. v.). n. *Schiffneria hyalina* (P. p. v.). o. *Odontoschisma denudatum* (D. p. v.). p. *Jackiella brunnea* (P. p. v.). q. *Lepidozia vitrea* (P. p. v.). r. *Bazzania albicans* (P. v.). s. *Calypogeia tosona* (P. p. v.). t<sub>1</sub>. *Radula oyamensis* (P. p. v.). t<sub>2</sub>. ditto (D. p. v.). t<sub>3</sub>. ditto (E. v.). u<sub>1</sub>, u<sub>2</sub>. *Porella ulophylla* (M.). v<sub>1</sub>, v<sub>2</sub>. *Frullania muscicola* (M.).





irregular-spherical or elliptical, diameter  $30(45)54 \times 40(55)66\mu$ ,  $48(55)63\mu$ . Exine about  $3\mu$ , polyforate and granulate, the foramina about  $4\mu$  wide, about  $1\mu$  hollow (concave) and scattered all over the surface at distance of two or three microns, the granules  $0.5-1\mu$  and covering the foramina. Color brown or dark-brown.

Specimen studied: Ohkubo-ji, Nagao-cho, Ohkawa-gun, Kagawa Pref., Apr. 4, 1963, N. Miyoshi.

5. **Frullania kagoshimensis** St. (Fig. 10-a, b)

External shape identical with *F. muscicola*. Diameter  $27(42)66 \times 33(53)80\mu$ ,  $30(48)63\mu$ . Exine about  $6\mu$  in large spores, but difficult to measure in small spores, polyforate and granulate, the foramina  $3-5\mu$  wide, about  $1\mu$  hollow, scattered all over the surface at distance of  $2-3\mu$ , and sometimes obscured in large spore type, the granules  $0.5-1\mu$  and covering the foramina. Color yellowish-brown.

Specimen studied: None, Toyo-cho, Aki-gun, Kohchi Pref., May 2, 1962, K. Nehira.

6. **Brachiolejeunea sandvicensis** (Gott.) Evans (Fig. 10-f, g) (Pl. 3-j, k)

Unicellular, apolar; tetrahedral shape and laesura unconfirmed apparently due to the enlargement in the early stage of the endogenous germination; external shape irregular-spherical or elliptical, difficult to distinguish the equatorial diameter and polar axis; diameter  $40(52)72 \times 54(70)102\mu$ ,  $51(59)69\mu$ . Exine about  $1\mu$ , echinulate and echinate; the spinules about  $1-2\mu$  long, densely covering the entire surface, the spines about  $3\mu$  wide at base and  $3-4\mu$  long, 6-10 spines gathered in a circle, the circles sporadically scattered at intervals of  $10-20\mu$ . Color yellowish-green with chloroplasts in the fresh spore, but yellow or yellowish-brown in dry condition.

Specimen studied: Ohkubo-ji, Nagao-cho, Ohkawa-gun, Kagawa Pref., Apr. 4, 1963, N. Miyoshi.

Illustrations: Erdtman (1957), Inoue (1958).

7. **Spruceanthus polymorphus** (Sde. Lac.) Verd. (Fig. 10-l, m)

Identical with *Brachiolejeunea sandvicensis* except for the size range, and the sculpture pattern; diameter  $27(36)42 \times 39(46)63\mu$ ,  $36(40)42\mu$ . Exine thick, about  $3\mu$ , granulate and echinate, the granules about  $1\mu$ , densely scattered throughout the surface, the spinules about  $3\mu$  wide at base and  $2\mu$  long, 5-8 spinules gathered in a circle, the circles scattered at intervals of  $10-20\mu$ .

Specimen studied: Anbo, Isl. Yakushima, Kagoshima Pref., Mar. 23, 1963, N. Miyoshi.

8. **Leptolejeunea subacuta** Evans (Fig. 10-h, i) (Pl. 3-c, d)

Unicellular, apolar, tetrahedral shape and laesura unconfirmed, external shape very irregular and angularly elliptical; diameter  $15(20)27 \times 24(40)60\mu$ . Exine  $0.5-1\mu$ , granulate; the granules about  $0.5\mu$ , scattered all over the surface with a few lumps of densely grouped granules. Color yellowish-brown.

Specimen studied: Hirose, Ino-cho, Agawa-gun, Kohchi Pref., May 1, 1962, K. Nehira.

9. **Ptychanthus striatus** (Lehm. & Lindenb.) Nees (Fig. 10-j, k) (Pl. 3-h, i)

Unicellular, anisopolar, bilateral, deformed-trilete, laesura broadly expanded and poorly observed, sometimes unconfirmed; external shape irregular elliptical or spherical, diameter

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Fig. 10. a-b. *Frullania kagoshimensis* (M.). c-d. *Jubula hutchinsiae* ssp. *javanica* (P. v.). e. ditto (E. v.). f-g. *Brachiolejeunea sandvicensis* (A.). h-i. *Leptolejeunea subacuta* (A.). j. *Ptychanthus striatus* (P. p. v., rarely observed). k. ditto (A.). l-m. *Spruceanthus polymorphus* (A.).

28(36)45×39(46)51 $\mu$ , 34(36)45 $\mu$ . Exine thin, 0.5-1 $\mu$ , echinulate; the spinules about 1 $\mu$  long, 5-10 spinules gathered in a circle, the circles sporadically scattered at intervals of 10-20 $\mu$ . Color yellowish-green in fresh spores.

Specimen studied: Mt. Kuroson, Kohchi Pref., May 1962, T. Seki.

Table 4. The range of size of spores in some species belonging to Jungermanniales acrogynae. (The spore are small, ranging from 8 $\mu$  to 21 $\mu$  in diameter, thin-walled and finely granular or smooth.)

Species	Size range ( $\mu$ )
<i>Trichocolea tomentella</i> .....	12(13)15*
<i>Chiloscyphus polyanthus</i> .....	17(19)21
<i>Heteroscyphus bescherelei</i> .....	11(12)15
<i>H. planus</i> .....	9(11)13
<i>Lophocolea heterophylla</i> .....	10(12)13
<i>L. horikawana</i> .....	10(12)13
<i>Jungermannia infusca</i> .....	16(17)19
<i>J. radiculosa</i> .....	11(13)14
<i>Plagiochila ovalifolia</i> .....	15(17)18
<i>Mylia verrucosa</i> .....	14(16)19
<i>Scapania spinosa</i> .....	9(11)13
<i>S. stephanii</i> .....	10(12)13
<i>Cephalozia otaruensis</i> .....	9(11)13
<i>Nowellia curvifolia</i> .....	9(10)11
<i>Schiffneria hyalina</i> .....	10(12)13
<i>Odontoschisma denudatum</i> .....	8(9)10
<i>Jackiella brunnea</i> .....	12(13)16
<i>Lepidozia vitrea</i> .....	10(14)16
<i>Bazzania albicans</i> .....	9(10)11
<i>Calypogeia tosana</i> .....	11(12)13
<i>Jubula hutchinsiae</i> ssp. <i>javanica</i> .....	9(10)12

\* Number in parenthesis indicates "mean value".

### Spore types

Five spore types are distinguishable by three characters; cell stages, polarity, and tetrad scar. They can be further divided into several subtypes based on their sculpture.

#### Spore type I

This type is characterized by having unicellular, anisopolar and trilete spores. Many species of Anthocerotales and Marchantiales belong to this type, the former have the sculpture originating in the exine, the latter in the perine. Among the Jungermanniales this type is encountered in only one genus, *Fossombronina*. This type is here recognized as the most primitive among the five types classified in this work, because:

(1) In the spore germination the character of distal dehiscence pattern of the spores is considered to be of the most primitive type (Inoue 1960). This pattern is observed in some species, e.g. *Riccia curtisii* and *R. compacta*, which have permanently adherent tetrads (Duthie & Gardise 1937, 1940). These adherent tetrads seem to have a triradiate tetrad scar on the proximal face of each spore, because the trilete mark is observed in *Riccia crystallina*, *R. huebeneriana*, etc. having unicellular and clearly trilete spores, and the type of tetrad scar is completely uniform in a genus.

(2) In Pteridophyta the spores with a triradiate scar are considered as being of a more

primitive type than monolete spores. For example, in the genus *Schizaia* the advanced group is characterized by bilateral, monolete spores, while aberrant spores with a tetrahedral, triradiate scar, occur occasionally in the most primitive group of the genus (Harris 1955).

(3) According to Knox (1938, 1939, 1959), fossil spores of Bryophyta and Pteridophyta from the Paleozoic and the Mesozoic eras have an almost triradiate tetrad scar, and the spores without trilete mark or monolete spores are very few.

These facts point to the trilete spores as being of a more primitive type than the spores with other features of tetrad scar.

The following species are included in spore type I:

- Spore type Ia (psilate) .....*Notothylas japonica*  
 Ib (granulate) ...*Phaeoceros laevis*, *Megaceros tosanus*  
 Ic (echinulate) ...*Anthoceros miyakeanus*  
 Id (echinate) .....*Anthoceros nagasakiensis*, *A. formosae* f. *gemmulosus*  
 Ig (reticulate) ...*Plagiochasma intermedium*, *P. nipponicum*, *Reboulia hemisphaerica*, *Asterella odora*, *A. pusilla*, *Riccia crystallina*, *R. glauca*, *R. huebeneriana*, *Ricciocarpus natans*, *Fossombronia japonica*  
 Ii (saccate) .....*Mannia levigata*

### Spore type II

This type is also unicellular and anisopolar. Immature spores of this type rarely show the triradiate mark, whereas mature spores usually show the triradiate, expanded scar and in extreme case almost rounded, tetrad scar (Fig. 8-a, c, g, l). The species belonging to this type show little divergence in both size and ornamentation of spores, except *Aspiromitus miyabeanus* which has large, verrucate spores. Five species grouped into spore type IIa have very small spores and it is difficult to recognize exactly their sculpture. Those of spore type IIb also have small spores, but their granulate sculpture is more distinct. As to the structure of the wall and fine granules of these small spores, the further investigation by electronmicroscope is desirable. I think that this type shows a more advanced character than spore type I (trilete spore).

The following species are included in spore type II:

- Spore type IIa (psilate) .....*Chiloscyphus polyanthus*, *Heteroscyphus bescherellei*, *H. planus*, *Lophocolea horikawana*, *L. heterophylla*  
 IIb (granulate) ...*Metzgeria conjugata* ssp. *japonica*, *Riccardia pinguis*, *R. miyakeana*, *R. nana*, *Calobryum rotundifolium*, *Jungermannia infusca*, *J. radiculosa*, *Scapania stephanii*, *Cephalozia otaruensis*, *Schiffneria hyalina*, *Odontoschisma denudatum*, *Jackiella brunnea*, *Lepidozia vitrea*, *Calypogeia tosanana*, *Radula oyamensis*, *Jubula hutchinsiae* ssp. *javanica*  
 IIc (verrucate) ...*Aspiromitus miyabeanus*  
 IIg (reticulate) ...*Makinoa crispata*, *Pallavicinia lyellii*, *Mylia verrucosa*

### Spore type III

The spores are unicellular, cryptopolar, indistinctly tetrahedral, and lacking the triradiate mark on the proximal face. The proximal side can be distinguished by the perine sculpture which is well developed in the species of Marchantiales except *Dumortiera hirsuta* with a bullate exine. In small spores, it is sometimes difficult to clearly separate spore type IIIb from spore type IIb, because the trilete mark is rarely observed in the spores of IIIb as in those of IIb.

The following species are included in spore type III:

Spore type IIIb (granulate) ... *Plagiochila ovalifolia*, *Scapania spinosa*, *Nowellia curvifolia*,

IIIId (baculate) ... *Dumortiera hirsuta*

IIIg (reticulate) ... *Targionia hypophylla*, *Preissia quadrata*

IIIh (bullate) ... *Marchantia cuneiloba*, *M. diptera*, *M. tosana*

IIIi (saccate) ... *Sauteria alpina*, *Peltolepis quadrata*, *Wiesnerella denudata*

#### Spore type IV

This type is characterized by having unicellular and apolar spores without tetrad scar. In Lejeuneaceae and Blasiaceae the premature spores may have the polarity, but the mature spores lack the polarity. It may be true that the mature spores are swollen and deformed in advance of the endogenous germination within the stretched exine, but they have not yet developed to the multicellular stage.

The following species are included in spore type IV:

Spore type IVa (psilate) ... *Trichocolea tomentella*, *Bazzania albicans*

IVb (granulate) ... *Cavicularia densa*, *Trichocoleopsis sacculata*, *Leptolejeunea subacuta*, *Spruceanthus polymorphus*

IVe (echinulate) ... *Brachiolejeunea sandvicensis*, *Ptychanthus striatus*

#### Spore type V

The spores of this type are always multicellular in mature capsule, and lack the polarity and tetrad scar. Such an endogenous germination pattern occurs frequently in epiphytic Hepaticae such as *Dendroceros* of Anthocerotales, *Frullania* and Lejeuneaceae of Jungermanniales acrogynae and in a few terrestrial Hepaticae such as *Conocephalum* of Marchantiales and *Pellia* of Jungermanniales anacrogynae. Nehira (1963) commented on this phenomenon as follow: "It is teleologically considered that the stretched spore coat serves as a guard structure to protect the naked protonema from being injured by dry environmental conditions."

The following species are included in spore type V:

Spore type Vb (granulate) ... *Dendroceros japonicus*, *Conocephalum supradecompositum*, *Pellia fabbroniana*, *P. neesiana*

Vc (verrucate) ... *Conocephalum conicum*

Ve (echinulate) ... *Porella ulophylla*

Vj (polyforate) ... *Frullania kagoshimensis*, *F. muscicola*

### Phylogenetic significance of spore morphology in Hepaticae

An attempt has been made to research the phylogenetic trends based on the combination of spore morphology and elater structures (Horikawa & Miyoshi 1965). Three principal orders of Hepaticae: Anthocerotales, Marchantiales and Jungermanniales, are individually considered.

Three spore types are observed in Anthocerotales, i. e. Spore type I, II and III. *Notothylas*, *Anthoceros* and *Phaeoceros*, having typical trilete spores (Spore type I), seem to be primitive. The former, without sculpture on the spore surface and with unicellular pseudo-elaters, seems to be more primitive than the latter two genera with well-developed sculpture and 2-5-celled pseudo-elaters. *Megaceros*, having poorly trilete spores and spiral elaters, is placed next in rank to the three above-mentioned genera. Spore type II is observed only in *Aspiromitus*, which has more advanced pseudo-elaters than in *Anthoceros* and *Phaeoceros*.

*Dendroceros* has spores showing the multicellular stage by the endogenous germination within the stretched exine and has spiral elaters, and is therefore considered to fall in a separate position from the preceding four genera. The interrelationship among the three types in Anthocerotales is shown in Fig. 12.

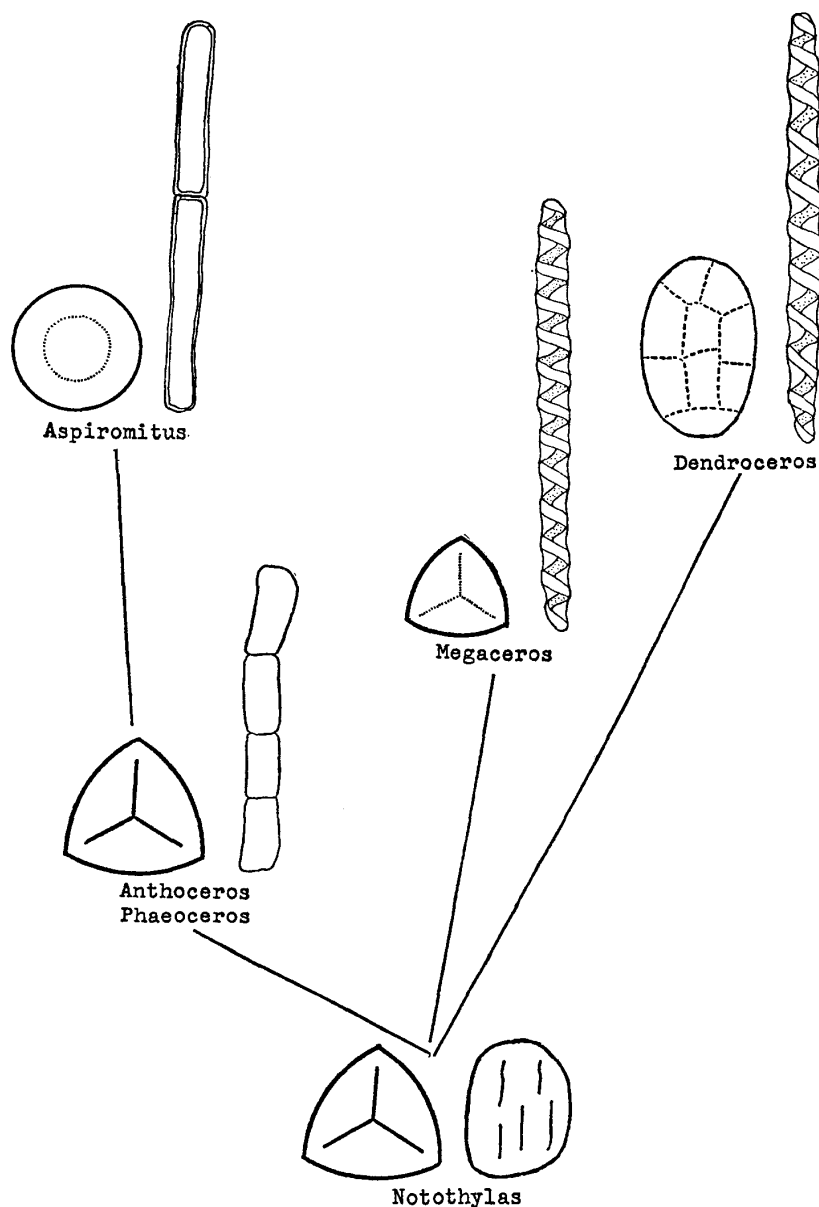


Fig. 12. Diagram showing the interrelationship in Anthocerotales based on the combination of spore types and elater structures.

In Marchantiales, three spore types are recognized, i. e. Spore type I, III and V. Spore type I is recognized in Ricciaceae and Grimaldiaceae. Ricciaceae has neither elater nor sterile cell with one exception, *Riccia crystallina*, and is considered to be most primitive in Marchantiales. Pagan (1932) stated, "In *Riccia crystallina* sterile or nutritive cells appear not only on the periphery of the sporangium, but also rarely in the interior." The sterile cells in this species may be considered as forerunners of the elaters of higher forms in Marchantiales.

In Grimaldiaceae, *Plagiochasma* has two types of elaters, one is the elaters with poor spiral such as seen in *P. intermedium*, the other is the elaters with two or three well-developed spirals such as those in *P. rupestre*. The former seems to be a primitive type of the

latter, which is also seen in other members of Marchantiales. *Asterella* and *Mannia* have short elaters with two or rarely three spirals, and *Reboulia* has the longest elaters among these three genera.

Spore type III is observed in Targioniaceae, Cleaviaceae and Marchantiaceae. *Preissia quadrata* of Marchantiaceae seems to have a near relation to Cleaviaceae from the viewpoint of spore and elater morphology. *Conocephalum*, which shows Spore type III, is placed in a separate position from the other genera of Marchantiales. The interrelationship of these three types in Marchantiales is schematized in Fig. 13.

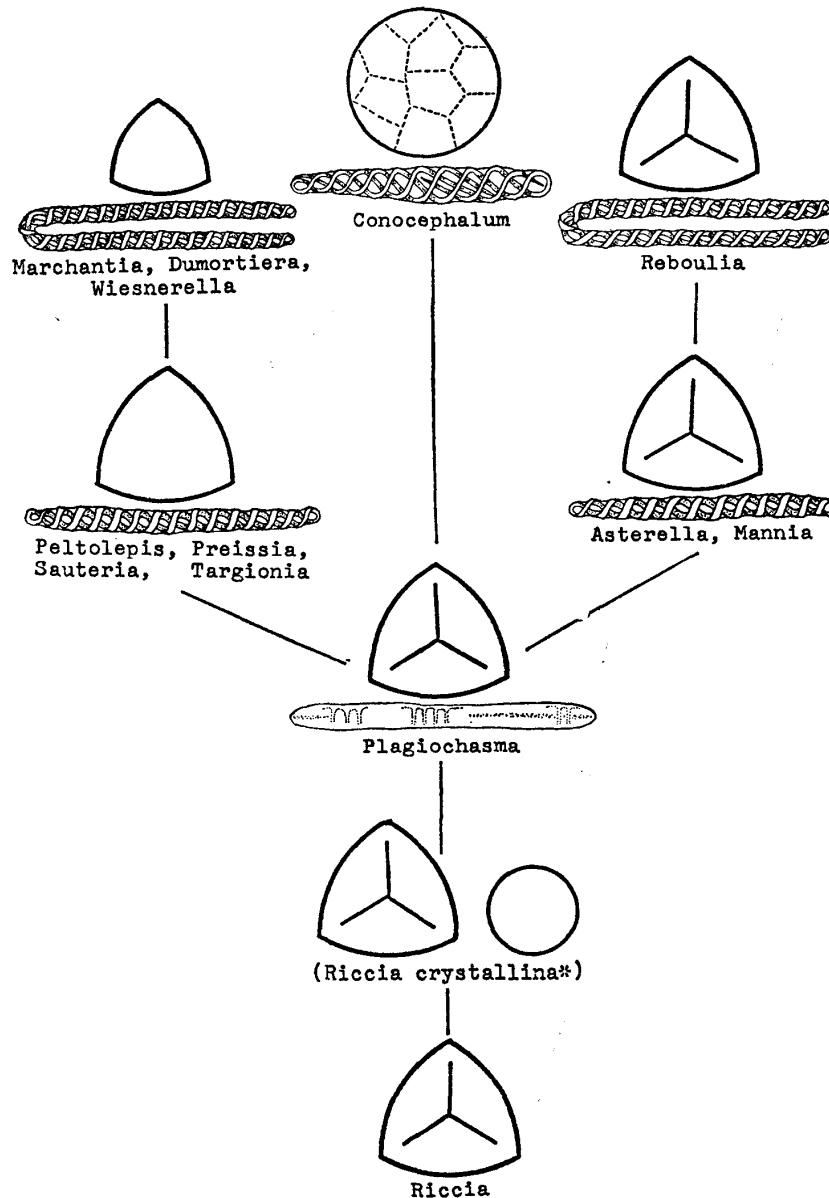


Fig. 13. Diagram showing the interrelationship in Marchantiales based on the combination of spore types and elater structures. \* Pagan (1932)

*Fossombronia* has an indistinct aperture, and is difficult to assign exactly to either Spore type I or II. Erdtman illustrated the aperture of the spore of *Fossombronia anulosa* with deformed triradiate mark and added a question mark (?). In this work, spores of *Fossombronia* are tentatively placed in Spore type I. *Fossombronia* seems to fall in a primitive position among Jungermanniales anacrogynae, the reasons being: *Fossombronia*

has spores with well-developed perine, which is mainly observed in Spore type I of Marchantiales, therefore the genus seems to have a relationship to primitive Marchantiales. Moreover, *Fossombronia* has two type of elaters, one is well-developed elaters with two spirals such as those in *F. pussila*, the other is poor elaters with ring-shaped bands and one spiral such as those observed in *F. japonica*. The latter seems to be a forerunner of the elater with spiral or ribbed thickening seen in genera of Jungermanniales anacrogynae such as *Riccardia*, *Pallavicinia*, *Pellia*, and *Makinoa*. But Goebel (1915-1918), who studied the elater of *Fossombronia luetzelburgiana*, states, "Von besonderem Interesse ist eine brasilianische *Fossombronia*-Art (*F. Luetzelburgiana*), weil sie zeigt, daß schon in der Jungermanniaceenreihe die Elateren stark rückgebildet werden können."

*Metzgeria*, *Riccardia* and *Pallavicinia*, all belonging to Spore type II, are placed in a higher position, and *Makinoa* is considered to be in middle position based on the size of spore and perinous sculpture, though it also belongs to Spore type II.

In my consideration the spores of Hepaticae follow a certain tendency or pattern: primitive species have larger spores and the more advanced species have smaller spores, except some families whose spores are of Spore type IV and V. The interrelationship of these four types in Jungermanniales anacrogynae is schematized in Fig. 14.

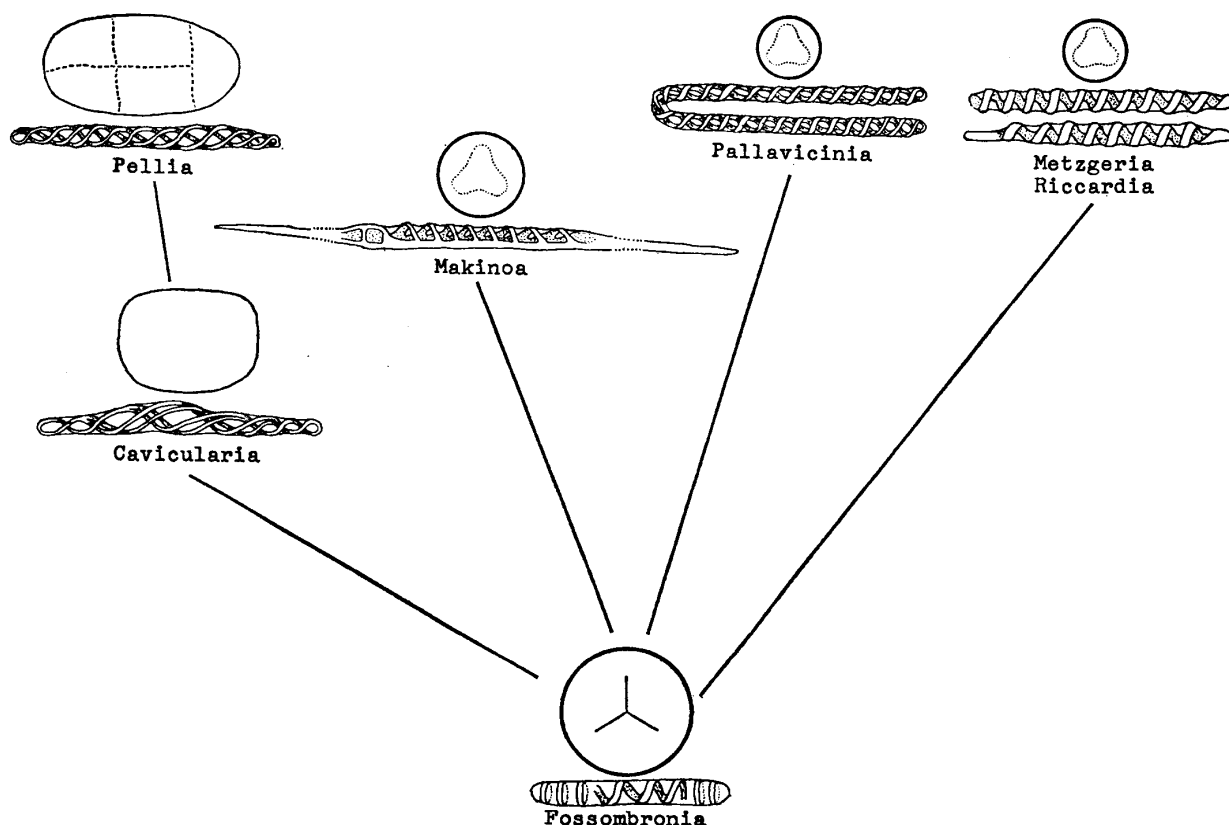


Fig. 14. Diagram showing the interrelationship in Jungermanniales anacrogynae based on the combination of spore types and elater structures.

As *Calobryum* (Spore type II) has small, deformed-trilete spores and long, advanced elaters with two spirals, I think that this genus is to be placed in a higher position among Jungermanniales, though it has been considered to be primitive from the result of previous studies on spore germination, morphology and karyotype.

In Jungermanniales acrogynae, which has four Spore type II, III, IV and V, it is usually difficult to distinguish exactly the spore type into families or genera and to consider the phylogenetic relation by spore morphology, especially in members with small spores belong-

ing to Spore type II, III and IV. Therefore, the study of the spore wall and sculpture by electron microscope is especially desirable.

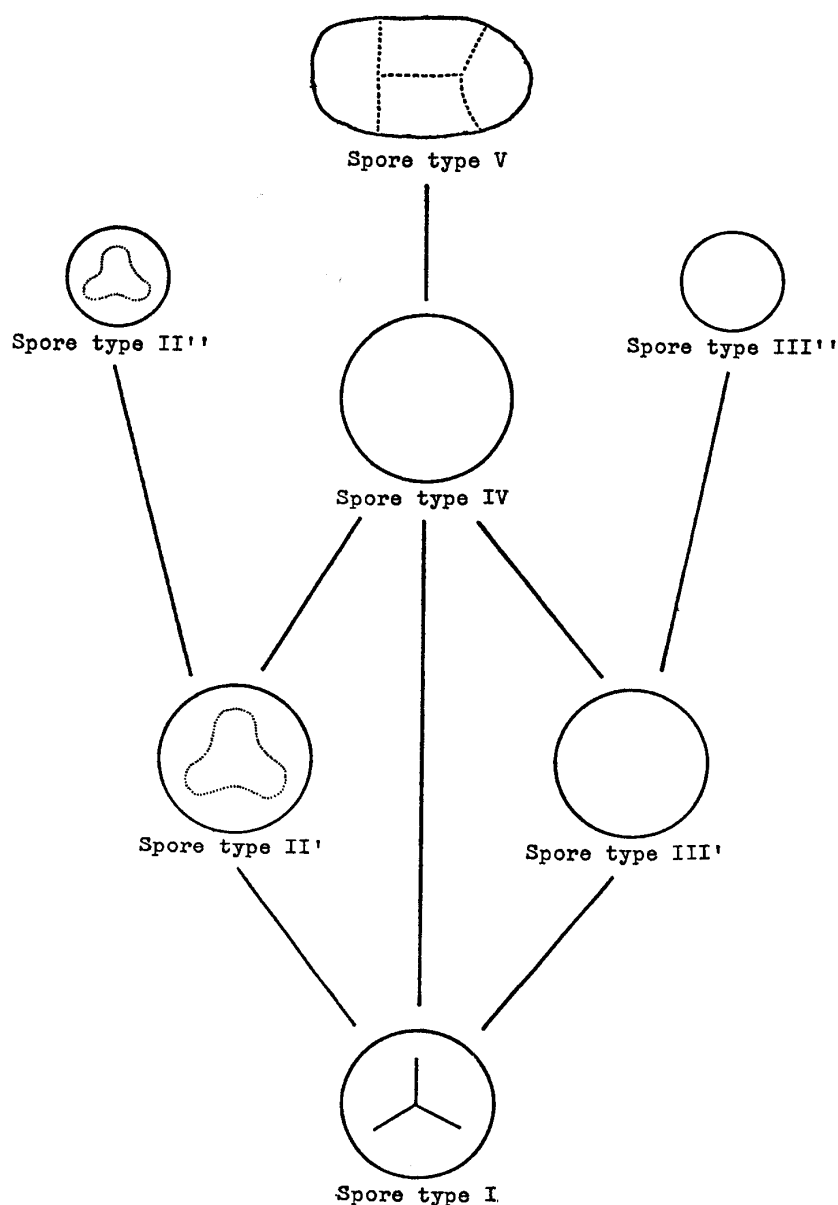


Fig. 15. Diagram showing the interrelationship among spore types in Hepaticae.

The interrelationship among the five spore types in Hepaticae is shown in Fig. 15. In the diagram, Spore type II and III are divided respectively into two groups by size of spore. Spore type II' and III' mean larger spores than  $25\mu$  in equatorial diameter, Spore type II'' and III'' mean smaller spores than  $25\mu$ . The small spores indicate the more advanced group than larger spores which means a primitive group. Certain tendencies of the five spore types in each order are as follow :

Anthocerotales .....	Spore type I—	II'—	V
Marchantiales .....	Spore type I—	III'—III''	V
Jungermanniales anacrogynae.....	Spore type I—	II'—II''	IV—V



If the permanent tetrad spore of Sphaerocarpaceae is added in this figure, I believe that the tetrad spore type would be placed in the more primitive position than Spore type I. As there is no any member of Sphaerocarpaceae in Japan, the tetrad spore type is not considered in this work.

### Summary

1. In this study, spores of 70 species, representing 3 orders and 28 families based mainly on collections made by myself in Japan, are described and illustrated.

2. Important characters considered in the spore morphology are: cell stages, external shape, polarity, tetrad scar, thickness of exine, sculpture, size and color.

3. Ten sculpture types are recognised in the spores of Hepaticae: psilate, granulate, verrucate, baculate, echinulate, echinate, reticulate, bullate, saccate and polyforate.

4. The spores are grouped into two types based on the size. The first type includes spores which are smaller than  $25\mu$  in diameter and morphologically almost similar to each other even among different families. Therefore such spores are very difficult to identify exactly. Spores of the second type are larger than  $25\mu$ , and their characters such as cell stages, polarity, shape, sculpture and color are remarkably diversified. It is relatively easy to distinguish the spores of this types into their families, genera or even into species.

5. By the cell stage, polarity and tetrad scar, five spore types are classified: trilete (Spore type I), deformed trilete (Spore type II), cryptopolar (Spore type III), apolar (Spore type IV) and multicellular spore (Spore type V).

6. By the spore characters, many species belonging to Anthocerotales, Marchantiales and some species of Jungermanniales, which have well-developed sculptures such as spines, verrucae, and reticula, can be quite easily distinguished into family or genus, and even into species. On the other hand, numerous species of Jungermanniales have such small spores with poorly defined sculpture that it is often difficult to determine exactly to which family or genus they belong.

7. From the study of spore types and measurement of size (equatorial diameter), the spores of Hepaticae seem to have evolved from large, well sculptured ones into two directions: retrogressively into small, unicellular, poorly figured spores and progressively into multicellular spores.

8. It is clear that results obtained from the study on spore morphology have phylogenetic significance. The interrelationship among spore types is shown in relation to morphology of elaters. It is concluded that Spore type I is considered to be more primitive except permanent tetrad spores of Sphaerocarpaceae, which may be the most primitive from the standpoint of spore morphology. Spore type II (deformed trilete) and Spore type III (cryptopolar) show the more advanced type than Spore type I. Lejeuneaceae and Blasiaceae of Spore type IV is a previous stage of endogenous germination to multicellular spores (Spore type V), which is placed in a higher position.

9. Conclusions on the relationship between the spore types and their sculptures in Hepaticae were not reached in this work, however the following tendencies were generally observed: (1) Spore type I and III have well developed sculptures derived from the perine, or exine with sculptures such as reticula, spines, and bacula except in *Notothylas japonica* in which the spores have the typical triradiate tetrad scar, but its exine is psilate; (2) Spore type II has a poor sculpture, mostly granulate, originating from the exine except in *Aspiromitus miyabeanus*, which has spores with well-developed verrucate projections; (3) Spore type IV and V have generally granules, and rarely verrucae, spines, spinules or foramina, which all seem to be derived from the exine

10. Polarity of small spores in Jungermanniales has not been treated by most investi-

gators. According to my observations, a tetrad scar which is usually deformed-trilete and sometimes rounded, is frequently recognized on the proximal side of a small spore in many species of Jungermanniales.

### Glossary

Most of the descriptive terms used in this work were taken from the literature on pollen or spore morphology such as the works of Potonié (1934), Faegri & Iversen (1950), Erdtman (1952, 1954), Harris (1955), and McClymont (1955). Some terms have been introduced by myself.

**Alete:** spores lacking a tetrad scar. (Harris 1955)

**Anisopolar:** having the proximal and distal portion of the spore dissimilar. (Harris 1955)

**Apolar:** the proximal and distal surface not differentiated. (Harris 1955)

**Baculate:** provided with small rods not thickened at the top end; possessing bacula (height of rod  $>$  greatest diameter of rod). (Faegri & Iversen 1950)

**Bullate:** used for the spore surface which is irregularly puckered or blistered.

**Commissure:** the line of dehiscence in the tetrad scar. (Harris 1955)

**Deformed trilete:** used for spores having expanded triradiate, in extreme case almost rounded, tetrad scar.

**Distal:** used of the part of the spore which was turned outward in the tetrad and is therefore opposite the tetrad scar. (Harris 1955)

**Double-reticulate:** forming a network with large lumina which possess 3-6 small pits in each.

**Echinate:** armed with spines over  $3\mu$  in length.

**Echinulate:** armed with spines less than  $3\mu$  in length.

**Equator:** region where the proximal surface, bearing the tetrad scar, meets the distal surface. (Harris 1955)

**Exine:** the main, outer, usually resistant layer of a sporoderm. (Erdtman 1952)

**Granulate:** covered with granules about  $1\mu$ , or less than  $1\mu$  in diameter.

**Laesura:** dehiscence fissure, including the commissure, and also the margo when this is distinguishable. (Harris 1955).

**Lumina:** refers to the space between the muri of a reticulum. (Potonié 1934)

**Margo:** a transition zone between the commissure(s) of the tetrad scar and remainder of the exine. (Harris 1955)

**Multicellular:** used for the spore which already germinated within the stretched exine.

**Muri:** ridges separating the lumina of a reticulum. (Potonié 1934)

**Perine:** the outermost layer, outside of the exine, in certain spores. (Erdtman 1954)

**Polyforate:** sculptural pattern with many circular apertures (foramina).

**Profile:** refers to the contour of spores seen in lateral view. (Harris 1955)

**Proximal:** used of the part of the spore that was turned inward in the tetrad and that usually bears a tetrad scar. (Harris 1955)

**Psilate:** smooth without adornments. (Erdtman 1954)

**Reticulate:** sculptural pattern consisting of muri separated by lumina.

**Saccate:** pouched, cavate, elevations approximately isodiametric. N.B.—The walls of saccate elevations tend to be flaccid and hollow looking, whereas verrucate projections are firmer and appear to be solid. (Harris 1955)

**Sexine:** the outer sculptured part of the exine. (Erdtman 1952)

**Trilete:** spores which have three ridges radiating from the proximal pole, the angles between the ridges being more or less equal. (McClymont 1955)

**Verrucate:** broad, or if more or less isodiametric, larger than granulate. (Harris 1955)

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## 摘 要

苔類胞子の形態は、分類学的形質の一つとして古くから記載し、図示されてきたが、胞子の形態を主体とした研究はごくわずかで、しかもそれらはほとんど断片的なものにとどまっている。この研究は、本邦産の苔類胞子を光学顕微鏡で観察して、胞子の識別に役立つ重要な特徴を追求し、それにもとづいて胞子分類表を作成し、さらに弾糸の形態を加味して苔類各目内における類縁関係ならびに胞子型相互の関連性を考察したものである。その概要は次の通りである。

### I. 苔類胞子の形態学的特徴

観察に用いた苔類は3目、28科、52属、70種で、これらの観察結果から胞子の識別に重要な特徴となる形質として次のようなものを認めた。

1. 複粒と多細胞胞子 胞子が成熟後も四分子胞子のまま結合している複粒は、*Sphaerocarpos* と *Riccia* の一部で報告されているが、今回研究した材料中には認められなかった。他方成熟した胞子は通常単細胞であるが、すでに胞子のう内で胞子膜内発芽をして多細胞化した胞子は、*Dendroceros*, *Conocephalum*, *Pellia* などで観察された。

2. 外部形態 (1) 極性 *Anthocerotales* と *Marchantiales* の大多数の種類では向心極面と遠心極面とははっきり区別することができる。また今までほとんどこの両極面の区別が無視されてきた *Jungermanniales* の大多数における  $25\mu$  以下の小

形胞子にも明らかに極性の存在が認められた。胞子膜内発芽をした胞子と、発芽寸前になっている *Blasiaceae* や *Lejeuneaceae* では極性が消失している。この極性の有無は胞子型区分の重要な特徴の一つとなる。(2) 極観 まるみをおびた三角形と円形のもとがあり、一般に *Anthocerotales* と *Marchantiales* では前者が多く、*Jungermanniales* では後者が多い。(3) 赤道観 向心極面がピラミッド状、遠心極面が半球状で、赤道観が扇形のもの *Anthoceros*, *Riccia* などで認められた。また向心極面が平らか、またはくぼみ、遠心極面が半球状で、赤道観が半月形～腎臓形のは *Aspiromitus*, *Marchantia*, *Makinoa* などで観察された。

3. 裂孔 単細胞胞子の向心極面には裂孔のあるものとなないものがある。また、多細胞胞子では裂孔の消失したものが多い。(1) 裂孔のあるもの a. 極の中心から三方に裂開し、その末端ほど狭くなった裂孔 (trilete) をもつもの… *Anthoceros*, *Plagioglossum* など。b. 四分子胞子から分離後広がり、しばしば円形になった裂孔 (deformed trilete) をもつもの… *Metzgeria*, *Radula* など。(2) 裂孔が全然認められないか、あるいは認められてもむじように発達の悪いもの… *Wiesnerella*, *Preissia* など。

4. 大きさ 赤道部直径がわずかに  $9\mu$  の小さな胞子から  $90\mu$  以上の大きな胞子までさまざまあり、このうち  $25\mu$  以上の胞子では、大きさは胞子による

科や属,あるいは種の識別の特徴の一つとして重要であったが,  $25\mu$ 以下の孢子については,その差が小さいため識別の特徴としてあまり役立たなかった。

5. 孢子膜 孢子膜は *exine* が最外層になったものと, *perine* が最外層になったものがあり,前者は *Anthocerotales* と *Jungermanniales* に多く,後者は *Marchantiales* に多い。また *exine* の厚さは各種によりかなり一定しているので,重要な特徴である。

6. 模様 孢子の模様は孢子膜の最外層である *exine* かまたは *perine* の一部から生じたものである。この模様には次のようなものが認められ,孢子型亜型の分類の特徴として用いられた。(1) 平滑状,(2) 棒状,(3) しわ状,(4) 顆粒状,(5) とげ状,(6) 小とげ状,(7) 多孔状,(8) 網目状,(9) 袋状,(10) いぼ状。

7. 色 淡黄褐色,黄褐色,褐色および暗褐色のものがみられ,その色は同一属ではかなり一定している。しかし大多数の属は黄褐色～褐色で,淡黄褐色や暗褐色のものはごくわずかである。また乾燥して古くなった孢子の色は,葉緑体をもった生時のものとかなり異なっていることが多く,*Ricciocarpus* (暗褐色)のような一部特殊なものを除いては,色は孢子の特徴としてあまり役立たない。

以上のような特徴をもとにすれば,赤道部直径約  $25\mu$  以上の大形孢子をもつ種類は,孢子の特徴だけでも科や属に識別できるものが多くあるので,その形態的特徴を記載し,図示した。一方  $25\mu$  以下の小形孢子は光学顕微鏡では識別に十分な特徴が認められないため,図示と孢子の赤道部直径の表示にとどめ,記載は省略した。これら小形孢子については,将来電子顕微鏡による微細形態の研究が期待される。

## II. 孢子型

孢子のいろいろな特徴のうち,細胞数,極性および裂孔をもとにして,これら孢子を大きく5型に大別し,模様によってさらに22亜型に細分した。大別された孢子型5型の概略は次の通りである。

孢子型I: 単細胞で向心極面と遠心極面の区別があり,典型的な *trilete* の裂孔をもっているもの…

*Notothylas*, *Anthoceros*, *Asterella*, *Plagioclasma*, *Riccia* など。

孢子型II: 細胞数と極性は孢子型Iと同じであるが,裂孔が変形して *deformed trilete* になっているもの…*Aspiromitus*, *Metzgeria*, *Makinoa*, *Chiloscyphus*, *Mylia* など。

孢子型III: 細胞数と極性は孢子型I, IIと同じであるが,裂孔がないかあるいは発達がよくないもの…*Preissia*, *Marchantia*, *Wiesnerella*, *Plagiocchila*, *Scapania* など。













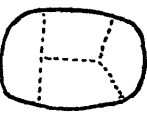





















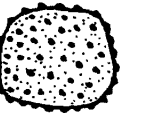






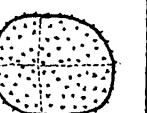



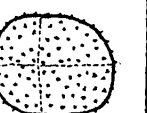
孢子型IV: 単細胞であるが,向心極面と遠心極面の区別がなく,裂孔も認められないもの…*Cavicularia*, *Leptolejeunea*, *Brachiolejeunea*, *Trichocolea*, *Bazzania* など。

孢子型V: 孢子膜内発芽により多細胞化して極性および裂孔が消失しているもの…*Dendroceros*, *Conocephalum*, *Pellia*, *Frullania*, *Porella* など。

## III. 類縁関係

孢子と同じように胞原細胞から生じた弾糸も科や属によって形態の異なるものが数多く認められ,このことについては,すでに報告した(堀川・三好: 1965)。この弾糸と,本研究により観察された孢子形態の特徴とをあわせて考察し,苔類各目内における類縁関係を追求した。その結果 *Anthocerotales*, *Marchantiales*, *Jungermanniales* *anacrogynae* では,これまでの分類体系(科や属との関係など)とかなりよく一致することが判った。また *Jungermanniales* *acrogynae* については孢子の資料不足のため今回は考察を省略した。

孢子型相互の類縁関係については,孢子型5型の中でもっとも原始的とみられる孢子型Iから孢子型II, III, Vの3つの方向への分化が考えられ,孢子型IVの *Blasiaceae*, *Lejeuneaceae* は孢子型Vへの前段階にあると考えられる。また,単細胞孢子の大きさは,  $60\mu$  以上の大きなものから  $10\mu$  以下の小さいものまでさまざまであるが,原始的とみなされる苔類の孢子は一般に大きく,分化が進むにつれて小さくなる傾向を示すようである。

Cell stage	Unicellular				Multi-cellular
Polarity	Anisopolar		Cryptopolar	Apolar	
Tetrad scar	Trilete	Deformed trilete			
Spore types	I	II	III	IV	V
Sculpture	  	  	  	  	
a	  	  			
b	  	  	  		
c		  			
d			  		
e	 				
Echinulate	 				

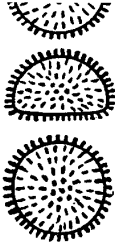
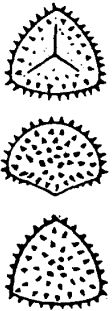
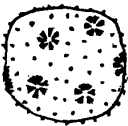
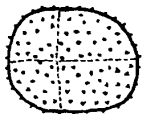
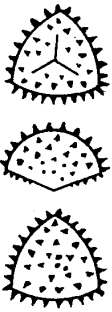
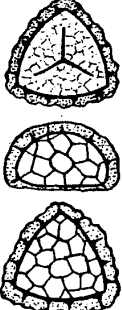

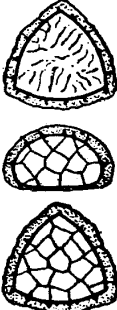
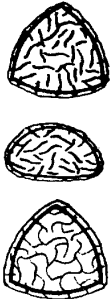



Baculate					
e Echinulate					
f Echinate					
g Reticulate					
h Bullate					
i Saccate					
j Polyforate					

Fig. II. Diagram showing the five spore types and their subtypes.



# PLATES

Magnification of Plates 1-4 is  $\times 1000$  except Plates 4-e, f, of which the magnification is  $\times 170$ .

Plate 1. a. *Anthoceros nagasakiensis* (P. p. v.). b. ditto (D. p. v.). c. ditto (E. v.). d. *Phaeoceros laevis* (P. p. v.). e. ditto (D. p. v.). f. *Aspiromitus miyabeanus* (P. p. v.?). g. *Anthoceros nagasakiensis* (tetrad spore). h. *Megaceros tosanus* (D. p. v.). i. *Notothylas japonica* (P. p. v.). j. *Dendroceros japonicus* (M.).

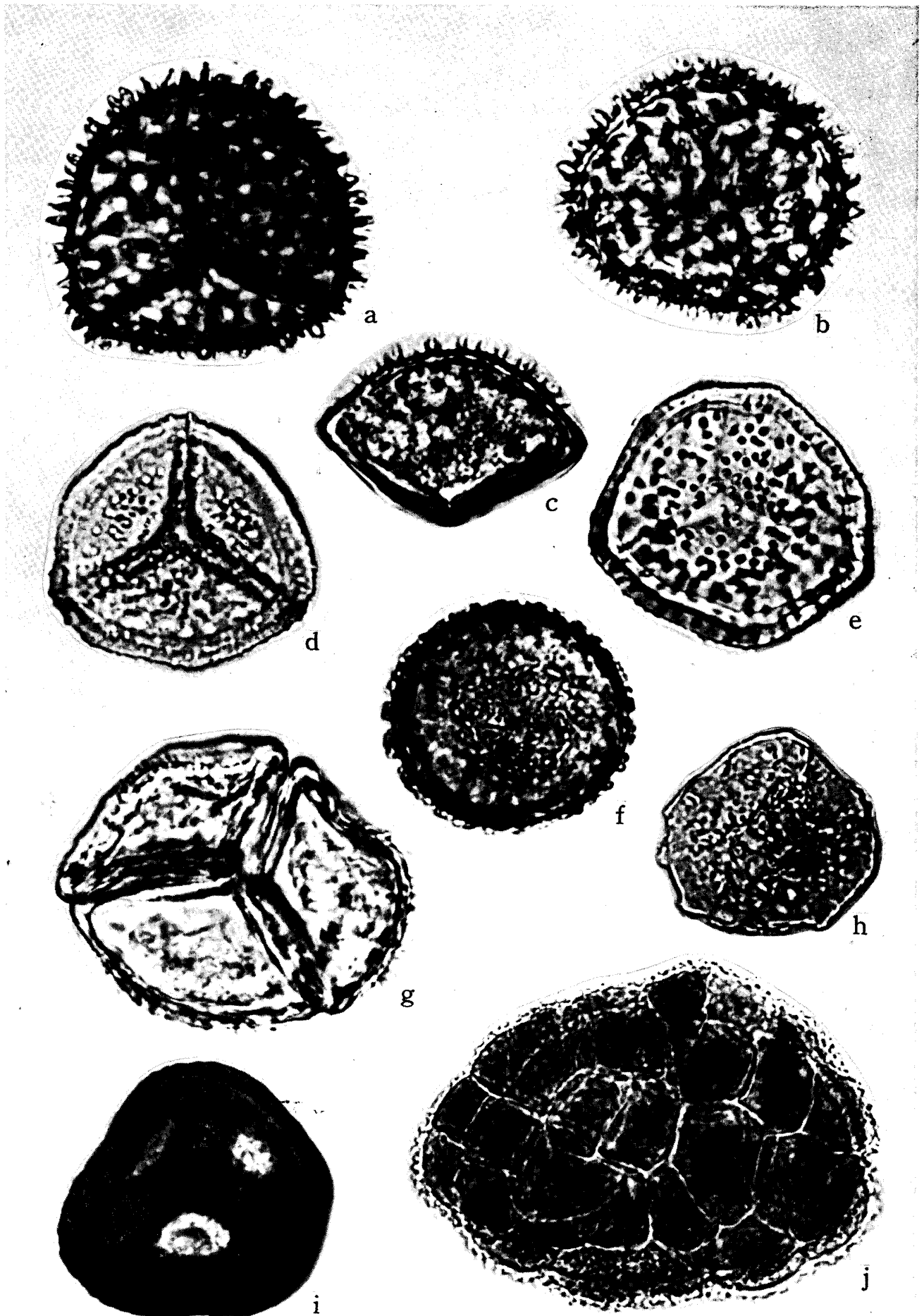


Plate 2. a-b. *Reboulia hemisphaerica* (P. p. v.). c. ditto (E. v.). d-e. *Wiesnerella denudata* (P. v.). f. ditto (E. v.). g. *Dumortiera hirsuta* (E. v.).

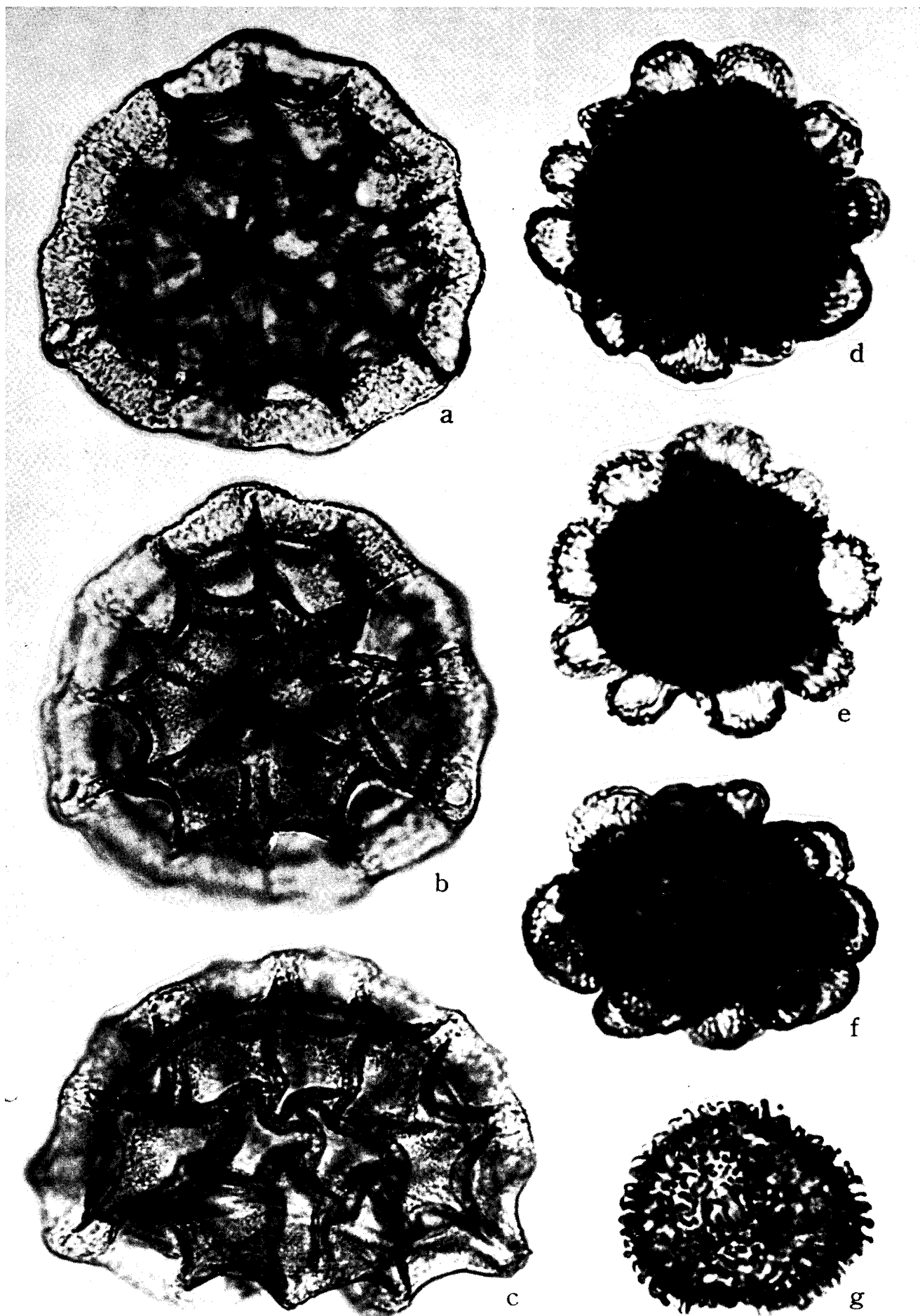


Plate 3. a. *Makinoa crispata* (P. p. v.). b. ditto (D. p. v.). c-d. *Leptolejeunea subacuta* (A.) e-f. *Frullania muscicola* (M). g. *Trichocoleopsis sacculata* (P. p. v., rarely observed). h-i. *Ptychanthus striatus* (A.). j-k. *Brachiolejeunea sandvicensis* (A.).

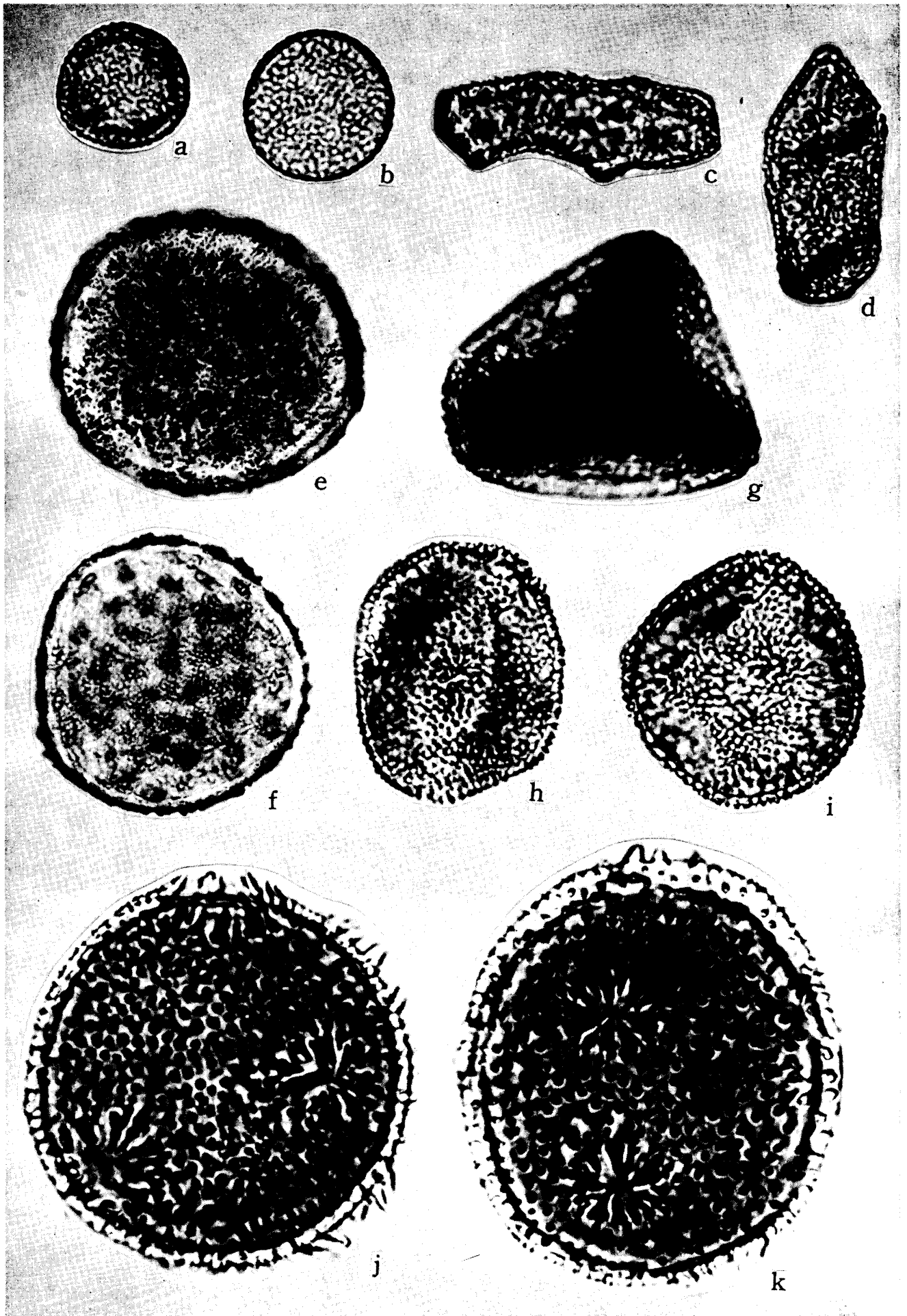
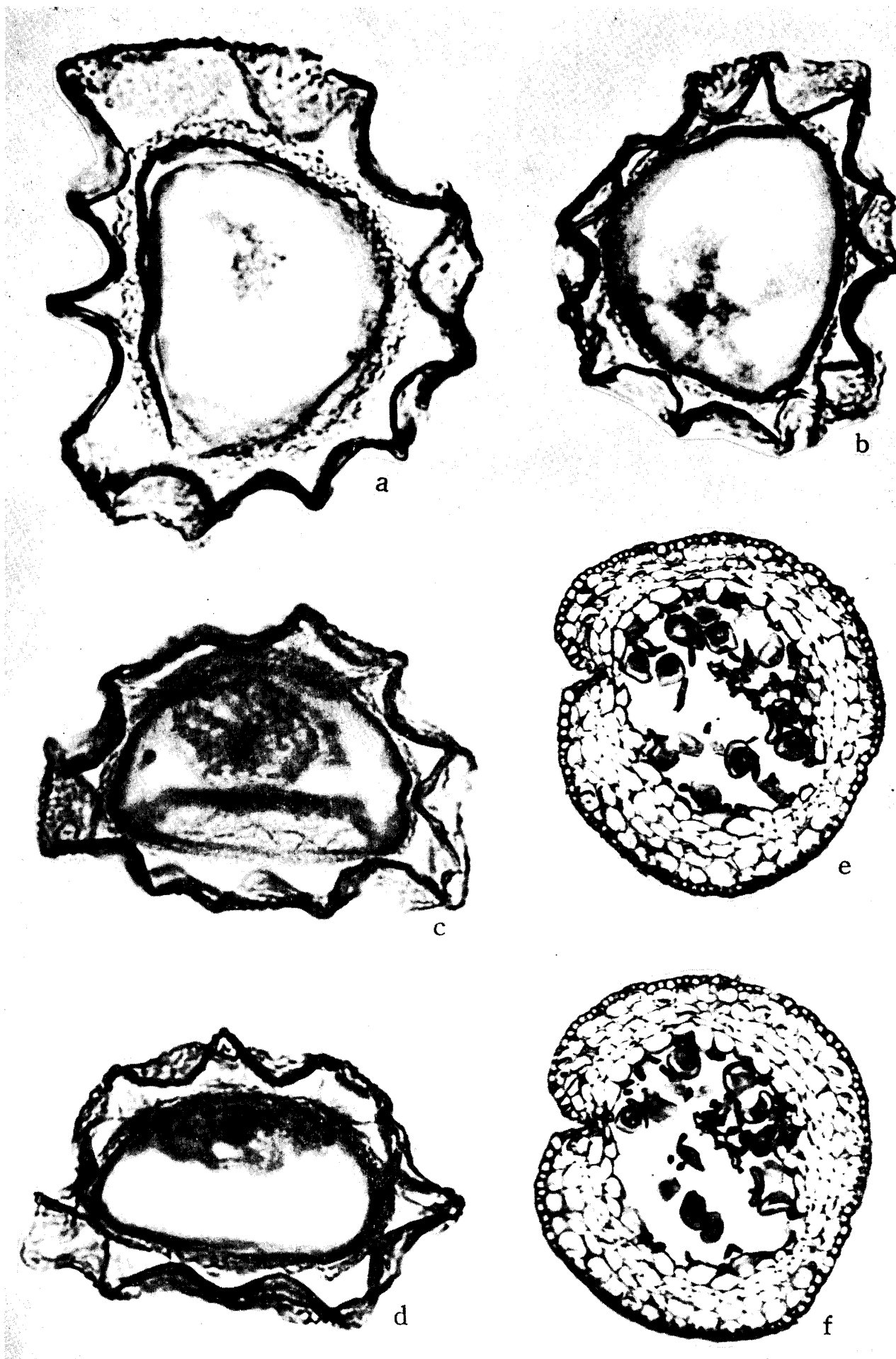


Plate 4. Microtome sections. a-b. *Plagiochasma intermedium* (P. v.). c-d. ditto (E. v.).  
e-f. *Aspiromitus miyabeanus* (sporangium).





# Errata & Corrigenda

page	line	for	read
2	30	K. Sasaki	Y. Sasaki
9	1	Table 8.	Table 3.
29	33	Table 4.	Table 5.
34	5	Table 4.	Table 5.