FLORA OF SOUTHERN AFRICA

HEPATOPHYTA

Editor O.A. Leistner

Part 1: Marchantiopsida

Fascicle 1: Marchantiidae

by Sarie M. Perold

NATIONAL
BOTANICAL
INSTITUTE

FLORA OF SOUTHERN AFRICA

which deals with the territories of

SOUTH AFRICA, LESOTHO, SWAZILAND, NAMIBIA AND BOTSWANA

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CONTENTS

INTRODUCTION

In contrast to the volume of work published on southern African mosses, the liverworts have been a rather neglected group. Bischoff (1846), Gottsche, Lindenberg & Nees (1844–1847) as well as Stephani (1886a, b, 1891, 1892, 1894, 1895a, b, 1898, 1899, 1901a, b, 1905, 1912, 1913) described a number of our liverworts, and during the present century Sim (1915, 1926, 1932), Duthie & Garside (1937, 1939) and S.W.Arnell (1952, 1953a, b, 1956b, 1957, 1963a, b) continued with the work. More recent studies on thallose liverworts are by Volk (1979, 1983), Volk & Perold (1984–1986, 1990), Perold & Volk (1988a, b), and by Perold (1986, 1989–1995), but much more work still needs to be done on the leafy liverworts of this region.

Vegetation formations in the *FSA* area

The thallose liverworts treated in this fascicle are found within six of the seven biomes as defined by Rutherford & Westfall (1986). The biomes are as follows: Desert, Savanna, Grassland, Nama-Karoo, Succulent Karoo, Fynbos and Forest. Some liverwort species are more or less restricted to only one of the biomes, but most exhibit a broader environmental tolerance and occur in two or more biomes. Only one species, *Riccia cavernosa*, occurs in all the biomes except the Desert Biome.

Desert Biome

This biome corresponds to the Namib Desert which forms a broad coastal belt north of the Lüderitz area in Namibia. The arid climate and sandy substrates are not suited to the requirements of the Hepatophyta, and there are no records of them growing in this area.

Savanna Biome

The Savanna Biome is the largest and extends into Namibia, Botswana, Northern Cape, North-West and Northern Province, central and eastern Swaziland, lower-lying areas of KwaZulu-Natal and Eastern Cape. Most of this biome occurs in the summer rainfall areas. The vegetation is described as a herbaceous, usually graminoid layer with an upper layer of woody plants. With increased canopy cover savanna is often referred to as woodland (Magill 1981). Almost all the major stratigraphic units of southern Africa occur in this biome. The rare *Riccia perssonii* occurs only in the far north of Namibia. Other species that are restricted to the Savanna Biome are *Riccia congoana*, *Athalamia spathysii*, *Plagiochasma appendiculatum*, *P. beccarianum* and *Marchantia paleacea*. Many of the other species that occur here, are also found in the Grassland Biome (see below). *Marchantia berteroana* is found here as well as in the Fynbos.

Grassland Biome

The Grassland Biome is found mainly on the high central plateau of South Africa, inland areas of the seaboard of KwaZulu-Natal and the mountainous areas of Eastern Cape. The name of this biome is self-explanatory. Here, *Riccia* species often grow around flat rock outcrops. *Riccia elongata* is a rare species and its distribution is restricted to a few localities in the northeastern part of this biome. Species that occur in both the Grassland and Savanna Biomes are the following: *Riccia argenteolimbata*, *R. atropurpurea*, *R. macrocarpa* (rare), *R. mammifera*, *R. microciliata*, *R. natalensis*, *R. volkii*, *Asterella muscicola*, *A. wilmsii*, *A. bachmannii*, *Exormotheca holstii*, *Marchantia debilis*, *Oxymitra cristata*, *Plagiochasma microcephalum* var. *microcephalum* and *P. rupestre* var. *volkii*.

Nama-Karoo Biome

This biome occurs on the central plateau in Northern Cape, the southwestern Free State and the southern interior of Namibia. Smaller areas are found in the Eastern Cape interior, Lesotho and the interior margin of the central Namib Desert. The most common soil group in the Nama-Karoo Biome is lime-rich. The vegetation is described as a grassy, dwarf shrubland. Except for some species in Lesotho, none of the other liverwort species that are treated in this fascicle are restricted to this biome. *Riccia bicolorata* and *R. namaquensis* occur here as well as in the Succulent Karoo. Others are found in the Nama-Karoo, Succulent Karoo and the Fynbos Biomes, for example *Riccia albornata, R. villosa* and *Asterella marginata. Riccia angolensis, R. pottsiana* and *R. pulveracea* occur in Grassland as well as in Nama-Karoo, whereas *R. albolimbata, R. albovestita, R. okahandjana, R. runssorensis* and *R. trichocarpa* grow in the Grassland, Savanna and Nama-Karoo Biomes. Those liverworts that are even more widespread, occurring in Grassland, Savanna, Nama-Karoo and Succulent Karoo include *Exormotheca pustulosa, Mannia capensis* and *Plagiochasma rupestre* var. *rupestre.*

The following species are restricted to the Nama-Karoo Biome of Lesotho [or the Afromontane archipelago-like region of White (1983)], *Riccia trachyglossum, R. montana* and *Cryptomitrium oreades. Riccia ampullacea* and *Plagiochasma eximium* also occur in the Grassland Biome, whereas *Riccia bullosa* and *R. sorocarpa*, occur here and in the Fynbos.

Succulent Karoo Biome

The Succulent Karoo Biome is found mostly west of the western escarpment from the Lüderitz District of Namibia through the western belt of Northern and Western Cape. This is a winter rainfall area and the most common soil group is lime-rich as in the Nama-Karoo Biome. A number of *Riccia* species are restricted to this biome, namely *R. alboporosa, R. furfuracea, R. hantamensis, R. hirsuta, R. schelpei, R. tomentosa* and *R. vitrea.* Other species that occur here, as well as in the Fynbos Biome, are *Riccia albomarginata, R. concava* and *R. limbata. Riccia bicolorata* and *R. namaquensis* occur in this biome and also in the Nama-Karoo. *Riccia albornata, R. villosa* and *Asterella marginata* are found here, in the Nama-Karoo and the Fynbos Biomes. *Exormotheca pustulosa, Mannia capensis* and *Plagiochasma rupestre* var. *rupestre* are found in the Succulent Karoo, Nama-Karoo, Grassland and Savanna Biomes.

Fynbos Biome

This biome occurs in the Western Cape and southern part of Eastern Cape. The topography is dominated by the Cape Folded Mountain Belt. Between the coast and the mountains, the lowlands also form part of this biome. It is a winter rainfall area and the vegetation formation contains a unique flora of ericoid and restioid elements. A few *Riccia* species are restricted to this biome, namely *R. alatospora, R. crozalsii, R. curtisii, R. garsidei, R. parvoareolata* and *R. purpurascens.* Other species such as *R. albomarginata, R. concava* and *R. limbata* occur here as well as in the Succulent Karoo. *Riccia bullosa* is found in the Fynbos, Succulent Karoo and the Nama-Karoo of Lesotho. *Riccia stricta, Dumortiera hirsuta, Lunularia cruciata* and *Marchantia pappeana* var. *pappeana* occur in the Fynbos, Savanna and Grassland Biomes. *Riccia cupulifera* and *R. nigrella* range from the Fynbos to the Succulent Karoo and Grassland. *Riccia simii* is very widespread and is found in the Fynbos, Nama-Karoo, Grassland and Savanna Biomes. *Targionia hypophylla* is equally widespread, occurring in the Fynbos, Succulent Karoo, Grassland and Savanna Biomes.

Forest Biome

This is by far the smallest biome in southern Africa and the only forest area of biome dimension occurs in the southern Western Cape. The very rare *Riccia rubricollis* is restricted to this biome. Other liverworts that also occur here are *Riccia crystallina, R. cupulifera, R. purpurascens, R. limbata, Dumortiera hirsuta* and *Marchantia berteroana.*

Collecting and preservation

It is often best to collect liverworts after rain, in other words during the rainy season, which will be in summer for most of the country and in winter for the western Cape areas. When dry, many thallose liverworts have their margins curved inwards, so that the dorsal face is covered. In this 'folded' state, they may be difficult to find.

The routine procedure for collecting liverworts is the same as that for moss specimens, except that the samples, when removed from the substrate with a small knife, are wrapped in strips of newspaper for protection. They are then placed into small paper bags and later allowed to air-dry (on the same day if possible), so as to prevent fungal growth. After identification, the specimens are rewrapped in good quality, soft absorbent paper before being stored in the same standard packets, folded from A4 paper, as those used for mosses, and described in the Introduction to Part 1, Fascicle 1 (Magill 1981). No other preparation is necessary; washing and pressing, or the use of glue to mount specimens on cardboard or preservation in spirit should be avoided (Jovet-Ast 1985).

Study and identification

A dissecting and a compound microscope, as well as the standard materials for preparing microscope slides, are needed for the identification of liverworts. Two pairs of fine-tipped forceps and two fine needle probes are used for the dissection of specimens; a thin razor blade is required to make cross and sometimes horizontal sections of the thallus branches as well as sexual and sporophyte structures.

Prior to dissection, some material from a specimen is removed to a microscope slide and moistened with a few drops of water (at room temperature) delivered by squirting from a Pasteur pipette. Dried thallose liverworts do not, however, always recover well when remoistened for examination. It is therefore preferable to examine fresh material whenever possible. The fresh or dried material (which has been allowed to revive as much as possible), is examined and observations concerning the habit, colour and consistency of the thallus, its shape, dorsal groove (if present) and margins as well as the presence or absence of scales, their number, colour and appendage(s) (if present), are noted. Some terminal branches are then cleaned of all soil particles by adding more water and by carefully and progressively removing the sand and debris with forceps. The presence of stolons, bulbils or gemmae (and the structure of gemma cups) should also be noted. The following should be examined, if available, after the material has been transferred to a drop of water on a clean slide, and a coverslip has been applied: cross sections of the cleaned branch cut by hand at mid-length or serially (for *Riccia* spp.) at intervals from the apex to the base; horizontal sections taken just below the dorsal covering as well as lower down through the assimilation tissue (if the tissues remain a little shrunken in the sections, they can be stretched lightly with the fine probes); some carefully detached ventral scales; sections of androecia and, if gametangiophores are present, cross sections of the stalk, and scales from its base, along its length and apex (if present); from the rarely raised male receptacle, the margin of the rays and ventral median scales; and from the carpocephalum, parts of the capsule wall, involucres and, if present, the pseudoperianth. As the water evaporates during examination under the compound microscope, more can be added. For taking measurements and for pho-

tography, water-mounted material is routinely used. To make more durable preparations, the sections and scales can be mounted in Hoyer's medium (Magill 1981: xiii); it, however, causes shrinkage and severe bleaching of the delicate tissues.

Characters used in keys and descriptions

Thallus. Characters describing the size, growth form, habit and colour are obtained from the specimens examined, but are frequently somewhat subjective. The nature of the margins, inflexed or not, is sometimes important in identification and should be observed in both wet and dry condition. The forking of the branches, whether shortly or deeply divided, the degree of divergence and the shape, which refers to that of the terminal segment, are also noted from the specimens. The size categories of the thallus branches referred to in the descriptions, more or less correspond to the following list, but are sometimes rather arbitrary and not universally applicable. Where taxa span more than one category, deviations are bound to occur. The length of the branches is measured from the apex to the base, and the width is taken across the widest part of the terminal segment.

Branch size categories. Very small to small: 1.0–4.0 (–5.0) × 0.6–1.5(–2.0) mm. Smallish to medium-sized: 5.0–10.0 × (0.6–)0.8–2.0 mm. Medium-sized: 5.0–10.0(–12.0) × (1.0–)3.0–4.0 mm. Large: up to 15.0 × 2.0–5.5 mm. Very large: more than 18.0 × 4.0–6.0(–8.0) mm. The thickness of the branches is measured medianly on cross sections; the ratio of the width to thickness is based on measurements taken in the same way. The slope of the flanks can also be observed in cross sections.

Scales. The presence (or absence), number of rows, and sometimes the fraction of the ventral face of the thallus covered by them, as well as the colour, size, shape, position, margins and appendages of the scales are often important taxonomic characters and are frequently used in the keys to identify species.

Cilia. A few species of *Riccia* have ciliate margins, and microscopic examination and measurement of the cilia should help to distinguish between them.

Dorsal epidermis (or epithelium). Under the dissecting microscope it can be observed whether the dorsal cells of the thallus are chlorophyllose or echlorophyllose and interrupted by defined pores, or form an even, ± homogeneous upper surface of echlorophyllose cells in one or two storeys, or whether they form free-standing, multicellular pillars. Subdorsal horizontal and cross sections are always taken to measure the cells and to note their shape as well as the occasional presence of trigones. In *Riccia* section *Pilifer* the cells of the dorsal pillars, as cited in the keys and descriptions, are used in conjunction with other characters, to distinguish between the different species. The first figure of the cell measurements refers to the long axis and the second to the width.

Air pores. The following should be noted: whether simple or compound (in *Marchantia* spp.), slightly or much raised, number of surrounding cell rings and the thickness of radial walls by using horizontal and cross sections. Only in *Marchantia* are air pores also viewed from below.

Assimilation tissue. Cross and horizontal sections reveal whether the assimilation tissue is spongy and a honeycomb of rather irregular walls and wide air chambers, the latter sometimes empty or filled with chlorophyllose filaments, or whether the cells in the assimilation tissue layer are closely packed together and only separated by narrow vertical air canals.

Male and *female receptacles*. Their position, size, shape, accompanying structures and membranes are studied. In *Riccia* species it should be noted whether the internally borne sporangia bulge dorsally or ventrally or whether they are deeply embedded.

Spores and *elaters* (when the latter are present). Mature, well-formed spores (and elaters) are mounted on microscope slides in Hoyer's medium to measure their size and other features. The shape and colour should also be observed, as well as details of the ornamentation. For SEM examination, spores from the same sample are mounted on aluminium stubs with double-sided tape and gold-coated. Spore characters are very important in distinguishing between species, particularly in *Riccia,* and many can easily be recognized solely by their ornamentation.

Descriptions and illustrations

Authors of plant names are abbreviated according to Brummitt & Powell (1992), with the exception of Jovet-Ast.

Descriptions of eight families, 13 genera and 75 species of the locally occurring Marchantiales are given. Only the genus *Riccia* has many species in southern Africa, whereas seven of the genera included here are represented by only one local species or are monotypic.

Illustrations were prepared by Mesdames Gillian Condy, Jill Kimpton (who did all but one of the Ricciaceae), Anne Pienaar and Marietjie Steyn. The habit drawings were done by direct observation of selected wet and sometimes dry plants as well, using a dissecting microscope. All other parts were drawn from photographs, taken by the author, using a photographic apparatus attached to a compound microscope.

CLASSIFICATION

Stotler & Crandall-Stotler (1977) and Bartholomew-Began (1990) are followed in considering the liverworts a separate division, the Hepatophyta (or Hepaticophyta), and not a class of the division Bryophyta (Schuster 1984b). The hornworts are also placed in a separate division, the Anthocerotophyta.

Schuster (1992b) includes the order Sphaerocarpales (and the extra-southern African Monocleales), together with the order Marchantiales, in the subclass Marchantiidae.

Here, only the order Marchantiales has been referred to the subclass Marchantiidae, which is dealt with in fascicle 1 of part 1: class Marchantiopsida. The order Sphaerocarpales (subclass Sphaerocarpidae) has not recently been studied in southern Africa as very little new material has been collected since the last treatments of its constituent genera, namely *Riella* by Wigglesworth (1937), *Riella* and *Sphaerocarpos* by Proskauer (1955) and *Monocarpus* by Schelpe (1969). Only if new collections come to hand, can these genera be revised meaningfully.

Schuster (1992c) is followed in recognizing the suborder Targioniineae, and the subfamily Dumortieroideae. The classification of the Aytoniaceae is after Grolle (1983a, b), and of the Ricciaceae partly after Grolle (1983a, b), and also partly after Jovet-Ast (1975), with the elevation of *Thallocarpus* to the status of subgenus. Schuster's rather controversial treatment of the Ricciaceae (Schuster 1992c), with the institution of many new sections, has not been followed here. Two other subgenera, unique to southern Africa, have been instituted: *Chartacea* and *Pannosae*. Section *Pilifer* (Volk 1983) is placed under subgenus *Riccia*, and not under subgenus *Pteroriccia* (Schuster 1985). Na-Thalang's (1980) example was partly followed in dividing section *Riccia* into the groups: Ciliatae, Mammillatae and Squamatae; section *Spongodes* was divided into two groups: Crystallina and Vesiculosa. The other two recently recognized subgenera, *Viridisquamata* and *Leptoriccia*, do not occur in southern Africa.

Extra-southern African families have generally not been included.

DIVISION BRYOPHYTA (mosses) (Magill 1981, 1987; Magill & Van Rooy 1998)

DIVISION HEPATOPHYTA (liverworts)
Part 1. Class Marchantiopsida *Stotler & Stotl.-Crand.* (1977)
Fascicle 1. Subclass Marchantiidae *R.M.Schust.* (1953)
Order Marchantiales *Limpr.* (1876)
Suborder Targioniineae *R.M.Schust.* (1958)
Family Targioniaceae *Dumort.* (1829)
Subfamily Targionioideae *Schiff.* (1893)
Cyathodioideae *Grolle* (1992)
Suborder Marchantiineae *Limpr.* (1876)
Family Lunulariaceae *H.Klinggr.* (1858)
Aytoniaceae *Cavers* (1911)
Subfamily Aytonioideae
Reboulioideae *Grolle* (1976)
Family Cleveaceae *Cavers* (1911)
Exormothecaceae *Müll.Frib.* in Grolle (1972)
Marchantiaceae *(Bisch.) Lindl.* (1836)
Subfamily Marchantioideae
Dumortieroideae *R.M.Schust.* (1984a)

Suborder Ricciineae *H.Buch.* (1936)
Family Oxymitraceae *Müll.Frib.* (1940)
Ricciaceae *Rchb.* (1828)
Fascicle 2. Subclass Sphaerocarpidae
Order Sphaerocarpales
Suborder Sphaerocarpineae
Family Sphaerocarpaceae
Suborder Riellineae
Family Riellaceae
Suborder Monocarpineae
Family Monocarpaceae
Part 2. Class Jungermanniopsida *Stotler & Stotl.-Crand.* (1977)
Fascicle 1. Subclass Metzgeriidae
Order Haplomitriales
Family Haplomitriaceae
Order Metzgeriales
Family Fossombroniaceae
Pallaviciniaceae
Aneuraceae
Metzgeriaceae
Fascicle 2. Subclass Jungermanniidae (Schuster 1953 as Jungermanniae)
Order Jungermanniales
Family Lepicoleaceae
Herbertaceae
Lepidoziaceae
Calypogeiaceae
Adelanthaceae
Cephaloziaceae
Cephaloziellaceae
Antheliaceae
Jungermanniaceae
Gymnomitraceae
Scapaniaceae
Geocalycaceae
Plagiochilaceae
Arnelliaceae
Acrobolbaceae
Schistochilaceae
Balantiopsidaceae
Pleuroziaceae
Radulaceae
Ptilidiaceae
Porellaceae
Jubulaceae (incl. Frullaniaceae)
Lejeuneaceae

DIVISION ANTHOCEROTOPHYTA (hornworts)

Class Anthocerotopsida
Order Anthocerotales
Family Anthocerotaceae

GLOSSARY

The terms used have for the most part been dealt with in the Glossary of Bryophyta (Magill 1981: 1–12). A few of the more commonly used ones are repeated here plus some which pertain only to liverworts.

acropetal—referring to organs developing from the base toward the apex.

air pores—minute, regular spaces or simple or compound, delimited stomata in dorsal covering of thallus, functioning in gas exchange.

air canals—narrow vertical interstices separating columns of chlorophyllose cells in the assimilation tissue.

air chambers—wide polyhedral air cavities, mostly enclosed by unistratose echlorophyllose or chlorophyllose cell plates in the assimilation tissue.

alveolus (pl. alveoli)—small angular or polygonal areas bordered by ridges and forming a pattern or network; applied to ornamentation in many spores; some workers, however, prefer to use the term 'areola'.

anastomose—interconnecting; applied to ornamentation in some spores.

androecium (pl. androecia)—antheridia grouped together.

anisopolar—proximal and distal spore faces differently ornamented.

annular thickenings—ring-like thickenings extending over both tangential and radial cell walls in liverwort capsules.

antheridiophore—specialized antheridium-bearing branch, the male gametangiophore, e.g. in *Marchantia.*

antheridium (pl. antheridia)—male gametangium, multicellular structure containing spermatozoids.

apical—at the apex or terminal end of the thallus branch.

apolar spores—spores with no obviously distinct polarity, lacking a conspicuous triradiate mark (opposed to polar).

archegoniophore—a specialized archegonium-bearing branch, the female gametangiophore, e.g. in *Marchantia.*

archegonium (pl. archegonia)—female gametangium; multicellular, flask-shaped structure containing ovum.

areolate—the cellular networkdk of a thallus or leaf.

autoicous—with antheridia and archegonia in separate clusters on the same plant.

basal—at the base or proximal end of the thallus branch.

bifurcate—divided or forked into two basically equal parts.

bulbil—vegetative propagule; a small, bulb-like bud.

calyptra—membranous covering of haploid tissue over developing sporophyte, derived from archegonial venter, ruptures near the apex and remains at base of seta.

carpocephalum—specialized, often radially symmetrical receptacle bearing sporangia, held aloft by a stalk.

cavernous—with numerous cavities in the tissue.

chlorophyllose—containing chlorophyll; green, as opposed to hyaline.

cilium (pl. cilia)—hair-like appendages along cupule margins or involucre margins in some *Marchantia* species or along thallus margins in some *Riccia* species.

cleistocarpous—referring to indehiscent capsules lacking valves and hence opening irregularly.

crenate—with rounded teeth; applied to scale margins.

crenulate—with minute, rounded teeth; applied to the spore wing in some species.

cupule—see **gemma cupule.**

dentate—with sharp teeth; applied to the scale margins in a few species.

dioicous—with archegonia and antheridia on separate plants.

distal—the outer, convex face of a spore, away from the sides of contact (opposed to **proximal**).

divergent—turned in different directions.

dorsal—the upper surface of the thallus, away from the substrate.

elater (pl. elaters)—a differentiated, elongate cell usually with helical wall thickenings, in most liverwort capsules admixed with spores.

emarginate—having a marginal indentation or notch at the thallus apex.

epidermis—the outer cell layer of the thallus in those species with defined stomata, sometimes becoming cavernous.

epithelium—the outer cell layer(s) of the thallus in those species of *Riccia* with minute spaces for air pores.

erose—irregularly and finely notched; applied to the spore wing in some species.

filiform—filamentous, threadlike.

flanks—sides of thallus.

foveolate—pitted; applied to the spore ornamentation in some species.

gametangium (pl. gametangia)—i.e. archegonium, antheridium which is vessel(s) bearing gametes.

gamete—male or female reproductive cell.

gametoecium—gametangia and surrounding bracts.

gemma cupule—cup-shaped, gemmae-containing structure of thallus origin, e.g. in *Marchantia, Lunularia.*

globose—spherical.

granular—with minute, blunt projections.

gregarious—growing together, but not closely touching as in mats.

gynoecium (pl. gynoecia)—female inflorescence often consisting of archegonia, surrounding calyptra and involucre.

habit—the aspect or general appearance of a thallus.

habitat—local environment.

hyaline—clear and colourless like glass, and transparent; applied to echlorophyllose cells of dorsal epithelium or to scales in some species.

idioblast—a uniquely differentiated cell, distinct in size and contents from the other cells of the same tissue.

imbricate—closely appressed and overlapping like shingles on a roof.

incrassate—with thickened cell walls.

inflexed—bent upward and inward; applied to thallus margins.

involucre—a protective sheath of tissue of thallus origin surrounding archegonium or sporophyte.

mammillose—(of cells) bulging, and/or with a hollow papilla-like protuberance.

monoicous—with antheridia and archegonia on the same plant.

neck—the narrow elongated upper end of the archegonium or antheridium.

oblique—slanted; applied to the slope of the flanks of the thallus in many species.

oil cell—cell characterized by the inclusion of a large oil body or organelle containing terpenes.

palea (pl. paleae)—scale(s) encircling androecia and gynoecia.

palmate—lobed or divided like fingers, referring to the female receptacle in some *Marchantia* species.

papilla (pl. papillae)—a minute protuberance of various forms.

papillate—loosely applied to minutely rough surface; bearing minute pimple-like protuberances.

paroicous—bearing the antheridia and archegonia close together in a single gametoecium but not mixed.

pedicel—stalk bearing gametangia.

polar spore—spores with a discernible to conspicuous triradiate mark on the proximal face.

postical—belonging to the undersurface or back.

proximal—applied to the internal face of a spore (opposed to **distal**).

pseudodichotomous—referring to the forking of the axis into two, more or less equal branches of the thallus, but not by equal division of an apical cell; false dichotomy.

pseudoperianth—tissue of thallus origin surrounding the archegonial cluster, calyptra and later the sporophyte, e.g. in *Asterella* and *Marchantia.*

receptacle—a disc, or wart-like mass of tissue, bearing antheridia or archegonia and found directly on the thallus or raised on a stalk.

reticulate—netted, referring to the network pattern produced by alveoli on spore faces.

rhizoid—roothair-like structures that theoretically function in absorption and anchorage, one-celled (in liverworts) and usually hyaline, smooth or pegged.

rhizoid furrow—a longitudinal, rhizoid-bearing channel or groove on the postical surface of a stalk.

rosette—growth habit with thalli radiating from a central point.

scales—thin, membranous structures, in two or more rows, on the undersides or flanks of the thallus.

sessile—affixed directly on the thallus, without a stalk.

seta—elongated portion of the sporophyte between capsule and foot.

sporangium—capsule; spore-producing structure, rarely embedded in thallus tissue.

sporophyte—the spore-bearing generation, typically consisting of foot, seta and capsule.

stalk—cylindrical structure carrying archegonial and rarely antheridial receptacles.

stolon—slender, ± vertical underground stem.

storage tissue—the ventral ± $^1/_2$–$^2/_3$ or more of thallus, composed of cells sometimes interspersed with oil or sclerotic cells or mucilage cavities.

succulent—thick and fleshy.

terete—circular in cross section.

tetrad—a group of 4 developing, or rarely mature, spores (permanently grouped so in a few *Riccia* species).

tetrahedral—four-sided.

thallus—a more or less flattened vegetative body, without differentiation into a stem and leaves.

triangular-globular—applied to a polar spore, the inner face of which has 3 facets separated by the arms of a triradiate mark; the outer face is convex.

trigone—generally triangular intracellular wall thickenings, at the point where 3 (or more) cells meet, often in epidermis of liverworts.

triradiate mark—prominent ridges in the shape of a 'y' on the proximal face of a spore.

tumid—swollen.

umbonate—convex with an abrupt, rounded central point.

undulate—wavy.

valve—one of the parts or partially detached flaps of tissue into which the capsule of many liverworts separates upon dehiscence.

venter—the expanded portion of the archegonium that encloses the egg.

ventral—referring to the lower surface, next to the substrate (opposed to **dorsal**).

vermiculate—long, narrow, somewhat wavy, usually with rounded ends; applied to the ornamentation of some spores.

verruculose—irregularly roughened; applied to the ornamentation of some spores.

wart—a small elevation or protuberance.

wing—loosely applied to the lamina of a thallus or to the thin, flat expansion at the margin of the spore.

SUBCLASS **MARCHANTIIDAE**

Marchantiidae *R.M.Schust.*, Boreal Hepaticae, a manual of the liverworts of Minnesota and adjacent regions. The American Midland Naturalist 49: 257–684 (1953).

Plants thallose, generally creeping, pseudodichotomously branching, dorsiventral, with marked tissue differentiation. Dorsal epidermis often lacking chloroplasts, interrupted by air pores (or small openings). Assimilation tissue with air chambers (or air canals), the former sometimes containing chlorophyllose filaments; storage tissue ventral; oil bodies large, spherical, solitary, in somewhat smaller cells that lack chloroplasts, scattered throughout all tissues, absent in *Athalamia* and *Riccia* species; ventral epidermis mostly bearing scales and dimorphic, smooth or pegged rhizoids.

Sexual reproduction by specialized propagules rare, very occasionally reproducing by multicellular gemmae.

Antheridia usually in groups, generally ellipsoidal, on short pedicel, often aggregated in sessile, very rarely stalked, androecial receptacles. *Archegonia* with neck normally formed of 6 rows of cells, frequently aggregated in stalked gynoecial receptacles, sometimes internal, rarely ventrally displaced; calyptra 1–4 cell layers thick, often surrounded by individual involucres. Sporophyte with capsule wall unistratose, except occasionally for a small, bistratose, apical area, dehiscing variously or not at all. *Spores* usually large, often clearly polar. *Elaters* mostly slender, twisted, sometimes absent.

Only the Marchantiales, with three local suborders, have been referred to the Marchantiidae in this treatment.

ORDER **MARCHANTIALES**

Marchantiales *Limpr.* Lebermoose. In F. Cohn, Kryptogamen-Flora von Schlesien: 225 (1876); R.M.Schust.: 1 (1992c).

Thalli small to very large, scattered or in loose or crowded patches, sometimes in rosettes; light green, green, glaucous green or dark green, usually firm but sometimes spongy and rather delicate. *Branches* simple or once to several times pseudodichotomously furcate, occasionally with ventrolateral or apical innovations, linear to oblong or obovate, apex entire or notched, tips of apical scales often recurved over edge; groove occasionally present or thallus dorsally flat to slightly concave, margins acute to obtuse; flanks sloping obliquely or sometimes almost vertical; ventral face medianly keeled or rounded. *Scales* ventral or ventrolateral, small to large, in 2–4(6) rows, hyaline or pigmented, variously shaped, with or without appendages, with or without oil cells.

Dorsal epidermis (or epithelium) unistratose, very occasionally partly or wholly bistratose, sometimes in free cell pillars; air pores simple, rarely much raised, occasionally only small spaces between cells, rarely compound, very seldom dorsal epidermis and pores absent. *Assimilation tissue* with one storey (or more) of partitioned air chambers, rarely subdivided, walls unistratose, cells with or without many small chloroplasts, spaces empty or containing chlorophyllose filaments, sometimes with narrow, vertical air canals enclosed by chlorophyllose cell columns; storage tissue parenchymatous; sometimes also present, oil cells, slime cells, sclerotic cells or cells with pitted walls.

Asexual reproduction usually lacking, occasionally by means of discoid gemmae borne in dorsal gemma cupules or sometimes perennating by ventral bulbils, tubers or stolons.

Monoicous, autoicous, dioicous or paroicous. *Antheridia* sometimes in median rows dorsally sunken into thallus or immersed in well-defined sessile cushions or discs, rarely in stalked receptacles, often opening into conical protuberances. *Archegonia* with moderately long necks, generally in stalked receptacles, sometimes sunken in thallus in dorsal median row, very occasionally in sessile gynoecia, rarely ventrally displaced below thallus apex and enclosed in black bivalved involucre (*Targionia*). *Sporophytes* with reduced foot and short seta present or absent, capsule globose, wall with or without thickenings, dehiscence various. *Spores* generally large, mostly polar, often triangular-globular, rarely retained in permanent tetrads, variously ornamented. *Elaters* usually bi- or trispiral, rarely reduced, sometimes absent. *Chromosome numbers:* n = 9 or multiples thereof, 18, 27, 36, or in Ricciineae 8, 10, 12, 15 or 24.

Members of the order have a worldwide distribution; many are pioneers of harsh biotopes, of semi-arid and arid areas, as well as arctic-antarctic, alpine and tropical mountain regions. Some also colonize disturbed mesic habitats and have become commensals of human activity (Bischler 1988).

The Marchantiales are said to form one of the summits of liverwort evolution (Schuster 1984b); tissue differentiation of the gametophyte is markedly complex and sporophyte reduction has been carried to the extreme in the Ricciaceae.

Locally, the order Marchantiales includes the following three suborders: Targioniineae, Marchantiineae and Ricciineae. The Corsiniineae have no representatives in southern Africa nor do the Monocleales. The subclass Sphaerocarpiidae has been excluded in this treatment for reasons already stated.

Key to local suborders of Marchantiales

1a Thalli medium-sized to robust, 2–10 mm wide, distantly or infrequently branching, sometimes with apical or ventrolateral innovations, not forming rosettes; archegonia in receptacles mostly raised on stalks, very rarely dorsally sessile on thallus or ventrally displaced below apex; sporophyte with distinct foot and seta; capsule wall persistent, not disintegrating at maturity; elaters present, mostly long and thin, rarely reduced:

2a Air pores of thallus simple, surrounded by several rings of differentiated cells, epidermal cells with distinct trigones; gemma cups absent; sporophyte single per receptacle, ventrally displaced below apex of thallus, thus inhibiting further apical growth; capsule wall with annular thickenings; calyptra smooth, delicate; involucre conspicuous, thick-walled, mussel-like, black; elaters long and thin . . . . . Targioniineae (p. 14)

2b Air pores of thallus simple, slightly or rarely much raised, sometimes compound, epidermal cells with or without trigones; very rarely epidermis and pores lacking; gemma cups sometimes present; sporophytes mostly 2 to several per receptacle, which is almost always raised on a stalk, very rarely dorsally sessile on thallus; calyptra delicate but pluristratose at maturity; elaters distinct, mostly long and thin, rarely reduced . . . . . Marchantiineae (p. 18)

1b Thalli usually small to medium-sized, 1–4 mm wide, mostly repeatedly pseudodichotomously closely furcate, frequently forming partial or complete rosettes; antheridia and archegonia (and sporophytes) embedded in thallus, very rarely dorsally sessile on thallus; sporophyte without foot and seta; capsule wall delicate, without thickenings, resorbed at maturity; elaters absent . . . . . Ricciineae (p. 107)

Key to local genera of Marchantiales

1a Thalli large, dark green, translucent, margins hirsute; dorsal epidermis, air pores and air chambers absent; male and female receptacles raised on stalks but male stalks very short . . . . . **Dumortiera** (p. 103)

1b Thalli small to large, various shades of green, margins not hirsute; dorsal epidermis (or epithelium), air pores (or openings), air chambers (or canals) present; gametangia stalked, sessile or embedded:

2a Thalli smallish to large, not in rosettes, dorsal groove absent; female receptacles raised on stalks, very rarely sessile; capsule dehiscence by lid or valves; elaters present:

3a Air chambers containing short, erect, chlorophyllose filaments or subdivided by secondary walls or plates:

4a Air chambers much elevated . . . . . **Exormotheca** (p. 73)

4b Air chambers not elevated:

5a Air pores of thallus compound, barrel-shaped (formed by 3–5 superimposed concentric rings of cells); round gemma cups present; male and female receptacles raised on longish stalks . . . . . **Marchantia** (p. 82)

5b Air pores of thallus simple, surrounded by 1–3 concentric rings of cells, with or without collapsed inner cell ring; rarely with crescentic gemma cups; female receptacle almost invariably raised on stalk:

6a Thalli dark green or bright green, margins purple; dorsal epidermal cells with distinct trigones; ventral scales dark purple, obliquely triangular, appendage(s) tapering, basally not constricted; gemma cups absent:

7a Air pores large, white-encircled; gynoecia ventrally displaced below thallus apex, sessile; involucre mussel-shaped, black, leathery . . . . . **Targionia** (p. 15)

7b Air pores less obvious, smaller; female receptacle raised on stalk; involucre bell-shaped, membranous . . . . . **Mannia** (p. 64)

6b Thalli bright yellow-green, margins hyaline; dorsal epidermal cells thin- or thick-walled, trigones lacking; ventral scales ± hyaline, appendage rounded, basally deeply constricted; crescentic gemma cups present . . . . . **Lunularia** (p. 21)

3b Air chambers empty, in one to several storeys, bounding walls chlorophyllose:

8a Female receptacle on stalk arising dorsally on thallus, away from apex; stalk lacking rhizoid furrow:

9a Thalli and ventral scales with scattered oil cells; rarely air pores tiny, stellate, appearing plugged; antheridia in sessile, cushion-like receptacles . . . . . **Plagiochasma** (p. 27)

9b Thalli and ventral scales lacking oil cells; radial walls of single ring of cells surrounding stellate air pores thickened, not appearing plugged; antheridia scattered medianly, sunken . . . . . **Athalamia** (p. 69)

8b Female receptacle on stalk arising from apical notch of thallus or at side of thallus; stalk with 1 rhizoid furrow:

10a Female receptacle round or umbonate, on stalk arising from apical notch of thallus; pseudoperianth present, basket-like; ventral scales of thallus with lanceolate or ovate appendages . . . . . **Asterella** (p. 43)

10b Female receptacle disciform-round, on stalk arising ventrolaterally and emerging at side of thallus; pseudoperianth absent; ventral scales of thallus with filiform appendages . . . . . **Cryptomitrium** (p. 59)

2b Thalli small to medium-sized, frequently in complete or partial rosettes; dorsal groove often present; sporangia very rarely sessile, otherwise always embedded in thallus; capsule cleistocarpous; elaters absent:
11a Air pores stellate, with thickened radial walls; oil cells absent; sporangia dorsally sessile on thallus, enclosed above by continuous crest-like involucre .... **Oxymitra** (p. 109)
11b Air pores not stellate, surrounded by undifferentiated cells or mere openings in epithelium; oil cells present or absent; sporangia embedded in thallus:
12a Thalli floating or terricolous; air chambers in several storeys; scales ventral, in long pendant purple ribbons, margins dentate, small in landform; oil cells present .... **Ricciocarpos** (p. 112)
12b Thalli terricolous, very rarely floating; air chambers mostly in single storey or in narrow canals; scales small to large, mostly rounded, very rarely triangular, margins smooth, rarely denticulate; oil cells absent .... **Riccia** (p. 115)

SUBORDER **TARGIONIINEAE**

Targioniineae *R.M.Schust.* in Bryologist 61: 33 (1958); R.M.Schust.: 1058–1060 (1984b); R.M. Schust.: 61 (1992c).

[excluding *Cyathodium* (Perold 1993c)]

Thalli medium-sized, in crowded patches, not in rosettes; dark green. *Branches* simple or repeatedly furcate, sometimes with ventrolateral innovations, linear to ligulate or obcordate, apex entire; groove absent, thallus dorsally flat, margins acute; flanks sloping obliquely; ventral face keeled. *Scales* ventral in 2 rows, one on either side of keel, large, deep purple, oil cells few.

Dorsal epidermis hyaline and firm, cells with distinct trigones; air pores conspicuous, surrounded by 3 concentric rings of differentiated cells. *Assimilation tissue* a low storey of air chambers, with chlorophyllose filaments; storage tissue parenchymatous.

Asexual reproduction absent.

Autoicous or dioicous. *Androecia* forming well- or poorly-defined groups at apex of reduced, basally stipitate, ventrolateral branches, antheridia embedded, each with a conical protuberance. *Gynoecial receptacles* displaced below ± entire apex of thallus. *Involucres* large, mussel-like, bivalved, thick-walled and black, opening along lips of valves. *Sporophyte* single in each involucre, subsessile, with short seta, foot distinct, capsule globose, wall with thickening bands, dehiscing by irregular breaking up of upper part. *Spores* alveolate with larger network of raised ridges enclosing polygonal areas, all covered by fine reticulum. *Elaters* up to ± 300 µm long, 12.5–18.0 µm wide, bi- or trispiral. *Chromosome number*: n = 9, 27.

The Targioniineae are divided into two families, Targioniaceae and Cyathodiaceae, by Hässel de Menéndez (1963) and Schuster (1992a), whereas Grolle (1972) treats these two taxa as subfamilies, Targionioideae and Cyathodioideae, in the single family Targioniaceae but concedes that 'die Verwandtschaft von *Targionia* und *Cyathodium* ist zwar locker'. Schuster (1992c) also regards affinities between the two taxa as 'probably rather remote'. Arnell (1963a) assigned the two genera *Targionia* and *Cyathodium* to the Targioniaceae and thought that species of *Cyathodium* would possibly be found in southern Africa. He misidentified a *Riccia* collection by Duthie as *Cyathodium* sp. (Perold 1993c). The presence of *Cyathodium* species in southern Africa has not been confirmed,

although the genus is widespread in the rest of Africa (Jones 1952). It is distinguished from *Targionia* by having thin, delicate thalli with reduced hyaline scales, ill-defined dorsal air pores and small, saccate, transparent involucres.

TARGIONIACEAE

Targioniaceae *Dumort.*, Analyses des Familles des Plantes: 68, 70 (1829); Nees, in Lindl.: 414 (1835).

Targionideae Gray: 678, 680 (1821).

Subfamily **TARGIONIOIDEAE**

Targionioideae Schiffn. in Engler et Prantl, Natürliche Pflanzenfamilien edn 1, 1,3: 24–26 (1893).

The diagnoses of the family and of the subfamily Targionioideae [after Grolle (1972) split off the subfamily Cyathodioideae in the Targioniaceae] are contained in the above description of the suborder Targioniineae.

TARGIONIA

Targionia *(P.Micheli) L.*, Species plantarum 2: 1136 (1753); Gottsche et al.: 574 (1844–1847); Schiffn.: 26 (1893); Steph.: 763 (1898); Macvicar: 33 (1926); Sim: 16 (1926); Müll.Frib.: 325 (1951–1958); Hässel de Menéndez: 68 (1963); S.W.Arnell: 46 (1963a); R.M.Schust.: 66 (1992c); Perold: 215 (1993c). Type: *Targionia hypophylla* L.

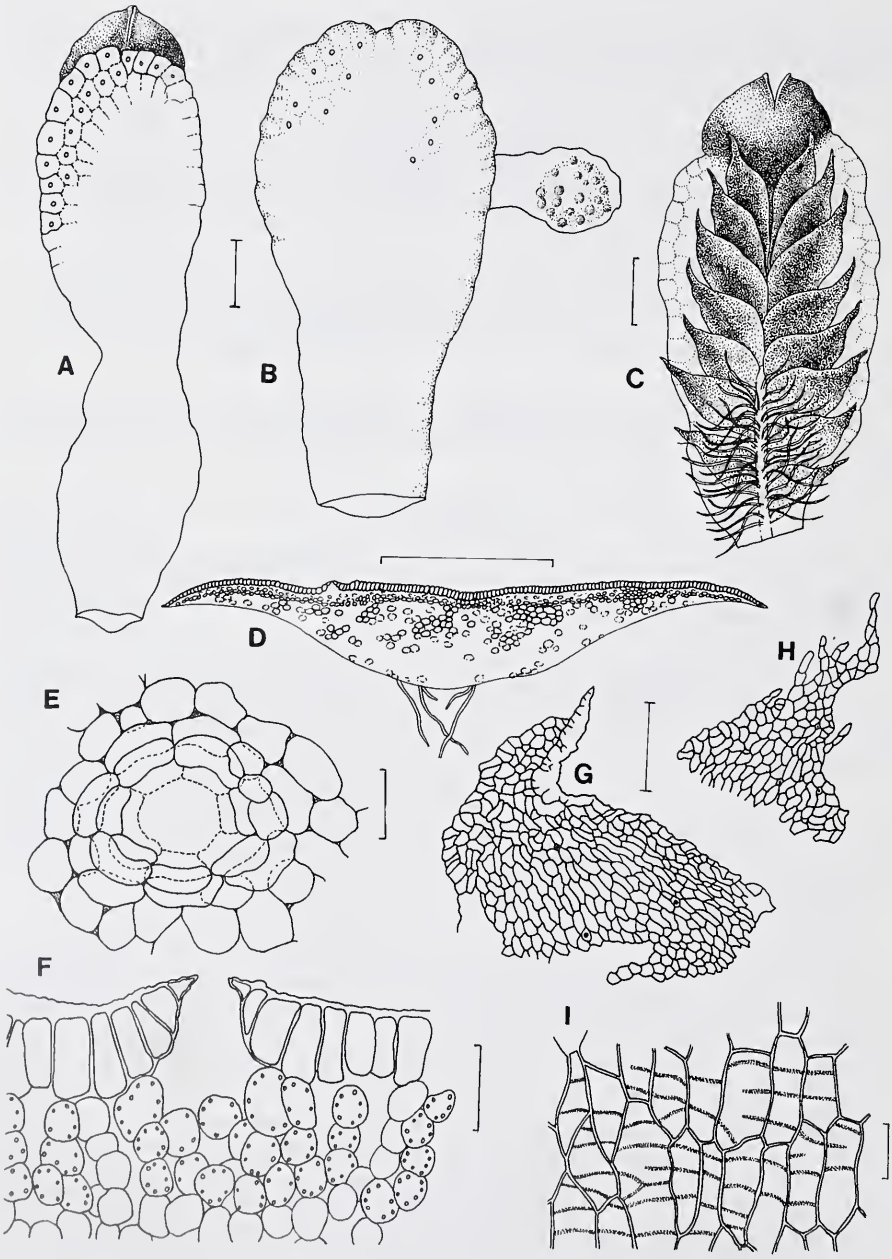
Thalli in crowded patches or extensive sheets, not in rosettes. *Branches* simple, sometimes repeatedly furcate or only apically branched or with ventrolateral innovations; groove absent, thallus dorsally flat. *Scales* ventral, in one row on each side of keel, large, obliquely triangular with long acuminate appendage, dark purple.

Dorsal epidermis hyaline, unistratose, with cell walls thickened, especially at corners; air pores simple, conspicuous, surrounded by 3 concentric rings of cells. *Assimilation tissue* with shallow, single storey of air chambers, containing chlorophyllose filaments; storage tissue well developed, cells variable in size; occasionally with an oil body.

Asexual reproduction absent.

Autoicous or dioicous. *Androecia* on terminal disc of short, stipitate, ventrolateral branches, antheridia with conical protuberances. *Gynoecia* terminal, below apex of thallus, enclosed in black, bivalved involucre; capsule subsessile, globose, wall with thickening bands. *Spores* anisopolar, ornamentation on distal face with a network of ridges covered by a fine reticulum of smaller ridges; proximal face with crowded, irregular, reticulated ridges. *Elaters* usually bispiral. *Chromosome number*: n = 9, 27 (in *T. lorbeeriana*).

Targionia hypophylla is the only representative of the genus in southern Africa. Other taxa placed here are: *T. lorbeeriana* Müll.Frib. from the Mediterranean, Australia, California, and questionably from East Africa and India; *T. stellaris* (Müll.Frib.) Hässel from Argentina, for which Schuster (1992c) has created a new subgenus, *Prototargionia*; *T. elongata* from Ethiopia and a new subspecies, *T. hypophylla* subsp. *linealis* W.Frey & Kürschner (1993) from Saudi Arabia; a new species was described from India by Udar & Gupta (1983).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Targionia hypophylla *L.*, Species plantarum: 1136 (1753); Steph.: 764 (1898); Macvicar: 33 (1926); Sim: 16 (1926); Müll.Frib.: 326 (1951–1958); Hässel de Menéndez: 69 (1963); S.W.Arnell: 46 (1963a); O.H.Volk: 241 (1979); Piippo: 274 (1991); R.M.Schust.: 70 (1992c); Perold: 215 (1993c). Types: 'Italia, Hispania, Constantinopoli' + citation (syn.); Dill.: 532. Lichen No. 9, tab. 78, fig. 9. (1741) (OXF, syn.); (H-SOL, isosyn.) [according to Isov. (1970) and quoted by Grolle (1976)].

T. michelii Corda in Opiz: 649 (1829). Type: Italy, leg. *Sieber.*

T. mexicana Lehm. & Lindenb. in Lehm.: 27 (1832). Type: Mexico, leg. *Schiede.*

T. capensis Huebener: 17 (1834).

T. bifurca Nees & Mont. in Mont.: 113 (1838a); Nees: 315 (1838a). Type: Chile, 'prope Quillota', leg. *Brotero.*

T. convoluta Lindenb. & Gottsche in Gottsche et al.: 576 (1846). Type: Mexico, ad Chinantla, leg. *Liebman.*

T. hypophylla var. *capensis* Huebener in Krauss: 135 (1846). Circa urbem Capstadt, Augusto.

T. hypophylla var. *fimbriata* Müll.Frib.: 326 (1951–1958).

Thalli medium-sized, in crowded patches; dark green, rather leathery, faintly areolate, air pores large, white-encircled, margins purple and entire to somewhat crenate; when dry, margins incurved, thalli almost tubular. *Branches* simple to repeatedly furcate or with ventrolateral or apical innovations, linear to ligulate, up to 30 mm long, 2.7–3.5 mm wide, 550 µm thick medianly, in section 5 or 6 times wider than thick, apex slightly notched or entire; groove absent, thallus margins acute, thin; flanks sloping obliquely; ventral face medianly keeled, mostly deep purple. *Scales* in 2 ventral rows, 875–1750 µm long, up to 1325 µm wide across base, tips not, or hardly reaching thallus margins, obliquely triangular, imbricate, reddish to dark purple, margins entire or sometimes with papillae or fimbria, apically continuing into long-acuminate appendage ± 375 µm long, oil cells few, scattered.

Dorsal epidermal cells unistratose, hyaline, rounded to oval, 22.5–37.5 × 17.5–25.0 µm, with conspicuous trigones; air pores somewhat raised, simple, oval, 52.5–67.5 × 35.0–40.0 µm, surrounded by 3 concentric rings of differentiated cells: innermost ring with ± 6 small, thin-walled, collapsed cells, outer 2 rows with 8–11 and ± 14 cells in each respectively, slightly thicker-walled. *Assimilation tissue* ± 80 µm thick, with air chambers in one storey, containing simple or branched, 2- or 3-celled chlorophyllose filaments, bounding walls hyaline; storage tissue ± 425 µm thick, cells closely packed; oil cells scattered throughout tissues.

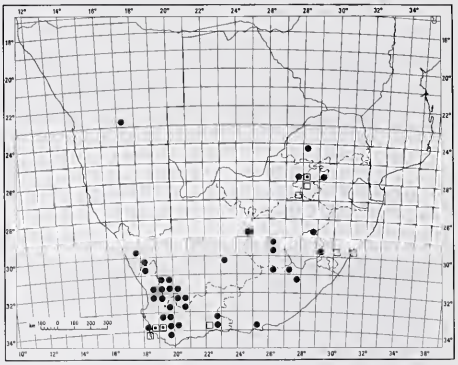
Asexual reproduction absent.

Autoicous or dioicous. *Androecia* terminal on short, ventrolateral branches, sessile discs, encircled above by low, frilly membrane; antheridia embedded, opening into conical protuberances. *Gynoecia* ventrally displaced below apex of thallus. *Involucres* enclosing single capsule, large, shiny black, mussel-like, bivalved, wall 4-layered, opening along narrow, central, vertical fissure. *Pseudoperianth* lacking. *Sporophyte* subsessile with distinct foot and short seta; capsule globose, wall with thickening bands, dehiscence by irregular rupturing. Figure 1. *Spores* (47–)62–77(–95) µm diam., light brown to dark reddish brown, anisopolar; distal face convex, ornamented with network of ridges, enclosing 16 or 17 polygonal areas, 12.5–17.5 µm wide, all covered by fine reticulum, alveoli smaller on sides and crests of primary ridges, larger within enclosures; proximal face flattish, generally with very irregularly contorted, crowded, reticulated ridges, separated by narrow fissures. *Elaters* yellowish brown, not tapering but sometimes branched, bispiral, up to 290 × 12.5 µm. *Chromosome number*: n = 9. Plate 1A, B.

FIGURE. 1.—**Targionia hypophylla**. A–D, thallus: A, dorsal face with tip of involucre protruding at apex; B, with short ventrally innovating branch bearing terminal disc with antheridia; C, ventral face with pouch-like involucre at apex and 2 rows of ventral scales; D, cross section. E, F, air pore: E, from above; F, c/s of dorsal cells and chlorophyllose filaments. G, H, scales: G, margins ± intact; H, fimbriate appendage. I, cells of capsule wall with thickening bands. A, C, D, F, I, *Koekemoer 477a*; B, E, G, *Garside 6674*; H, *Schelpe 4947*. Scale bars: A–D, 1 mm; E, F, I, 50 µm; G, H, 250 µm. Drawings by G. Condy.

Targionia hypophylla is a widespread almost cosmopolitan species, occurring mostly in temperate and seasonally dry areas, on soil in rock crevices, over rock outcrops or under rock overhangs, or as a pioneer on disturbed earth banks, like road cuttings, sometimes in association with *Riccia* spp., *Plagiochasma* spp. and *Mannia capensis* (Steph.) S.W.Arnell.

In the *FSA* area the species has been rather rarely collected in Namibia [from whence Volk (1979) recorded 14 collections], Northern Province, Gauteng, Mpumalanga, Free State, KwaZulu-Natal, Lesotho, Northern, Western and Eastern Cape, but frequently in the winter rainfall areas of the western Northern Cape and Western Cape. Map 1.



MAP 1.—● **Targionia hypophylla**
□ **Lunularia cruciata**

Targionia hypophylla L. var. *fimbriata* Müll.Frib. is not treated as a distinct variety, as was done by Arnell (1963a) and Hässel de Menéndez (1963), because the presence of fimbria along the ventral scale margins is very variable, even in thalli from the same population. Schuster (1992c) also comments that in his opinion, 'the intrapopulational variation in this feature is so great that no taxonomic segregation of the two extremes seems possible'.

When fertile, *T. hypophylla* is recognized by the ventrally displaced capsule contained in a shiny black pouch at the apex of the thallus; sterile plants are distinguished by their dark green, somewhat leathery appearance, the conspicuous white-encircled air pores and reddish to purple-black, obliquely triangular ventral scales with a single appendage.

Although reported by Arnell (1963a), the presence of *T. lorbeeriana* in southern Africa has not been confirmed. It is distinguished from *T. hypophylla* by a strong smell of acid pear drops when fresh; by the cordate shape and light green colour of the thallus; by larger, oval air pores and by having different cell dimensions of the thallus margins at the apex and dorsal epidermis, as well as the scales in the middle of the body and below the appendage; the spore ornamentation is also different and the chromosome count is n = 27.

Vouchers: *Cholnoky 182; S.M. Perold 898; Van Rooy 2345, 2961; Volk 11357.*

SUBORDER **MARCHANTIINEAE**

Marchantiineae *Limpr.*, Lebermoose. In F. Cohn, Kryptogamen-Flora von Schlesien: 225 (1876); Müll.Frib.: 320 (1951–1958); R.M.Schust.: 78 (1992c).

Thalli large to very large, in gregarious patches, not in rosettes; green, glaucous green or dark green. *Branches* simple or once to several times furcate, sometimes with apical or ventrolateral innovations, linear to oblong or obovate, apex entire or notched; groove mostly absent, thallus margins generally acute; flanks sloping obliquely; ventral face medianly keeled. *Scales* ventral, small to large, in 2–4(–6) rows, hyaline or pigmented, shape various, with or without appendages, with or without oil cells.

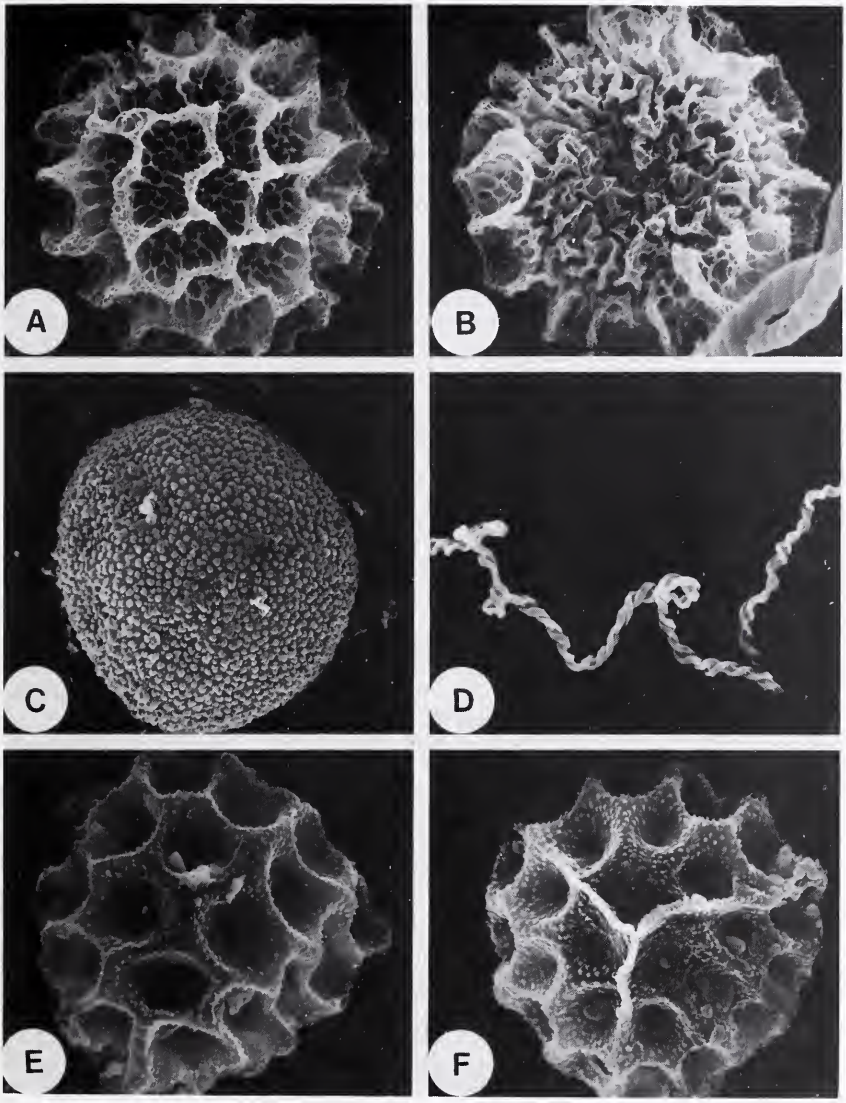


PLATE 1.—Spores and elater. A, B, **Targionia hypophylla**: A, distal face; B, proximal face. C, D, **Lunularia cruciata**: C, spore; D, elater. E, F, **Plagiochasma rupestre** var. **rupestre**: E, distal face; F, proximal face. A, B, *S.M. Perold 2365*; C, D, *S. Strauss s.n.*; E, *G.W. Sim CH1145*; F, *Pole Evans 458*. A, × 660; B, × 690; C, × 2450; D, × 450; E, F, × 580.

Dorsal epidermis generally unistratose, sometimes with bistratose patches; air pores simple, rarely much raised (in *Exormotheca* spp.), sometimes compound (in *Marchantia* spp.). *Assimilation tissue* with one (or more) storey(s) of air chambers, rarely subdivided, empty or containing chlorophyllose filaments, very rarely (in *Dumortiera*) dorsal epidermis and air pores absent; storage tissue occupying ventral $^1/_3$ to almost entire thickness of thallus; rhizoids some smooth, others pegged.

Asexual reproduction rarely by discoid gemmae.

Monoicous or dioicous. *Androecia* mostly sessile, occasionally subsessile, rarely raised on stalk, antheridia sunken. *Gynoecia* almost always in distinct stalked receptacles. *Stalk* short or long, with or without 1 or 2 rhizoid furrows, sometimes with 1 or 2 bands of air chambers. *Involucre* bilabiate or bivalved, rarely tubular, occasionally bell-shaped and wide-mouthed, mostly membranous, often continuous with edges of carpocephalum lobes. *Pseudoperianth* mostly absent, sometimes present, divided into cage-like segments or not, and then bell-shaped. *Sporophytes* with short or long seta; capsule globose, rarely obovoid, never cleistocarpous, opening by a lid and/or longitudinal valves, wall with or without thickening bands. *Spores* reticulate or with conical spines, ridges, bullae or nodules. *Elaters* long and tapering, bi- or trispiral, rarely short and thick, unispiral or ringed. *Chromosome number*: n = 8 or multiples thereof, or 9 or multiples thereof or 10.

Five of the seven families placed here occur in the *FSA* area.

Key to local families of Marchantiineae

1a Air pores of thallus simple, not or slightly raised, sometimes elevated to ± apices of highly inflated air chambers, surrounded by 1–3(4) concentric rings of differentiated cells, rarely stellate; male receptacles sessile, often ill-defined; ventral scales in 2 rows; (crescent-shaped gemma cups only present in *Lunularia cruciata*):
2a Air chambers of thallus highly inflated, basally containing chlorophyllose filaments . . . . . **Exormothecaceae** (p. 72)
2b Air chambers of thallus not or only slightly raised, with or without chlorophyllose filaments:
3a Air chambers of thallus containing chlorophyllose filaments; crescent-shaped gemma cups usually present; sporophytes very rare . . . . . **Lunulariaceae** (p. 21)
3b Air chambers of thallus without chlorophyllose filaments, rarely (in *Mannia*) subdivided by chlorophyllose supplementary partitions ending in short filaments; gemma cups absent; sporophytes commonly produced:
4a Plants rare; air pores of thallus (in southern African species) surrounded by 1 ring of cells, radial walls often thickened and pores stellate; oil bodies absent throughout; capsule wall with annular thickenings . . . . . **Cleveaceae** (p. 67)
4b Plants generally common; air pores of thallus usually surrounded by several concentric rings of cells, rarely by 1 ring, pores rarely stellate; oil bodies present; capsule wall lacking thickenings (except in the very rare *Cryptonitrium oreades* from Lesotho, p. 61) . . . . . **Aytoniaceae** (p. 25)
1b Air pores of thallus compound, surrounded by 6 or 7 superimposed concentric rings of cells or else lacking, together with dorsal epidermis and air chambers (in *Dumortiera hirsuta*); male receptacle raised on long or rarely on very short stalk; ventral scales in 4–6 rows or rarely vestigial; round gemma cups often present in *Marchantia* spp. . . . . **Marchantiaceae** (p. 79)

LUNULARIACEAE

Lunulariaceae *H.Klinggr.*, Die höheren Cryptogamen Preussens: 9 (1858); Müll.Frib.: 364 (1951–1958); R.M.Schust.: 80 (1992c). Subtribe *Lunulariinae* Nees: 9 (1838) (as 'Lunularieae'). Type: *Lunularia* Adans.

Thalli large, in overlying patches; bright green to yellowish green, somewhat glossy. *Branches* pseudodichotomously or irregularly furcate, ribbon-like; groove absent, thallus dorsally flat, margins acute, hyaline; flanks sloping very obliquely; ventral face keeled. *Scales* ventral, in curved parallel rows stretched across flanks on either side of keel, hyaline.

Dorsal epidermis hyaline; air pores conspicuous, surrounded by several concentric rings of differentiated cells. *Assimilation tissue* with one low storey of air chambers, containing erect, chlorophyllose, branched filaments, floored by chlorophyllose cells; storage tissue well developed; oil cells scattered throughout tissues.

Asexual reproduction by gemmae produced in crescent-shaped gemma cups.

Dioicous. *Androecia* with antheridia sunken in thickened, sessile discs, originally terminal, becoming laterally displaced in a deep notch. *Gynoecial receptacles* also originally terminal, eventually laterally situated; when young, small, sessile, weakly 4-lobed, almost entirely sheathed in layers of white scales. *Stalk* elongating when sporophytes nearly ripe, lacking rhizoid furrow. *Involucres* tubular, initially drooping, later spreading outwards, cross-like. *Pseudoperianth* absent. *Sporophytes* 1 or 2(3) per involucre, seta long, foot bulbous, capsules obovoid, becoming exserted, wall lacking thickenings, spores released by shedding tiny distal cap and dehiscing into 4 lanceolate valves. *Spores* small, apolar, spherical or ovoid, densely granulate. *Elaters* long, tapering, bispiral. *Chromosome number*: n = 8, 9.

Sporophytes exceedingly rare in southern Africa. The family contains a single genus, *Lunularia*.

LUNULARIA

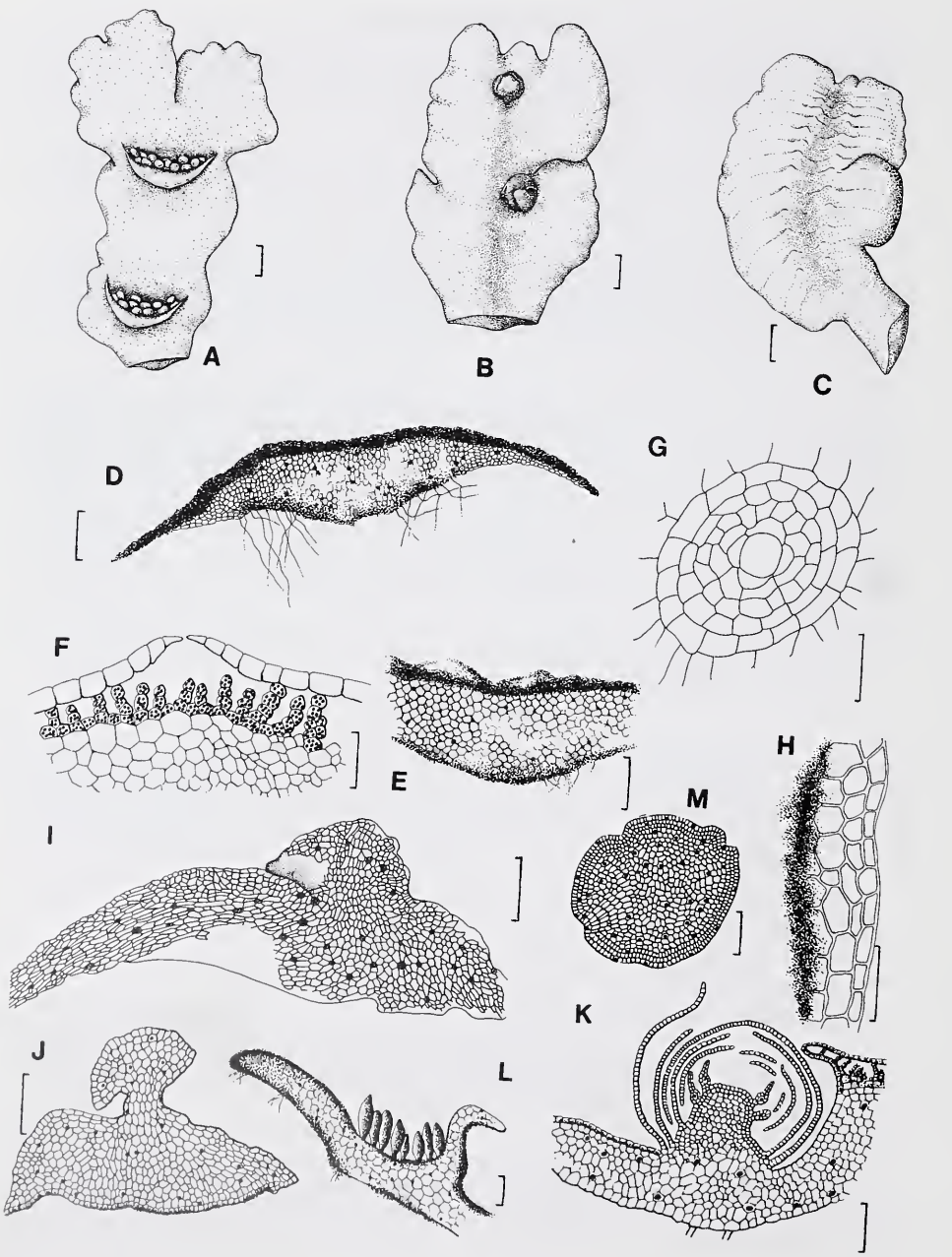
Lunularia *Adans.*, Familles des plantes 2: 15 (1763); P.Micheli: 4 (1729); Nees: 29 (1838); Gottsche et al.: 510 (1844 –1847); Schiffn.: 35 (1893); Steph.: 216 (1899); M.Howe: 59 (1899); Macvicar: 38 (1926); Sim: 123 (1926); Müll.Frib.: 366 (1951–1958); S.W.Arnell: 73 (1963a); Hässel de Menéndez: 125 (1963); R.M.Schust.: 84 (1992c); Perold: 53 (1993a). Type: *Lunularia cruciata* (L.) Dumort. ex Lindb.

Selenia Hill: 120 (1773) nom. illeg.
Dichominum Neck.: 345 (1790) (as subgenus).
Staurophora Willd.: 101 (1809).
Sedgwickia Bowdich: 35 (1825).
Marsilia Kuntze: 837 (1891).

With characters of the family.

Only one species is now recognized although a second species, *L. thaxteri*, was described from South America by Evans & Herzog in Herzog (1938); it is now treated as a subspecies by Schuster (1992c) or as a forma by Hässel de Menéndez (1963).

Lunularia cruciata *(L.) Dumort. ex Lindb.* in Notiser Sällskap pro Fauna et Flora Fennica Förhandlingar 9: 298 (1868); M.Howe: 60 (1899); Macvicar: 40 (1926); Sim: 24 (1926); Müll.Frib.: 366 (1951–1958); S.W.Arnell: 73 (1963a); Hässel de Menéndez: 126 (1963);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E.O.Campb.: 31 (1965); R.M.Schust.: 85 (1992c); Perold: 55 (1993a); Perold: 239 (1995e).

Lunularia vulgaris Micheli: 4 (1729) nom. illegit.

Marchantia cruciata L.: 1137 (1753). Type: Europe.

Staurophora pulchella Willd.: 101 (1809) nom. illegit.

Lunularia vulgaris Raddi: 355 (1818) nom. illegit.

Sedgwickia hemisphaerica Bowdich: 35 (1825). Type: Portugal, Madeira Island, behind Mr Veitch's Quinta, leg. *Bowdich.*

Lunularia michelii Jolis and *L. dillenii* Jolis: 192 (1853). Type: Italy, Micheli: Nova plantarum genera: 4, t.4.

Dichominum cruciatum (L.) Trevis.: 785 (1874). Type: sub *Marchantia.*

Dichominum vulgare (Raddi) Trevis.: 436 (1877). Type: sub *Lunularia.*

Cyathophora cucullata (Mont. & Nees) Kuntze: 834 (1891). Type: sub *Preissia.*

Marsilia cruciata (L.) Kuntze: 837 (1891). Type: Europe.

Lunularia thaxteri A.Evans & Herzog in Herzog: 5 (1938). Type: Chile, Prov. Concepción, Dep. Coronel: Concepción, leg. *R. Thaxter* (1905).

Thalli moderately large, in crowded patches; glossy, turning dull with age, bright green to yellowish green; faintly areolate, air pores whitish, margins hyaline, irregularly undulate, somewhat scalloped; when dry, rather leathery. *Branches* repeatedly pseudodichotomously or irregularly furcate with apical or ventrolateral innovations, ribbon-like, 40–55 mm long, 5(–10) mm wide, 650(–1000) µm thick medianly, in section ± 7–10 times wider than thick, apex notched or sinusoidal; groove absent, thallus dorsally flat, margins acute; flanks sloping obliquely, to becoming slightly recurved; ventral face medianly keeled. *Scales* in 2 well-spaced rows, stretched across ventral face of wings, 1000–1375 µm long, up to 4250 µm wide across base, broadly and shallowly crescentic, hyaline, apically constricted where joined with rounded appendage, ± 400 × 250–600 µm, margin entire or crenate, ± 20 oil cells scattered throughout scale and appendage.

Dorsal epidermal cells unistratose, hyaline, 35–50 × 20–30 µm, thin- to thick-walled or only thickened at corners; air pores slightly raised, simple, oval, 17–25 × 12–20 µm, surrounded by 3 or 4 concentric rings of differentiated cells, innermost row often with 4 cells, outer rings with 10–15 cells in each. *Assimilation tissue* ± 90 µm thick, air chambers in one storey, containing 3- or 4-celled, branched, chlorophyllose filaments, bounding walls hyaline, unistratose, floor densely chlorophyllose; storage tissue with ± 15(–20) rows of cells medianly, gradually decreasing in wings; some cells with pitted walls; oil cells scattered throughout tissues.

Asexual reproduction by gemmae in crescent-shaped cupules, ± 3 mm wide, with crenate to entire ridge on proximal side.

Dioicous. *Androecia* on alternate sides of thallus, slightly raised, ovate, flattish discs, encircled by membranous sheath with crenate edge, containing numerous sunken antheridia. *Gynoecial receptacles* lateral on alternate sides of thallus, when young small, sessile, domed, weakly 4-lobed, bearing 4 groups of archegonia in radiating rows and below attached to thallus, sheathed in several layers of white scales, upper edges irregularly fringed with filiform cellular appendages. *Stalk* eventually elongating and up to ± 34 mm long, pale green to whitish, tender, ± 950 µm diam., lacking rhizoid furrow and air chambers, externally shaggy with scattered, white, thread-like filaments. *Involucres* tubular, rather delicate, enclosing sporophytes carried to underside of receptacle by expansion of central dome, initially drooping, later almost horizontally spreading outwards in a cross. *Pseudoperianth* absent. *Sporophyte* with subspherical foot and

FIGURE 2.—**Lunularia cruciata**. A–D, thallus: A, dorsal face with gemma cups; B, female with young archegoniophores; C, ventral face with young lateral branch; D, cross section. E, c/s of midrib region, much enlarged; F, G, air pore: F, c/s dorsal cells and air chamber; G, from above. H, margin of thallus with hyaline cells, seen from above. I, J, scales: I, older; J, younger. K, l/s through young archegoniophore; L, l/s through gemma cup; M, gemma. A, D–H, J, L, M, *S.M. Perold 2821*; B, C, *S.M. Perold 1996*. Scale bars: A–C, 2 mm; D, E, K, L, 1 mm; I, J, 500 µm; F, M, 100 µm; G, H, 50 µm. Drawings by A. Pienaar. Figure 2K partly after Benson-Evans & Hughes (1954: fig. 4).

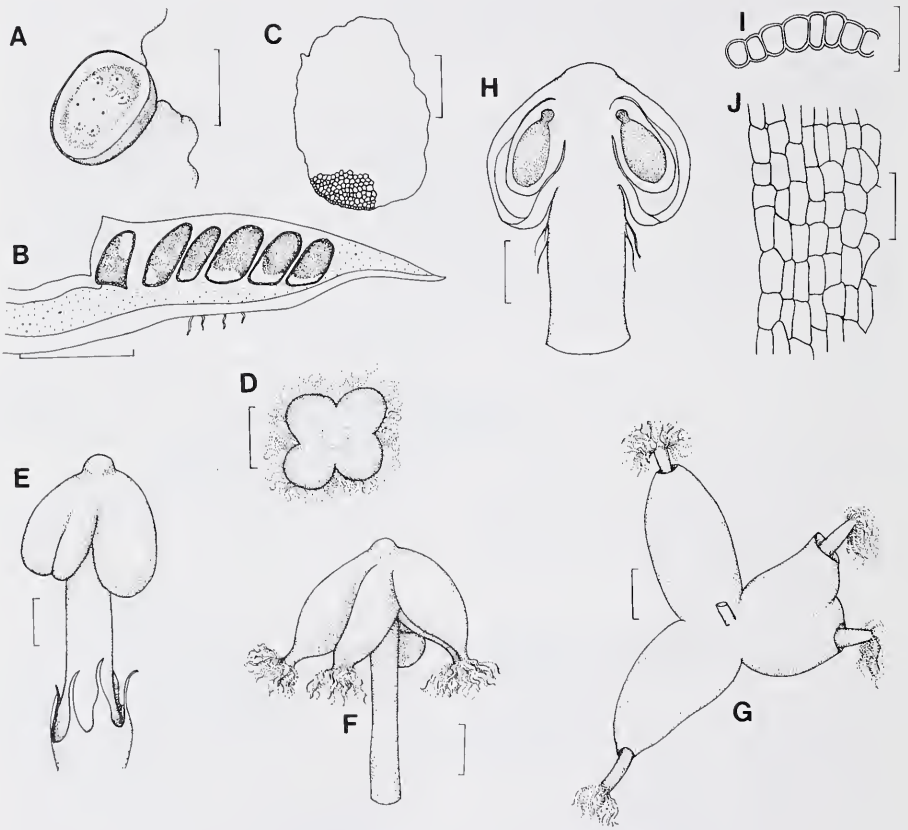


FIGURE 3.—**Lunularia cruciata**. A, B, androecial disc: A, from above; B, longitudinal section. C, c/s of stalk. D–G, gynoecial receptacle: D, young receptacle from above; E, older receptacle from side; F, mature receptacle from side; G, mature receptacle from below. H, l/s through gynoecial receptacle and upper part of stalk; I, J, capsule wall: I, cross section; J, portion. A–J, *S. Strauss 64*. Scale bars: A, 2 mm; B, D–H, 1 mm; C, 100 µm; I, J, 50 µm. Drawings by M. Steyn.

rapidly elongating seta, supporting obovoid capsule (1–3), exserted beyond involucre, capsule wall unistratose, lacking thickenings, dehiscence by shedding tiny distal bistratose cap and lanceolate valves folding back. Figures 2 & 3. *Spores* (12.5–)15.0–22.5 µm diam., apolar, triradiate mark absent, mostly spherical or ovoid, light brown, wall thin, densely granulate. *Elaters* light brown, bispiral, long-tapering at both ends, 320–350 µm long, in centre 5–6 µm wide, at tips 2.5 µm. Plate 1C, D. *Chromosome number*: n = 8 (Heitz 1927); n = 9 = 8 + x/y^2 (Lorbeer 1934); n = 9 (Bornefeld 1987).

A widespread species, *L. cruciata* is known from North and South America, the Mediterranean region, Asia, central and southern Africa, Australia and New Zealand. In the *FSA* area

many collections are from nurseries or city gardens, so it would appear that *L. cruciata* may have been introduced into southern Africa. It is not frequently found here, most collections being from the southern Western Cape, a few from Gauteng and some from KwaZulu-Natal. Map 1.

Lunularia cruciata is easily recognized because of the crescent-shaped gemma cupules that are always present.

Vouchers: *Perold 645; Sim 1279, 1280; Stirton 9415.*

AYTONIACEAE

Aytoniaceae *Cavers* in New Phytologist 10: 42 (1911). Type: *Aytonia* G.Forst. (= *Plagiochasma* Lehm. & Lindenb.).

Grimaldieae Rchb. ex Rabenh.: 6 (1848).

Grimaldiaceae (Rchb. ex Rabenh.) Müll.Frib.: 220 (1940b).

Thalli smallish to large, in dense or loose patches; dull, glaucous green and waxy to velvety, or shiny, lime-green to bright green, firm or somewhat spongy. *Branches* simple to pseudodichotomously or variously furcate, sometimes articulate with ventrolateral or apical innovations, lingulate, apex notched or entire, tips of apical scales often recurved over edge; groove absent, thallus dorsally flat or slightly concave, margins acute, mostly purple or black, scalloped or sometimes irregularly crenate; flanks sloping obliquely, sometimes black and shiny; ventral face medianly keeled or rounded. *Scales* ventral, in 2 rows, one on either side of keel, generally large, body ovate to obliquely triangular or transversely rectangular, apically with lanceolate, ovate, orbicular or filiform appendages, rarely constricted at base, mostly purple, reddish or black, scattered oil cells present throughout.

Dorsal epidermis mostly lacking chloroplasts, thin- or thick-walled, with or without trigones; air pores simple, sometimes stellate, very small and inconspicuous to large and slightly raised, surrounded by up to 3 concentric rings of (4)5–8 cells in each. *Assimilation tissue* with air chambers almost always empty, single or storeyed, mostly shallow, rarely tall; storage tissue well developed, occupying ventral $^1/_2$ or more of thallus.

Asexual reproduction absent.

Monoicous, autoicous or paroicous, rarely dioicous. *Androecia* on main or on reduced ventrolateral branches, with antheridia sunken into thallus dorsally, in clusters or rows or in sessile discs or cushions, base sometimes encircled by short paleae. *Gynoecial receptacle* raised on stalk, sometimes arising terminally at apical notch and mostly inhibiting further growth of branch, rarely ventrolaterally, or more usually, dorsally at intervals along length of main branch; carpocephala domed, disciform or variously lobed, with compound air pores. *Stalk* short or long, with or without rhizoid furrow, with or without air chambers, at base and summit with or without paleae. *Involucre* swollen and bilabiate, or membranous and bell-shaped. *Pseudoperianth* sometimes present, with cage-like segments. *Sporophyte* with short seta, foot rounded, capsule globose, wall mostly lacking thickenings, dehiscence by shedding small, well-defined apical lid or by an irregularly decaying, usually bistratose cap. *Spores* alveolate, with thick or thin walls, and then with subsidiary alveoli, or with swollen bullae, or ridges, always winged. *Elaters* tapering, bi- or trispiral. *Chromosome number*: n = 9, 10, 18.

Two subfamilies are recognized, Aytonioideae and Reboulioideae Grolle (p. 43).

A key to the two subfamilies is not included, but a key to the local genera and two of the species of the Aytoniaceae is given, as *Plagiochasma* is the only local genus referred to the Aytonioideae.

Subfamily **AYTONIOIDEAE**

Thalli medium-sized to large, in crowded, extensive mats; dull glaucous green or purplish, then waxy to velvety, otherwise bright green to yellowish green, firm and somewhat leathery. *Branches* simple or pseudodichotomously to variously furcate, with ventrolateral or apical innovations, sometimes articulate, lingulate, apex mostly notched with scale appendages recurved over edge; groove absent, thallus dorsally flat, margins thin, attenuate, narrowly purple, scalloped; flanks sloping obliquely to very obliquely, purple or dark red; ventral face medianly keeled. *Scales* ventral, in 2 rows, one on either side of keel, body broadly ovate, apically with linear-lanceolate or ovate to orbicular appendage, sometimes constricted or folded at base, purple-red to violet, scattered oil cells present throughout.

Dorsal epidermis mostly lacking chloroplasts, cells thin- or thick-walled, with or without trigones, roughened or smooth, with or without waxy granular deposit externally; air pores simple, sometimes stellate, minute and inconspicuous or larger and slightly raised, surrounded by 1 or 2(3) concentric rings of (4)5–8 cells in each, radial walls often forming ± continuous lines, sometimes thickened. *Assimilation tissue* with small, empty air chambers, in several irregular storeys, cells in bounding walls chlorophyllose; storage tissue with closely packed cells.

Monoicous, autoicous or paroicous. *Androecia* away from branch apex, with antheridia sunken in tumid, sessile, crescentic to broadly U- or V-shaped, dorsal cushions, base encircled by short paleae. *Gynoecial receptacle(s)* single to several along main branch away fron apex, usually with tuft of slender paleae around base, eventually transferred to apex of stalk; carpocephalum with top slightly raised or nearly flat or ± depressed, 3- or 4-sided. *Stalk* very short to long, lacking rhizoid furrow. *Involucre* bilabiate, with vertically, slightly overlapping, somewhat swollen lips. *Pseudoperianth* absent. *Sporophyte* with short seta, capsule globose, wall thickenings lacking, dehiscing by irregularly decaying lid. *Spores* triangular-globular, winged, both faces coarsely alveolate. *Elaters* long, tapering, bi- or trispiral. *Chromosome number*: n = 9, 18.

Only the genus *Plagiochasma* is classified in the subfamily Aytonioideae.

Key to local genera and two species of Aytoniaceae

1a Thalli often large, firm and leathery; air pores minute to large, surrounded by 1 or 2(3) concentric rings of cells; carpocephala dorsal on thallus, away from apex; stalk sometimes very short, always lacking rhizoid furrow ..... *Plagiochasma*

1b Thalli generally smaller, often thin and somewhat delicate; air pores medium-sized, surrounded by 2 or 3 concentric rings of cells; carpocephala on stalk arising from apical notch of thallus or at bifurcation of branches, very rarely ventrolaterally, with 1 rhizoid furrow:

2a Air chambers of thallus much subdivided by supplementary chlorophyllose partitions ..... *Mannia capensis* (p. 65)

2b Air chambers of thallus empty, not subdivided, lacking chlorophyllose filaments, cells in bounding walls with chloroplasts:

3a Carpocephala always with basket-like pseudoperianths, divided into lanceolate segments; capsule wall lacking thickenings; stalk arising from apex of thallus or at bifurcation of branches ..... *Asterella* (p. 43)

3b Carpocephala lacking pseudoperianths; capsule wall with thickenings; stalk arising ventrolaterally ..... *Cryptomitrium oreades* (p. 61)

PLAGIOCHASMA

Plagiochasma *Lehm. & Lindenb.* in Lehm., Novarum et minus cognitarum stirpium pugillus quartus: 13 (1832); Nees: 33, 40 (1838); Gottsche et al.: 511 (1844–1847); Steph.: 775 (1898); A.Evans: 262 (1915); Sim: 16 (1926); Müll.Frib.: 331 (1951–1958); Hässel de Menéndez: 83 (1963); S.W.Arnell: 65 (1963a); Bischl.: 71 (1977); R.M.Schust.: 264 (1992c); Perold: 13, 14 (1995a). Type: *P. cordatum* Lehm. & Lindenb.

Aytonia J.R.Forst. & G.Forst. in G.Forst.: 147 (1776); Lindb.: 291 (1868); Schiffn.: 30 (1893). Type: *A. rupestris*.

Aitonia J.R. Forst. & G.Forst. in G.Forst.: 46, 73 (1787) orth. var. [not of Thunb.: 166 (1776)].

Rupinia L.f.: 69 (1781) nom. illegit.

Ruppinia L.f.: 204 (1783) orth. var. Type species *R. rupestris*.

Antrocephalus Lehm.: 682 (1838). Type: *A. nepalensis*.

Teldea Mont. ex Webb & Berthel.: 59 (1840) nom. illegit. Type: *T. elastica*.

With characters of the subfamily Aytonioideae (p. 26).

Two subgenera, namely *Micropylum* and *Plagiochasma* have been instituted by Bischler (1977), based mainly on the compactness and colour of the thalli, the structure of the dorsal air pores and on the shape, size and margins of the scale appendages.

Key to subgenera and species of *Plagiochasma*

1a Thalli glaucous to greyish green, dull and velvety, dorsally granular, with numerous air pores, tiny and obscure, surrounded by a single ring of 4–6 cells but never by an inner hyaline ring of collapsed cells; ventral scales with 1, 2(3) narrow appendages, hardly or not constricted at base, with margins not differentiated and lacking teeth and/or papillae . . . subgenus **Micropylum** Bischl.):

2a Ventral scales reddish pink to purple, rarely more than 2000 µm long, including pink, purple or hyaline appendage(s) (1 or 2), narrowly to broadly triangular, up to 900 µm long, apically shortly pointed, with 1 or 2 (rarely 3) cells in series, thin-walled and quadrate or rectangular; spores up to 92.5 µm diam. ..... 1a. *P. rupestre* var. *rupestre*

2b Ventral scales dark red or purple, large, up to 3000 µm long, including hyaline appendage(s) (1–3), narrowly triangular, up to 1500 µm long, apically with a long point, with 3–5 elongated cells in series, thick-walled; spores more than 92.5 µm diam. ..... 1b. *P. rupestre* var. *volkii*

1b Thalli green to yellow-green, shiny and dorsally smooth with fewer air pores, large and quite conspicuous, raised and surrounded by an inner hyaline ring of collapsed cells and then by 2 or 3 concentric rings of 5-8 cells in each; ventral scales with 1-3 appendages, wide or narrow, often constricted or folded at base with margins differentiated into smaller cells, teeth and/or papillae . . . subgenus **Plagiochasma**, p. 33):

3a Scales mostly with 1 appendage, sometimes with two, round or oval or broadly triangular, widest across middle, constricted or folded at base; along margins 1 or 2 rows of regular, smaller cells or alternating with them, cells of usual size, lacking teeth; elaters with evenly thickened spirals:

4a Thalli robust; carpocephalum on short, thick stalk; scale appendage single, rarely double, rounded, large, hyaline above, red or pink below, markedly constricted at base; margins smooth, with small cells here and there alternating with somewhat larger ones ..... 2. *P. appendiculatum*

4b Thalli medium-sized; small carpocephalum on thin, short or long stalk; scale appendage single or double, oval or broadly triangular, pink or violet, slightly constricted or folded or horizontally pleated at base; margins with 1 or 2 rows of smaller, regular cells, occasionally with papillae ..... 3. *P. microcephalum* var. *microcephalum*

3b Scales with 1, 2 (or 3) appendages, narrowly triangular, slightly constricted to folded at base or evenly tapered; sometimes toothed along margins; elaters with spirals interrupted or evenly thickened:

5a Thalli robust but carpocephala relatively small; dorsal air pores of thalli surrounded by hyaline ring and 3 concentric rings of cells; scale appendages red, not acuminate, slightly constricted or folded at base; elaters with spirals often interrupted ..... 4. *P. eximium*

5b Thalli less robust and carpocephala of usual size; air pores surrounded by hyaline ring and 2 concentric rings of cells; scale appendages purple, acuminate, lanceolate, not constricted at base; elaters with spirals evenly thickened ..... 5. *P. beccarianum*

Subgenus **Micropylum** *Bischl.*

Thalli glaucous-green, dull, velvety, firm, covered with water-repellent, granular deposit. *Scales* with acuminate appendages, margins undifferentiated, lacking teeth and papillae.

Dorsal epidermis with air pores numerous, tiny and inconspicuous, lacking surrounding small, inner hyaline ring of collapsed cells.

Only *Plagiochasma rupestre* with two varieties is placed here.

1. **Plagiochasma rupestre** *(J.R.Forst. & G.Forst.) Steph.* in Bulletin de l'Herbier Boissier 6: 783 (1898). Müll.Frib.: 332 (1951–1958); A.Evans: 277 (1915); Sim: 18 (1926); Hässel de Menéndez: 84 (1963); S.W.Arnell: 67 (1963a); Bischl.: 264 (1978); O.H.Volk: 237 (1979); Bischl. & Sérgio: 173 (1984); R.M. Schust.: 292 (1992c); Perold: 14 (1995a). Type: Madeira, Funchal, Quinta do Bom Sucesso, *Sérgio & Nóbrega 3873* [LISU, neo.! selected by Bischl. & Sérgio (1984); PC, BM, G, MADJ, iso.].

Aytonia rupestris J.R.Forst. & G.Forst.: 147 (1776); Lindb.: 291 (1868); Schiffn.: 30 (1893).

P. dschallanum Steph.: 778 (1898). Type: Tanzania, Kilimandscharo, ad lacum Dschalla, leg. *Holst*.

P. tenue Steph.: 779 (1898). Types: S. Africa, Transvaal, leg. *MacLea, Wilms*; Tanzania, Usambara, leg. *Holst*; Angola, leg. *Welwitsch*.

P. algericum Steph.: 780 (1898). Type: Algeria, leg. *Trabut*.

P. muricatum Steph.: 310 (1901a) nom. illegit.

P. abyssinicum Gola: 62 (1914). Type: Ethiopia, Erythraea, in regione Hamasen prope Asmara n. 132, 24. IV. 1909, leg. *Chiovenda*.

P. capense Sim: 17 (1926). Type: S. Africa, Herschel, Cape Province, 5000 ft, leg. *Hepburn*.

The list of synonyms includes only African plants and was taken from Bischler (1978).

Thalli medium-sized to large, in gregarious patches; firm, leathery, glaucous to greyish green, dull, surface ± water-repellent, hardly areolate, air pores almost imperceptible, margins purple, scalloped and undulate; when dry, margins incurved. *Branches* simple or once, rarely twice furcate or articulate with apical or ventrolateral innovations, oblong to ligulate, 8–25 mm long, (3–)4–6 mm wide, 375–650 µm thick medianly, in section 9 or 10 times wider than thick, apex notched, acute scale appendages recurved over edge; groove absent, thallus dorsally flat, margins acute, thin; flanks sloping obliquely; ventral face medianly keeled, green. *Scales* in 2 ventral rows, asymmetric, obtusely triangular, reddish pink or purple, sometimes partly hyaline, body 600–1500 µm long, margins lacking teeth and papillae, base flatly arched, 900–1250 µm wide, narrowed above without constriction to acuminate or ovate-lanceolate appendage, 900–1450 µm long, oil cells scattered throughout.

Dorsal epidermal cells unistratose, hyaline, polygonal, 25–47 × 20–37 µm, thin-walled, thickened at corners, externally covered with granules; air pores not raised, simple, tiny, appearing plugged, numerous, surrounded by one ring of 3–5 small cells, radial walls often thickened, lacking small inner hyaline ring of collapsed cells. *Assimilation tissue* 175–220 µm thick, air chambers empty, in several storeys, cells in bounding walls containing chloroplasts; storage tissue well developed; oil cells scattered throughout tissues.

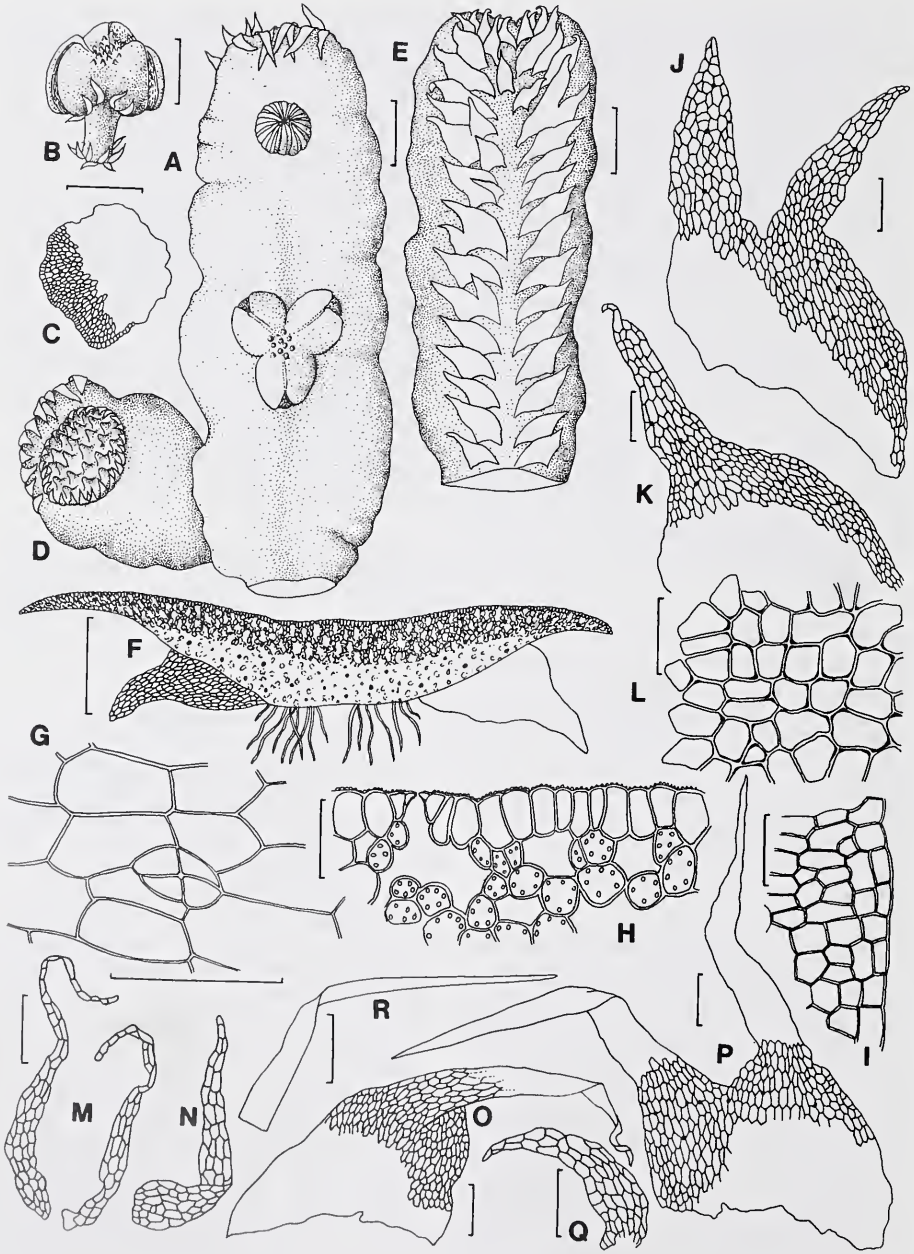
Monoicous. *Androecia* medianly on leading branch or on apical or ventrolateral innovations, sessile cushions, round or crescentic, base encircled by tapering, purple paleae, antheridia sunken, opening above into raised conical papillae. *Gynoecial receptacles* in acropetal sequence medianly along main branch, or paired on furcate branches, enclosed by tall tuft of tapering, purple-red paleae, most of them later carried to top of stalk; carpocephala 2–3 mm wide, on top initially slightly raised, later becoming depressed, air pores compound, below with 1–3(–5) lobes. *Stalk* at maturity usually remaining very short, only rarely up to 6 mm long, ± 640 µm wide, lacking rhizoid furrow and air chambers. *Involucre* bilabiate, lips vertical and swollen, slightly overlapping. *Sporophyte* with short seta, capsule ± globose, wall unistratose, lacking thickening bands, dehiscing by decaying lid. *Spores* 80–105 µm diam., triangular-globular, polar, light brown to yellow brown; wing ± 12 µm wide, margin undulate, crenulate; ornamentation similar on 2 faces; distal face with ± 4 alveoli across, ± 20 µm wide, walls wide and studded with granules; proximal face with narrow triradiate mark, each of 3 facets with 6–9 alveoli, up to 25 µm wide, walls raised and wide, studded with granules. *Elaters* light brown to yellow brown, 175–235 µm long, 12.5 µm wide in middle, tapering toward ends, ± 5 µm wide, bispiral. *Chromosome number*: n = 9, 18 (Bischler 1978).

Two varieties are recognized: *P. rupestre* var. *rupestre* and *P. rupestre* var. *volkii*. They are distinguished by the longer, acuminate, hyaline appendages of the ventral scales and slightly larger spore dimensions of var. *volkii*.

1a. **P. rupestre** var. **rupestre**

Ventral scales obliquely lunate, rarely longer than 2000 µm, 1050 µm wide across base; 1 or 2 narrowly to broadly triangular appendages up to 900 µm long, 1.7–2.7 times longer than wide, apically acuminate with uniseriate 1 or 2(3) terminal cells, margins entire. Male paleae around base of androecium 550–580 µm long, 110–180 µm wide at base, tapering to narrow tip, with 1–3 cells in series; female paleae 1030–1375 µm long, 150–220 µm wide at base, tapering to narrow tip, with up to 4 cells in series. Figure 4A–N. *Spores* 80.0–92.5 µm diam. Plate 1E, F.

The typical variety is subcosmopolitan and widely distributed, especially in xerothermic regions. In the *FSA* area *P. rupestre* var. *rupestre* is quite common and frequently collected in rocky crevices, moist ledges, under boulders, or at seepages, on calcareous substrates or on soil overlying cave sandstone or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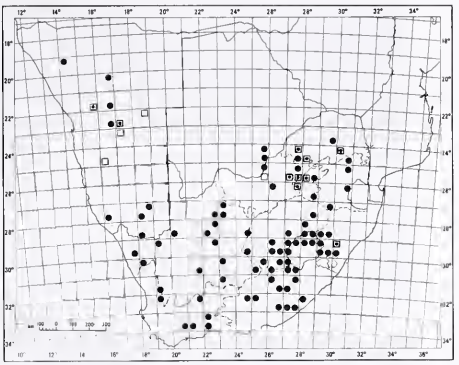
dolomite. It sometimes grows together with *Targionia hypophylla* and *Riccia* spp. It is known from Namibia, Botswana, Northern Province, North-West, Gauteng, Mpumalanga, Free State, KwaZulu-Natal, Lesotho, Northern, Western, and Eastern Cape. Map 2.

Plagiochasma rupestre var. *rupestre* is easily identified by its dull, velvety and glaucous thalli with simple, very inconspicuous pores and by its reddish pink or purple scales, with ovate-lanceolate or acuminate appendages and entire margins.

Vouchers: *Brusse 4123; Condy 45; Germishuizen 5393; Perold 2167; Van Rooy 2726.*



MAP 2.—● **Plagiochasma rupestre** var. **rupestre**
□ **P. rupestre** var. **volkii**

1b. **P. rupestre** var. **volkii** *Bischl.* Type: Namibia, Neudamm bei Windhoek, *Volk 948* (JE).

Ventral scales larger, up to 3000 × 1350 µm, more conspicuous than those of typical variety, especially 2 or 3 hyaline or white appendages, which are narrowly triangular, 1370–1450 µm long and 4 or 5 times longer than wide; apex rather fragile, 3–5 elongated cells in series, walls thickened. Male paleae ± 600 µm long, 150 µm wide at base, tapering to narrow tip with 4 cells in series; female paleae up to 1500 µm long, 100–150 µm wide at base, tapering to a narrow tip with 3 or 4 cells in series. Figure 4O–R. *Spores* 92.5–105.0 µm diam., slightly larger but very similar in appearance to those of typical variety. Plate 2A, B.

This variety is quite rarely collected in southern Africa, but both varieties grow together fairly frequently. In the *FSA* area *P. rupestre* var. *volkii* is known from Namibia, Northern Province, North-West, Gauteng and KwaZulu-Natal. Map 2.

Bischler (1978) had also studied plants from the Western Cape, Free State, Lesotho and Zimbabwe; it therefore occurs throughout most of southern Africa. Schuster (1992c) states that *P. rupestre* var. *volkii* also occurs in Peru and Argentina and it is accordingly not endemic to southern Africa.

In *P. rupestre* var. *volkii* the thallus is generally somewhat narrower than in the typical variety, but otherwise it is very similar in colour, appearance and composition. The very long, decolorate scale appendages are conspicuous, however, and make it easily separable.

Vouchers: *H. Anderson CH13512; Glen 1644; Mogg 37590; Perold 2586; Volk 00948.*

FIGURE 4.—A–N, **Plagiochasma rupestre** var. **rupestre**: A, E, F, thallus: A, dorsal face with archegoniophore and carpocephalum; E, ventral face; F, cross section. B, carpocephalum, side view; C, c/s of stalk; D, androecium at apex of ventrolateral branch. G, H, air pore: G, dorsal cells from above; H, c/s of dorsal cells and air chambers. I, margin of thallus. J, K, scales: J, with 2 appendages; K, with 1 appendage. L, cells in capsule wall; M, female paleae; N, male palea. O–R, **Plagiochasma rupestre** var. **volkii**: O, P, scales: O, with 1 appendage; P, with 2 appendages. Q, male palea; R, female palea. A, B, D, E, L, N, *Heilgendorff CH13611*; *C. Manning CH13590*; F, H, *H. Anderson 1230*; G, I–K, M, *S.M. Perold 3058*; O–R, *Mogg 37590*. Scale bars: A, B, D, E, 2 mm; F, 1 mm; C, J, K, M–R, 250 µm; G–I, L, 50 µm. Drawings by G. Condy.

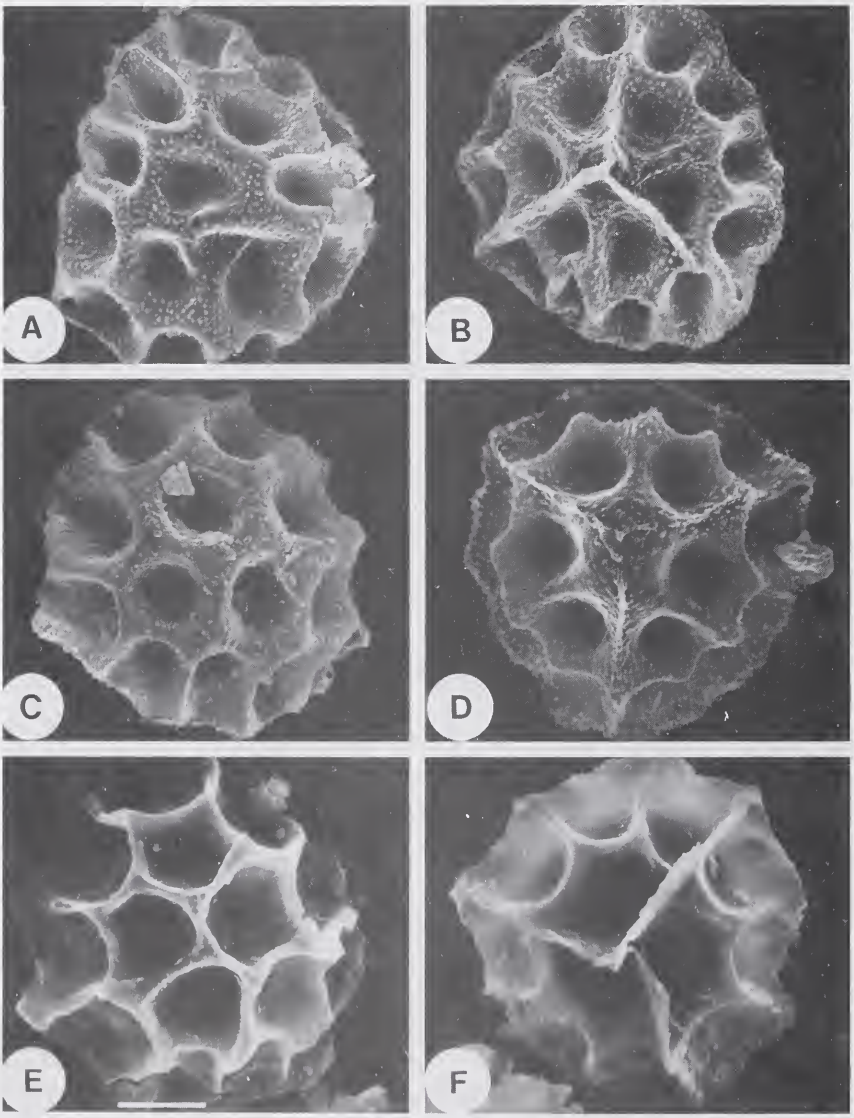


PLATE 2.—Spores. A, B, **Plagiochasma rupestre** var. **volkii**: A, distal face; B, proximal face. C, D, **P. appendiculatum**: C, distal face; D, proximal face. E, F, **P. microcephalum** var. **microcephalum**: E, distal face; F, proximal face. A, B, *Mogg 37590*; C, *Hook 8204*; D, *Perold & Koekemoer 3135*; E, F, *Holst 362*. A, B, × 520; C, × 630; D, × 700; E, × 770; F, × 750.

Subgenus **Plagiochasma**

Thalli green or yellow-green, less compact than in subgenus *Micropylum*, dorsally ± smooth, faintly areolate. *Scales* and appendage margins differentiated with smaller cells, teeth or papillae.

Dorsal epidermis with air pores quite large, surrounded by collapsed hyaline ring and 2 or 3 concentric rings of cells, radial walls generally forming ± continuous radiating lines, sometimes thickened.

The other *Plagiochasma* species are assigned here.

2. **Plagiochasma appendiculatum** *Lehm. & Lindenb.* in Lehm., Novarum et minus cognitarum stirpium pugillus quartus: 14 (1832); Gottsche et al.: 517 (1844–1847); Steph.: 782 (1898); Kashyap: 318 (1914); Bischl.: 228 (1978); Perold: 19 (1995a). Type: Nepal, Punjab, Dehra Doon, *Wallich*.

P. fischerianum (Steph.) Steph.: 786 (1898) (*P. fischeri*). Type: Kenya, Ligaijo, *Fischer 692* [as *Aitonia fischeriana* Steph.: 301 (1895)].

P. appendiculatum Lehm. & Lindenb. var. *erythraeum* Gola: 62 (1914). Type: Ethiopia, Eritrea, Hamasen, sul Monte Bizen nella valle Nabaret a Mai Electi, *Ragazzi 253*.

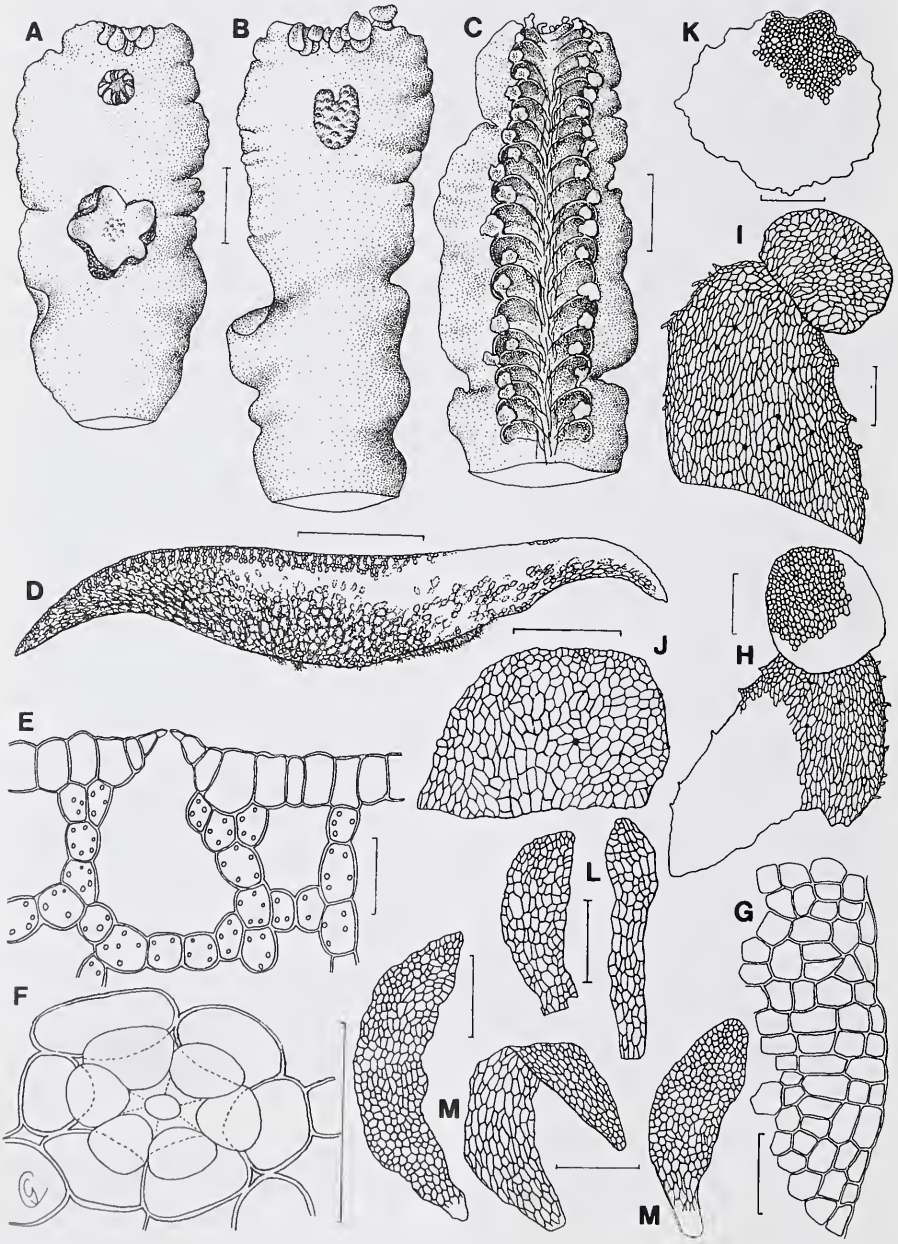
For a complete synonymy see Bischl. (1978).

Thalli robust, in gregarious patches; bright green, shiny, areolate, air pores small, faintly visible, margins purple, scalloped and slightly undulate; when dry, margins tightly incurved. *Branches* simple or once, sometimes twice furcate, rarely articulate with apical or ventrolateral innovations, broadly lingulate, 10–20 mm long, 5–8 mm wide, 750–925 µm thick medianly, in section 6–8 times wider than thick, apex notched with large, orbicular appendages recurved over edge; groove absent, thallus margins acute, thin; flanks sloping very obliquely; ventral face medianly keeled, green. *Scales* in 2 ventral rows, body up to 1250 µm long, margins occasionally with projecting papillae, base flatly arched, ± 1100 µm wide, gradually narrowed above, deeply constricted and folded where joined with large, mostly single, orbicular, often decolorate appendage, 750 µm long, 550 µm across widest part, margins smooth with 1 or 2 rows of small rectangular cells, alternating with somewhat larger cells, some smaller oil cells scattered throughout scale.

Dorsal epidermal cells unistratose, hyaline, thin-walled, thickened at corners, polygonal, 22.5–42.5 × 15.0–27.5 µm, smooth externally; air pores slightly raised, simple, 7.5–10.0 µm wide, surrounded by innermost ring of tiny, collapsed cells, then by 2 (or 3 partly) concentric rings of 5 or 6 larger cells in each, radial walls not thickened. *Assimilation tissue* 375–500 µm thick, air chambers empty, in several storeys, bounding walls chlorophyllose; storage tissue well developed; oil cells scattered throughout tissues.

Monoicous, but male and female receptacles often on separate plants. *Androecia* medianly on leading branch near apex, sessile cushions, oval, horseshoe- or heart-shaped, base encircled by blunt, hyaline or partly purple paleae, 550–580 × 130–180 µm. *Gynoecial receptacles* medianly along main branch, single or several in acropetal sequence, initially enclosed by arching, hyaline paleae, ± 850 × 120 µm; carpocephala 2 × 2 mm when 4 lobes present. *Stalk* 1.25–2.00 mm long, ± 750 µm wide. *Involucre* bilabiate. Sphorophyte with *capsule* ± globose. Figure 5. *Spores* 75–85 µm diam., triangular-globular, polar, light brown, translucent; wing ± 10 µm wide, porate at corners, margin undulate, finely crenulate; ornamentation similar on 2 faces; distal face with 5 alveoli across, ± 22 µm wide, walls finely granular; proximal face with very narrow triradiate mark, each of 3 facets with 6 or 7 alveoli, walls wide and studded with granules. *Elaters* pale brown, 187–240 µm long, 10 µm wide in middle, tapering toward ends, 5 µm wide, bi- or trispiral. *Chromosome number*: n = 9 (Bischler 1978). Plate 2C, D.

Plagiochasma appendiculatum is chiefly an Asiatic species and has been reported from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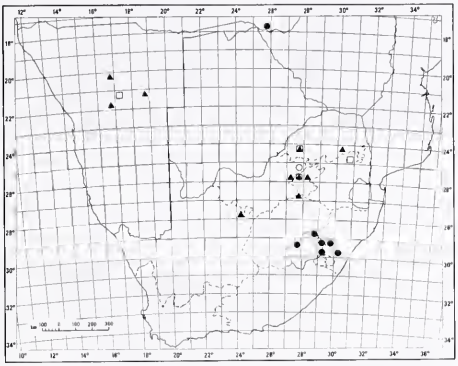
Afghanistan, Burma, Celebes, China, Taiwan [Formosa], India, Kashmir, Nepal, Pakistan, Philippines, Sikkim and Vietnam. It is also known from the Arabian Peninsula, Socotra and Yemen, and in Africa from Ethiopia, Kenya, Tanzania and Zimbabwe. In southern Africa the species is very rare and has been collected at only two localities in the North-West. Map 3.

Generally *P. appendiculatum* is a large plant and easily recognized by its mostly single, very rarely double, large, orbicular scale appendages.

Vouchers: *Bottomley CH268; Perold 854; Perold & Koekemoer 3135.*



MAP 3.— ○ **Plagiochasma appendiculatum**
▲ **P. microcephalum** var. **microcephalum**
● **P. eximium**
□ **P. beccarianum**

3. **Plagiochasma microcephalum** *(Steph.) Steph.* var. **microcephalum** in Bulletin de l'Herbier Boissier 6: 781 (1898); Bischl.: 237 (1978); O.H.Volk: 240 (1979); Perold: 21 (1995a).

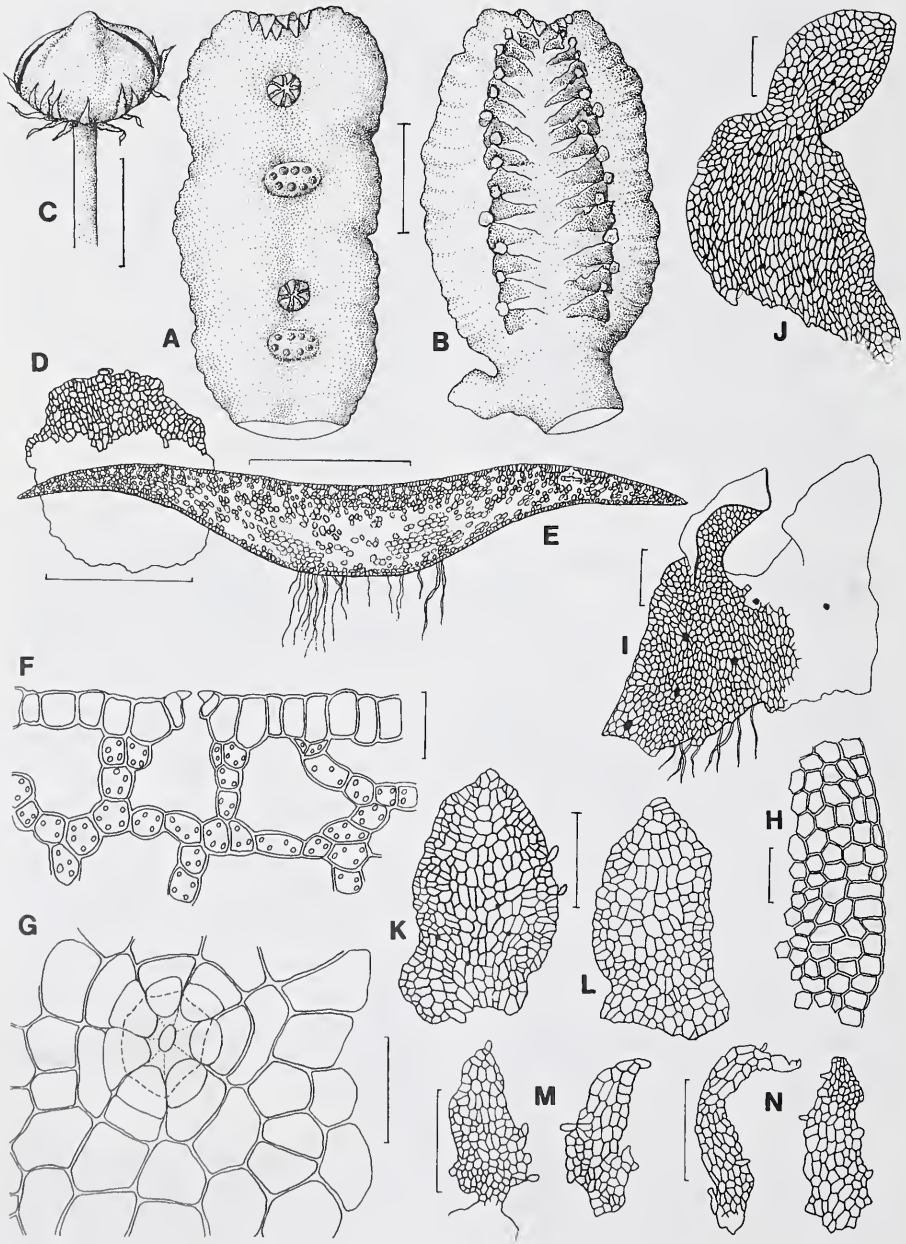
Aitonia microcephala Steph.: 301 (1895b). Type: Tanzania, Usambara, leg. *Holst 362* (G, holo.!).

P. dinteri Steph.: 762 (1901b). Type: Namibia (= Deutsch-Südwest-Afrika). Hereroland: Kransfontein, leg. *Dinter.*

Thalli smallish to medium-sized, in gregarious patches; bright green, finely and irregularly areolate, air pores faintly visible, margins red-brown to purple, scalloped; when dry, margins tightly inflexed. *Branches* simple to several times pseudodichotomously furcate, occasionally with apical or ventrolateral innovations, ligulate to oblong, 6–12 mm long, 3–4(–6) mm wide, 450–850 µm thick medianly, in section 6 or 7 times wider than thick, apex notched, broadly ovate, purple or partly decolorate scale appendages recurved over edge; groove absent, thallus dorsally flat, margins acute, thin; flanks sloping obliquely, deep purple or dark red; ventral face medianly keeled, green. *Scales* in 2 rows, asymmetric, obliquely triangular, purple or reddish, body up to 675 µm long, margins with few projecting papillae, base flatly arched, 800–1500 µm wide, narrowed above and constricted or folded or transversely pleated, where joined with 1 or sometimes 2 broadly ovate or triangular appendages, 350–600 µm long, 350–450 µm across middle, along margins with 1 or 2 rows of small, thin-walled, regular cells, occasionally with a projecting papilla, a number of smaller oil cells scattered throughout scale.

Dorsal epidermal cells unistratose, hyaline, polygonal, 22.5–35.0(–40.0) × 17.5–25.0 µm, thin-walled, but with trigones, smooth externally; air pores slightly raised, simple, 7.5–12.5 µm wide, surrounded by innermost ring of small, collapsed cells, then by 2 concentric rings of 5–7(8) larger cells in each, radial walls sometimes thickened. *Assimilation tissue* 200–400 µm thick, air chambers empty, in several storeys, bounding walls chlorophyllose; storage tissue well developed; oil cells scattered throughout tissues.

FIGURE 5.—**Plagiochasma appendiculatum**. A–D, thallus: A, dorsal face with archegoniophore and carpocephalum; B, dorsal face with androecium; C, ventral face; D, cross section. E, F, air pore: E, c/s dorsal cells and air chambers; F, with surrounding cells from above. G, margin of thallus; H, I, scales; J, scale appendage; K, c/s of stalk; L, male paleae; M, female paleae. A, C, F, G, K, M, *Bottomley CH268*; B, D, E, H–J, L, *S.M. Perold 854*. Scale bars: A–C, 2 mm; D, 1 mm; E–G, 50 µm; H–M, 250 µm. Drawings by G. Condy.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Monoicous. *Androecia* medianly spaced along length of thallus, small sessile cushions, rounded or V-shaped, basally encircled by inconspicuous purple, tapering paleae, ± 400 × 200 µm, several mucilage papillae at margins and apex. *Gynoecial receptacles* acropetally arranged along length of thallus and alternating with androecia, initially enclosed by arching, tapering, hyaline or purple paleae, ± 500 × 150 µm, sometimes marginally with few mucilage papillae; carpocephala small, 1.0 × 2.0 mm, when 2 lobes present. *Stalk* up to 15 mm long, ± 310 µm wide, variously twisted, striate and dark red. *Involucre* bilabiate. Figure 6. *Spores* 70–75 µm diam., triangular-globular, polar, light brown; wing ± 10 µm wide, margins undulate, finely crenulate; ornamentation similar on 2 faces; distal face with 4 alveoli across, 15–20 µm wide, walls narrow, almost smooth to granular; proximal face with distinct triradiate mark, arms thin, 5.0–7.5 µm high, 4 alveoli on each of 3 facets, walls almost smooth to granular. *Elaters* light brown, 212–300 µm long, 7.5 µm wide in middle, tapering toward ends, ± 5 µm wide, bi- or trispiral. *Chromosome number*: n = 9 (Bischler 1978). Plate 2E, F.

Bischler (1978) recognized two varieties of *P. microcephalum*, namely var. *microcephalum* and var. *tunesicum* Bischl. The latter appears to be restricted to Tunisia, whereas she reported the former from the following African countries: Ethiopia, Uganda, Angola, Namibia and South Africa. It is also known from Madagascar, Yemen and southwest India. In southern Africa the species has infrequently been collected in Namibia, Northern Province, North-West, Gauteng and Northern Cape. Map 3.

Plagiochasma microcephalum can be distinguished by the green colour of the fresh thallus and by the generally large, broadly ovate or triangular scale appendages which have one or two rows of smaller cells along the margin. Bischler (1978) reported that plants growing in dry habitats have scales with a single, broadly ovate appendage which is constricted at the base, whereas those from more humid sites usually have one or two triangular scale appendages horizontally folded at the base and hardly constricted. Plants with mature female receptacles are rare. The carpocephala are small (hence the specific epithet) and are raised on a slender, short or long, dark red stalk.

Vouchers: *Bottomley CH175; Burtt Davy 15176; Perold 2976; Volk 81/183.*

4. **Plagiochasma eximium** *(Schiffn.) Steph.* in Bulletin de l'Herbier Boissier 6: 781 (1898); Bischl.: 248 (1978); Perold: 23 (1995a).

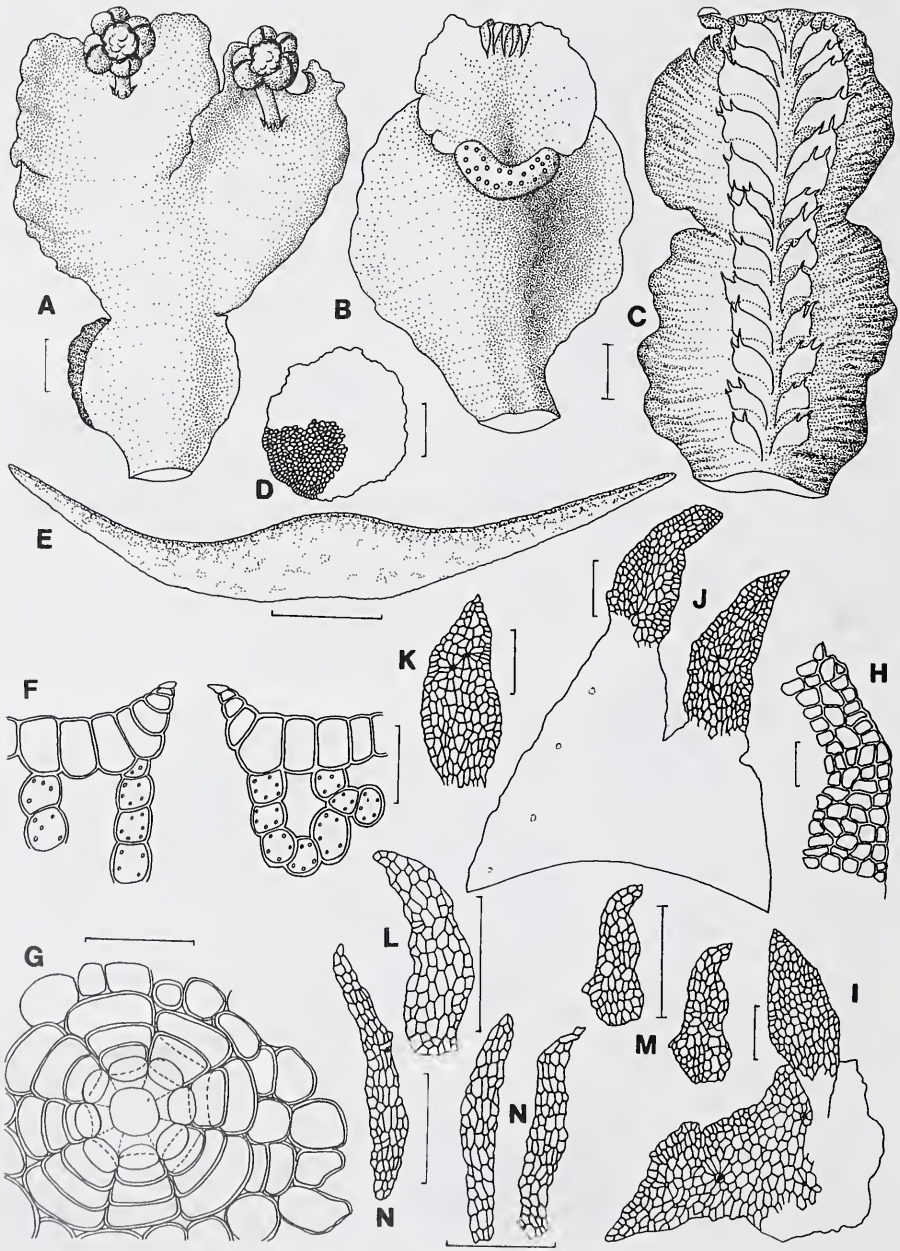
Aitonia eximia Schiffn. in Steph.: 300 (1895b). Type: Kamerun, Buea, an den Höhlen eine Stunde östlich von Manus-Quelle, 2 500 m, 4-II-1891, leg. *Preuss 731* (FI, lecto.!).

P. schimperi Steph.: 788 (1898). Type: Ethiopia (Abyssinia). In monte Semen, leg. *Schimper.*

Grimaldia abyssinica Gola: 63 (1914). Type: Abyssinia, leg. *Chiovenda 2993* (FI).

Thalli robust, in gregarious patches; yellow-green, finely and irregularly areolate, air pores faintly visible, margins narrowly to widely dark red, scalloped and undulate; when dry, margins tightly inflexed. *Branches* simple or once pseudodichotomously furcate, sometimes articulate with one or more apical innovations, 16.5–22.0 mm long, 5.0–8.5 mm wide, ± 750 µm thick medianly, in section 7–11 times wider than thick, apex notched, with lanceolate, reddish pink or dark red scale appendages recurved over edge; groove absent, thallus margins acute, thin; flanks sloping obliquely; ventral face medianly keeled, green. *Scales* in 2 ventral rows, asymmetric, obtusely triangular, deep pink

FIGURE 6.—**Plagiochasma microcephalum** var. **microcephalum**. A, B, E, thallus: A, dorsal face with young receptacles; B, ventral face; E, cross section. C, carpocephalum on stalk; D, c/s of stalk. F, G, air pore: F, c/s dorsal cells and air chambers; G, dorsal cells from above. H, margin of thallus. I–L, scales: I, with 2 appendages; J, with 1 appendage; K, L, appendages. M, male paleae; N, female paleae. A, B, F, G, *Condy 47*; C, D, *Holst 362*; E, *S.M. Perold 2976*; H–K, M, N, *Bottomley CH175*; L, *Burtt Davy 15176*. Scale bars: A–C, E, 1 mm; D, 100 µm; F–H, 50 µm; I–N, 250 µm. Drawings by G. Condy.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to wine red, body ± 950 µm long, margins occasionally with projecting papillae, base arched, ± 1650 µm wide, narrowed above and slightly constricted or pleated where joined with 1 or 2, sometimes 3 tapering appendages, 650–900 µm long, basally 250–350(–400) µm wide, apex not acuminate but often unicellular, ± 14 smaller oil cells scattered throughout scale.

Dorsal epidermal cells unistratose, hyaline, polygonal, 25–40 × 20–35 µm, walls with trigones at corners, smooth externally; air pores slightly raised, simple, 12.5–27.5 µm wide, surrounded by innermost ring of small, collapsed cells, then by 3 concentric rings of 7 or 8 larger cells in each, radial walls sometimes thickened. *Assimilation tissue* 375–475 µm thick, air chambers empty, in several storeys, bounding walls chlorophyllose; storage tissue well developed; oil cells scattered throughout tissues.

Monoicous, but male and female receptacles sometimes on separate plants. *Androecia* medianly at base of smaller, articulate, apical innovation of leading branch, sessile cushions, kidney- or sausage-shaped, basally encircled by apically tapered, dark red paleae, 250–500 × (90–)100–120 µm, margins sometimes with projecting papillae. *Gynoecial receptacles* medianly near apex of branch, single or occasionally paired when branches bifurcate, enclosed by arching, hyaline, tapering paleae, ± 550 × 80 µm, margins sometimes with papillae; carpocephala 3.25 × 3.25 mm, when 4 lobes present. *Stalk* 3–6(–9) mm long, ± 850 µm wide, striate and dark red. *Involucre* bilabiate. Figure 7. *Spores* 82.5–90.0 µm diam., triangular-globular, polar, brown, translucent; wing up to 12.5 µm wide, porate at corners, margins undulate, finely crenulate; ornamentation similar on two faces; distal face with 4 or 5 alveoli across, 22.5–32.5 µm wide, walls wide and finely granular; proximal face with distinct triradiate mark, arms ± 5 µm high, mostly 4 shallow alveoli on each of 3 facets, walls sparsely sprinkled with granules. *Elaters* light brown, 175–225 µm long, 15–20 µm wide in middle, tapering toward ends, 5.0–7.5 µm wide, laxly bispiral or spirals interrupted. *Chromosome number*: n = 9 (Bischler 1978). Plate 3A–C.

The species is widespread in Africa and has been reported by Bischler (1978) from Sierra Leone, Guinea, Cameroons, Zaïre, Djibouti, Ethiopia, Uganda, Kenya, Tanzania, Malawi and the following islands: Cape Verde, Réunion and Madagascar (Bischler 1990). Its distribution extends to the Arabian Peninsula: Saudi Arabia, Yemen, Oman and to Socotra.

Several of the southern Africa collections are from high altitudes, such as the Drakensberg in KwaZulu-Natal and Lesotho, where the plants grow in shady kloofs, on muddy rock faces or on soil covering rocks or under boulders. Map 3.

Plagiochasma eximium is a rather variable species, but can be distinguished by its robust, yellow-green thalli with large, deep pink to wine-red ventral scales narrowed above into (1)2 or 3 tapering appendages which are only a little constricted or pleated at the base. Ventrally the flanks are wrinkled and deep red, not dark purple. Elaters from the few spore-bearing plants studied are bispiral, but Bischler (1978) also found them to be tri- or quadrispiral and spirals generally distinct along only a small part of their length.

Vouchers: *H. Anderson CH4500; Esterhuysen 26166* (BOL); *Perold 2498; Sim CH1186; Volk 84/650* p.p.

5. **Plagiochasma beccarianum** *Steph.* in Bulletin de l'Herbier Boissier 6: 781 (1898); Bischl.: 257 (1978); O.H.Volk: 240 (1979); Perold: 27 (1995a). Type: Abyssinia (Bogos),

FIGURE 7.—**Plagiochasma eximium**. A–C, E, thallus: A, with 2 carpocephala; B, with androecium; C, ventral face; E, cross section. D, c/s of stalk. F, G, air pore: F, c/s dorsal cells and air chambers; G, dorsal cells from above. H, margin of thallus. I–K, scales: I, with 1 appendage; J, with 2 appendages; K, appendage. L, M, male paleae; N, female paleae. A–C, L, *S.M. Perold 2498*; D–I, *Sim CH1163*; J, K, *H. Anderson CH4498*; M, *Sim CH1200*. Scale bars: A–C, 2 mm; D, 100 µm; E, 1 mm; F–H, 50 µm; I–N, 250 µm. Drawings by G. Condy.

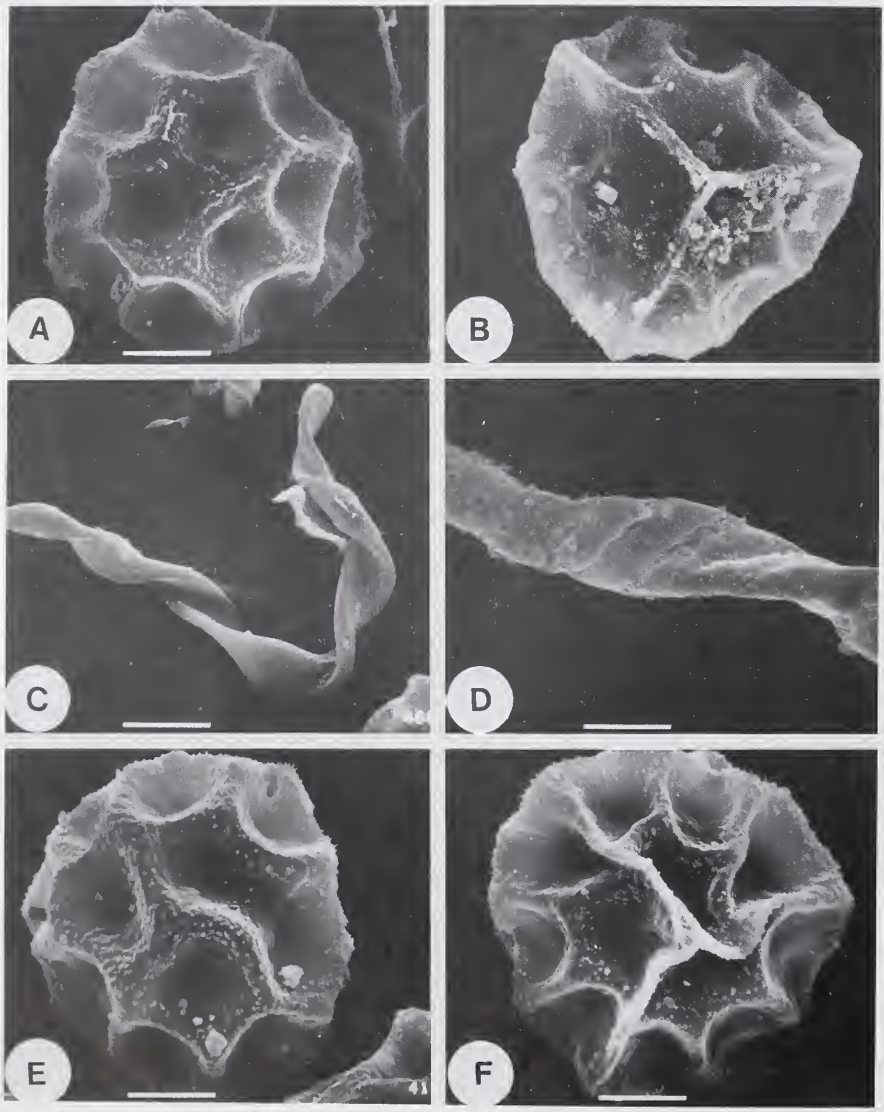


PLATE 3.—Spores and elaters. A–C, **Plagiochasma eximium**: A, distal face; B, proximal face; C, elater. D–F, **P. beccarianum**: D, elater; E, distal face; F, proximal face. A, C, *Sim 9076*; B, *Sim CH1163*; D–F, *Volk 00950*. A, × 630; B, E, × 600; C, × 400; D, × 500; F, × 580.

Keren, in Monte Deban, inter 4500' & 5500', 1870, *Beccari* (FI, holo.; *G009583*, iso.!).

Thalli medium-sized to rather large, in gregarious patches; bright green and shiny, finely and irregularly areolate, air pores distinctly visible, margins narrowly purple, sparsely scalloped and slightly undulate; when dry, margins tightly inflexed. *Branches* once or twice pseudodichotomously furcate, sometimes articulate with apical innovations, ligulate to lingulate, 8–20 mm long, 3.5–5.0(–6.0) mm wide, 600–850 µm thick medianly, in section 6–8 times wider than thick, apex notched with several purple, ovate-lanceolate scale appendages recurved over edge; groove absent, thallus dorsally flat, margins acute, thin; flanks sloping obliquely; ventral face medianly keeled, green. *Scales* in 2 ventral rows, asymmetric, obliquely triangular, deep purple to violet, body ± 850 µm long, margins sometimes with a few prominent, 1–3-celled teeth, base flatly arched, ± 1750 µm wide, gradually tapered above into 2 or 3 lanceolate appendages, up to 1000 µm long, not constricted at base, ± 400 µm wide, margins also occasionally toothed, ± 10 small oil cells scattered throughout scale.

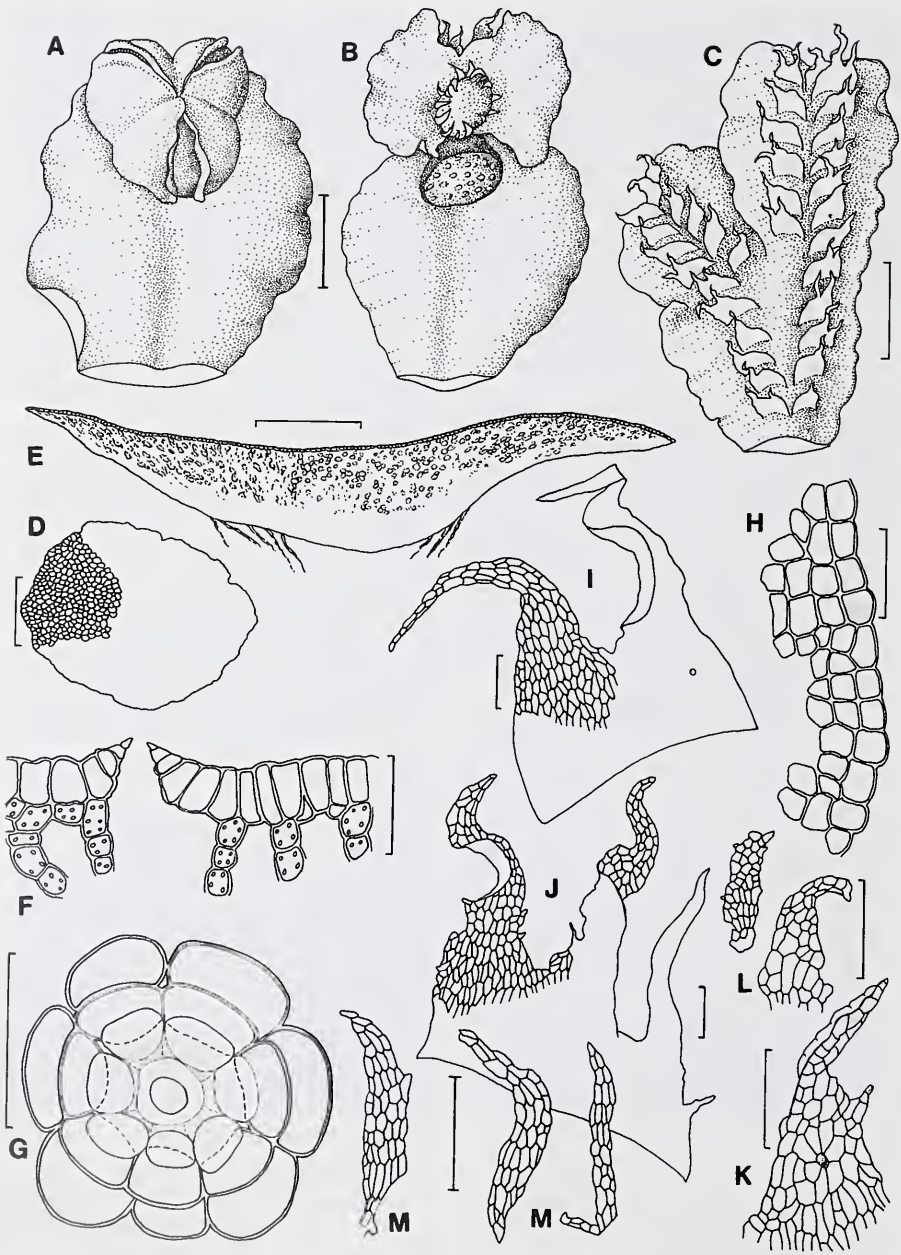
Dorsal epidermal cells unistratose, hyaline, polygonal, 25.0–37.5 × 20.0–27.5 µm, walls thin, at corners with trigones; air pores slightly raised, simple, 15–30 µm wide, surrounded by innermost ring of small, collapsed cells, then by 2 (or 3 partly) concentric rings of 6–8 larger cells in each, radial walls not thickened. *Assimilation tissue* 300–400 µm thick, air chambers empty, in several storeys, bounding walls chlorophyllose; storage tissue occupying ventral part of thallus; oil cells scattered throughout tissues.

Monoicous, but receptacles often on separate plants. *Androecia* medianly and generally just proximal to apical innovation, sessile cushions, kidney-shaped or rounded, basally surrounded by purple paleae, 300–400 × 160–200 µm, apically pointed or blunt, margins sometimes with projecting papillae. *Gynoecial* receptacles medianly near apex of main branch or on apical innovation, single, sometimes 2 in acropetal sequence, basally surrounded by dark paleae with pointed apex, up to 500 × 80 µm, sometimes a few papillae at margins; carpocephala up to 3.5 × 3.5 mm, when 4 lobes present. *Stalk* 1.2–3.5 mm long, ± 825 µm wide. *Involucre* bilabiate. Figure 8. *Spores* 80–90 µm diam., triangular-globular, polar, light brown; wing 10 µm wide, porate at corners, margin finely crenulate; ornamentation similar on 2 faces; distal face with 3 or 4 alveoli across, 20–25 µm wide, walls ± 7.5 µm wide and finely granular; proximal face with distinct triradiate mark, ridge ± 7.5 µm high, each of 3 facets with 4 alveoli, walls wide and sprinkled with granules. *Elaters* light brown, 195–258 µm long, 12.5 µm wide in middle, tapering toward ends, 7.5 µm wide, occasionally branched, bispiral except at tips. *Chromosome number*: n = 9 (Bischler 1978). Plate 3D–F.

The species is rare and has been reported from relatively few places in Africa; except for Namibia (*Volk 00950*), it is mostly found along the eastern part of the continent, namely Ethiopia, Tanzania and Zambia (Bischler 1978). It has also been reported from the Arabian Peninsula (Frey & Kürschner 1988) and from Socotra (Bischler 1978; Frey & Kürschner 1988). Some specimens from Northern Province and Mpumalanga have recently been collected, where they grew in a shady kloof under boulders or in a rocky crevice in Blyde River Canyon respectively. Map 3.

Plagiochasma beccarianum is regarded as quite a heterogeneous species, but so closely resembling *P. eximium* that the two species are often difficult to distinguish when sterile (Bischler 1978). In the few southern African specimens of *P. beccarianum* available for study, it appears that the fresh thalli are a clear green dorsally, not yellow green, and the underside of the wings as well as the scales are deep purple and not dark red as in *P. eximium*. The two or three scale appendages of *P. beccarianum* are ± acuminate or narrowly triangular and not constricted at the base; their margins are irregularly toothed.

Bischler (1978) states that *P. beccarianum* belongs to a complex represented by several species in Asia and America. She thinks that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this group probably diversified more rapidly on these two continents than in Africa and that the heterogeneity of *P. beccarianum* could be due to a slower African evolution of the complex which has not as yet achieved separation into distinct taxonomic units.

Vouchers: *Glen 1250; Perold 2992, 2995; Volk 00950* (BOL).

Subfamily **REBOULIOIDEAE**

Reboulioideae *Grolle* in Feddes Repertorium 87: 244 (1976). Type: *Reboulia* Raddi.

Thalli smallish to large, in loose or crowded patches or in dense mats; lime green to bright green, sometimes becoming reddish or bronzed. *Branches* simple or rarely once/twice pseudodichotomously furcate, or with ventrolateral or apical innovations, apex slightly notched or entire; groove mostly absent, thallus dorsally flat to slightly concave, margins thin, somewhat scalloped or irregularly crenate, hyaline or purple or black; flanks sloping obliquely to very obliquely, often deep purple or black and shiny, sometimes transversely wrinkled; ventral face medianly keeled. *Scales* ventral, smallish to large, in 2 rows, one on either side of keel, body obliquely triangular or semilunate, hyaline or reddish pink to dark red or purple or black to reddish black, apically with lanceolate, ovate or filiform appendages, scattered oil cells present throughout.

Dorsal epidermis mostly lacking chloroplasts, cells thin- or thick-walled, trigones present or absent; air pores simple, rarely stellate, slightly raised, surrounded by 3 concentric rings of cells. *Assimilation tissue* with air chambers very rarely containing a few chlorophyllose filaments, mostly empty and in storeys, rarely in 1 layer and then tall; storage tissue with closely packed parenchymatous cells.

Monoicous, paroicous or autoicous, rarely dioicous. *Androecia* sessile, well defined or not, antheridia sunken in disc or clustered or in 1 or 2 rows on main or ventrolateral branch. *Gynoecial receptacle* on stalk emerging from apical notch or at bifurcation of branches or rarely ventrolateral; carpocephalum with top almost smooth or with prominent papillae, domed to low conical, or umbonate, or disciform-round, not or scarcely lobed beneath. *Stalk* elongate, with 1 rhizoid furrow, sometimes with air chambers. *Involucres* membranous, bell-shaped or bilabiate. *Pseudoperianth* only present in *Asterella* spp. *Sporophyte* with short seta, capsule globose, wall thickenings rarely present, dehiscing along well-defined line. *Spores* triangular-globular, winged, both faces alveolate, with thick or thin walls and then with subsidiary alveoli or with swollen bullae. *Elaters* tapering, bi- or trispiral. *Chromosome number*: n = 9 or multiples thereof, or 10.

The genera *Asterella*, *Mannia*, *Cryptomitrium* and *Reboulia* are classified in the subfamily Reboulioideae. The presence of *Reboulia* in southern Africa has not been confirmed.

ASTERELLA

Asterella *P.Beauv.* in Dictionnaire des sciences naturelles 3: 257 (1805); A.Evans: 247 (1920); Frye & L.Clark: 69 (1937); Hässel de Menéndez: 100 (1963); S.W.Arnell: 59 (1963a); Vanden

FIGURE 8.—**Plagiochasma beccarianum.** A–C, E, thallus: A, with mature carpocephalum; B, with archegoniophore and androecium; C, ventral face; E, cross section. D, c/s of stalk. F, G, air pore: F, c/s dorsal cells and air chambers; G, from above. H, margin of thallus. I–K, scales: I, with 2 appendages; J, with 3 appendages; K, appendage. L, male paleae; M, female paleae. A, B, D–K, M, *Volk 00950*; C, *S.M. Perold 2992*; L, *S.M. Perold 2995*. Scale bars: A–C, 2 mm; D, 100 µm; E, 1 mm; F–H, 50 µm; I–M, 250 µm. Drawings by G. Condy.

Berghen: 169 (1972); R.M.Schust.: 224 (1992c); Perold: 133 (1994c). Type: *A. tenella* (L.) P.Beauv. (= *Marchantia tenella* L.; lecto., designated by Long & Grolle 1992).

Fimbraria Nees: 44 (1820); Gottsche et al.: 555 (1844–1847); Schiffn.: 33 (1893); Steph.: 84 (1899); Sim: 22 (1926); Müll.Frib.: 353 (1951–1958) nom. illegit. Lectotype: *F. marginata* Nees.

Hypenantron Corda: 648 (1829). Type: *H. ciliatum* Corda.

Dictyochiton Corda ex Nees: 258 (1838) non rite publ.

Rhacotheca Bisch.: 12 (1844). Type: *R. azorica* Bisch.

Octokepos Griff.: 343 (1849). Type: *O. khasyanum* Griff.

Thalli medium-sized to fairly large, in crowded patches or dense mats; lime green to bright green, firm or rarely somewhat spongy. *Branches* simple, rarely once or twice pseudodichotomously furcate, or with ventrolateral or apical innovations, ligulate, obovate or obcordate, apex slightly notched, with tips of ventral scales recurved over edge; groove absent, rarely present at apex only, otherwise thallus dorsally flat, margins thin, somewhat scalloped, attenuate, frequently purple; flanks sloping obliquely, purple or black or green; ventral face medianly keeled. *Scales* ventral, in 2 rows, one on either side of keel, body ovate to obliquely triangular, mostly purple or wine-red, apically with 1, rarely 2 or 3 lanceolate or ovate appendage(s), margins mostly entire, scattered oil cells present throughout.

Dorsal epidermis mostly without chloroplasts, cells thin-walled, lacking trigones; air pores small, simple, slightly raised, surrounded by 2 or 3 concentric rings of 6–8 cells in each, radial walls of cells rarely thickened, pores then stellate. *Assimilation tissue* with small, empty air chambers in several irregular, low storeys, or in single tall storey, cells in bounding walls chlorophyllose; storage tissue with rounded or angular cells, closely packed together.

Monoicous, paroicous, or autoicous, rarely dioicous. *Androecia* with antheridia in paroicous species in a vaguely defined cluster or a row immediately or somewhat more proximal to foot of archegoniophore stalk; in autoicous or dioicous species, androecia well-defined, on reduced ventrolateral branches or as median oval disc on main branch. *Gynoecial receptacle* raised on stalk, emerging from apical notch of main or ventrolateral branch, base encircled by paleae; carpocephalum rounded or umbonate, nearly smooth to distinctly papillose, air chambers opening via compound pores, below with (1–)2–4(–5) lobes. *Stalk* elongate, with one rhizoid furrow, with or without air chambers, at summit with paleae, rarely without. *Involucres* membranous, continuous with edges of lobes. *Pseudoperianths* present, mostly pendulous, conical or blunt, vertically split into segments, connate at tips, covering and projecting beyond capsules in all but one southern African species. *Sporophyte* with very short seta, capsule globose, wall lacking thickening bands, dehiscing by well-defined lid. *Spores* triangular-globular, winged, both faces with regular or irregular network of large, angular to rounded alveoli, bordered by ridges and generally lined with small subsidiary alveoli; proximal face also with pronounced triradiate mark. *Elaters* short or of medium length, uni- to trispiral. *Chromosome number*: n = 9 or multiple thereof, or 10.

Asterella is one of the larger genera of the Marchantiales and occurs world-wide. It has been divided into three subgenera: *Brachyblepharis, Asterella* and *Phragmoblepharis*, the latter with three sections, namely *Pappiae, Lindenbergianae* and *Saccatae* (Grolle 1976). Four of the southern African species of *Asterella* are placed in subgenus *Phragmoblepharis* Grolle, since the segments of the pseudoperianths remain connate at their tips for a long time, in contrast to those in subgenera *Brachyblepharis* and *Asterella*, where they separate at maturity; only *A. abyssinica* is placed in subgenus *Brachyblepharis*.

Asterella species are easily recognized when fertile, by the presence of the basket-like pseudoperianth, which soon splits into narrow segments.

Key to the southern African species of *Asterella*

1a Pseudoperianth with segments apically free at maturity . . . subgenus **Brachyblepharis:** . . . . . 1. *A. abyssinica*

1b Pseudoperianth with segments remaining apically connate at maturity . . . subgenus **Phragmoblepharis**:

2a Thalli spongy, with tall air chambers mostly in one storey, and then not subdivided by supplementary partitions, each opening dorsally by a stellate pore; ventral scales occasionally fimbriate at single lanceolate appendage; carpocephalum round or umbonate and lacking paleae at summit of stalk; pseudoperianth extending ± 300 µm beyond involucre and subdivided into 12 or 13 segments; spores 75–95 µm diam., dark brown, ornamentation with irregular zig-zagging ridges . . . . . 2. *A. muscicola*

2b Thalli compact, firm, with small, low air chambers in several storeys, only some top ones opening above by a dorsal, non-stellate pore; ventral scales with 1 (or 2) lanceolate or ovate appendages, margin ± entire; carpocephalum round or umbonate, papillose or ± smooth, with paleae at summit of stalk; pseudoperianth extending more than 1000 µm beyond involucre and subdivided into 14–16 segments; spores more than 100 µm diam., yellow or brown, ornamentation with larger alveoli generally containing subsidiary alveoli:

3a Thalli smallish to large; carpocephalum covered with distinct papillae, projecting ± 200 µm; paleae at summit of stalk shaggy, dense, pale mauve or colourless, up to 3000 µm long and 4 or 5 cells wide at base; ventral scales with lanceolate appendage; spores elaborately ornamented with 6–8 alveoli across distal face, 20–30 µm wide and ridges extending across wing, containing numerous subsidiary alveoli (common, mostly summer rainfall species) . . . . . 3. *A. bachmannii*

3b Thalli medium-sized to very large; carpocephalum ± smooth or with low papillae; paleae at summit of stalk colourless or purple, length variable; ventral scales with lanceolate or ovate appendages; spores less elaborately ornamented:

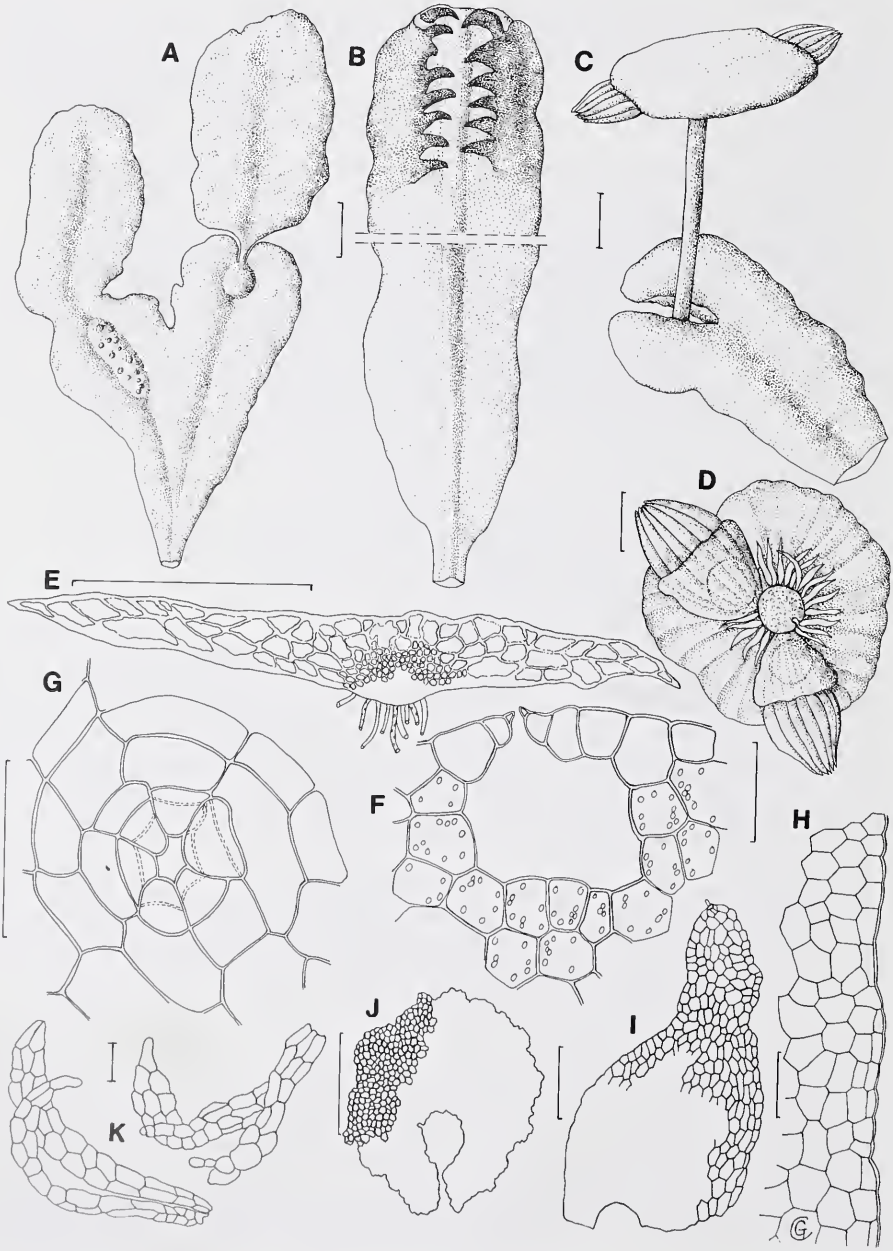
4a Thalli medium-sized; carpocephalum with umbonate head; paleae at summit of stalk mostly colourless, some very long, more than 8000 µm in length, ± 4 cells wide at base; ventral scales with 1 or 2 lanceolate appendages; spores on distal face with (4–)6–9 alveoli across, ± 32 µm wide, very high ridges seldom extending across wing, usually containing small subsidiary alveoli (winter rainfall species) . . . . . 4. *A. marginata*

4b Thalli large to very large; carpocephalum with rounded head, distinctly lobed below; paleae at summit of stalk almost colourless to purple, 2000–3000 µm long, some up to 7 cells wide at base; ventral scales with single, large-celled, ovate appendage, constricted at base; spores on distal face with 5–8 alveoli across, 25–30 µm wide and extending to wing margin, almost empty of subsidiary alveoli and hollow (summer rainfall, mostly Afromontane species) . . . . . 5. *A. wilmsii*

1. **Asterella abyssinica** (*Gottsche*) *Grolle* in Vanden Berghen: 170 (1972).

Fimbriaria abyssinica Gottsche in Gottsche et al.: 569 (1844–1847); *Hypenantron abyssinicum* (Gottsche) Trevis.: 441 (1877); Steph.: 109 (1899). Type: Abyssinia cum *Targionia elongata*, in caespite Un. itin. n. 500 a *Kotschy* lecto (not seen).

Thalli smallish to medium-sized, in crowded mats; green to light olive-green, hardly areolate, air pores not visible, margins hyaline or tinged with mauve to deep purple, weakly scalloped, slightly undulate; when dry, thallus margins flat or raised to partly inflexed. *Branches* simple or once pseudodichotomously furcate, with apical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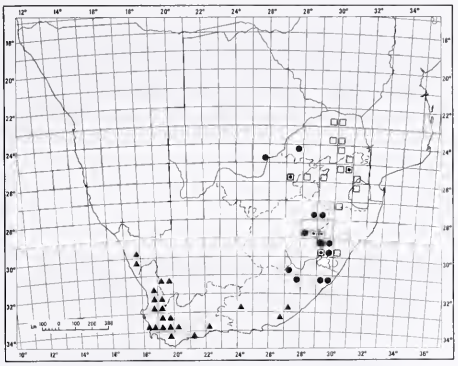
or ventrolateral innovations, widening gradually from a stipitate base, 15–18 mm long, 2.3–5.0 mm wide, 400–450 (–630) μm thick medianly, in section 6–11 times wider than thick, apex slightly notched, tips of few ventral scales recurved over edge; groove absent, thallus dorsally flat, margins acute, thin; flanks sloping obliquely, entirely or only distally purple; ventral face medianly keeled, green. *Scales* in 2 ventral rows, obliquely triangular, in different shades of mauve to purple, body up to 800 μm long, margins ± entire, base occasionally crescentic, 650–750 μm wide, narrowed above and sometimes constricted where joined to single oblong or elliptical appendage, 420–430 μm long, ± 200 μm wide basally, tapering above to conical apical cell, up to 12 small, colourless oil cells scattered throughout scale.



MAP 4.— ■ **Asterella abyssinica**
● **Asterella muscicola**
▲ **A. marginata**
□ **A. wilmsii**

Dorsal epidermal cells unistratose, containing chloroplasts, thin-walled, 5- or 6-sided, (40.0–)45.0–65.0(–72.5) × 22.5–37.5 μm; air pores hardly raised, simple, ± 12.5 × 10.0 μm, surrounded by innermost ring of small collapsed cells, then by 2 concentric rings of 6 or 7 larger cells in each, radial walls not thickened. *Assimilation tissue* 215–260 μm thick, air chambers small, empty, in 2 or 3 storeys, bounding walls chlorophyllose; storage tissue confined to keel, cells closely packed together; oil cells scattered throughout tissues.

Autoicous. *Androecia* in sessile, thickened cushions, elongated or oval, occasionally furcate, near apex of branch or more proximally at constriction, opening above into conical papillae. *Gynoecial receptacles* proximal to apical notch of main branch or just proximal to stipitate innovation of apical branch, single, occasionally paired at apices of 2 furcate branches, ± sessile when young, later raised on stalk; carpocephalum rather flat to weakly convex, suborbicular, 3.5–4.0 mm across, above almost smooth. *Stalk* arising ± 1.7 mm proximal to apex of branch in apical notch, 4–5 mm long, whitish green or streaked with purple, widening slightly toward base, at midlength ± 520 μm wide, with rhizoid furrow, at summit of stalk and scattered along its length, colourless or purple paleae, up to 820 μm long, 2 or 3 cells wide basally, above 3–5 cells wide, tapering to apical cell. *Involucre* membranous, partly covering capsules below. *Pseudoperianths* extending up to 1250 μm beyond involucre, generally with 8–10 white segments, tapering to narrow tips that become free before capsule dehiscence. *Sporophyte* with obovoid capsule, thin-walled and lacking thickening bands. Figure 9.

Spores 62.5–72.5 μm diam., triangular-globular, pale yellow to yellow, translucent; wing undulate, up to 10 μm wide, margin crenulate; distal face convex, reticulate, with network of ± 6 larger, primary alveoli across, ± 10–15 μm wide and extending over wing, their delimiting ridges only slightly raised and not clearly defined among the numerous walls of small, subsidiary alveoli, alveolar floor highly porate; proximal face with prominent triradiate ridge,

FIGURE 9.—**Asterella abyssinica**. A, B, E, thallus: A, dorsal view with gametoecia on separate branches of same plant; B, ventral view; E, cross section. C, carpocephalum raised on stalk; D, ventral view of carpocephalum. F, G, air pore: F, c/s with air chamber; G, from above. H, marginal cells of thallus; I, ventral scale; J, c/s of stalk; K, paleae. A–J, *Duckett & Matcham 6049*; K, *S.M. Perold 2674*. Scale bars: A–E, 1 mm; F–H, 50 μm; I, J, 250 μm; K, 100 μm. Drawings by G. Condy.

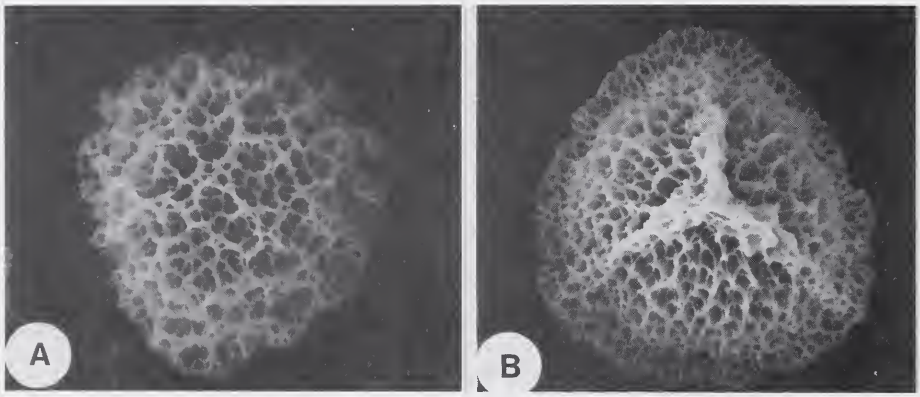


PLATE 4.—Spores of **Asterella abyssinica**, *Duckett & Matcham 6049*. A, distal face; B, proximal face. A, × 745; B, × 710.

its arms continuous from pole to wing, but not clearly extending across, each of 3 facets with numerous alveoli, larger at pole and smaller toward wing, but not clearly arranged in primary and subsidiary alveoli, floor also highly porate. Plate 4A, B. *Elaters* 135–150 µm long, 10 µm wide in centre, slightly tapering toward rounded ends, bispiral. *Chromosome number*: unknown.

The species has only very recently been collected in the *Flora* area, namely in KwaZulu-Natal. Map 4. The range of *A. abyssinica* extends northwards into Zimbabwe, Malawi (Perold 1997), Tanzania, Rwanda, Burundi, Ethiopia, Zaïre, Cameroun and Sierra Leone (Wigginton *et al.* 1996). It frequently grows at high altitudes on streambanks or on damp rocks in association with other liverworts such as *Targionia hypophylla* and *Asterella bachmannii*.

It is easily recognized by the rather flattened round discs of the carpocephala, by horizontally protruding pseudoperianths, their rather short segments becoming free at the tips before the capsules dehisce.

Voucher: *Duckett & Matcham 6049*.

2. **Asterella muscicola** *(Steph.) S.W.Arnell*, Hepaticae of South Africa: 60 (1963a); Perold: 135 (1994c).

Fimbraria muscicola Steph.: 121 (1892); Steph.: 97 (1899); Sim: 22 (1926). Type: Mpumalanga [Transvaal], Spitzkop bei Lydenburg, Febr. 1888, leg. *Wilms G001664*, holo.! (G); *G024589*, iso.! (G).

Thalli medium-sized to fairly large, in crowded patches; bright green, areolate, somewhat spongy, air pores tiny, white specks, very slightly raised, margins soon turning purple, becoming wider proximally and pinkish purple, scalloped and undulate, in older parts dead; when dry, thallus margins tightly clasped together. *Branches* simple or once/twice pseudodichotomously furcate, oblong, up to 18 mm long, 2.5–3.5(–6.5) mm wide, ± 1250 µm thick medianly, in section 2–5 times wider than thick, apex notched, tips of ventral scales recurved over edge; groove faintly present toward apex, thallus dorsally concave more proximally, margins acute, thin; flanks sloping obliquely; ventral face medianly keeled, green. *Scales* in 2 ventral rows, obliquely triangular, wine red to deep purple, body 700–800 µm long, margins sometimes with several 1- or 2-celled papillae, base curved, 1100–1250 µm wide, narrowed above to acuminate appendage, 170–350 µm long, apex tapered and occasionally fimbriate, 2–8 small, colourless oil cells scattered throughout scale.

Dorsal epidermal cells unistratose, hyaline, thin-walled, without trigones, 4- or 5–(–7)-sided, (37.5–)45.0–72.5 × 15.0–25.0 µm; air pores very

slightly raised, simple, ± 7.5 µm wide, surrounded by innermost ring of small collapsed cells, then by 2 concentric rings of 6 larger cells in each, radial walls mostly thickened and pores stellate. *Assimilaton tissue* ± 650 µm thick, air chambers tall and empty, mostly in one storey, bounded by chlorophyllose, unistratose walls; storage tissue with cells tightly packed together; oil cells scattered throughout tissues.

Paroicous. *Androecia* with antheridia grouped or in 1 or 2 short rows along midline of thallus, generally immediately proximal to stalk, very rarely on separate plant, immersed, opening above into prominent, conical papillae. *Gynoecial receptacles* single, rarely paired at apices of 2 furcate branches, almost sessile when young, later raised on stalk; carpocephalum rounded to somewhat umbonate, ± 3 mm across, air pores compound, below with 3–5 capsules (sometimes 2 together in same involucre). *Stalk* arising at bifurcation of branches, the latter continuing in growth, yellowish, shiny, ribbed, stout, erect or somewhat bent, 5–8 mm long, ± 675 µm wide at midlength, becoming thicker toward base and tapering toward naked summit, with one rhizoid furrow and narrow to wide air chambers. *Involucre* ± bilabiate, enclosing base of pseudoperianth and capsule. *Pseudoperianths* extending obliquely downward, projecting ± 300 µm beyond involucre, somewhat flattened sideways, with 12 or 13 cage-like, hyaline segments, connate at tips. *Sporophyte* with swollen foot and very short seta, capsule globose, ± 875 µm diam., wall unistratose, lacking thickening bands. Figure 10. *Spores* 75–95 µm diam., triangular-globular, dark brown, opaque; wing somewhat pleated, 5 µm wide, margin undulate; distal face convex, reticulate, with very irregular, mostly incomplete alveoli, ridges forming an irregular, zigzagging maze; proximal face with distinct triradiate mark, facets also with irregular, incomplete alveoli, ranging from small and crowded to larger and more widely dispersed. *Elaters* 150–175 µm long, 17.5 µm wide in centre, slightly tapering toward ends, bispiral, light brown. *Chromosome number*: n = 10 (T. Bornefeld pers. comm.). Plate 5A, B.

The range of *A. muscicola* extends into Malawi (Kasunga Nat. Park, *Perold 2682*) and Zimbabwe (*Eyles 932, 933; Miller 7869*) from where it is also reported by Best (1990). The species is probably endemic to southern Africa and in the *FSA* area is known from Botswana, Northern Province, North-West, Mpumalanga, Free State, KwaZulu-Natal, Lesotho, and Eastern Cape. Map 4.

It frequently grows at high altitudes on soil overlying sandstone or basalt outcrops in association with other liverworts such as *Plagiochasma* spp. and *Riccia* spp.

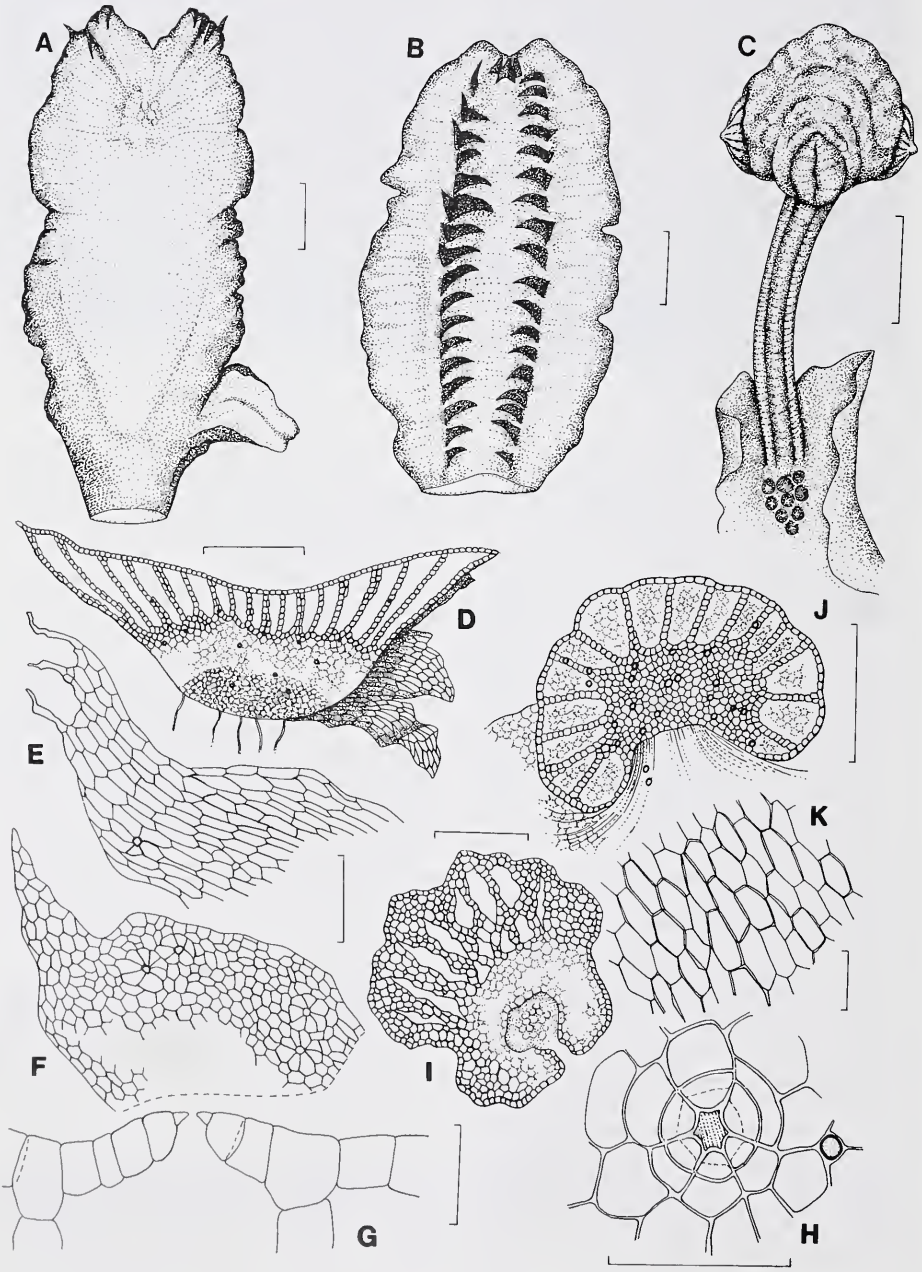
Sterile specimens of *A. muscicola* have been confused with *Athalamia spathysii*, since the dorsal air pores of the thallus in both spp. are stellate. In *A. muscicola* the air chambers are devoid of chlorophyllose filaments, but oil bodies are present and their remains are present in the scales which have cells half as wide as those of *A. spathysii*. It differs from *Athalamia* species mainly in sporophyte characters: the stalk arises at the bifurcation of the branches, it is thicker and has a rhizoid furrow, it is also devoid of scales both at the base and summit; the cells in the capsule wall lack annular or semi-annular thickenings; pseudoperianths are present; the spores are larger, dark brown and winged, their ornamentation is reticulate (not papillose); the elaters are shorter and wider.

Vouchers: *H. Anderson 1248; Marais 832; Mott 861; Perold & Koekemoer 2968; Smook 8237.*

3. **Asterella bachmannii** *(Steph.) S.W.Arnell*, Hepaticae of South Africa: 62 (1963a); Perold: 137 (1994c). Type: Pondoland, Port Grosvenor, *Bachmann* (*G13866*, lecto.!; *G13867*!).

Fimbraria bachmannii Steph.: 7 (1894); Steph.: 105 (1899); Sim: 22 (1926).

Thalli smallish to quite large, in crowded mats; light green, rather crystalline to shiny, firm and compact, faintly areolate or not, air pores tiny, scattered, margins turning purple, slightly scalloped, somewhat undulate; when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dry, thallus margins raised or inflexed, sometimes inrolled. *Branches* simple or occasionally once, rarely several times pseudodichotomously furcate, often with apical or ventrolateral innovations, broadly ligulate, widening rapidly from narrow base, 18–25 mm long, (1.9–)2.5–4.0 (–4.9) mm wide, (450–) 500–600 (–775) µm thick medianly, in section 5 or 6 times wider than thick, apex notched, tips of ventral scales recurved over edge; groove absent, thallus dorsally flat, margins acute, thin; flanks sloping obliquely, red to deep purple; ventral face medianly keeled, green. *Scales* in 2 ventral rows, obliquely triangular, red to deep purple, body up to 1000 µm long, margins ± entire, base crescentic, ± 1500 µm wide, narrowed above and constricted where joined to single lanceolate appendage, occasionally 2, 450–650 (–800) µm long, 150–200 µm wide basally, tapering above to conical apical cell, ± 8 or more small, colourless oil cells scattered throughout scale.

Dorsal epidermal cells unistratose, generally containing chloroplasts, thin-walled, (4-)5- or 6-sided, (30.0)–50.0–67.5(–90.0) × 22.5–30.0 µm; air pores slightly raised, simple, ± 17.5 × 12.5 µm, surrounded by innermost ring of small collapsed cells, then by 2 concentric rings of 6–8(–10) larger cells in each, radial walls not thickened. *Assimilation tissue* up to 280 µm thick, air chambers small, empty, in 2–4 storeys, bounding walls chlorophyllose; storage tissue mostly confined to keel, cells closely packed together, walls thick and pitted; oil cells scattered throughout tissues.

?Dioicous, rarely autoicous. *Androecia* naked, sessile, elongated or oval cushions, medianly near apex of main branch, rarely also at ± midlength constriction, sometimes on short apical or lateral innovations, antheridia immersed, opening above into stout, raised, purple-red papillae. *Gynoecial receptacles* proximal to apical notch of main branch or rarely on short ventrolateral innovations, single, occasionally paired at apices of 2 furcate branches, almost sessile when young, with numerous (± 75), long, pale, sometimes purple paleae arching over disc, at maturity raised on stalk; carpocephalum rounded, ± 3 mm across when bearing 4 or 5 capsules, frequently with only 1 or 2 and then smaller, above with numerous prominent papillae, containing air chambers which open via compound air pores. *Stalk* arising 1.5 mm proximal to apex of branch in apical notch, length variable, (1–)5–13(–20) mm long, at midlength ± 550 µm wide, widening toward base, whitish to purple, with single rhizoid furrow, at summit ± 32 slender, shaggy paleae, white or purple, up to 3250 µm long, 4 or 5 cells wide at base, gradually tapering to conical apical cell. *Involucre* membranous, partly covering capsule below. *Pseudoperianths* descending obliquely downward and extending ± 1000 µm beyond involucre, generally split into 14 cage-like segments, shiny white or purple-stained, tapering to narrow, connate tips. *Sporophyte* with globose capsule, ± 1000 µm diam., wall unistratose, lacking thickening bands, dehiscing along well-defined line. Figure 11. *Spores* 102.5–125.0 µm diam., triangular-globular, mostly yellow, sometimes brown, translucent; wing undulate, up to ± 20 µm wide, margin crenulate; distal face convex, with network of 6–8 angular alveoli across, 20–30 µm wide, ridges 7.5–10.0 µm high and laterally extending across wing, floor of alveoli highly porate and generally with smaller subsidiary alveoli, these also extending over crests of main ridges; proximal face with prominent triradiate ridge, its arms ± 15 µm high, continuous from pole and across wing to margin, each of 3 facets with alveoli, ± 10 µm wide, also extending across wing and containing many or few, smaller, subsidiary alveoli that cross over crests of main alveoli and onto wing to margin,

FIGURE 10.—**Asterella muscicola**: A, B, D, thallus: A, dorsal face; B, ventral face; D, cross section. C, carpocephalum raised on stalk and antheridia proximal to foot of stalk. E, F, scales: E, with fimbriate apex; F, with acuminate apex. G, H, air pore: G, c/s with air chamber; H, cells and oil cell from above. I, c/s of stalk; J, l/s of young archegoniophore; K, capsule wall cells. A–C, E, G, I, J, *Perold & Koekemoer 2968*; D, F, H, *Condy 13*; K, *H. Anderson 1248*. Scale bars: A–D, 2 mm; E, F, I, 250 µm; J, 1 mm; G, H, K, 50 µm. Drawings by A. Pienaar.

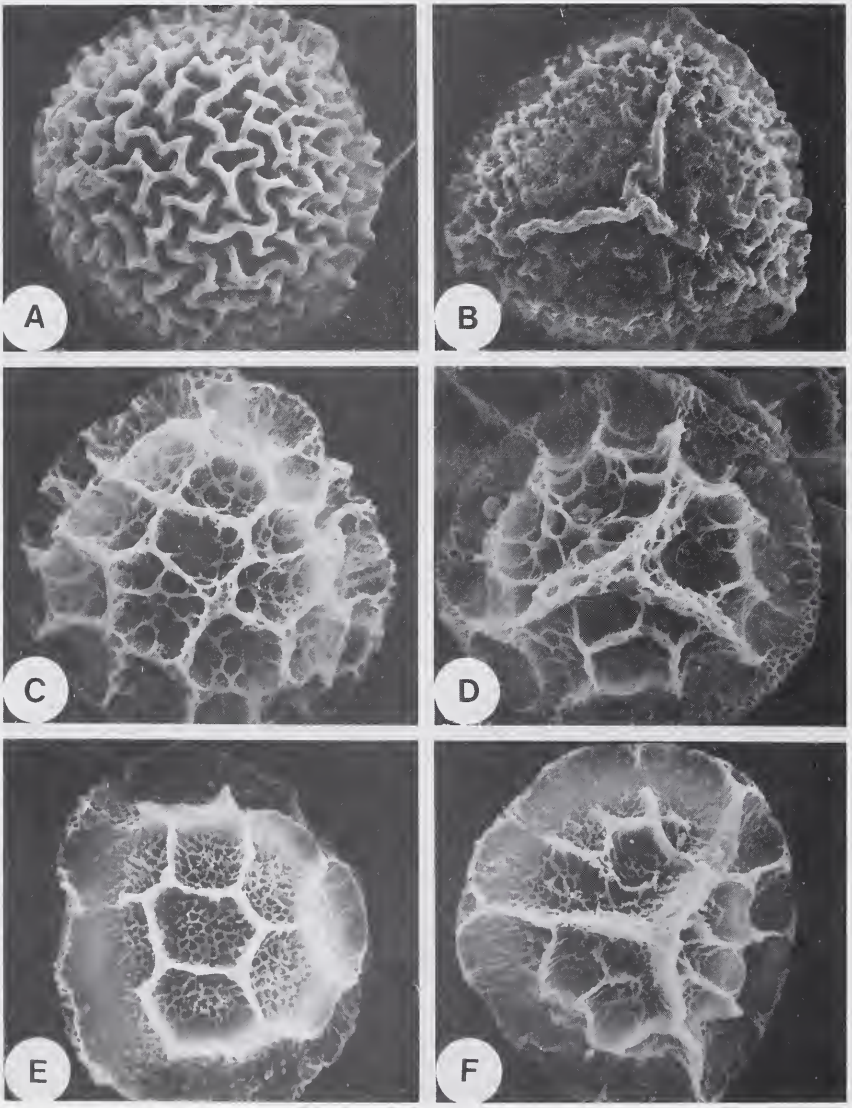


PLATE 5.—Spores. A, B, **Asterella muscicola**: A, distal face; B, proximal face. C, D, **A. bachmannii**: C, distal face; D, proximal face. E, F, **A. marginata**: E, distal face; F, proximal face. A, B, *Perold & Koekemoer 2968*; C, *Glen 2155*; D, *Perold & Koekemoer 2917*; E, *S.M. Perold 2418*; F, *Arnell 505*. A, B, × 640, C, × 520, D, × 530; E, × 545; F, × 400.

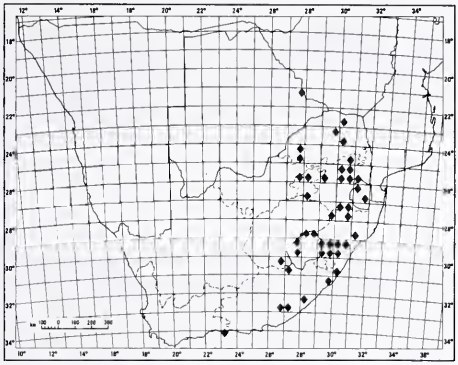
which is finely ornamented on both faces. *Elaters* 142–165 (–180) µm long, 15 µm wide in centre, slightly tapering to ends, bispiral, yellow. *Chromosome number*: n = 9 (T. Bornefeld pers. comm.). Plate 5C, D.

The range of *Asterella bachmannii* extends into Zimbabwe and Malawi (Nyika Nat. Park). Best (1990) also reported it from Zimbabwe. It is by far the most frequently collected *Asterella* species in the summer rainfall areas of southern Africa. It is known from Botswana, Northern Province, Gauteng, Mpumalanga, Swaziland, Free State, KwaZulu-Natal, Lesotho, Western and Eastern Cape. Map 5. It is mostly found on damp soil along stream banks, at waterfalls or in shaded gulleys or kloofs, sometimes on soil-covered vertical rock walls, at seepages or on soil overlying sandstone, in light shade or in full sunlight. It occasionally grows together with *A. wilmsii*, *Symphyogyna* species and *Fossombronia* species.

Asterella bachmannii is a variable species and can range in size from smallish to quite large. The thallus margins and ventral face can be very deeply pigmented or hardly at all, depending on whether it is exposed to intense sunlight or not. The ventral scales can likewise be deeply pigmented and the appendages are then not clearly discernible against the purple flanks.

Fertile plants are easily recognized by the mostly pronounced papillae covering the carpocephalum as well as by the dense, narrow, stringy or shaggy paleae which are usually white, but occasionally can be purple-stained. The spores are highly ornamented with the main alveoli containing numerous smaller subsidiary alveoli on both faces, giving it a lacey appearance. Sterile specimens can be distinguished from *A. muscicola* by the compactness of the assimilation tissue and from *A. wilmsii*, by its smaller size and the lanceolate appendages (occasionally double) of the purple or reddish purple ventral scales and from *A. marginata* by its generally purple, not wide, black thallus margins and by its mostly summer rainfall distribution.

Vouchers: *Glen 2150*; *Perold & Koekemoer 2856, 2913*; *Phelan 375*.

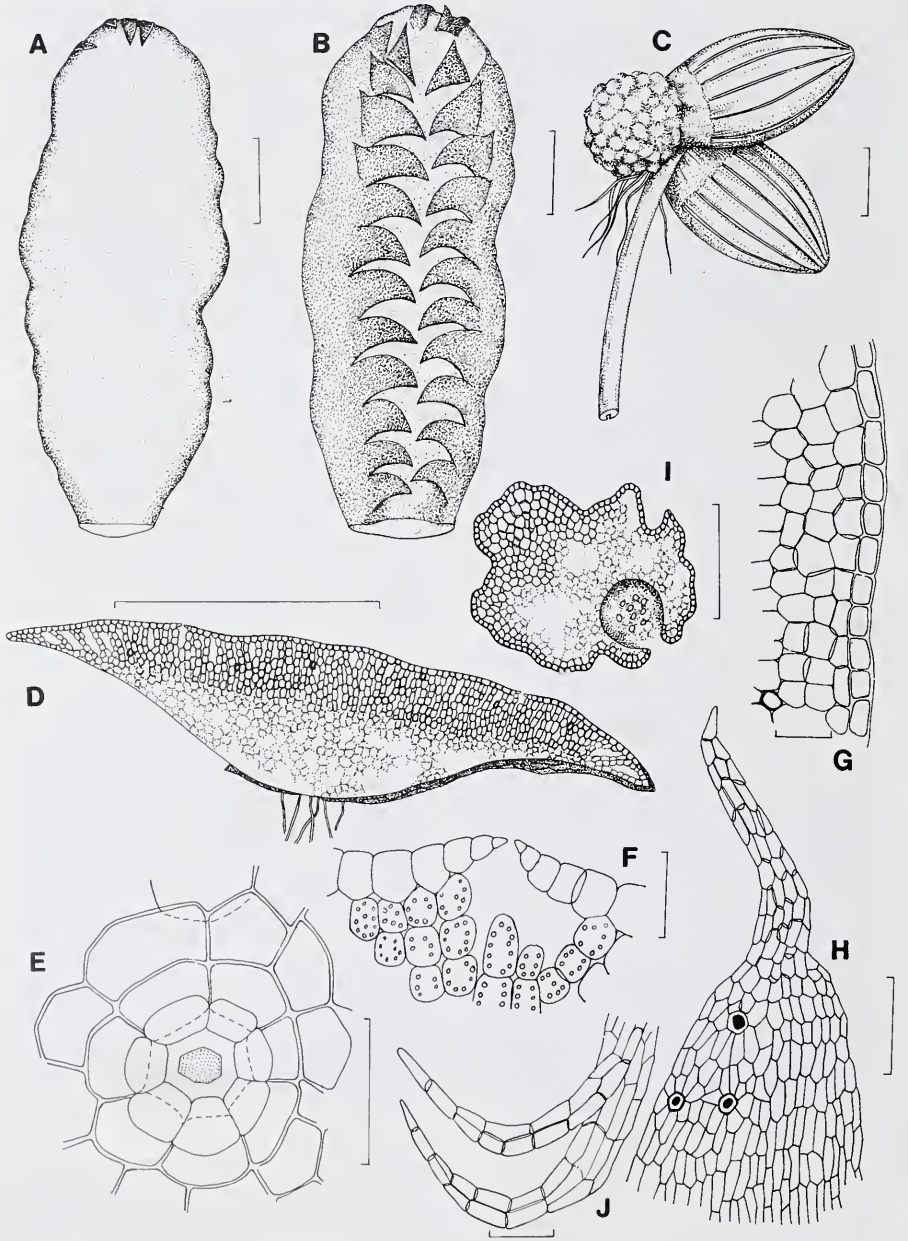


MAP 5.— **Asterella bachmannii**

4. **Asterella marginata** *(Nees) S.W.Arnell*, Hepaticae of South Africa: 63 (1963a); Perold: 140 (1994c). Type: Capite b. spei, crescit iuxta viam in monte Leuwenstaart ad terram, leg. *Bergius s.n.* (BM).

Fimbraria marginata Nees: 44 (1820); Gottsche et al.: 559 (1844–1847); Steph.: 104 (1899).

Thalli medium-sized, in crowded mats; bright green, firm and compact, hardly areolate, air pores slightly raised, scattered, margins with narrow to wide black border, occasionally reddish purple, very wavy to almost frilly; when dry, thallus margins raised to inrolled. *Branches* simple or once, rarely twice pseudodichotomously furcate, sometimes with apical or ventrolateral innovations, obovate to obcordate or ligulate, frequently widening rapidly from narrow base, up to 23 mm long, 2.3–5.0 mm wide, 550–565 µm thick medianly, in section 4–9 times wider than thick, apex notched, tips of ventral scales recurved over edge; groove absent, thallus dorsally flattish to somewhat concave, margins acute, thin; flanks sloping obliquely, purple to black; ventral face medianly keeled. *Scales* in 2 ventral rows, obliquely triangular, deep purple to lightly pigmented, body ± 675 µm long, at margins few small papillae, base crescentic, 825–925 µm wide, narrowed above, not constricted where joined to 1 or 2(3) lanceolate appendages, equally long or not, length 675–925 µm, tapering above to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single apical cell, basally ± 375 µm wide, up to 20 smaller oil cells scattered throughout scale.

Dorsal epidermal cells unistratose, mostly hyaline, walls thin, slightly thickened at corners, 5- or 6-sided, 30.0–45.0 × 17.5–20.0 µm; air pores slightly raised, simple, ± 10.0 × 7.5 µm, surrounded by innermost ring of small, collapsed cells, and then by 2 concentric rings of 5–7 larger cells in each. *Assimilation tissue* 200–250 µm thick, air chambers small, empty, in 2 or 3 storeys, bounding walls chlorophyllose; storage tissue confined to keel, cell walls porate, thickened, often with striate network of bands; oil cells scattered throughout tissues.

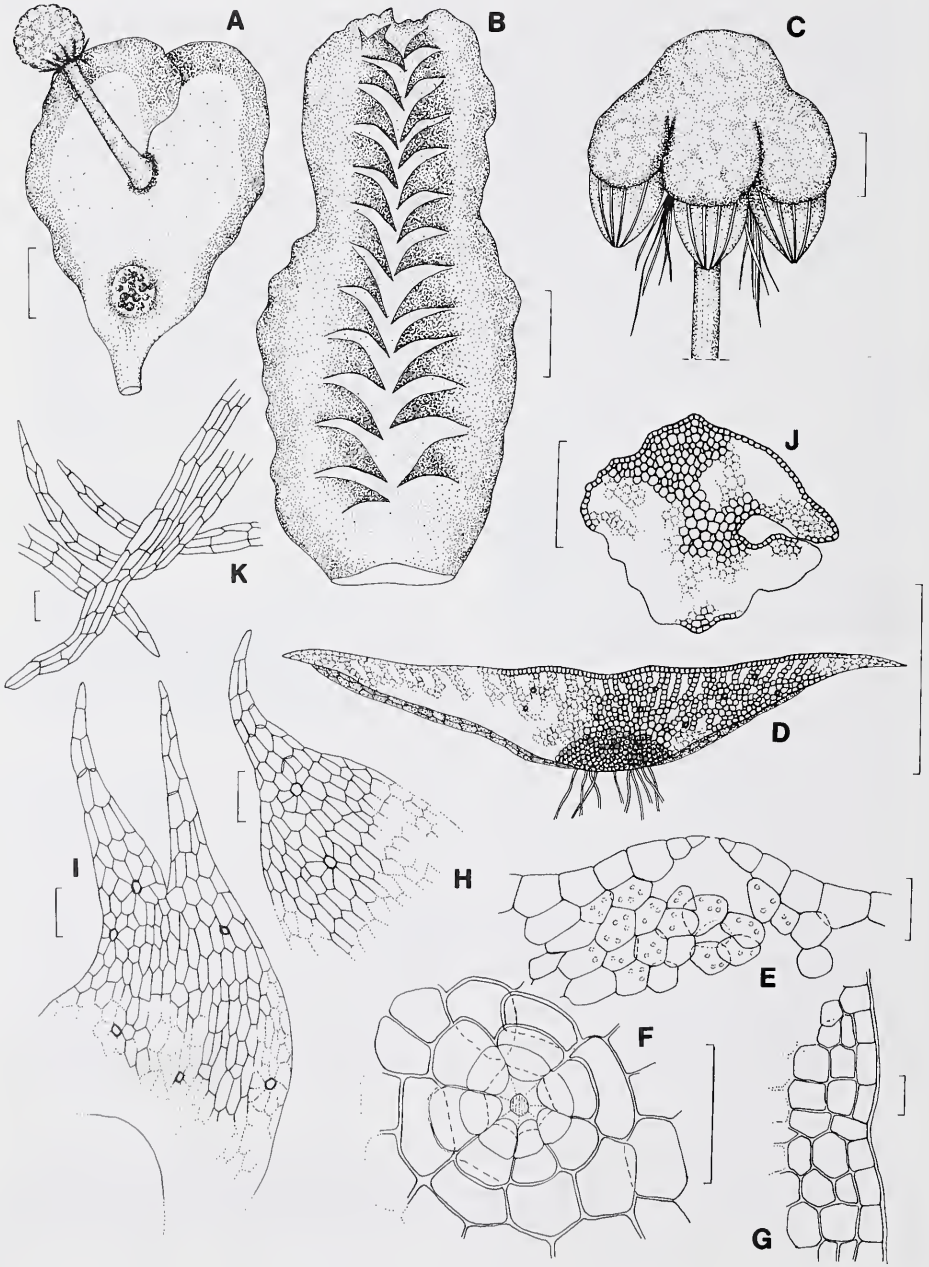
Autoicous or monoicous. *Androecia* in sessile cushions on ventrolateral innovations or at base of main branches, antheridia immersed, opening above into raised, purple papillae. *Gynoecial receptacles* proximal to apical notch of main branch, single, occasionally paired at apices of 2 furcate branches, almost sessile when young, at maturity raised on stalk; carpocephalum ± 3 mm across, umbonate, air pores compound, slightly raised, sometimes quite conspicuous, (1–)3–5(–6) capsules borne below. *Stalk* arising ± 1 mm proximal to branch apex in notch, foot slightly wider than at midlength, width ± 575 µm, with single rhizoid furrow, length variable, 2.5–18.0 mm, white or reddish purple, at summit (and along length) numerous pale, occasionally purple paleae, some very long, up to 8400 µm, others 1250–2750 µm, base ± 100 µm or 4 cells wide, tapering to single apical cell. *Involucre* membranous, partly covering capsule. *Pseudoperianths* descending obliquely downward, extending ± 1100 µm beyond involucre and divided into 15 segments, tapering toward connate tips. *Sporophyte* with globose capsule, ± 600 µm diam. Figure 12. *Spores* (102–)125–140 µm diam., triangular-globular, yellow; wing undulate, 20 µm wide, margin crenulate; distal face convex, centrally with (4–)6–9 complete alveoli, ± 32.5 µm wide, outer alveoli incomplete, ridges up to 12.5 µm high, seldom extending across wing, smaller, subsidiary alveoli, 2.5–5.0 µm wide (and occasionally even further divided up), generally covering floor of larger alveoli and extending over crests of main ridges; proximal face with prominent triradiate mark, its arms 15 µm high and continuous from pole across wing to margin, each of 3 facets with complete or mostly incomplete alveoli, main ridges sometimes extending across wing, small subsidiary alveoli covering floor and ridges of main alveoli, as well as arms of triradiate mark. *Elaters* ± 145 µm long, 12.5 µm wide in centre, slightly tapering to ends, bispiral, yellow. *Chromosome number*: unknown. Plate 5E, F.

The distribution of *A. marginata* appears to be confined to the mostly winter rainfall areas of the Northern, Western and Eastern Cape. Map 4.

Asterella marginata grows in dense mats on clayey soil or on weathered, soil-covered rocks at seepages or riverbanks, between rock crevices and under ledges, sometimes in association with *Fossombronia* spp., *Bryum* spp. and *Riccia* spp.

Fertile specimens of *A. marginata* are easily recognized by the umbonate head of the carpocephalum, which lacks prominent papillae; the frequently very long, pale paleae, and the spore ornamentation mostly with numerous fine, ± regular, subsidiary alveoli contained within the highly ridged, larger ones, which usually do not extend across the wing. Sterile collections of *A. marginata* are, however, difficult to place and have frequently been confused with *A. bachmannii*; in fact, Arnell (1963) stated that he could find no real differences between them, basing his opinion on their scale

FIGURE 11.—**Asterella bachmannii.** A, B, D, thallus: A, dorsal face; B, ventral face, appendages of scales mostly not visible against dark purple flanks; D, cross section. C, carpocephalum with papillose disc and 2 pseudoperianths. E, F, air pore: E, from above; F, c/s with air chamber. G, marginal cells; H, appendage and upper part of scale; I, c/s of stalk; J, paleae. A–D, I, *Glen 2150*; E, G, H, J, *Perold & Koekemoer 2856*; F, *Condy 7*. Scale bars: A–D, 1 mm; E–G, 50 µm; H, I, 250 µm; J, 100 µm. Drawings by A. Pienaar.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appendages, air pores, epidermal cells and spores.

Vouchers: *Arnell 5359* (BOL); *Bottomley CH263; Dyer 863; Garside 6585; Koekemoer 869; Oliver 1474.*

5. **Asterella wilmsii** *(Steph.) S.W.Arnell*, Hepaticae of South Africa: 62 (1963a); Perold: 142 (1994c). Type: Spitzkopf bei Lydenburg, Transvaal (Mpumalanga), leg. *Dr Wilms* (ex Herb. Jack, *G001666*, lecto. fide Grolle in litt.).

Fimbraria wilmsii Steph.: 122 (1892); Steph.: 103 (1899); Sim: 23 (1926).

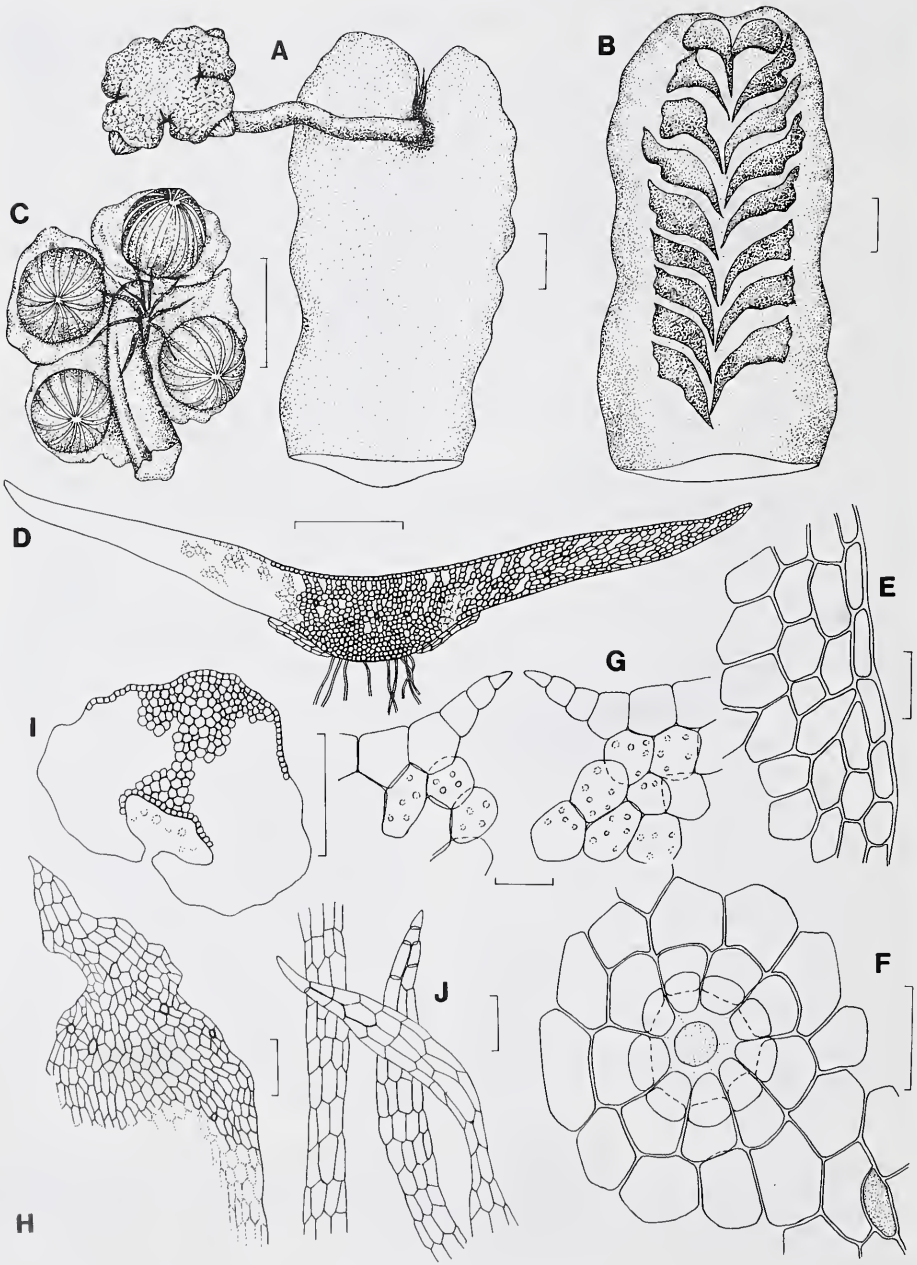
F. angolensis Steph.: 100 (1899); *Asterella angolensis* S.W.Arnell: 64 (1963a). Type: Angola, Huilla, waterfall, *Newton 25a* (*G001673*, holo.!).

Thalli large, in crowded, overlying mats; yellowish green, not areolate, pores hardly raised, margins dark red, gently scalloped, somewhat undulate; when dry, thallus margins slightly raised to inflexed. *Branches* simple or once pseudodichotomously furcate, sometimes with apical or ventrolateral innovations, broadly ligulate, widening rapidly from narrow base, 30–40(–75) mm long, 4.7–7.1 mm wide, 600–800(–950) µm thick medianly, in section 7 or 8 times wider than thick, apex notched, tips of scale appendages recurved over edge; groove absent, thallus dorsally flat to slightly concave, margins acute, thin; flanks sloping obliquely, reddish purple; ventral face medianly keeled, green. *Scales* in 2 ventral rows, obliquely triangular, purple-red, pink or hyaline, body 1000–1100 µm long, margin ± entire, base 950–1050 µm wide, continuing into long tail below, narrowed above, constricted where joined to large, ovate or roughly triangular appendage, (850–)1050–1200 µm long, apex apiculate, width 420–500 µm across widest part, cells distinctly larger than in base, ± 9 oil cells scattered throughout scale.

Dorsal epidermal cells unistratose, containing chloroplasts, thin-walled, 5- or 6-sided, 50–95 × 25–35 µm; air pores very slightly raised, simple, ± 17.5 × 8.0 µm, surrounded by innermost ring of small, collapsed cells and then by 2 concentric rings of (6–)7–9 larger cells in each. *Assimilation tissue* (150–) 250–320 µm thick, air chambers small, empty, in several storeys, bounding walls chlorophyllose; storage tissue 450–650 µm thick over keel, thinning out laterally, absent at margins, cells angular, walls thick, porate and sometimes with a network of striations; oil cells scattered throughout tissues.

Autoicous. *Androecia* in sessile, thickened cushions, oval or elongated or heart-shaped, near apex of main branch, or of ventrolateral innovation, antheridia immersed, opening above into conspicuous papillae. *Gynoecial receptacles* proximal to apical notch of main branch, single, occasionally paired at apices of 2 furcate branches, ± sessile when young, surrounded by up to 70 purple paleae, not arching over disc, at maturity raised on stalk; carpocephalum rounded, 3.5–5.0 mm across when bearing 4 or 5 capsules, sometimes with only 1 or 2, then smaller and asymmetric, above almost smooth or with low papillae further down. *Stalk* arising ± 2 mm proximal to apex of branch in apical notch, length variable, (2–)4–10(–20) mm long, often purple, widening toward base, at midlength ± 600 µm wide, with rhizoid furrow, at summit of stalk (and protruding from notches in head), dark purple paleae, occasionally pink or colourless, length variable, up to 2000 µm long, rarely as much as 3250 µm long, but then narrower, and only 3 cell rows wide, mostly up to 7 cell rows or ± 325 µm wide at base, gradually tapering to conical apical cell. *Involucre* membranous, partly covering capsule below. *Pseudoperianths* extending up to 1500 µm beyond involucre, generally with 16 segments, white or

FIGURE 12.—**Asterella marginata.** A, B, D, thallus: A, dorsal face with young carpocephalum raised on stalk and sessile androecium; B, ventral face; D, cross section. C, carpocephalum and pseudoperianths. E, F, air pore: E, c/s with air chamber; F, from above. G, marginal cells. H, I, scales: H, with 1 appendage; I, with 2 appendages. J, c/s of stalk; K, paleae. A, B, D–F, H, I, *S.M. Perold 2787*; C, *Pillans 3991*; G, *Arnell 505*; J, *Arnell 206*; K, *Koekemoer 316*. Scale bars: A–D, 1 mm; E–G, 50 µm; H–J, 250 µm; K, 100 µm. Drawings by A. Pienaar.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purple-stained, tapering to narrow, connate tips. *Sporophyte* with globose capsule, thin-walled and lacking thickening bands. Figure 13. *Spores* 115.0–152.5 µm diam., triangular-globular, mostly yellow; wing thin, somewhat scalloped, 20.0–22.5 µm wide, margin crenulate; distal face convex, with network of 5–8, ± smooth, angular, complete or incomplete alveoli across and extending over wing to margin on both sides, 25–30 × 20–25 µm, small subsidiary alveoli sometimes present and extending over crests of main ridges, 7.5–10.0 µm high; proximal face with prominent triradiate ridge, its arms up to 25 µm high and continuous from the pole across wing to margin, each of 3 facets with rounded alveoli, up to 20 × 20 µm, some with small, subsidiary alveoli, others appearing smooth and hollowed out. *Elaters* 225–230 µm long, 17.5 µm wide in centre, slightly tapering to ends, 12.5 µm wide, sometimes branched, bispiral, yellow. *Chromosome number*: unknown. Plate 6A–C.

In the *FSA* area *A. wilmsii* is known from Northern Province, Gauteng, Mpumalanga, Swaziland and KwaZulu-Natal. Map 4. The range of the species extends northward into Zimbabwe and Angola (the type specimen of *A. angolensis*) as well as Malawi (Bizot *et al.* 1976). It may also grow in Zaïre, a tentative conclusion based on the ovate scale appendages illustrated by Vanden Berghen (1972: fig. 74H, I and the distal spore face in fig. 74K), which suggest this species, although the material was merely designated as *Asterella* sp. by him. *Asterella wilmsii* was also reported from Mozambique by Arnell (1963a). The main distribution pattern along the mountains of the eastern part of the subcontinent suggests that it is an Afromontane species with isolated western outliers. It grows on damp soil along streambanks and waterfalls, sometimes in forested areas, forming dense mats, occasionally in association with *A. bachmannii* and *Symphyogyna* spp.

Asterella wilmsii is the largest of the southern African species in this genus. It can be distinguished from the others by the single, ovate or roughly triangular, large-celled appendage of the ventral scales, by the distinctly lobed disc of the carpocephalum, with purple paleae protruding from the notches and by the slightly broader-based paleae (up to 7 cells wide). The young, almost sessile archegoniophore is surrounded by purple paleae, which do not arch over it, as in *A. bachmannii*. The disc is less papillose and the spores are not as highly ornamented as those of *A. bachmannii*, often lacking smaller subsidiary alveoli in the large alveoli, which then appear to be almost smooth and hollow and extend across the wing. It is also not as widespread in southern Africa as *A. bachmannii* and it is far less frequently collected.

Vouchers: *Edwards CH1270; Glen 1675; Hardy 930; Kresfelder CH163; Mogg 37642; Perold 2914.*

CRYPTOMITRIUM

Cryptomitrium *Austin ex Underw.* in Bulletin Illinois State Laboratory of Natural History 2: 36 (1884); Schiffn.: 33 (1893); Steph.: 221 (1899); M.Howe: 43 (1899); A.Evans: 45 (1923); Hässel de Menéndez: 120 (1963); Perold: 149 (1994d). Type: *C. tenerum* (Hook.) Austin.

Platycoaspis Lindb. in Lindb. & Arnell: 11 (1889).

FIGURE 13.—**Asterella wilmsii**. A, B, D, thallus: A, dorsal face with stalk and carpocephalum; B, ventral face; D, cross section. C, carpocephalum from below; E, marginal cells. F, G, air pore: F, cells and oil cell from above; G, c/s with part of air chamber. H, ventral scale; I, c/s of stalk; J, paleae from summit of stalk. A, I, J, *S.M. Perold 2632*; B, C, *H. Anderson 1219a*; D, E, *Perold & Koekemoer 2836*; F–H, *Perold & Koekemoer 2830*. Scale bars: A–D, 1 mm; E–G, 50 µm; H, I, 250 µm; J, 100 µm. Drawings by A. Pienaar.

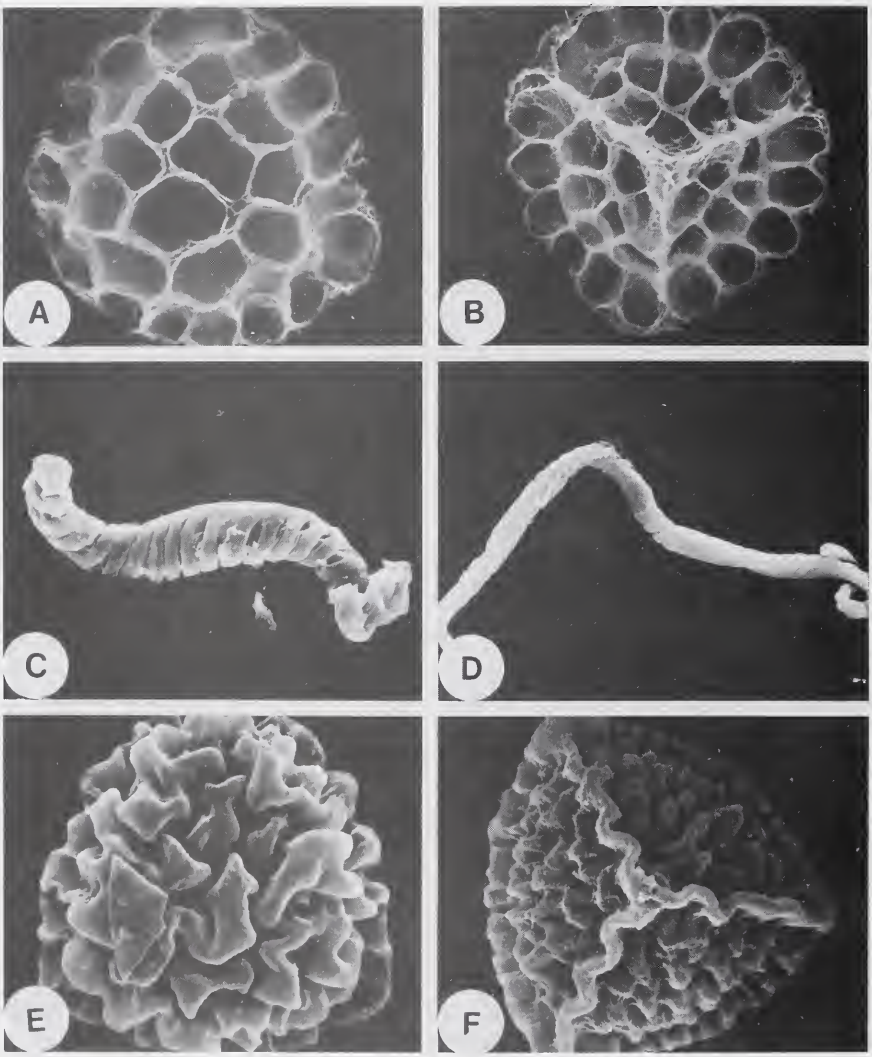


PLATE 6.—Spores and elaters. A–C, **Asterella wilmsii**: A, distal face; B, proximal face; C, elater. D–F, **Cryptomitrium oreades**: D, elater; E, distal face; F, proximal face. A, *Sim CH12679*; B, *Doidge 3187*; C, *Perold & Koekemoer 2836*; D, E, *Van Rooy 3051*; F, *Perold & Duckett 3228*. A, D, × 420; B, × 350, C, × 440; E, × 600; F, × 570.

Thalli smallish to medium-sized, in loose patches; green, somewhat spongy and delicate. *Branches* simple or rarely 1–3 times pseudodichotomously furcate, sometimes with apical or ventrolateral innovations, oblong to obovate, apex slightly notched, with scale appendages recurved over edge; groove absent, thallus dorsally rather flat to slightly concave, margins thin, acute, scalloped or irregularly crenate, green or brownish purple; flanks sloping very obliquely, deep purple and striate or green; ventral face medianly keeled. *Scales* ventral, small, in 2 rows, one on either side of keel, roughly triangular or broadly ovate, dark red or reddish pink, with 1 or 2(3) filiform appendages, margins occasionally with slime papillae, a few scattered oil cells present.

Dorsal epidermis hyaline, cell walls slightly thickened, with trigones prominent but not bulging, or lacking trigones, oil cells occasional or absent; air pores small, simple, slightly raised, surrounded by 3 or 4 concentric rings of 6–8 cells in each, radial walls not thickened. *Assimilation tissue* medianly with 3 or 4 storeys of empty air chambers, reduced to single storey at margin, bounding walls unistratose, chlorophyllose; storage tissue with closely packed, angular cells, not restricted to keel.

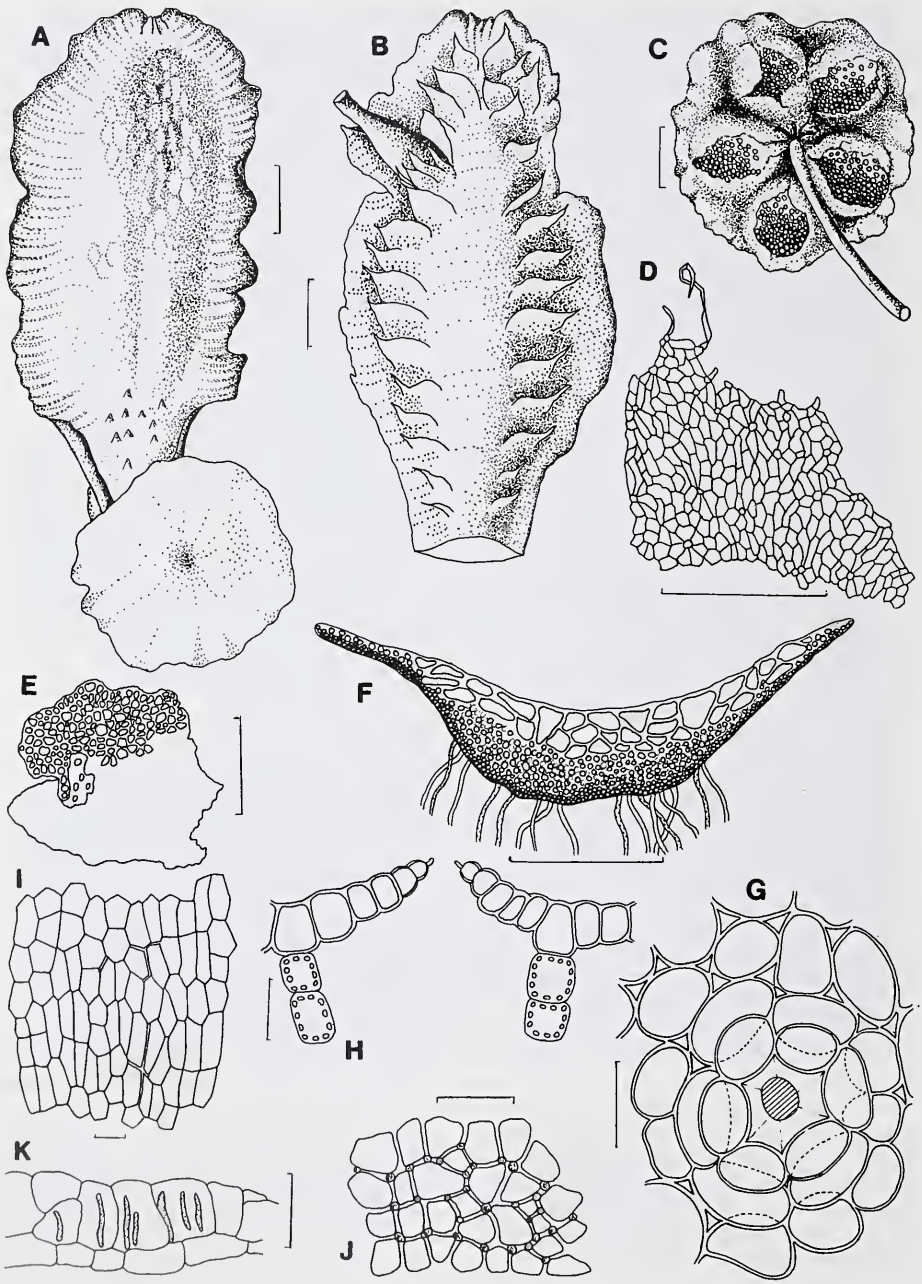
Autoicous, sometimes protandrous. *Androecia* in groups or rows, with sunken antheridia opening into conical papillae above. *Gynoecial receptacle* raised on stalk arising ventrolaterally at margin (in single southern African species) or dorsally at apical notch of thallus in extra southern African species; carpocephalum disciform-round, flattish on top, margins crenate, with one layer of air chambers opening above via compound air pores, below with (2)3–6 capsules. *Stalk* naked, slender, yellowish, lacking air chambers, but with 1 rhizoid furrow. *Involucre* membranous, bilabiate, lips parted by elongated radial cleft, this eventually opening and gaping. *Pseudoperianth* absent. *Sporophyte* with very short seta, foot bulbous, capsule nearly globose, wall thin, unistratose, apically bistratose, inner cells with thickening bands, dehiscing by operculum shed at annulus. *Spores* triangular-globular, winged; distal face with ± reticulate ornamentation, or with thick sinuate ridges; proximal face with thin, tall, conspicuous triradiate mark, each facet with incomplete alveoli. *Elaters* long, tapering, bispiral. *Chromosome number*: n = 9 [in *C. himalayense* (Mehra (1948)].

Worldwide only three species have been described in this genus: *C. tenerum* from North America (California and Washington State), as well as from Latin America (Mexico, Costa Rica, Guatemala, Chile and Argentina); *C. himalayense* is from India; recently, the genus was reported for the first time for the African continent, with the description of *C. oreades* from the Mountain Kingdom of Lesotho (Perold 1994d).

Cryptomitrium species can be recognized, when fertile, by a flattish disciform-round carpocephalum, with 3–6 ventrally borne capsules, each protruding from a bilabiate, radially arranged involucre; it is raised on a stalk with one rhizoid furrow but no air chambers.

Cryptomitrium oreades *Perold* in Bothalia 24: 149 (1994d). Type: Lesotho, 1 km from New Oxbow Lodge on road to Mokhotlong, ± 1/2 km from bridge, to the left, along Tiholohatsi River, at interface between basalt rock slope and grassy fringe, under large boulder in wet seepage area, on soil, in alpine heath-grassland, alt. ± 2 900 m, April 1994, *Perold & Duckett 3228* (PRE, holo.).

Thalli medium-sized, in loose patches; green, faintly areolate, air pores small, enlarging proximally, margins irregularly crenate to wavy, deep purple underside visible through thin dorsal tissue; when dry, thallus margins incurved or clasped together. *Branches* simple or once pseudodichotomously furcate, broadly linear to oblong, up to 12 mm long, 3–5(–6) mm wide, (450–)600–800 µm thick medianly, in section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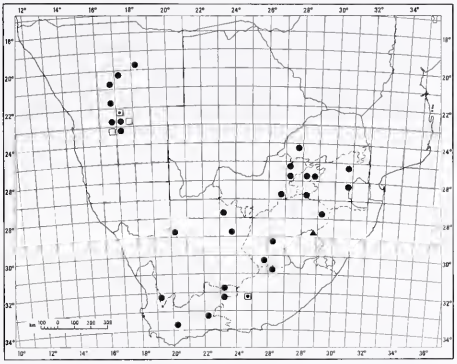
6–8 times wider than thick, apex slightly notched, with purple filiform tips of scale appendages recurved over edge; groove absent, thallus dorsally flat to slightly concave, margins acute, thin; flanks sloping very obliquely, purple; ventral face medianly keeled. *Scales* in 2 ventral rows, roughly triangular to transversely rectangular, dark red or reddish pink, smallish, body 300–410 µm long, margins here and there with slime papillae, base flat, 600–750 µm wide, narrowed above, with 1 or 2(3) filiform appendages, 150–590 µm long, basal cells in 2 rows, soon uniseriate, small oil cells scattered throughout scale.

Dorsal epidermal cells unistratose, hyaline, walls slightly thickened, trigones prominent, irregularly shaped or oval, 25.0–42.5 × 20.0–32.5 µm; air pores slightly raised, simple, 32.5 × 27.5 µm, surrounded by innermost ring of 6–8 small collapsed cells, then by 2 concentric rings of 6–8 larger cells in each, radial walls not thickened. *Assimilation tissue* 280–450 µm thick, air chambers empty, in 3 storeys, bounding walls chlorophyllose; storage tissue cells closely packed; oil cells scattered throughout tissues.

Autoicous. *Androecia* in diffusely arranged groups of antheridia sunken into dorsal tissue of thallus, opening into conical papillae. *Gynoecial receptacles* raised on stalk at maturity, mostly single, rarely 2 adjacent; carpocephalum disciform-round, not lobed, green, turning brown with age, 2.5–4.2 mm diam., rather flattish on top, with one layer of elongated air chambers, opening via compound air pores, 3–6 capsules borne below. *Stalk* erect, arising ventrally from below flank at side of keel, emerging laterally, close to dorsally borne antheridial group, 3–5 mm long, up to 490 µm wide, with single rhizoid furrow, base red, partly covered with purple scales, otherwise yellowish, summit surrounded by a few hyaline, filiform paleae.



MAP 6.— ▲ **Cryptomitrium oreades**
● **Mannia capensis**
□ **Athalamia spathysii**

Involucre membranous, formed by lips of elongated radial clefts, which eventually widen, exposing capsules. *Sporophyte* with short seta, capsule globose, 1100 µm diam., wall unistratose, apical cap bistratose, cells in inner layer thicker-walled, smaller, with rod-like thickenings, cap shed at annulus by dehiscence. Figure 14. *Spores* (77.5–)85.0–95.0 µm diam., light brown, semitransparent, triangular-globular; wing 7.5 µm wide, undulating and somewhat plicate, margin irregular; distal face convex with ornamentation hardly reticulate or with thick, sinuate ridges up to 5 µm high, irregularly branched and wavy, separated by deep fissures; proximal face with conspicuous triradiate mark, thin, tortuous, ± 7.5 µm high, extending onto wing, each facet with irregular, branching ridges, forming incomplete alveoli. *Elaters* light brown, bispiral, 210–275 µm long and 10 µm wide at widest part, tapering to tips, 5 µm wide. *Chromosome number*: unknown. Plate 6D–F.

Up to now *C. oreades* is known from only two localities in Lesotho, growing at high alti-

FIGURE 14.—**Cryptomitrium oreades.** A, B, F, thallus: A, dorsal face with carpocephalum on stalk emerging at side; B, ventral face; F, cross section. C, carpocephalum seen from below; D, ventral scale; E, c/s of stalk. G, H, air pore: G, from above; H, c/s with part of air chamber. I–K, capsule wall: I, thin, unistratose portion; J, bistratose apical portion with thickenings, from above; K, c/s of bistratose portion. A–C, E, F, I–K, *Van Rooy 3051*; D, G, H, *Perold & Duckett 3228*. Scale bars: A–C, F, 1 mm; D, 500 µm; E, 250 µm; G–K, 50 µm. Drawings by G. Condy.

tude in association with the moss *Gymnostomum aeruginosum* J.E.Sm. Map 6.

The species is characterized by a disciform-round carpocephalum borne on an erect, single-furrowed stalk which arises ventrally at the side of the keel and emerges laterally at the thallus margin in close proximity to the dorsally situated antheridial group.

Cryptomitrium oreades differs from the other two species in the genus mainly by the lateral position of its stalk. In *C. tenerum* and *C. himalayense* the stalk is dorsally situated near the apex of the thallus; the thalli are also thinner and more delicate than those of *C. oreades*.

Vouchers: *Perold & Koekemoer 3749, 3750*; *Van Rooy 3051*.

MANNIA

Mannia *Opiz*, Beiträge zur Naturgeschichte 12: 646 (1829); Frye & L.Clark: 60 (1937); R.M.Schust.: 601 (1953); Shimizu & S.Hatt.: 60 (1953); S.W.Arnell: 267 (1957); S.W.Arnell: 71 (1963a); R.M.Schust.: 177 (1992c); Perold: 9 (1994a). Type: *M. raddii* Opiz = *M. triandra* (Scop.) Grolle.

Grimaldia Raddi: 356 (1818); Steph.: 792 (1898); M.Howe: 40 (1899); A.Evans: 43 (1923); Sim: 21 (1926). Type: *G. dichotoma* Raddi, nom. illegit.

Synonymy partly after Grolle: 56 (1983a).

Thalli smallish to medium-sized, in crowded patches; bright green, sometimes laterally reddish or bronzed, margins black, somewhat scalloped, firm, compact, rather leathery, lacunose proximally. *Branches* simple or once, rarely twice, pseudodichotomously furcate, or with apical or ventrolateral innovations, linear or strap-shaped, apex ± entire, black tips of scale appendages recurved over edge; groove absent, thallus dorsally flat to slightly concave, margins rather thin, acute; flanks sloping obliquely, black and shiny; ventral face medianly broadly keeled. *Scales* ventral, in 2 rows, obliquely triangular or semilunate, red-black, with 1 or 2 linear-lanceolate appendages, not constricted at base, a few scattered oil cells present.

Dorsal epidermis hyaline, cell walls thin to thickened, with trigones; air pores simple, inconspicuous, slightly raised, surrounded by 2 or 3 concentric rings of 5–7 cells in each, radial walls not thickened. *Assimilation tissue* with 2 or more storeys of repeatedly subdivided air chambers, generally without chlorophyllose filaments, bounding walls complete or incomplete; storage tissue well developed, with closely packed, angular cells; few cells with an oil body.

Dioicous, rarely autoicous, then androecia and gynoecia generally on different branches. *Androecia* with antheridia sunken in 2 to several rows along centre of branches in the single southern African species, otherwise in small, median, round or oval discs, opening above into conical papillae. *Gynoecial receptacle* emerging from apical sinus formed by subsequent growth of thallus lobes of main or ventrolateral branch; carpocephalum domed to low conical, centrally papillose with compound air pores, not, or scarcely lobed beneath. *Stalk* length variable, with one rhizoid furrow, at base and summit often with paleae. *Involucre* membranous, wide-mouthed and bell-shaped, not bilabiate. *Pseudoperianth* absent. *Sporophyte* with short seta, globose capsule protruding, wall lacking thickening bands, dehiscing by discrete apical lid. *Spores* roughly triangular-globular; distal face with conspicuous hemispherical bullae, sometimes collapsed; wing thick and undulating; proximal face on raised platform, with low triradiate mark. *Elaters* tapering, bi- or trispiral. *Chromosome number*: n = 9.

Mannia is said by Schuster (1992c) to be a relatively large genus with ± 18 species worldwide, but Engel (1990) states that there are only six. All of them, except *M. capensis*, are from the northern hemisphere.

The genus was originally known as *Grimaldia* Raddi, but the specimen on which it was based, contained two elements. Evans (Herzog 1938) showed that the name, *Grimaldia*, is illegitimate and recently Grolle (1983b) submitted a proposal to conserve the name, *Mannia* Opiz (1829) against *Cyathophora* Gray (1821). Grolle created two subgenera: *Arnelliella* (Mass.) Grolle, with section *Neesiella* (Schiffn.) Shimizu & S.Hatt. and *Xeromannia* Grolle with sections *Xeromannia* and *Sindonisce*.

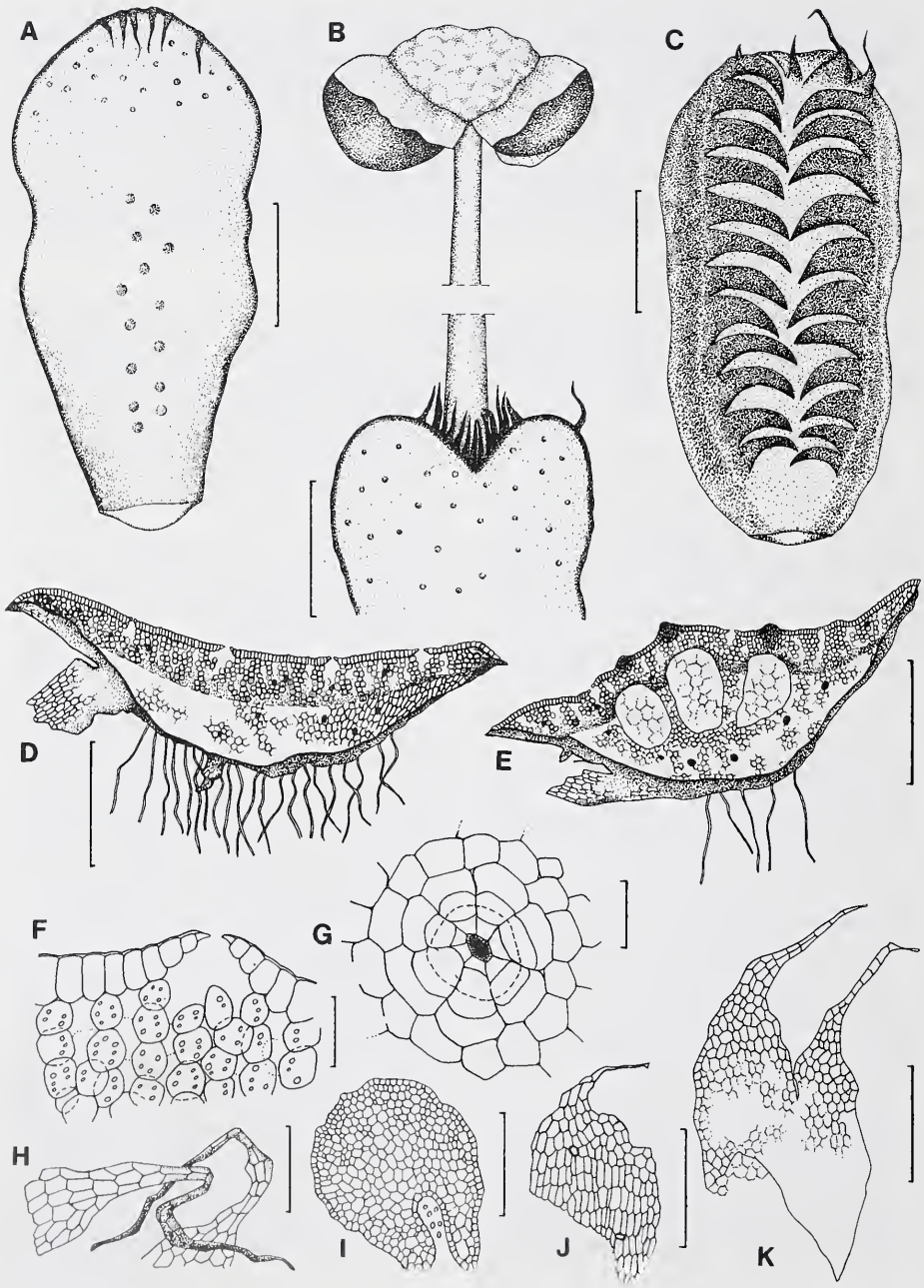
Schuster (1953, 1992c) is, however, convinced that the division of *Mannia* into subgenera, based largely on the form of the aerenchyma tissue 'compact' versus 'loose', is artificial. He concluded that it 'is perhaps an artifact based on environmentally induced distinctions' (Schuster 1956).

Mannia capensis *(Steph.) S.W.Arnell* in Mitteilungen der Botanischen Staatssammlung, München 16: 263 (1957); S.W.Arnell: 72 (1963a); O.H.Volk: 233 (1979); Perold: 9 (1994a). Type: Bloemfontein, leg. *Rehmann* (G, holo.!).

Thalli smallish to medium-sized, in crowded patches; bright green, sometimes laterally reddish or bronzed, firm, compact, faintly areolate, air pores numerous, small, margins with narrow black borders distally, gradually widening proximally, somewhat scalloped; when dry, thallus margins tightly incurved and branches almost tubular. *Branches* simple or once, rarely twice, pseudodichotomously furcate, sometimes with apical or ventrolateral innovations, linear or strap-shaped, up to 12 mm long, 2–4 mm wide, 525–775 µm thick medianly, in section 4 or 5 times wider than thick, apex entire, tips of ventral scales reflexed over edge; groove absent, thallus flat to slightly concave dorsally, margins acute, quite thin; flanks sloping obliquely; ventral face medianly broadly keeled, black. *Scales* in 2 ventral rows, obliquely triangular or semilunate, black to reddish black, body ± 600 µm long, margins sometimes with few mucilage papillae, base concave, ± 600 µm wide, narrowed above without constriction to 1 or 2(3) linear-lanceolate appendages, up to 110 µm long, ± 17 µm wide at base, tapering to acute apex, oil cells scattered throughout.

Dorsal epidermal cells unistratose, hyaline, trigones conspicuous but not bulging, externally covered with minute spicules, polygonal, 27–30 × 15–25 µm; air pores slightly raised, simple, ± 25 × 15 µm, surrounded by innermost ring of 7 small, collapsed cells, then by 2 concentric rings of 7(8) larger cells in each, radial walls not thickened. *Assimilation tissue* 200–250 µm thick, air chambers in several storeys, densely crowded and incompletely bounded by unistratose walls, difficult to distinguish between bounding cells and those forming chlorophyllose filaments; storage tissue well developed, cells angular; oil cells scattered throughout tissues.

Dioicous, rarely monoicous, but gametangia generally on different branches. *Androecia* with 2 to 4 rows of sunken antheridia along centre of branches, opening into conical papillae. *Gynoecial receptacles* terminal when young, sessile, knob-like, in V-shaped, apical sinus, surrounded by numerous, arched, dark purple lanceolate paleae, up to 1150 µm long, 4–6 cells wide at base, narrowing to one cell wide at apex, at maturity raised on stalk; carpocephalum ± 2 mm across, straw-coloured, domed to low conical, papillose centrally with compound pores, not or scarcely lobed below, bearing (1)2–4 capsules. *Stalk* 5–25 mm long, cylindrical, 400 µm wide, with single rhizoid furrow, only a few paleae carried along and also present at summit, but obscured. *Involucres* membranous, wide-mouthed and bell-shaped, each with single capsule. *Sporophyte* with short seta, capsules protruding, globose, dark brown, wall lacking annular thickenings, dehiscing by well-formed lid along row of smaller cells. Figure 15. *Spores* 75–80 µm diam., polar, roughly triangular-globular, light brown, semitransparent; wing lighter, straw-coloured, 7.5 µm wide, porate at each of 3 angles (or in between as well), wavy and undulating, inflated and twisted in side view; distal face convex, bearing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10–13 crowded and very conspicuous, hemispherical bullae, ± 22 µm wide, mostly well separated from each other, occasionally 1 or 2 collapsed, proximal face with raised base, triradiate mark present but weak, slightly raised or not, arms not extending to edge, with shallow, crowded and overlying alveoli in centre, both faces generally covered with granules. *Elaters* reddish brown, tapering toward ends, 212–275 µm long, 12.5 µm wide in centre, 7.5 µm wide at tips, bi- or trispiral. *Chromosome number*: n = 9. Plate 7A–C.

The species has been reported from Zimbabwe (Best 1990) and Bizot & Pócs (1982) reported its occurrence as disjunct in East Africa on the Uluguru Mountains, where it grows in open, exposed sites. Although not common, *Mannia capensis* has been collected over a wide area in southern Africa. It is known from Namibia, Northern Province, North-West, Gauteng, Mpumalanga, Free State, Northern, Western and Eastern Cape. Map 6. It is found in rocky clefts or on shallow soil covering granite, quartzite, sandstone or sometimes dolomite, occasionally in association with other liverworts such as *Riccia* spp., *Plagiochasma* spp. or with *Exormotheca pustulosa*. It is a pronounced xerophyte, with the storage tissue markedly thicker than the assimilation tissue.

Fertile plants of *M. capensis* can be distinguished quite readily from other members of the Marchantiales by the stalked, domed and unlobed carpocephala, lacking a pseudoperianth. Sterile specimens are more difficult to distinguish, particularly from *Targionia hypophylla* and small *Asterella* plants. In *T. hypophylla*, however, the dorsal air pores are larger, and, when dry, white-encircled; in *Asterella* species, with the exception of *A. muscicola*, the air pores and air chambers are generally difficult to detect from above, fresh or dry.

Vouchers: *Brusse 4206; Burrows 2521; Glen 2461; Koekemoer 637a; Mogg 37590; Perold 947.*

CLEVEACEAE

Cleveaceae *Cavers* in New Phytology 10: 42 (1911); Müll.Frib.: 368 (1951–1958); Hässel de Menéndez: 133 (1963); R.M.Schust.: 103 (1992c). Type: *Clevea* Lindb.

Astroporae Leitg. (1881).

Cleveideae Solms: 15 (1899).

Cleveoideae Lotsy: 103, 114 (1909).

Sauteriaceae A.Evans: 35 (1923).

Thalli medium-sized, in crowded patches; bright green or glaucous green, sometimes purple along margins. *Branches* simple or once pseudodichotomously furcate, occasionally with ventrolateral or apical innovations, ligulate or oblong to broadly ovate to obovate, apex hardly notched, tips of some apical scales projecting beyond or recurved over edge; groove absent, thallus medianly concave dorsally, margins acute, thin, attenuate, scalloped and undulate, occasionally somewhat erect; flanks sloping obliquely or steep, sometimes deep purple; ventral face medianly keeled

FIGURE 15.—**Mannia capensis**. A–E, thallus: A, dorsal face of male with rows of antheridia; B, apical portion of female with stalk arising from apical sinus and at its tip bearing unlobed archegoniophore, involucres partly covering 2 capsules; C, ventral face showing scales; D, cross section; E, c/s of male through antheridia. F, G, air pore: F, c/s dorsal cells and assimilation tissue; G, from above. H, paleae from foot of stalk; I, c/s of stalk. J, K, scales: J, with 1 appendage; K, with 2 appendages. A–D, G–I, K, *Glen 2117*; E, F, J, *Koekemoer 637*. Scale bars: A–C, 1 mm; D, E, 500 µm; F, G, 50 µm; H, I, 250 µm; J, K, 500 µm. Drawings by A. Pienaar.

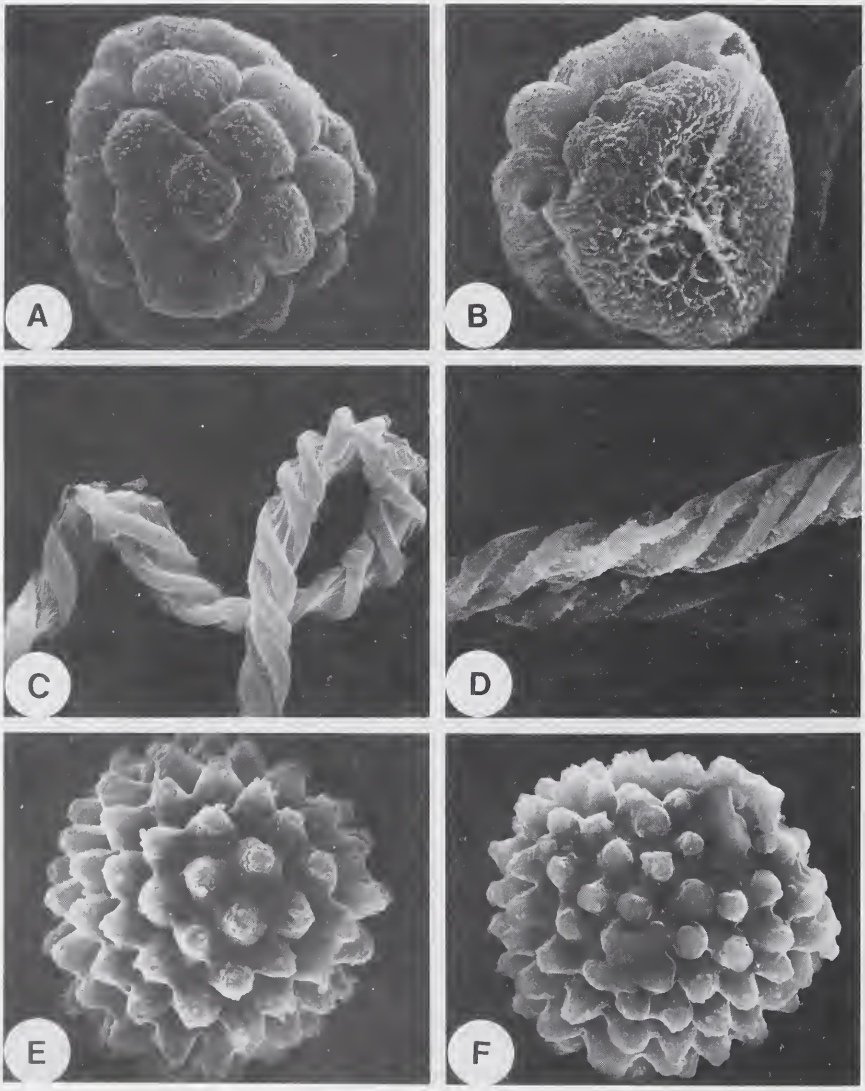


PLATE 7.—Spores and elaters. A–C, **Mannia capensis**: A, distal face; B, proximal face; C, elater. D–F, **Athalamia spathysii**: D, elater; E, distal face; F, proximal face. A, B, *Eyles CH1179*; C, *Volk 00828*; D–F, *Volk 00589*. A, B, × 700; C, × 410; D, × 1290; E, × 740; F, × 620.

or flattish. *Scales* ventral, in 2 or more, regular or irregular rows, obtusely triangular, hyaline or purple-red, with long-acuminate appendage, not constricted at base, margins sometimes with slime papillae, tips extending beyond thallus margins or not, oil cells absent.

Dorsal epidermis hyaline or with chloroplasts, cell walls thin, with or without minute trigones; air pores simple, small, slightly raised, encircling wall ± thickened, often stellate, surrounded by one ring of cells, radial walls generally thickened. *Assimilation tissue* with one or several storeys of empty air chambers, cells in bounding walls chlorophyllose; storage tissue poorly or well developed; with occasional oil cell, but mostly without; with or without mycorrhiza.

Asexual reproduction absent.

Monoicous or dioicous. *Androecia* with antheridia hardly aggregated, in loose, sessile, ill-defined groups or in median rows along length of thallus, opening into projecting papillae. *Gynoecial receptacle* single or several along midline, arising from dorsal depression, proximal to apex of branch; carpocephalum sessile when young, surrounded by tuft of hyaline or reddish paleae, at maturity raised on stalk, developing (1–)2 or 3 arms, air chambers and pores vestigial or absent. *Stalk* ± colourless, lacking rhizoid furrow, at summit with few paleae. *Involucres* directed obliquely upwards, often somewhat beaked or pointed at upper ends, basally connate. *Sporophyte* with globose capsule on short seta, obliquely erect, wall with thickening bands, dehiscing by irregular valves. *Spores* rounded distally, somewhat flattened proximally, lacking triradiate mark, densely covered with conical spines. *Elaters* long, tapering, bispiral. *Chromosome number*: n = 9, 18.

Three genera, *Athalamia* Falc., *Peltolepis* Lindb. and *Sauteria* Nees are classified in the family Cleveaceae, but neither of the latter two occur in southern Africa. The above family description excludes them.

The family is known from alpine and arctic or sometimes from warm, low-lying areas.

ATHALAMIA

Athalamia *Falc.* in Annals and Magazine of Natural History, Ser. 2,1: 375 (1848); Falc.: 397 (1851); Shimizu & S.Hatt.: 52 (1954); S.W.Arnell: 57 (1963a); Perold: 207 (1993b). Type: *Athalamia pinguis* Falc.

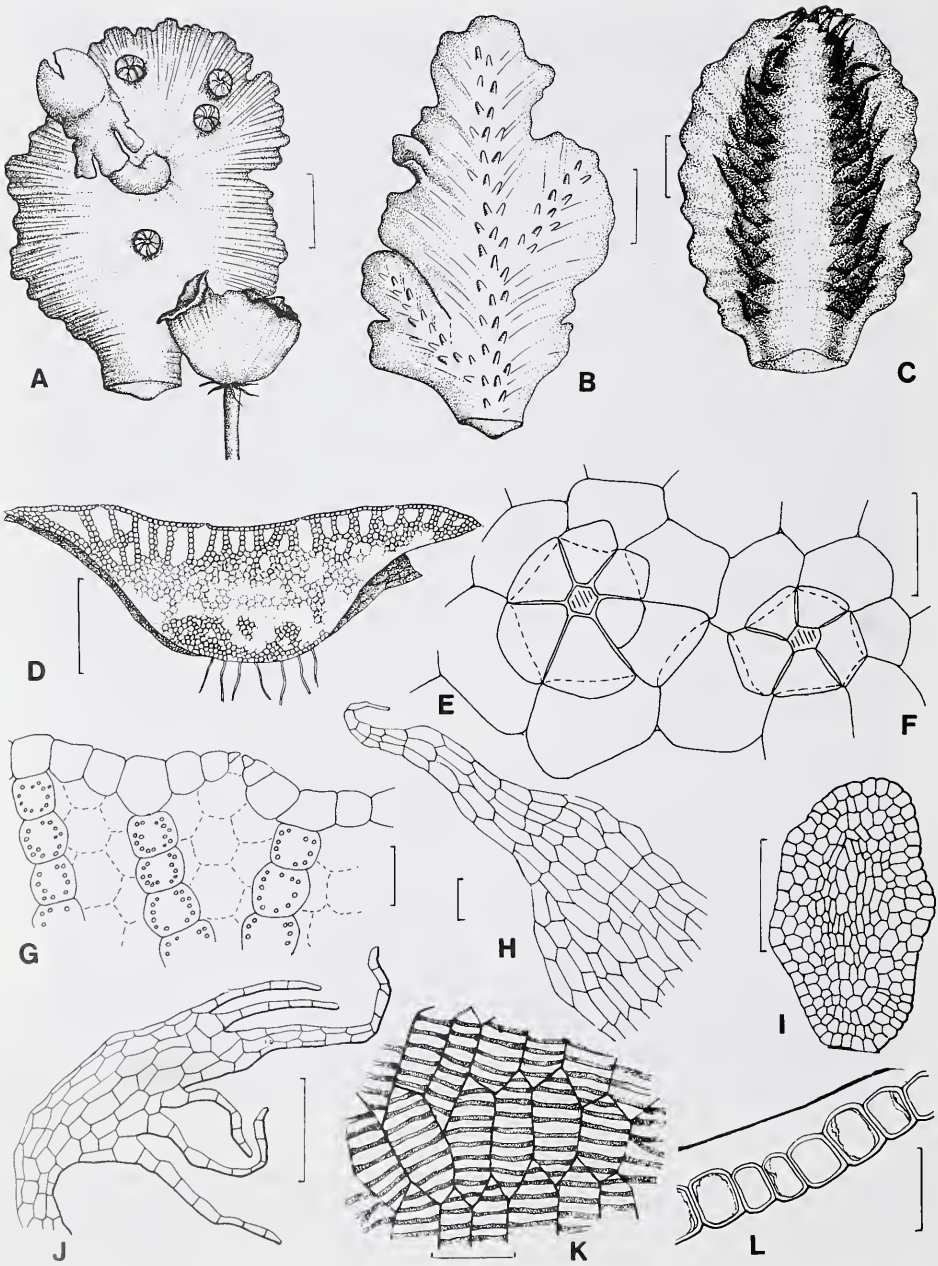
Clevea Lindb. 9: 289 (1868); Steph.: 769 (1898); Schiffn.: 29 (1893); M.Howe: 36 (1899); Müll.Frib.: 368 (1951–1958); Hässel de Menéndez: 133 (1963). Type: *Clevea hyalina* (Sommerf.) Lindb.

Spathysia Nees ex Trevis.: 439 (1877). Type: *Spathysia lindenbergii* Trevis. nom. illegit.

Gollaniella Steph.: 74 (1905). Type: *Gollaniella pusilla* Steph.

Characters the same as those of the family as represented in southern Africa.

There are at least 10 or even 15 species world-wide in the genus *Athalamia*, with *A. spathysii* the only representative in southern Africa; *A. pulcherrima* (Steph.) S.Hatt. from Ethiopia is distinguished by larger, hyaline, ventral scales and cells with much thickened radial walls surrounding the dorsal air pores. Another species recorded from Africa in Algeria, is *Clevea (Athalamia) trabutiana* Steph., but it is regarded by Grolle (1976) as conspecific with *A. hyalina* (Sommerf.) S.Hatt.; *Clevea (Athalamia) crassa* Trabut from the Atlas Mountains (Magreb) is also very similar to *A. hyalina* (Müll.Frib. 1951–1958), but Grolle (1976) considers it to be a '*nom. inval.*'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According to Müller (1939), Arnell (1963a), Vanden Berghen (1965) and Volk (1979) oil bodies are absent in the genus *Athalamia* (= *Clevea*). Perold (1993b) also found them to be absent in *A. spathysii*, but fresh material was not available for study. Shimizu & Hattori (1954), however, reported oil cells in *Athalamia glauco-virens* as well as in *A. nana* (Shimizu & Hattori 1955). Schuster (1992c) states that sparse, scattered oil cells may be present or absent.

Shimizu & Hattori (1954) also stated that 'whether the pores of the thallus are stellate or not, should not be considered a characteristic of generic value'. Sometimes they had observed pores with both thickened radial walls (stellate) or with thin walls (not stellate) on the same plant.

Asexual reproduction is said to be absent. Stephani (1895) suspected that adventitious growth in the form of ventral shoots from the costa was partly the reason for the 'dichten verfilzten niedrigen Rasen' in *Clevea pulcherrima* Steph. As in *Plagiochasma* spp., the apical part of the thallus continues to grow and increase in length, beyond the archegoniophore, after the latter has differentiated.

Athalamia spathysii *(Lindenb.) S.Hatt.* in Shimizu & S.Hatt. in Journal of the Hattori Botanical Laboratory 12: 54 (1954); S.W.Arnell: 57 (1963a); Vanden Berghen: 168 (1965); O.H.Volk: 230 (1979); Perold: 207 (1993b). Type: Greece, Corfu, leg. *Spathys* (W, holo.!; STR, iso.).

Marchantia spathysii Lindenb.: 104 (1829); Bisch.: 1018 (1835). *Dumortiera spathysii* (Lindenb.) Nees: 171 (1838); Gottsche et al.: 546 (1844–1847). *Clevea spathysii* (Lindenb.) Müll.Frib.: 75 (1940a); Müll.Frib.: 374 (1951–1958).

Plagiochasma rousselianum Mont.: 334 (1838b). *Clevea rousseliana* (Mont.) Leitg. in Steph.: 771 (1898). Type: Algeria, 'Boudjareah', *Roussel.*

Thalli medium-sized, in crowded patches; bright green, areolate, air pores tiny, slightly raised, margins wine-red, scalloped, undulate, often somewhat erect, older parts dead; when dry, thallus margins incurved and tightly clasped together above. *Branches* simple or once pseudodichotomously furcate, oblong to broadly ovate or obovate, (3.5–)5.0–12.0 mm long, 2.5–7.5 mm wide, 825–1075 µm thick medianly, in section 3–7 times wider than thick, apex slightly notched, with tips of 2 or 3 purple-red scales recurved over edge; groove absent, thallus dorsally slightly concave medianly, margins acute, thin; flanks sloping obliquely, purple; ventral face medianly keeled, green. *Scales* in 2 ventral rows, obtusely triangular, purple-red, body 550–600 µm long, margins entire or sometimes bluntly toothed on oblique side, base ± straight to slightly concave, 850–1000 µm wide, narrowed above without constriction to acuminate, apically tapering and pointed appendage, 575–750 µm long, 150–200 µm wide at base, oil cells absent.

Dorsal epidermal cells unistratose, hyaline, ± polygonal, (32.5–)57.5–62.5 ± 30.0–42.5 µm, thin-walled, but frequently thickened at corners; air pores very slightly raised, simple, 7.5–12.5 µm wide, surrounded by one ring of 4–6(–7) bluntly triangular cells, partly overlying adjacent dorsal cells, encircling and radial walls mostly thickened, pores thus stellate. *Assimilation tissue* 350–500 µm thick, air chambers empty, in one storey, sometimes in several, walls unistratose, chlorophyllose; storage tissue with cells fairly densely packed together, rounded.

FIGURE 16.—**Athalamia spathysii**. A–D, thallus: A, dorsal face with stalked archegoniophore and several young sessile ones; inset with archegoniophore and 2 dehiscing capsules; B, dorsal face with rows of antheridia; C, ventral face; D, cross section. E–G, air pore: E, F, with thickened radial walls; G, c/s with dorsal epidermis and air chambers. H, ventral scale; I, c/s of stalk; J, palea from top of stalk; K, L, capsule wall: K, cells with annular thickenings; L, cross section. A, I–L, *Volk 00589*; B, *Volk 6124*; C–H, *Volk 00904*. Scale bars: A–C, 2 mm; D, 1 mm; E–G, K, L, 50 µm; H, J, 200 µm; I, 100 µm. Drawings by A. Pienaar.

Monoicous, but occasionally only antheridia or archegonia found. *Androecia*, with antheridia in rows along entire middle of thallus, sunken, opening into raised, conical papillae. *Gynoecial receptacle* single or several, ± linearly and acropetally arranged on dorsal face, sessile when young, rounded and basally surrounded by inconspicuous, filiform paleae, at maturity raised on stalk; carpocephalum white to greenish white, central disc absent. *Stalk* cylindrical, pellucid, 1.6–7.0 mm long, 250 µm diam., without rhizoid furrow; paleae eventually carried upwards and only present at its summit, hyaline or pink, basally 750 × 500 µm, apically with 4 or 5 filiform strands, up to 750 µm long. *Involucres* 1–3(4), connate at their bases, attached to top of stalk, bilabiate by vertical cleft, each one with single capsule. *Sporophyte* with capsule globose, 1250 µm diam., borne obliquely erect on seta with bulbous foot, dehiscing by several irregular valves, wall unistratose, cells with annular thickening bands. Figure 16. *Spores* (60–)65–75(–78) µm diam., globular, golden brown, semitransparent, both faces thickly covered with dense conical spines, 5 µm high and 15 µm wide at base, sprinkled with fine granules; distal face convex; proximal face without triradiate mark, somewhat flatter. *Elaters* yellow-brown, slightly tapering toward ends, 275–350 µm long, 7.5–10.5 µm wide in middle, bispiral, very occasionally branched, sometimes bent. *Chromosome number*: n = 9 (Bornefeld 1987); as *Clevea rousseliana*: n = 9 (Heitz 1927). Plate 7D–F.

Athalamia spathysii is known from Israel, North Africa, the Canary Islands and the Mediterranean countries (Müll.Frib. 1951–1958); the type specimen was collected at Corfu. Frey & Kürschner (1988) report it from Yemen and Oman in the Arabian Peninsula, and state that its distribution includes Turkey and Jordan. It has also been reported from eastern Africa, i.e. from Tanzania (= Tanganyika) by Vanden Berghen (1965).

Athalamia spathysii has rarely been collected in southern Africa; the gatherings by Volk (1979) are restricted to Namibia. It was recently also collected in the Eastern Cape. Map 6. It grows in periodically dry areas, on soil overlying slate, granite or sandstone, in rocky crevices or under overhangs, where runoff may be concentrated and some protection against radiation is afforded; sometimes it occurs together with *Plagiochasma* spp. and *Targionia hypophylla*.

The species is distinguished by the areolate dorsal surface of the thallus, small and slightly raised, mostly stellate air pores, empty air chambers, scales with acuminate appendages, lack of oil cells, cell walls of capsule with spiral thickenings and by bluntly spinous spores.

Sterile specimens of *A. spathysii* have been confused with *Asterella muscicola* (Arnell 1957), because of the stellate dorsal pores, but the latter does not grow in Namibia (Volk 1979), its ventral scales have scattered oil cells, the stalk has a rhizoid furrow and the capsule wall lacks thickenings.

Vouchers: *Perold 945; Schelpe 4763; Volk 00952, 6124.*

EXORMOTHECACEAE

Exormothecaceae *Müll.Frib.* in Grolle, Journal of Bryology 7: 208 (1972); Müll.Frib.: 275 (1940b); Müll.Frib.: 397 (1951–1958); Hässel de Menéndez: 192 (1963); S.W.Arnell: 74 (1963a). Type: *Exormotheca* (Godm.) Mitt.

Thalli small to medium-sized to quite large, in crowded patches; silvery glaucous-green, margins not differentiated, dorsally completely covered with numerous conical evaginations of epidermis, ventrally fleshy. *Branches* simple or once, sometimes twice (–3 times) pseudodichoto-

mously furcate, ligulate or narrowly to broadly linear or ovate, apex entire to shallowly notched, apical (and other) scales mostly erect, only when dry recurved over edge; groove absent, thallus dorsally slightly concave medianly, otherwise flat, margins somewhat obtuse, becoming more acute proximally; flanks sloping obliquely to rather steeply; ventral face medianly rounded. *Scales* ventrolateral, oblong to rounded or obliquely triangular, purple or hyaline with purple base, occasionally with 1 or 2 appendages, or with long, filiform appendages at acute apex, margins often toothed, extending to or above thallus margins, oil cells absent.

Dorsal epidermis unistratose, hyaline, thin-walled, without trigones, raised as pustular or conical evaginations over low or tall air chambers; air pores simple, at or near apices of evaginations, surrounded by thin-walled cells. *Assimilation tissue* with air chambers elevated, low or tall, basally occupied by densely crowded, chlorophyllose filaments in one storey; storage tissue occupying ventral part of thallus, in somewhat loose mesh of open, round spaces, surrounded by smaller, angular cells; with scattered oil cells.

Asexual reproduction rare.

Monoicous or ?dioicous. *Androecia* with antheridia sunken in rows in shallow groove, along middle of thallus, sometimes interrupted, necks protruding conspicuously, development of air chambers here temporarily suppressed. *Gynoecial receptacle* raised on stalk or sessile; carpocephalum with central core of parenchymatous tissue, supporting filament-containing air chambers that open above via simple air pores, capsules usually borne laterally. *Stalk*, when present, with single rhizoid furrow, lacking paleae. *Involucre* tubular or not, bilabiate, lateral extensions of central area or dome. *Sporophyte* 1 or 2 per involucre, sometimes none, capsules globose, exserted on seta or not, wall with semi-annular thickenings, dehiscing by 4 or 5 irregular valves. *Spores* smallish to large, triangular-globular; distal face with large, hollow, conical papillae covered with granules; proximal face without distinct triradiate mark, heavily encrusted with granules. *Elaters* long or short, tapering or blunt, tri- or unispiral. *Chromosome number*: n = 16, 18, 32.

Three genera, *Exormotheca* (Godm.) Mitt., *Aitchisoniella* Kashyap and *Stephensoniella* Kashyap are classified in the family Exormothecaceae, but the last two are restricted to India. The family description above excludes them. The genus *Exormotheca* is widespread and is known from several Mediterranean countries, Atlantic and Indian Ocean islands, north, tropical and southern Africa, the Middle East, India, and Sri Lanka (Ceylon), as well as from South America (Brazil and Argentina) and possibly Mexico.

EXORMOTHECA

Exormotheca *(Godm.) Mitt.* in Natural history of the Azores or Western Islands: 325 (1870); Schiffn.: 29 (1893); Solms: 2 (1897); Steph.: 218 (1899); Müll.Frib.: 292 (1905–1916); Schiffn.: 40 (1942); Müll.Frib.: 398 (1951–1958); Hässel de Menéndez: 193 (1963); Perold: 15 (1994b). Type: *E. pustulosa Mitt.*

Myriorrhynchus Lindb. & Arnell: 8 (1884). Type: *M. fimbriatus* Nees.

Corbierella Douin & Trab.: 321 (1916). Type: *C. algeriensis* Douin & Trab.

Characters the same as those of the family as represented in southern Africa.

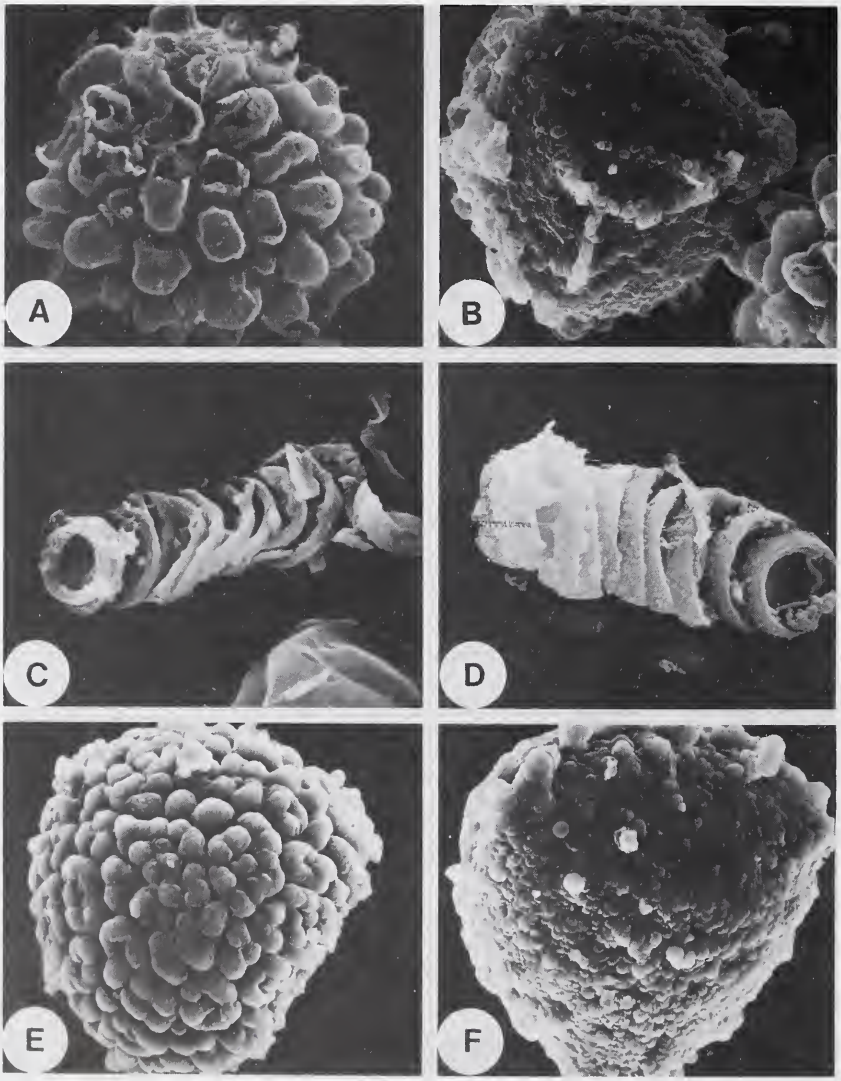


PLATE 8.—Spores and elaters. A–C, **Exormotheca pustulosa**: A, distal face; B, proximal face; C, elater. D–F, **E. holstii**. D, elater; E, distal face; F, proximal face. A, B, *Arnell 791*; C, *Perold & Koekemoer 3133*; D–F, *Holst 3107*. A, × 690; B, × 660; C, × 930; D, × 860; E, × 380; F, × 390.

Three sections are recognized in the genus *Exormotheca*: *Exormotheca,* for *E. pustulosa, E. tuberifera* and *E. ceylonensis*; *Corbierella* (Douin & Trab.) Schiffn., for *E. welwitschii, E. algeriensis* and *E. holstii*; and *Myrriorhynchus* Lindb. & Arnell, for *E. fimbriata* (Schiffner 1942). The last section does not occur in southern Africa, only in Brazil and Argentina, and is distinguished by scales with fan-shaped, multibranched, filamentous appendages.

Key to sections and species of *Exormotheca* in southern Africa

Thalli smallish; assimilation tissue with air chambers inflated into low, conical protuberances, basal $^2/_3$ occupied by chlorophyllose filaments; ventral scales small, oblong to rounded, often purple, with 1 or 2 filiform appendages; gynoecial receptacle mostly on longish stalk; elaters long, trispiral . . . . . section *Exormotheca*: 1. *E. pustulosa*

Thalli medium-sized to quite large; assimilation tissue with air chambers inflated into tall conical protuberances, basal $^1/_5$–$^1/_3$ occupied by chlorophyllose filaments; ventral scales large, ± obliquely triangular, hyaline, apex with up to 5 filiform appendages; gynoecial receptacle sessile; elaters short, unispiral or ringed . . . . . section *Corbierella*: 2. *E. holstii*

Exormotheca section **Exormotheca**

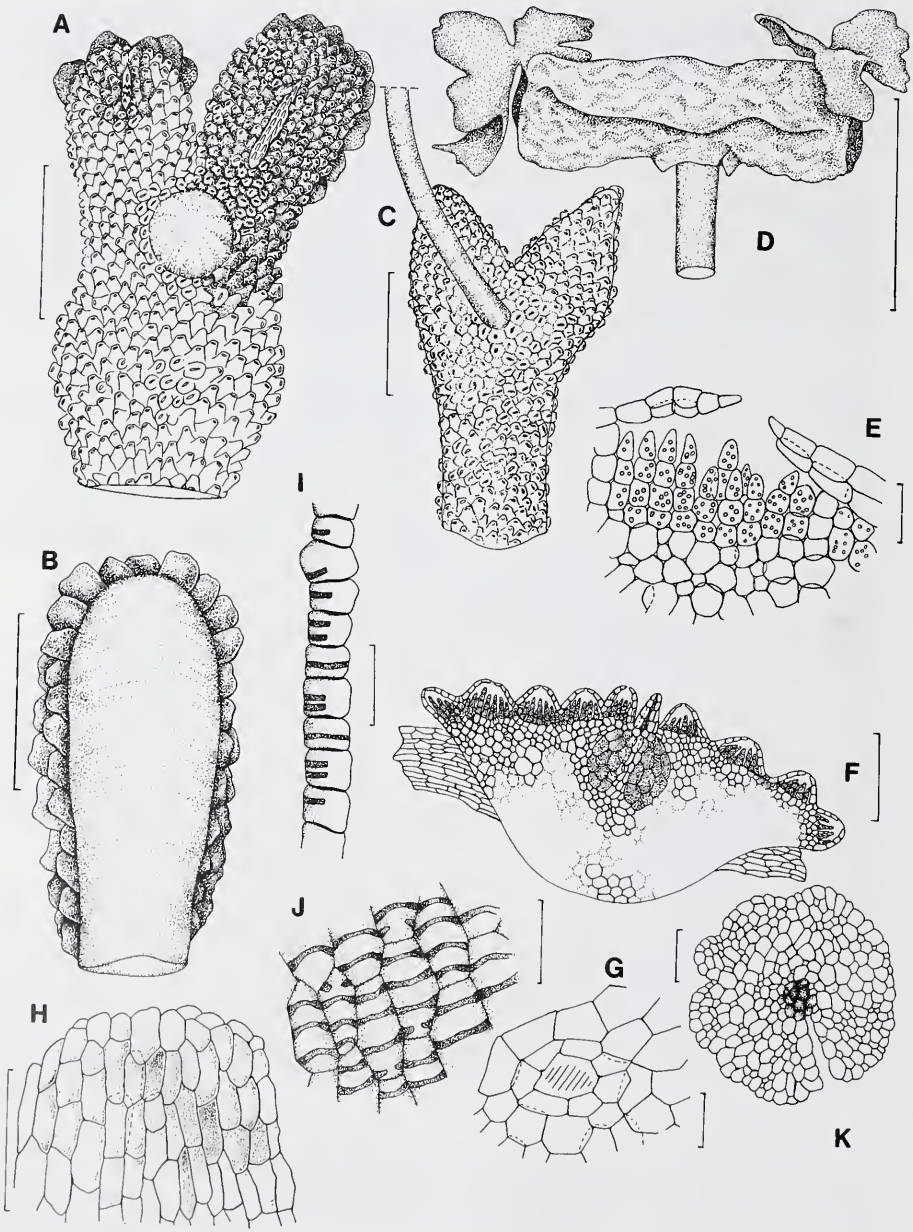
Thalli smallish with low, conical air chambers, lower ± $^2/_3$ filled with chlorophyllose cell filaments. *Scales* oblong or rounded, purple or partly hyaline. *Gynoecial receptacles* stalked. *Elaters* rather long, trispiral. *Exormotheca pustulosa* belongs here.

1. **Exormotheca pustulosa** *Mitt.* in Natural history of the Azores or Western Islands: 326 (1870); Solms: 2 (1897); Steph.: 218 (1899); K.I.Goebel: 244 (1905); Müll.Frib.: 292 (1905–1916); Schiffn.: 46 (1942); Müll.Frib.: 399 (1951–1958); S.W.Arnell: 74 (1963a); O.H.Volk: 232 (1979); Perold: 15 (1994b). Type: Madeira, Pico de Barcellos, leg. *Johnson* (NY, holo.!).

E. africana Steph.: 18 (1917). Type: Transvaal, in waterfall gorge near Belfast, leg. *Pole Evans* (G).

Thalli rather small, in crowded patches; glaucous-green, with numerous conspicuous, partly adjoined conical or pustular evaginations of dorsal epidermis into air chambers, pores raised, at or near their apices; when dry, flanks covered by imbricate, purple or partly hyaline scales, generally tightly incurved over whitish, dorsal face. *Branches* simple, or once, occasionally twice (–3 times) pseudodichotomously furcate, linear to ligulate, up to 8 or 9 mm long, 2(–3) mm wide, ± 1000 µm thick medianly, in section 2 or 3 times wider than thick, apex slightly concave medianly, scales not reflexed over edge; groove absent, thallus dorsally ± flat, margins rather obtuse, covered by air chambers, scales extending above or hardly so; flanks sloping obliquely; ventral face quite strongly keeled medianly, green. *Scales* covering flanks, imbricate, oblong or rounded, purple or partly hyaline, 500–1000 × 540–850 µm, occasionally with 1 or 2 appendages at margin, oil cells absent.

Dorsal epidermal cells unistratose, hyaline, polygonal, 30–75 × 22–25 µm, fairly thin-walled, without trigones, elevated into conical protuberances ± 300 µm high, 150–180 µm wide, in (8)9–11 irregular rows across width of thallus; air pores raised to or near top of cone, simple, round or oval, up to 62 µm wide, surrounded by innermost ring of ± 8 slightly bent, ± rectangular, thin-walled cells, then by an irregular ring of smaller, polygonal, thicker-walled cells. *Assimilation tissue* ± 200 µm thick, occupying lower ± $^2/_3$ of air chambers, consisting of densely crowded filaments, sometimes branching, containing numerous chloroplasts; storage tissue loosely composed, with larger empty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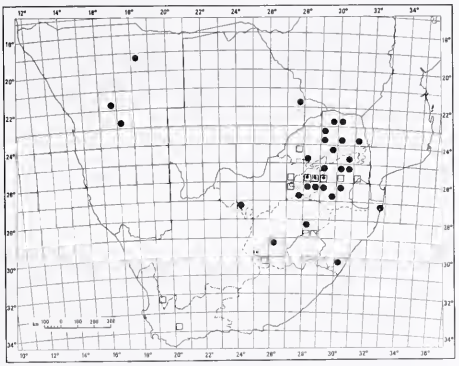
spaces (so-called 'slime' cells), encircled by smaller cells; a few oil cells in between.

Asexual reproduction by ventral, scale-clad, spherical tubers (Knöllchen).

Monoicous (or rarely ?dioicous). *Androecia* in 1–3 rows along middle of thallus, close to female receptacle (distal or proximal to it), antheridia sunken, in shallow groove, necks protruding, air chambers here suppressed. *Gynoecial receptacles* apical or just proximal to bifurcation of 2 terminal branches, when young sessile, at maturity raised on stalk; carpocephalum above with filament-containing air chambers opening via hardly raised, simple air pores, frequently hammer-like in shape, up to 3 mm across, capsules exserted laterally, one on either side, sometimes bearing only 1 capsule, and then erect and oblong. *Stalk* basally purple-streaked, remainder yellowish, length variable, up to 10 mm, 350 µm diam., with single rhizoid furrow, top of stalk loosely sheathed in short, collar-like outgrowth at base of head. *Involucres* bilabiate. *Sporophyte* with long seta, capsule ± globose, wall unistratose, upper part forming an operculum, its cells somewhat smaller, otherwise similar to the rest, with semi-annular thickenings, dehiscing by shedding lid and by 4 or 5 irregularly shaped valves folding back, petal-like. Figure 17. *Spores* 70–75 µm diam., polar, triangular-globular, honey-brown; distal face rounded, with up to ± 50 crowded, hollow, conical papillae, 10 µm high, 10 µm wide, walls of papillae composed of numerous adjoining granules, stacked into tiny pillars in some areas and only exposed where wall breaks down; proximal face with vestigial triradiate mark or only part of it occasionally present, entirely encrusted with fine granules, wing absent, margin scalloped by protruding papillae on distal face. *Elaters* honey-brown, not tapering toward ends, sometimes coiled, up to 150 × 10 µm, trispiral. *Chromosome number* n = 16 (Bischler 1976). Plate 8A–C.



MAP 7.—❑ **Exormotheca pustulosa**
● **E. holstii**

Exormotheca pustulosa is quite widespread and is known from the following Mediterranean countries: Portugal, Spain, France and Italy, as well as from the Atlantic islands of Azores, Madeira, the Canaries, Cape Verde and St Helena, also from two island groups (or islands) in the Indian Ocean: the Comores and Réunion (Bischler 1976). It is further known from Saudi Arabia, United Arab Emirates and Oman (Frey & Kürschner 1988) as well as from the following African countries: Morocco, Chad, Ethiopia, and also from Kenya, Tanzania (Bizot & Pócs 1979), Angola, Zimbabwe and southern Africa. In southern Africa *E. pustulosa* has been quite rarely collected in the North-West and Northern Province, Gauteng, Mpumalanga, as well as in Free State, Lesotho and Western Cape. Map 7.

FIGURE 17.—**Exormotheca pustulosa**. A, B, F, thallus: A, dorsal face from above, toward apices with rows of antheridia in grooves and with young gynoecium at furcation; B, ventral face, showing scales; F, c/s, showing 2 antheridia. C, stalk (cut off) emerging just proximal to furcation of thallus; D, 'hammer-like' head of carpocephalum with 2 dehisced capsules; E, G, air pore: E, with air chamber, assimilation tissue filaments and some storage tissue cells; G, from above. H, scale. I, J, capsule wall: I, cross section; J, from above. K, c/s of stalk with one rhizoid furrow. A, B, F, H, *Perold 2604*; C, D, I–K, *S.W. Arnell 791*; G, *Reid 1107a*. Scale bars: A–D, 1 mm; E, G, I, J, 50 µm; F, H, 500 µm; K, 100 µm. Drawings by A. Pienaar.

Exormotheca pustulosa grows in association with other liverworts, such as *Riccia* species and *Mannia capensis*, on soil around granite or sandstone outcrops, which are generally only temporarily wet.

The species can be distinguished by its low conical air chambers ± $^2/_3$ filled with chlorophyllose cell filaments, by its small size, oblong or rounded, mostly purple scales, its stalked carpocephala, its spore ornamentation and its spherical tubers.

Vouchers: *Arnell 7913; Bosman CH1533; Glen 2140; Perold 1207; Schelpe 5284.*

Exormotheca section **Corbierella** *(Douin & Trab.) Schiffn.*

Thalli medium-sized to quite large; with tall conical air chambers, basal $^1/_5$–$^1/_3$ filled with chlorophyllose cell filaments. *Scales* ventral, large, ± obliquely triangular. *Gynoecial receptacles* sessile. *Elaters* short, unispiral or ringed. *Exormotheca holstii* is placed here.

2. **Exormotheca holstii** *Steph.* in Bulletin de l'Herbier Boissier 7: 145 (1899); Schiffn.: 66 (1942); S.W.Arnell: 76 (1963a); O.H.Volk: 231 (1979); Perold: 18 (1994b). Type: Deutsch-Ost-Afrika (= Tanzania), Muse, plains, in moist sandy spots [regio campestris, in locis arenosis humidis], leg. *Holst 3107* (*G024591*, holo.!).

E. megastomata C.Marquand: 237 (1930). Type: Transvaal, Krantz, 3 miles N of Middelburg, leg. *F. van der Merwe CH214* (BM, holo.), *CH214* (PRE, iso.!); *BOL54643* (*Duthie 5042*) (iso.!).

E. youngii S.W.Arnell: 283 (1953b). Type: Transvaal, Pilgrim's Rest, Hendriksdal, on dry rocky veld, leg. *E.M. Young* (*Duthie 5211*) (*BOL54651*, holo.!).

Thalli medium-sized to quite large, in crowded patches; silvery green, dorsal epidermis evaginated into numerous conspicuous, tall, conical air chambers, medianly narrow, somewhat lower, laterally mostly wider and taller, air pores raised to near or at apices; when dry, dorsally concave to grooved along midline, scales incurved over margins or erect. *Branches* simple or once, rarely twice or 3 times pseudodichotomously furcate, broadly linear to ± ovate, 8–15(–22) mm long, (2.5–) 3.0–5.0(–7.0) mm wide, 2125–2900 µm thick over midrib, in section ± $1^1/_2$ times wider than thick, apex with shallow notch; groove shallow toward apex, thallus otherwise dorsally flat to medianly slightly concave, margins obscured by air chambers, scales mostly hidden; flanks sloping steeply; ventral face rounded to flattish, green or sometimes purple. *Scales* covering flanks, hyaline with purple base, imbricate, obliquely triangular, 1250–1625 µm long, vertical margins facing distally, ± entire, sloping margins often toothed, apex with several branched or unbranched, filiform appendages, base 900–1500 µm wide, oil cells absent.

Dorsal epidermal cells unistratose, hyaline, variable in shape and size, ± thin-walled, raised into tall 4–6-sided air chambers, in 8–12 irregular rows across thallus width, attached to each other except for free, conical, apical part; air pores located at or away from tip of cones, simple, rounded or elongated, surrounded by one ring of smaller cells. *Assimilation tissue* 350–400 µm thick, occupying basal $^1/_5$–$^1/_3$ of air chambers, composed of densely crowded, sometimes branched filaments, 7 or 8 cells long, filled with chloroplasts; storage tissue an open mesh with 'rounded spaces', surrounded by smaller, mostly angular cells; oil cells toward top and base of storage tissue.

Monoicous or dioicous or ?protandrous, very rarely producing gametangia of both sexes simultaneously. *Androecia* in 2–4 irregular rows along midline of thallus, in 1 or 2 successive linear groups, antheridia sunken, necks protruding conspicuously, development of central air chambers temporarily suppressed. *Gynoecial receptacles* developing near apex of thallus (which con-

tinues growth), sessile, mostly in single groups, ± 4 mm wide; carpocephalum supported on central core of parenchymatous tissue, on either side 1 (or 2) slightly obliquely held capsules, domed above, containing elongated air chambers, basally with cellular filaments, opening via simple air pores. *Involucres* continuous with outer layer of dome on both sides, as deeply purple-stained extensions partly covering capsules. *Sporophyte* with capsule on short seta, globose, ± 1500 µm diam., wall cells with semi-annular thickenings. Figure 18. *Spores* 117.5–142.5 µm diam., polar, triangular-globular, dark red; distal face rounded, with 6–8 highly convoluted, raised areas across, 22.5–27.5 µm wide, bordered by superimposed layers of granules and hollowed in the centre, distinctly or poorly separated by deep furrows; proximal face with triradiate mark absent, but with slight flattening of 3 facets, entirely encrusted with numerous, tiny granules, wing absent, margin scalloped by projecting convoluted areas from distal face. *Elaters* brownish red, tapering slightly at one end, blunt and thicker at the other, 70–90 × 20 µm, unispiral or ringed. *Chromosome number*: n = 18, 32 (T. Bornefeld pers. comm. via O.H. Volk). Plate 8D–F.

Exormotheca holstii is known from the following African countries, Tanzania (*locus classicus*), Zimbabwe (Best 1990) and southern Africa, where it has been reported from Namibia—several collections recorded by Volk (1979)—Botswana, North-West, Northern Province, Gauteng, Mpumalanga, Free State and KwaZulu-Natal. Map 7.

It is found mainly on quite dry, somewhat sandy or gravelly soil, sometimes between grass or in exposed areas that are only occasionally wet and that overlie sandstone or quartzitic or granitic rock. It sometimes grows in association with *Riccia* species, such as *R. volkii*, *R. rosea* and *R. albovestita*.

Exormotheca holstii can be distinguished from other species in the genus by its large size, its tall air chambers, basal $^1/_5$–$^1/_3$ occupied by chlorophyllose filaments, and laterally adjoined except for the apical 250 µm toward the centre of the thallus and marginally for the apical ± 500 µm; by the large, hyaline, triangular scales with long filiform appendages and its subsessile gynoecia. Tubers were not found.

Vouchers: *Bottomley CH3566; M.J.A.W. Crosby 1115; Germishuizen 2839; Giess 15383; Glen 2243; Perold 2702; Volk 81/124.*

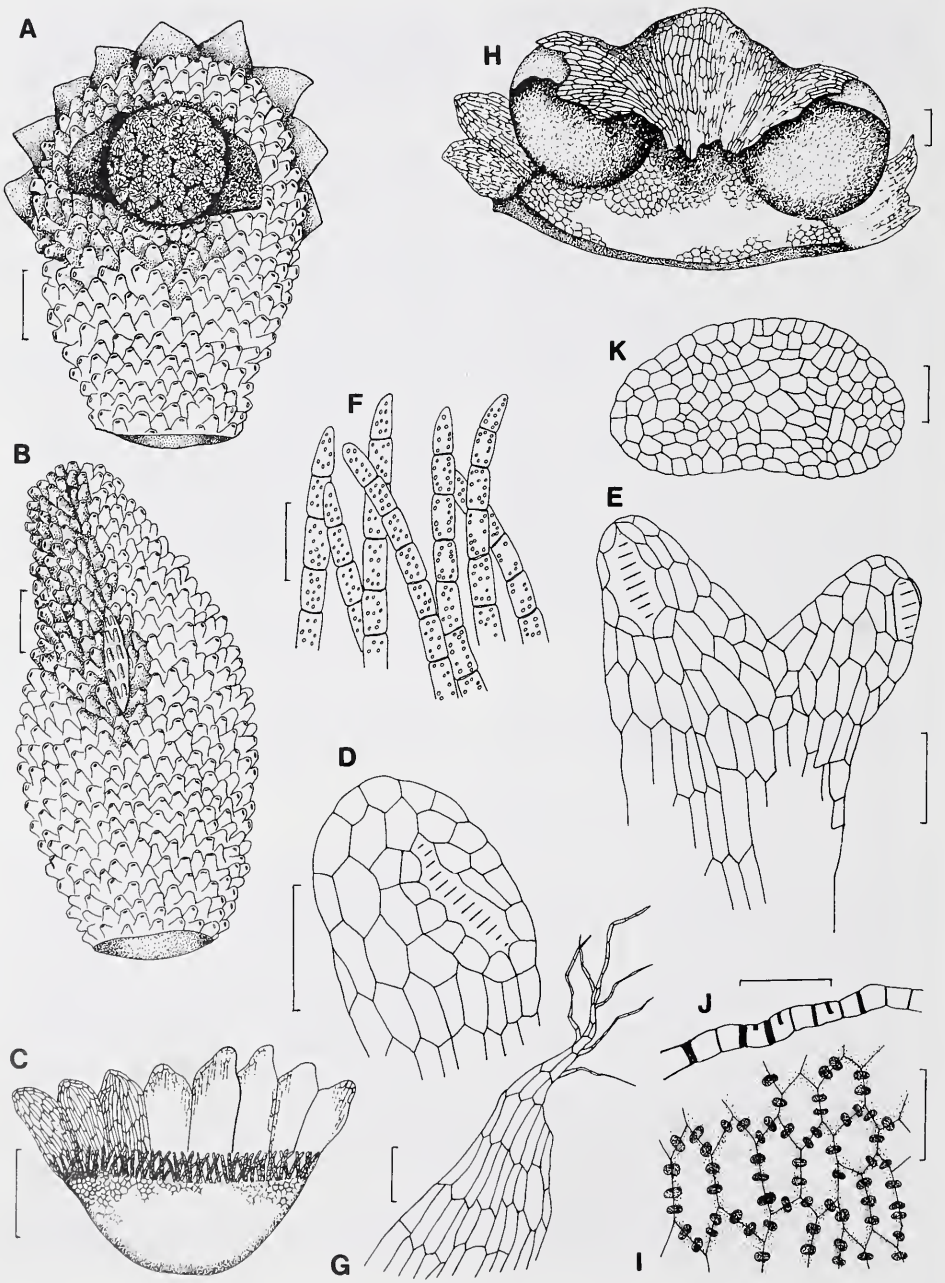
Note: *E. bulbigena* sp. nov. by Bornefeld *et al.* (1996) is not included here, as my treatment was completed before their paper was published.

MARCHANTIACEAE

Marchantiaceae *(Bisch.) Lindl.*, An introduction to the natural system of botany, edn 2: 26, 412 (1836); Dumort.: 69 (1829), emend. Müll.Frib.: 264 (1940b); Müll.Frib.: 382 (1951–1958); Hässel de Menéndez: 141 (1963); S.W.Arnell: 52 (1963a); R.M.Schust.: 299 (1992c). Type: *Marchantia* L.

Thalli medium-sized to very large, in crowded mats; green to dark green, sometimes leathery, rarely translucent. *Branches* pseudodichotomously furcate, with or without apical and ventrolateral innovations, broadly band-shaped or narrowly ribbon-shaped, apex notched, often with median scale appendages recurved over edge; groove absent, thallus dorsally flat, margins lobulate, crenulate or undulate, sparsely hirsute in *Dumortiera*; flanks sloping very obliquely; ventral face medianly strongly keeled. *Scales* in 4 or 6(8) rows, 2 or 3(4) on either side of keel, covering part or all of ventral face, rarely projecting beyond margins; *median scales* bluntly triangular, constricted where joined to appendage; *laminal scales* smaller, lacking appendage; *marginal scales* rarely present; in *Dumortiera* scales vestigial and evanescent.

Dorsal epidermis often lacking chloroplasts, mostly unistratose, cell walls thin or slightly thickened, without trigones, absent in *Dumortiera*; air pores, when present, compound, surrounded by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several superimposed concentric rings of cells, some above epidermis, others projecting into air chambers. *Assimilation tissue* with shallow air chambers in 1 storey, densely packed with 2–4(5)-celled chlorophyllose filaments, absent in *Dumortiera*; storage tissue occupying ventral part of thallus or almost all of thallus in *Dumortiera*, compact, sometimes with a few slerotic cells and/or mucilage cavities; oil cells scattered, these also present elsewhere in thallus and scales.

Asexual reproduction in *Marchantia* spp. only, by discoid gemmae contained in hollow cupules borne dorsally on thalli, contracted below, flaring above, margin ciliate, lobed-ciliate, dentate or nearly entire.

Monoicous or dioicous (in *Marchantia* spp.). *Antheridiophore* with stalk fairly long in *Marchantia* spp., very short in *Dumortiera*, disc lobed or divided into rays in *Marchantia* spp., unlobed in *Dumortiera*, antheridia sunken in dorsal side, air pores present only in *Marchantia* spp., ventral side with several rows of scales. *Stalk* usually with 2 rhizoid furrows, air chambers present in *Marchantia* spp., absent in *Dumortiera*. *Archegoniophore* with carpocephalum convex above, lobed or divided into rays, dorsally with compound air pores in *Marchantia* spp., absent in *Dumortiera*, below with scales and sporophytes in groups, alternating with lobes or rays (in African *Marchantia* species). *Stalk* basally sometimes surrounded by large scales, generally without appendage, along its length bearing filiform scales, 2–4 rhizoid furrows and 0–2 bands of air chambers. *Involucre* bivalved, membranous in *Marchantia* spp., fleshy and saccate in *Dumortiera*. *Pseudoperianths* present in *Marchantia* spp., membranous and delicate, bell-shaped, enclosing sporophytes individually, absent in *Dumortiera*. *Sporophyte* with foot, short seta and subglobose to ovoid capsule, wall unistratose, with annular thickenings, dehiscing irregularly in *Marchantia* spp. or by valves in *Dumortiera*. *Spores* small, thin-walled, ± triangular-globular, ornamentation with numerous thin, irregularly convoluted ridges or with few wide ridges separated by granules, the 2 faces similar or dissimilar in *Marchantia* spp., ornamented with nodules in *Dumortiera*. *Elaters* tapering at ends, bi- or trispiral. *Chromosome number*: n = 9 (basically).

Five genera, *Marchantia* L., *Dumortiera* Nees, *Preissia* Corda, *Bucegia* Radian and *Neohodgsonia* H.Perss. are classified in the family Marchantiaceae, but only the first two are found in southern Africa. Each one of the two locally occurring genera has been placed in its own subfamily: *Marchantia* (and extra-territorial *Preissia*) in Marchantioideae and *Dumortiera* in Dumortieroideae; *Bucegia* and *Neohodgsonia* have been referred to the subfamily Bucegioideae.

Key to local subfamilies of Marchantiaceae

Air pores of thallus compound; epidermis and air chambers present; thallus margins not hirsute; male receptacles on long stalks; cupules bearing gemmae present . . . . . Marchantioideae

Air pores, epidermis and air chambers of thallus absent; thallus margins hirsute; male receptacles on very short stalks; cupules absent . . . . . Dumortieroideae

FIGURE 18.—**Exormotheca holstii**. A–C, thallus: A, with sessile carpocephalum from above; B, with antheridial necks emerging in midline between air chambers; C, c/s showing tall air chambers, chlorophyllose cell filaments and storage tissue. D, air pore and surrounding cells from above; E, top part of 2 partly adjoining air chambers; F, assimilation tissue with cell filaments; G, scale with branched filiform appendages; H, carpocephalum, upper half three-dimensional, lower half in c/s. I, J, capsule wall: I, from above; J, cross section. K, c/s of seta. A, H, K, *Germishuizen 2839*; C, *Perold & Koekemoer 2872*; D, *Perold 2702*; E, F, *Glen 2190*; G, I, J, *Holst 3107*. Scale bars: A–C, H, 1 mm; D–F, I–K, 100 µm; G, 500 µm. Drawings by A. Pienaar.

Subfamily **MARCHANTIOIDEAE** (excluding *Preissia*)

Type: *Marchantia* L.

Thalli medium-sized to large, in crowded mats; green, sometimes leathery. *Branches* pseudodichotomously furcate, without innovations, broadly band-shaped or narrowly ribbon-shaped, apex notched, median scale appendages recurved over edge; groove absent, thallus dorsally flat, margins lobulate, crenulate or undulate, sometimes purplish; flanks sloping very obliquely; ventral face medianly strongly keeled. *Scales* in 4 or 6 rows, covering part or all of ventral face, rarely projecting beyond margins.

Dorsal epidermis often hyaline, mostly unistratose, cell walls thin or slightly thickened, without trigones; air pores compound, surrounded by several superimposed, concentric cell rings, cells of inner opening sometimes covered with black granular deposit. *Assimilation tissue* with one storey of shallow air chambers, densely packed with chlorophyllose filaments; storage tissue sometimes with a few sclerotic cells and/or mucilage cavities; oil cells scattered throughout thallus.

Asexual reproduction by discoid gemmae.

Dioicous. *Antheridiophore* with receptacle lobed or divided into rays. *Stalk* with 2 rhizoid furrows and 0–2 bands of air chambers. *Archegoniophore* with carpocephalum lobed or divided into rays. *Stalk* with 2–4 rhizoid furrows and 0–2 bands of air chambers, basally sometimes surrounded by large scales. *Involucre* bivalved, membranous. *Pseudoperianth* membranous, bell-shaped. *Sporophyte* with subglobose capsule, dehiscing irregularly. *Spores* ± triangular-globular, ornamented with thin, irregularly convoluted ridges or with wide ridges and granules between. *Elaters* bi- or trispiral. *Chromosome number*: n = 9 (basically).

MARCHANTIA

Marchantia *L.*, Species plantarum, edn 1: 1137 (1753) emend. Raddi, Opuscoli scientifici, Bologna: 358 (1818); Sim: 27 (1926); S.W.Arnell: 53 (1963a); Bischl.: 6 (1984); Bischl.: 13 (1989a); Bischl.: 13 (1993); R.M.Schust.: 305 (1992c); Perold: 183 (1995c). Type: *Marchantia polymorpha* L. [lecto. fide Léman: 115 (1823)].

Marchantiopsis Douin & R.C.V.Douin: 135 (1918).

Chlamidium Corda in Opiz: 647 (1829).

The generic diagnosis is contained in the diagnosis of the subfamily.

The genus is subdivided into three subgenera: *Marchantia*, *Chlamidium* (Corda) Bischl. and *Protomarchantia* R.M.Schust. on the basis of differences in, *inter alia*, spore morphology, germination patterns and flavonoid patterns. *Protomarchantia* is absent from our region.

Key to local subgenera, sections and species of *Marchantia*

1a Thalli with margins plicate-crisped, crenulate or lobulate; dorsally with or without dark median band; cells bordering inner opening of epidermal air pores with slightly or strongly projecting walls, pores then cruciate; scales in 4–6 rows, covering $^3/_4$ or all of ventral surface, then also extending beyond margins; appendages of median scales orbicular or reniform or ovate, marginal cells slightly or strikingly smaller than inner cells; laminal scales much wider than long; cupule margins with ciliate lobes, exter-

nally with papillae; male receptacles peltate, shallowly dissected into 6–10 broad lobes; membranous margins of rays crenulate or entire, then with very small cells; female receptacles deeply dissected into 9–11 terete rays, with or without papillae; stalks with single broad band of air chambers; involucre margins with ciliate lobes; spores 8–16 µm diam., ornamentation on 2 faces similar, with numerous narrow, convoluted ridges . . . subgenus **Marchantia** (p. 84):

2a Thalli with margins entire or crenulate; dorsally often with dark median band; cells bordering inner opening of epidermal pores with slightly convex inner walls, pores not cruciate; ventral scales in 6 rows, extending beyond thallus margins; median scale appendage small, margins bordered with somewhat smaller cells; membranous margin of male receptacle crenulate, with slightly smaller cells; rays of female receptacle with numerous papillae . . . . . 1. *M. polymorpha*

2b Thalli with margins lobulate; dorsally without dark median band; cells bordering inner opening of epidermal pores with strongly convex inner walls, pores cruciate; ventral scales in 4(–6) rows, not extending beyond thallus margins, marginal scales sometimes partly or altogether absent; median scale appendage large, margins entire or slightly crenulate, bordered with strikingly small marginal cells; membranous margin of male receptacle not distinctly crenulate, composed of very small cells; rays of female receptacle without papillae . . . . . 2. *M. berteroana*

1b Thalli with margins entire, nearly flat or sometimes slightly undulate; dorsally with or without dark median band; cells bordering inner opening of epidermal pores with straight or convex walls, rarely with strongly projecting processes, pores then cruciate; scales in 4 rows, covering $^1/_4$ to almost $^2/_3$ of ventral surface; median scale appendage orbicular, ovate or ± triangular, apically acuminate, acute or apiculate, marginal cells rather smaller than inner ones; laminal scales as long as or longer than wide; cupule margins ciliate, almost entire or rarely with ciliate lobes, externally rarely with papillae; male receptacles palmate or rarely peltate, shallowly or deeply dissected into rays; membranous margin of rays entire or slightly crenulate; female receptacles dissected into 5–9 apically ± flat lobes; stalks with air chambers in 1 or 2 bands; involucre margins ciliate or entire, rarely with ciliate lobes; spores 20–35 µm diam., ornamentation on 2 faces dissimilar, distally mostly with wide ridges . . . subgenus **Chlamidium** (p. 92):

3a Thalli medium-sized to large, 6–8(–11) mm wide; cells bordering inner opening of epidermal pores with strongly projecting walls, pores cruciate; median scale appendages with margins entire or slightly denticulate; cupule margins with triangular, ciliate lobes, externally with numerous papillae; female receptacle deeply dissected into lobes, apically truncate or emarginate; involucre margins with ciliate lobes . . . section *Paleaceae* (p. 92) . . . . . 3. *M. paleacea*

3b Thalli smallish to large, 3.5–10.0 mm wide; cells bordering inner opening of epidermal pores with straight or convex walls; median scale appendages with margins often distinctly toothed; cupule margins with long or short cilia or almost entire, externally without or with few papillae; female receptacle shallowly or deeply dissected into lobes; involucre margins ciliate or ± entire:

4a Thalli 6.0–8.5(–10.0) mm wide; dorsally without dark median band; median scale appendages large, inner cell structure 'loose' with large cells; cupule margins with cilia up to 6 cells long; female receptacle large, shallowly dissected into broad lobes, sometimes bearing a male ray; involucre margins ciliate . . . section *Chlamidium* (p. 95) . . . . . 4. *M. pappeana*

4b Thalli 3.0–7.5 mm wide; mostly with distinct dark median band dorsally; median scale appendages small, inner cells not markedly large and structure not 'loose'; cupule margins crenulate or with short cilia, up to 3 cells long; female receptacle rather small, deeply dissected into narrow lobes; involucre margins entire or crenulate . . . section *Papillatae* (p. 99) ..... 5. *M. debilis*

Subgenus **Marchantia**

Marchantia L. sect. *Astromarchantia* Nees: 60, 61 (1838) (nom. illegit.).

Marchantia L. (without rank) *Stellatae* Gottsche et al.: 522 (1844–1847, published 1846).

Marchantia L. (without rank) *Marchantiotypus* Dumort.: 150 (1874).

Thalli with wide branches, from nearly 7 mm to almost twice that; margins crenulate, lobulate or plicate-crisped. *Scales* in 4–6(–8) rows, covering $^3/_4$ to all of ventral face: *median scale* appendages ovate, orbicular or reniform, not acuminate at apex, margins crenulate, toothed or entire, sometimes cells in outer row very much smaller than inner ones; *laminal scales* wider than long, apically rounded, lacking papillae, upper cell walls with trigones; *marginal scales* sometimes present, projecting beyond thallus margins or not.

Dorsal epidermis with or without papillae; air pores surrounded by 4–5(6) concentric rings of cells, at inner openings sometimes with rounded walls, otherwise with pronounced processes, pores then cruciate; storage tissue lacking sclerotic cells.

Cupule margins with acutely triangular, toothed lobes, externally papillate.

Dioicous. *Antheridiophores* with receptacles ± symmetrical, peltate, rays very short and broad. *Archegoniophores* with receptacle deeply dissected into terete lobes. *Stalks* of gametangiophores with 2 rhizoid furrows. *Involucre* margins toothed or ciliate. *Spores* small, 8–16 µm diam.; 2 faces similarly ornamented, with numerous thin, highly convoluted ridges, triradiate mark on proximal face distinct to absent, wing absent.

Marchantia polymorpha (with three subspecies), *M. berteroana* and *M. plicata* (from central and South America) are classified in subgenus *Marchantia*.

1. **Marchantia polymorpha** *L.*, Species plantarum, edn 1: 1137 (1753); Bischl.: 34 (1993); Perold: 185 (1995c). Type: Europe, *Dill.*: t. 76, fig. 6E, F (1741) [OXF, lecto., typo., fide Bischl. & Boisselier-Dubayle: 363 (1991) (photo. of typo. in PRE!)].

Synonymy see Bischl. (1993).

Thalli large, in crowded patches; bright, yellowish or deep green, medianly with or without dark band, arcolate, air pores small to large, margins reddish brown, crisped, entire, sometimes crenulate; when dry, margins not raised. *Branches* prostrate to somewhat erect, repeatedly pseudodichotomously furcate, broadly obovate, total length up to 35 mm, 7–10 mm wide, 325–375 um thick medianly, in section 21–27 times wider than thick, apex notched, median scale appendages recurved over edge; groove absent, thallus margins acute, thin; flanks sloping obliquely; ventral face medianly keeled. *Scales* in 6 rows, entirely covering ventral face and extending beyond thallus margins: *median scales* closest to keel, with body obliquely triangular, pale mauve, up to 750 µm long, base 1575–2250 µm wide, narrowed above and deeply constricted where joined with appendage, oil cells sparsely scattered throughout

scale, appendage of median scale broadly rounded, brown or purple, (350–)400–640 × 500–700 µm, margins toothed, crenulate or almost entire, bordered by slightly smaller cells; *laminal scales* lateral to median scales, wedge-shaped, much wider than long, hyaline or pale mauve, 600–825 µm long, apex rounded, margin papillate, base flatly arched, 1450–1750 µm wide, oil cells rare; *marginal scales* usually projecting beyond thallus margins, oblong or ovate, hyaline or brownish, 700–750 µm long, apex rounded, base 550–650 µm wide, with 5 or 6 scattered oil cells.

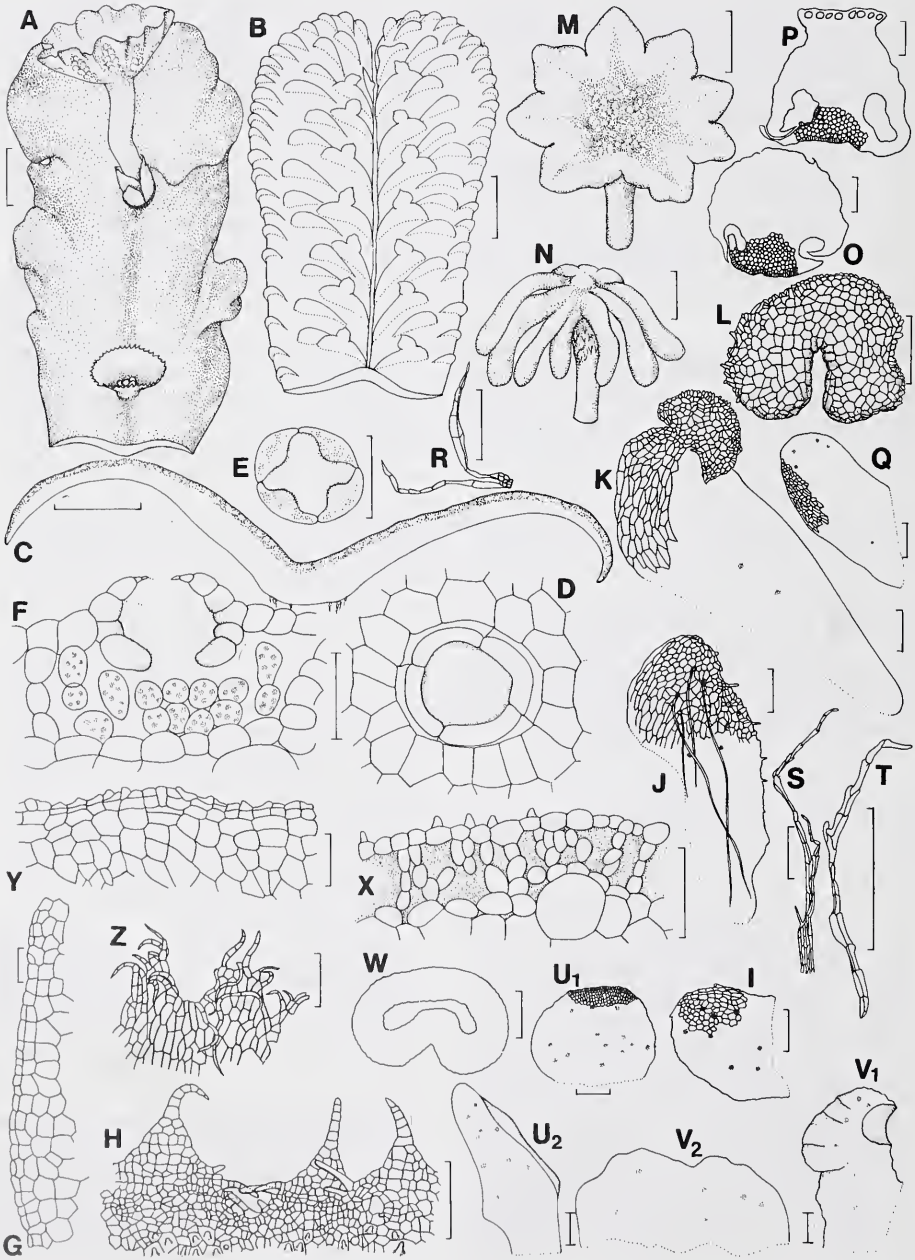
Dorsal epidermal cells unistratose, mostly hyaline, 4–6-sided, 35–74 × 18–30 µm, thin-walled, lacking trigones; air pores raised, compound, 30.0–62.5 × 40.0–60.0 µm, surrounded by (3)4 or 5 concentric rings of 4–6 cells in each, 2 or 3 above epidermis and 2(3) projecting into air chambers, inner opening mostly surrounded by 4 cells protruding into cavity. *Assimilation tissue* 50–100 µm thick, air chambers in one storey, containing densely chlorophyllose, mostly 3-celled filaments, bounding walls without chloroplasts; storage tissue with ± 11 rows of cells medianly, decreasing laterally, sclerotic cells and mucilage cavities absent; oil cells scattered throughout tissues.

Cupule margins with ciliate, triangular lobes, cilia at apex of lobes vertical, up to 5 or 6 cells long, basally on either side transverse; cupule wall lower down, several cell layers thick, exteriorly with numerous 1–3-celled papillae.

Dioicous. *Antheridiophore* arising from apex of terminal segment of main or short lateral branch, raised on stalk; receptacle ± 8 mm diam., shallowly dissected into 8(–10) lobes, ± 375 µm long, symmetric, basal sinus up to 30° wide, lobe margins membranous, hyaline, crenulate, cells small in outer 1 or 2 rows; *median scales* on ventral side of lobes hyaline, oblong, with rounded apex, lacking appendage, 1375–1575 × 600–850 µm, margins toward base sometimes with small papillae, 4–10 oil cells present. *Stalk* ± 4.5–15.0 mm long, 975–1000 µm diam., with 2 rhizoid furrows, air chambers absent; *scales at base of stalk* large, 1250–2000 × 800 µm, round or oblong, lacking appendage, bases purple, sometimes with protruding papillae, up to 8 scattered oil cells present; *scales along length of stalk* hyaline, filiform, (1)2–3 cells wide. *Archegoniophore* arising from apex of terminal segment of main or short lateral branch, raised on stalk; carpocephalum 9.5–10.0 mm diam., nearly symmetric, with small round projection dorsally, deeply divided into 9–11 rays, 2.5–3.2 mm long, basal sinus ± 40°, margins distally incurved and terete in cross section, toward apices with numerous conical papillae; *scales of carpocephalum* hyaline, up to 2000 µm long, 80 µm wide at base, sometimes branched along length. *Stalk* 17–40 mm long, 600–1250 µm diam., with 2 rhizoid furrows, 1 band of air chambers; *scales at base of stalk* large, 750 × 1000(–1750) µm, shape irregular, mostly without appendage, purple or brown or hyaline, lateral margins sometimes with papillae; *scales along length of stalk* hyaline or brown, filiform, 2 cells wide. *Involucre* with margins hyaline or occasionally purple-tinged, with tapering, ciliate lobes, 300–350 µm long, 90–150 µm wide at base, cilia (1–)2–5 cells long. *Sporophyte* with short seta, capsule subglobose, wall dehiscing by irregular slits. Figure 19. *Spores* 10.0–12.5 µm diam., triangular-globular, yellow; distal face with numerous highly convoluted and branched, smooth ridges; proximal face with faint, collapsed triradiate mark, facets finely and densely granular, narrowly winged. *Elaters* yellow-brown, 350–435 µm long, 5 µm wide, gradually tapering to narrow tips, bispiral. *Chromosome number*: n = 9 (Bischler-Causse 1993a). Plate 9A, B.

Marchantia polymorpha is widespread and is known from Europe, Russia, Japan, China, India and the Americas. It has frequently been described, but its taxonomy was unresolved because proper lectotypification had not been done.

Lectotypification of *M. polymorpha* was recently done by Bischler-Causse & Boisselier-Dubayle (1991) who used a Dillenian illustration and a specimen held in OXF (i.e. a typotype). This corresponds to the first of three Linnean varieties, namely var. [α], which was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later called '*aquatica*'. This first variety [α] forms the basis for the application of the specific name (Isoviita 1970). However, since the lectotype of *M. polymorpha* var. *polymorpha* of Linnaeus corresponds to the taxon '*aquatica*' (at any rank), it renders that name illegitimate, because the epithet '*polymorpha*' would be used for a taxon not including its type. The best procedure seemed, therefore, for Bischler-Causse & Boisselier-Dubayle to describe their three newly separated electrophoretic groups (in three enzyme systems: esterases, peroxidases and acid phosphatases) as subspecies, give two of them new names and select good, recent type specimens. *Marchantia polymorpha* L. subsp. *polymorpha* thus corresponds to the taxon formerly called '*aquatica*'; *M. polymorpha* L. subsp. *ruderalis* Bischl. & Boisselier corresponds roughly to the former '*polymorpha sensu stricto*' and *M. polymorpha* L. subsp. *montivagans* Bischl. & Boisselier roughly to the former '*alpestris*'.

Specimens recently collected in Gauteng (Map 8) are clearly introduced. They have been referred to *M. polymorpha* subsp. *ruderalis* Bischl. & Boisselier, since they grow as weeds in man-made habitats (nurseries) and agree in other respects with this subspecies, as distinguished by Bischler-Causse & Boisselier-Dubayle (1991).

Arnell (1963a) reported the species from southern Africa, namely Golden Gate, near Clarens in the eastern Free State and from Zimbabwe (Southern Rhodesia), near Odnazi River Bridge, Umtali. These specimens are not held at PRE or at BOL and up to now, the natural presence here of *M. polymorpha* has not been confirmed.

Typical characters of the subspecies: fresh thalli prostrate and bright green, with a dark, rather indistinct and discontinuous median band with elongated air chambers; dorsal air pores 50.0–62.5 µm wide, dorsal epidermal cells 35–55 µm long and median scale appendages, 350–500 × 510–760 µm, with toothed margins.

Marchantia polymorpha is very similar to *M. berteroana*, but can be distinguished from it by the marginal scales which are always present and which mostly extend beyond the crisped, sometimes crenulate thallus margins, by the air pores not being cruciate, by the presence of numerous papillae on the rays of the female receptacle and by the appendages of the median scales bordered by larger cells.

Vouchers: *Glen 3468, 3728.*

2. **Marchantia berteroana** *Lehm. & Lindenb.* in Lehm., Novarum et minus cognitarum stirpium, pugillus 6: 21 (1834); Gottsche et al.: 481 (1844–1847); Steph.: 393 (1898, 1899, 1900); Schiffn.: 41–44 (1896); A.Evans: 246 (1917); Hässel de Menéndez: 160 (1963); S.W.Arnell: 55 (1963a); E.O.Campb.: 122 (1965); Bischl.: 44 (1984); Bischl.: 81 (1989a); Bischl.: 56 (1993); Perold: 189 (1995c). Type: 'in insula Juan Fernandez legit cl. *Bertero* (Herb. Hookeri)' (*W8294*, holo.; FH, G, NY, PC, STR, W, iso.).

M. tabularis Nees: 71 (1838); Sim: 28 (1926). Type: South Africa, Tafelberg, [leg. *Ecklon W8289*! (female), syn.; leg. *Bergius* (male) STR, syn.].

M. contracta Bisch.: 135 (1846) fide Bischl. (1993a). Type: South Africa, Cap, Duyvelsberg, *Krauss s.n.* (BM, FH, G!, PC, W).

FIGURE 19.—**Marchantia polymorpha** subsp. **ruderalis**. A–C, thallus: A, dorsal face of male with antheridiophore and cupule; B, ventral face; C, cross section. D–F, air pore: D, from above; E, from below; F, c/s with dorsal epidermal cells and air chamber. G, margin of thallus; H, cupule margin; I, marginal scale; J, laminal scale; K, median scale; L, appendage of median scale; M, male receptacle; N, female receptacle from side; O, c/s of male stalk; P, c/s of female stalk; Q, median scale of male receptacle; R, scale from along male stalk; S, scale from female receptacle; T, scale from along female stalk; U_1, U_2, scales from foot of male stalk; V_1, V_2, scales from foot of female stalk; W, c/s of female ray; X, part of section of female ray, showing papillae on epidermal cells and air chambers; Y, margin of male ray; Z, margin of involucre. A, M, O, Q, R, U_1, U_2, Y, *Perold & Koekemoer 3248*; B–L, N, P, S, T, V_1, V_2, W_1, X, Z, *Glen 3728*. Scale bars: A, B, M, N, 2 mm; C, 1 mm; D–F, 50 µm; G, X, Y, 100 µm; H–L, O–W, 250 µm. Drawings by M. Steyn.

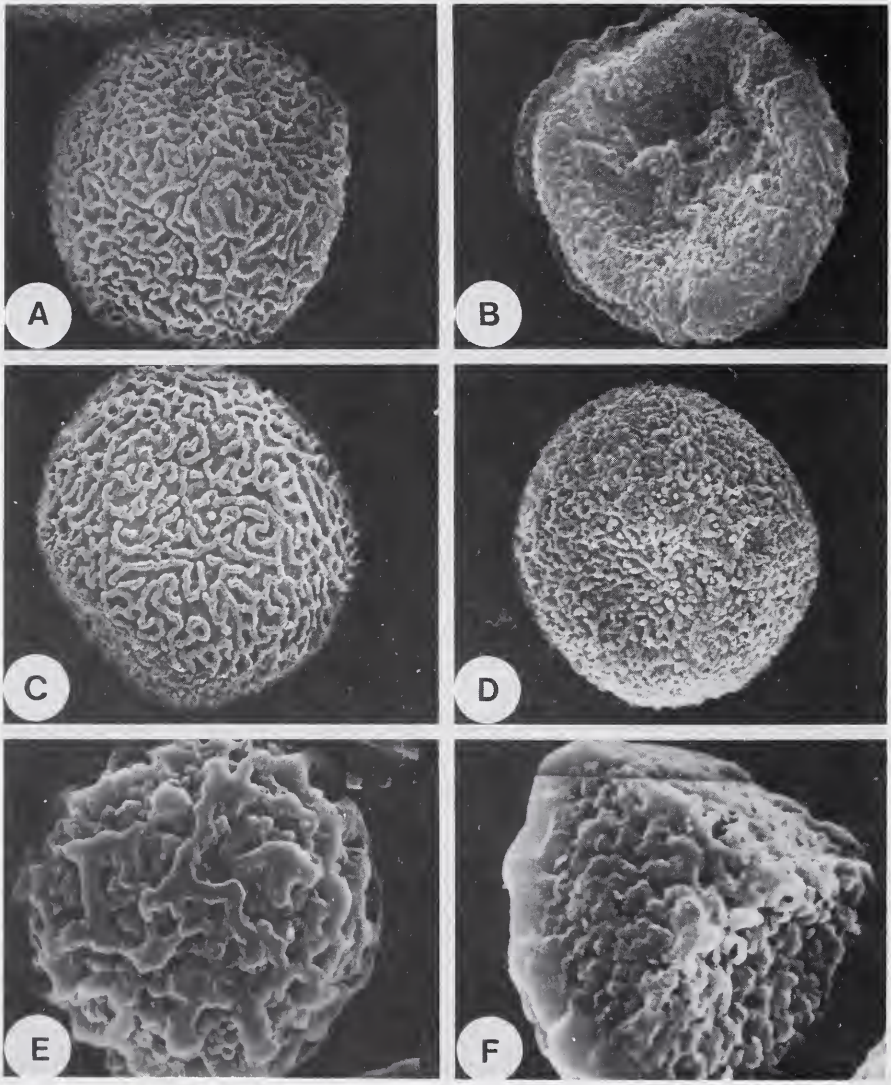


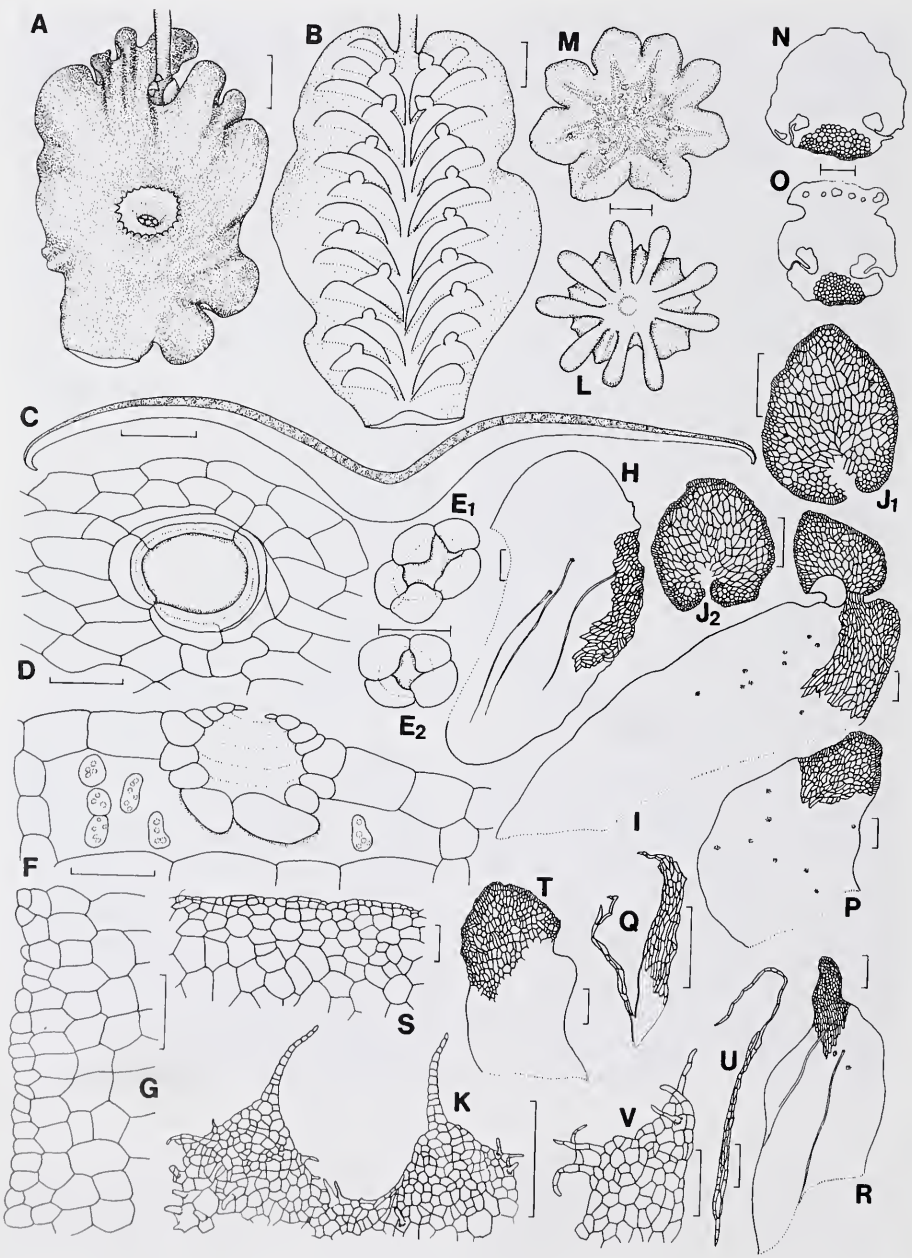
PLATE 9.—Spores. A, B, **Marchantia polymorpha**: A, distal face; B, proximal face. C, D, **M. berteroana**: C, distal face; D, proximal face. E, F, **M. pappeana**: E, distal face; F, proximal face. A, B, *Perold & Koekemoer 3249*; C, D, *Geldenhuys 1332*; E, F, *H. Anderson CH13278*. A, B, × 3900; C, × 3950; D, × 3720; E, × 1580; F, × 1540.

Thalli robust, in crowded, overlying mats; green, yellowish green or bluish green, almost leathery, without distinct median band, faintly areolate, air pores numerous, small, almost closed, margins hyaline, purplish or brownish, irregularly lobulate, ± plicate but not crisped, entire or minutely crenulate; when dry, margins not raised. *Branches* repeatedly furcate, but rather irregularly so, terminal segments broadly oblong, up to 20 mm long, 9.5–12.0(–15.0) mm wide, 600–900 µm thick medianly, in section 13–16 times wider than thick, apex notched, median scale appendages recurved over edge; groove absent, thallus dorsally rather flat, margins acute, thin, slightly recurved; flanks sloping obliquely; ventral face medianly keeled, brownish or purplish. *Scales* in 4 (sometimes 6) ventral rows, extending over $^3/_4$–$^9/_{10}$ of thallus width, but mostly not right up to margin: *median scales* with body obliquely triangular, hyaline or purplish, up to 1450 µm long, base hardly arched, 2875–3500 µm wide, gradually narrowing upwards, abruptly and deeply constricted where joined with appendage, ± 35 oil cells scattered throughout, appendage of median scales orbicular to broadly ovate, brownish, hyaline or purplish or both, 675–950 × 650–800 µm, apex rounded to somewhat obtusely narrowed, basally cordate, margins entire or minutely crenulate, bordered by 1 or 2(3) rows of cells very much smaller than inner ones; *laminal scales* lateral to, and alternating irregularly with median scales, broadly rounded, mostly hyaline, yellowish brown or reddish, 850–1125 µm long, base flatly arched, 1875–3375 µm wide, much wider than long, margins entire or slightly crenulate, ± 12 scattered oil cells present; *marginal scales* rarely to sometimes present, when ± scattered and not extending to thallus margins, crescent-shaped with rounded apex, hyaline, 675–1250 × 775 µm.

Dorsal epidermal cells mostly unistratose, hyaline, polygonal, (50–)57.5–77.5 × 20.0–30.0 µm, walls slightly thickened; air pores raised, compound (37.5–)57.5–75.0 × 27.5–47.5(–55.0) µm, surrounded by (4)5–7 concentric rings of 3 or 4 cells in each, 3(4) above epidermis and 3 or 4 projecting into air chambers, inner opening mostly with 4 or 5 cells, inside walls strongly protuberant, leaving only a small, usually cruciate opening. *Assimilation tissue* 45–50(–60) µm thick, air chambers in one storey, containing densely chlorophyllose filaments, bounding walls 3 or 4 cells high; storage tissue occupying most of ventral part of thallus medianly, decreasing laterally, cells containing scattered starch grains, but sclerotic cells and mucilage cavities absent; oil cells scattered throughout tissues.

Cupule margins with ciliate, ± triangular lobes, cilia at apex of lobes vertical, 10 or 11 cells long, basally on either side transverse, (2–)3 or 4–(–6)-celled; cupule wall lower down, several cell layers thick, exteriorly with numerous 1 or 2(–3)-celled papillae.

Dioicous. *Antheridiophore* arising from apex of terminal segment of main or short lateral branch, raised on stalk; receptacle up to 10 mm diam., shallowly dissected into 8(9) ± symmetric lobes, basal sinus ± 80° wide, lobe margins membranous, brownish or hyaline, minutely crenulate, with 1 or 2 rows of very small cells; *median scales* on ventral side of lobes hyaline, 750–1375 × 1000–1875 µm, appendage absent or present, ± 267.5 × 200.0 µm, oblong, rounded apically, not or hardly constricted at join with scale. *Stalk* 23–30 mm long, ± 1000 µm diam., with 2 rhizoid furrows, air chambers absent; *scales at base of stalk* large, up to 1200 × 1400 µm, roughly triangular or oblong, lacking an appendage, hyaline or purplish, along upper margins 1 or 2 rows of very small cells, ± 10 oil cells scattered throughout; *scales along length of stalk* hyaline, filiform, 3–9 cells wide. *Archegoniophore* arising from apex of terminal segment of main or short lateral branch, raised on stalk; carpocephalum up to 10 mm diam., nearly symmetric, dorsally with small round median projection, deeply divided into 9 linear rays, up to 2.6 mm long, basal sinus ± 45° wide, margins distally slightly incurved, terete in cross section, lacking papillae toward apex; *scales of carpocephalum* hyaline, filiform, up to 2150 µm long, 35.0–87.5 µm wide at base, often splitting further along and strands mostly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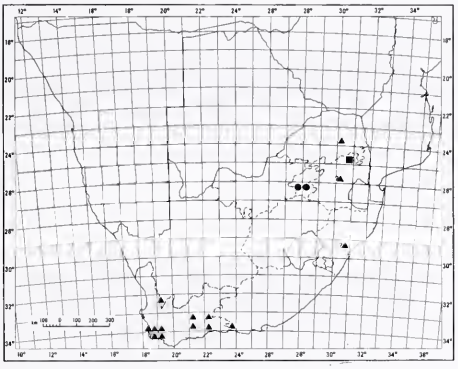
only 2 cells wide. *Stalk* 48–65 mm long, up to 1000 µm diam., with single band of air chambers and 2 rhizoid furrows; *scales at base of stalk* oblong or ovate, without appendage, apex rounded, brownish or hyaline, large, 1575–2000 × 800–1250 µm, margins apically occasionally slightly crenulate, with very small cells; *scales along length of stalk* hyaline, filiform, up to 6500 µm long, 2 or 3(4) cells wide. *Involucre* with margins hyaline or purplish, with tapering, ciliate lobes, 100–175 µm long, 125–180 µm wide at base, cilia apically and at sides numerous, tapering, branched and intertwined, up to 220 µm long. Figure 20. *Spores* 7.5–12.5 µm diam., ± globular, brownish; distal face with numerous, much convoluted and branched ridges; proximal face with faint triradiate mark, winged and densely covered with numerous fine granules and tiny irregular ridges. *Elaters* yellow-brown, (550–)600–640(–770) µm long, 5 µm wide, gradually tapering at both ends for 150–200 µm, bispiral. *Chromosome number*: n = 9 (Bischler-Causse 1993). Plate 9C, D.

The species is widely distributed in the southern hemisphere, from South America, south to the Antarctic Peninsula and north to Costa Rica, islands of the Atlantic and south Indian Ocean, southern Africa, Australia, Tasmania, New Zealand, New Guinea, New Caledonia, Java and Sulawesi (Bischler-Causse 1993). In southern Africa it is known from Northern Province, Mpumalanga and from KwaZulu-Natal, which receive summer rain, also from Western and southwestern Eastern Cape, which receive winter rain. Exact localities of two of the collections by Wilms and by McLea are not known and a question mark precedes the symbol on the map. Map 8.



MAP 8.—● **Marchantia polymorpha** subsp. **ruderalis**
▲ **M. berteroana**
■ **M. paleacea**

Marchantia berteroana generally grows on damp soil, and sometimes on wet rocks, at stream banks, near waterfalls, along paths, in kloofs, passes, ravines, gorges, in forests under trees or in burnt-over areas.

Specimens of *M. berteroana* are easily distinguished by the tiny marginal cells of the median scale appendages, by the cruciate dorsal pores and by the lobulate thallus margins. The membranous margins of the rays of the male receptacle also have very small cells. Otherwise it is quite similar to *M. polymorpha*, except for the latter having papillae on the rays of the carpocephalum. The ornamentation of their spores is also quite similar.

Vouchers: *Arnell 1058* (BOL); *Barnard CH1315; Bolus CH1319; Duthie CH1320; Garside 6185.*

FIGURE 20.—**Marchantia berteroana**. A–C, thallus: A, dorsal face with cupule; B, ventral face; C, cross section. D–F, air pore: D, from above; E_1, E_2, from below; F, c/s with dorsal epidermal cells and air chamber. G, margin of thallus; H, laminal scale; I, median scale; J_1, J_2, appendages of median scales; K, cupule margin; L, female receptacle; M, male receptacle; N, c/s of male stalk; O, c/s of female stalk: P, scale from foot of male stalk; Q, scale from along male stalk; R, median scale of male receptacle; S, margin of male ray; T, scale from foot of female stalk; U, scale from female receptacle; V, margin of involucre. A, F, G, L, N, P, R, S, *A.E. van Wyk 2066*; B–E_1, E_2, H–J_1, J_2, M, O, T–V, *Geldenhuys 1332*; K, Q, *Pillans 4048*. Scale bars: A, B, L, M, 2 mm; C, 1 mm; D–G, 50 µm; H–K, N–R, T, 250 µm; S, U, 100 µm. Drawings by M. Steyn.

Subgenus **Chlamidium**

Subgenus **Chlamidium** *(Corda) Bischl.* in Cryptogamie, Bryologie et Lichénologie 3: 362 (1982); Bischl.: 89 (1989a); Bischl.: 65 (1993); Perold: 192 (1995c). Type: *Chlamidium indicum* Corda ('Sieber flora mart. exsicc. No. 375') = *Marchantia chenopoda* L. Type: *Sieber 378* p.p. [W, neo.; STR, iso., fide Bischl. (1984)].

Chlamidium Corda in Opiz: 647 (1829).

Marchantia L. sect. *Chlamidium* (Corda) Nees: 60, 101 (1838).

Thalli with branches rather narrow, ± 2.4 mm wide to 4 times that; margins nearly flat, entire, sometimes slightly undulate, rarely crisped. *Scales* in 4 rows, covering $^1/_4$ to $^2/_3$ of ventral face, oil cells present or absent: *median scales* with appendages variously shaped, orbicular, ovate or triangular, apically often acuminate, acute or apiculate, seldom rounded, margins entire, crenulate-serrate, coarsely toothed or lobed; *laminal scales* as long as, or longer than wide, sometimes in 2 incomplete rows on either side of median scales, apically acute or obtuse, with papillae, upper cell walls lacking trigones.

Dorsal epidermis without papillae; air pores surrounded by (4)5–7 concentric rings of cells, at inner openings with straight or convex walls, rarely with pronounced, rounded processes and pores then cruciate; storage tissue often with scattered sclerotic cells.

Cupules with margins ciliate, almost entire, or with ciliate lobes, externally without, or rarely with papillae.

Dioicous. *Antheridiophores* with receptacle symmetric or asymmetric, palmate or rarely peltate, rays shallowly or deeply dissected. *Archegoniophores* with receptacle symmetric, or sometimes asymmetric, dissected into 5–9 rays, flat or convex but never terete; scales of receptacle in African species apically with marginal cells rectangular and long axis parallel to margins. *Stalks* of gametangiophores with 2(–4) rhizoid furrows. *Involucre* with margins ciliate or crenulate to entire, rarely with ciliate lobes. *Spores* larger than in subgenus *Marchantia*, 20–35 µm diam.; distal face generally ornamented with thick ridges separated by dense granules; proximal face with coarse granules only, triradiate mark and thick wing usually present.

Subgenus *Chlamidium* contains three sections, *Paleaceae, Chlamidium* and *Papillatae*. All three are represented in southern Africa by a single species.

Subgenus **Chlamidium** section **Paleaceae** *Bischl.* in Bryophytorum Bibliotheca 38: 90 (1989a); Bischl.: 67 (1993); Perold: 192 (1995c). Type: *M. paleacea* Bertol. [lecto. fide Grolle: 210 (1976)].

Thalli with branches (3.5–)6.0–8.0(–11.0) mm wide, irregularly spaced, narrowly divergent; *median scales* with appendage oblong, ovate or suborbicular, apically rounded, acute or shortly apiculate, basally cordate, width across broadest part 650–750 µm, margins entire, crenulate or slightly denticulate.

Dorsal epidermis without papillae; air pores with inner opening cruciate, inside walls of bordering cells strongly protuberant.

Cupules with margins triangularly lobed and ciliate, externally with 1- or 2-celled papillae.

Dioicous. *Antheridiophore* with receptacle peltate, shallowly dissected into 6–10 broad, rounded lobes, dorsal surface lacking papillae. *Archegoniophore* with receptacle bearing prominent median projection dorsally, deeply divided into 8 or more convex lobes, basally costate, apically truncate or hardly broadened, emarginate. *Stalks* of gametangiophores basally surrounded by large scales. *Involucre* margin with ciliate lobes. *Spores* 19–25 µm diam.; ornamentation on distal face lacking alveoli, mostly covered with a rather featureless, granular layer or with very irregular ridges, broken up or folded in or convoluted; proximal face different, thickly winged, triradiate mark faint, covered with dense granules or centrally with narrow, irregular granular ridges.

Only the two subspecies of *M. paleacea* belong to this section. The ornamentation of the spores is distinctive. Additional differences from the other two sections in subgenus *Chlamidium* are the shape of the female receptacle and the ciliate, lobed margins of the involucres and cupules.

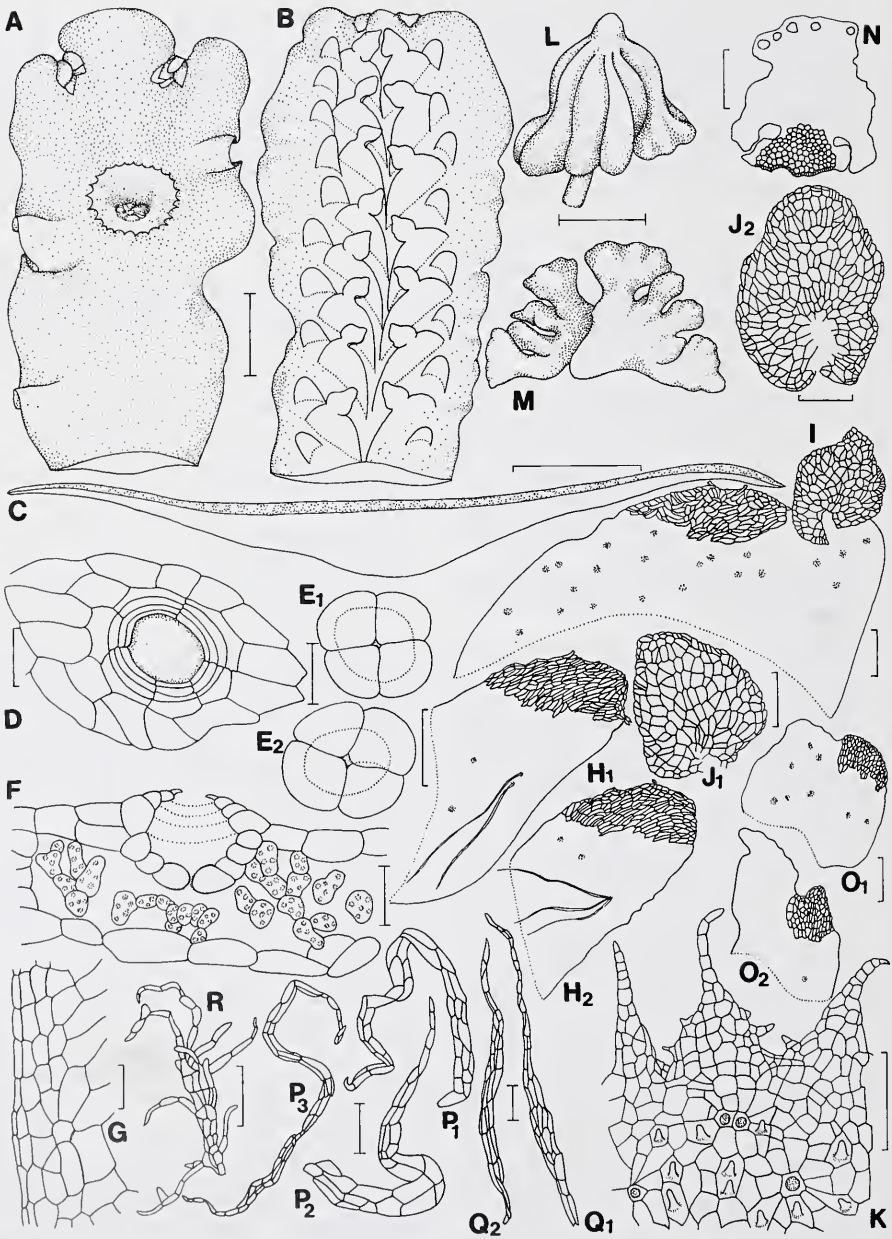
3. **Marchantia paleacea** *Bertol.* in Opuscoli scientifici. Bologna 1: 242 (1817); Bischl.: 55 (1984); Bischl.: 91 (1989a); Bischl.: 68 (1993); Perold: 193 (1995c). Type: Italy, Borgonuovo secus valles in Liguria orientali, *D. Turio*, 1810 [BOLO, lecto. fide Grolle (1976)].

M. papillata Raddi var. *italica* Raddi: 20 (1822). Syntypes: Italy, Contorni di Firenze, *Raddi s.n.* (BOLO, FH, FI, G, PC, STR).

For further synonymy see Bischler-Causse (1993).

Thalli medium-sized to large, in crowded mats; bright green to bluish green, sometimes blotched with dark red pigmentation, firm, rather leathery, without dark median band, areolate, flecked with numerous white oil bodies, pores numerous, small, generally closed, margins mostly deep red or pink, entire, proximally undulate and scalloped; when dry, margins crinkled, not raised or incurved. *Branches* repeatedly furcate, terminal segments oblong, up to 15 mm long, (3.5–)6.0–8.0(–11.0) mm wide, 750–800 µm thick medianly, in section ± 8–10 times wider than thick, apex notched, median scale appendages recurved over edge; groove absent, thallus dorsally flat, margins acute; flanks sloping obliquely; ventral face medianly keeled, dark red entirely or only medianly, the remainder green. *Scales* in 4 ventral rows, extending over $^1/_3$–$^1/_2$ of thallus width: *median scales* with body obliquely triangular, mauve, up to 1050 µm long, base arched, ± 3250 µm wide, gradually narrowing upwards, abruptly and deeply constricted at join with appendage, up to 25 oil cells scattered throughout, appendage of median scales ovate, oblong or suborbicular, marginally orange-brown or purplish, internally pink or occasionally hyaline, 810–875 × 650–750 µm, apex rounded, acute or shortly apiculate, basally generally ± cordate, margins entire, crenulate or slightly denticulate, bordered by 1 row of smaller cells, oil cells absent or 1, 2 or more present; *laminal scales* lateral to and alternating irregularly with median scales, asymmetrically oblong, mauve or internally mauve and marginally hyaline, 750–1575 µm long, base slightly arched or oblique, 500–650 µm wide, longer than wide, margins entire or slightly crenulate, up to 10 oil cells present.

Dorsal epidermal cells mostly unistratose, hyaline, long-rectangular or polygonal, (45.0–)60.0–80.0 × 27.5–37.5 µm, walls thin or slightly thickened; air pores raised, compound, 40.0–50.0 × 35.0–42.5 µm, surrounded by 4–6(–7) concentric rings of cells, 2 or 3 above epidermis and up to 4 projecting into air chambers, inner opening with 4 or 5 cells, inside walls strongly protuberant, leaving only a small cruciate opening. *Assimilation tissue* 75–100 µm thick, air chambers in one storey, containing densely chlorophyllose filaments, bounding walls 3 or 4(5) cells high; storage tissue occupying most of ventral part of thallus medianly, decreasing laterally, cell walls pitted, central area sometimes stained purple, sclerotic cells and mucilage cavities absent in specimens seen, but reportedly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sometimes present; oil cells scattered throughout tissues, numerous in dorsal epidermis.

Cupule margins with ciliate, ± triangular lobes, cilia at apex of lobes up to 6 vertical cells long, basally on either side transverse, 1–3(4)-celled; cupule wall lower down several cell layers thick, exteriorly with 1- or 2-celled papillae. *Chromosome number*: n = 9 (Bischl. 1984, 1988, 1989a). Figure 21.

Only sterile plants are known from southern Africa. Archegoniophores from a specimen from Madeira, *Tavares s.n.*, were illustrated in Perold (1995c: fig. 5L–R). This widespread species is known from the southern states of the USA, Mexico and Central America, the Mediterranean, northern Yemen, the Caucasus, Himalayas and the Far East. In Africa (and islands) it has been collected in Algeria, Ethiopia, the Azores, Madeira, Cape Verde and Réunion. In the *FSA* area it is only known from Pilgrim's Rest, Mpumalanga, where it grows on a steep bank of the Blyde River and from Forest Falls, near Graskop. Map 8.

M. paleacea subsp. *paleacea* has been placed in subgenus *Chlamidium* on account of the 4 rows of ventral scales restricted to the median part of the thallus. It differs from other species in the subgenus by its cruciate epidermal pores, cupules with ciliate lobes at the margins and median scale appendages which are ovate to orbicular. The species is assigned to the monotypic section *Paleaceae* because of the shape of the female receptacle and the structure of the margins of the involucres and cupules, which have ciliate lobes that are externally papillate.

In the Far East, a subspecies, *M. paleacea* subsp. *diptera* (Nees et Mont.) S.Hatt., is recognized (Bischler-Causse 1989a). It is distinguished from subsp. *paleacea* by the epidermal pores of the thallus usually surrounded by 7 or 8 rings of cells, by the frequent presence of non-functional female receptacles and by the marginal cells in the median scale appendage with the long axis oblique to perpendicular to the margins (not parallel to, as in the typical subspecies).

Vouchers: *Perold 3264, 3265*; *Perold & Koekemoer 4031*.

Subgenus **Chlamidium** section **Chlamidium** *(Corda) Nees*

Thalli with branches (6.0–)7.0–8.5(–10.0) mm wide, generally rather remotely spaced and narrowly divergent; *median scales* with appendage ovate to orbicular or broadly triangular, apically rarely obtuse, mostly acute, sometimes shortly apiculate, basally rounded or cordate, width across broadest part 375–530 µm, margins entire or sometimes bluntly toothed, with 1 or 2 oil cells, rarely more numerous.

Dorsal epidermis without papillae; air pores with inner opening bordered by cells, their inside walls convex to nearly straight or with short, rounded processes.

Cupules with ciliate margins, cilia up to 6 or 7 cells long and 3 cells wide basally, externally sometimes also with several cilia.

Dioicous. *Antheridiophore* with receptacle palmate, shallowly to deeply dissected into 6–8 (–10) rays, dorsal surface with or without papillae. *Archegoniophore* with receptacle bearing

FIGURE 21.—**Marchantia paleacea.** A–C, thallus: A, dorsal face; B, ventral face; C, cross section. D–F, air pore: D, from above; E_1, E_2, from below; F, c/s with dorsal epidermal cells and air chamber. G, margin of thallus; H_1, H_2, laminal scales; I, median scale; J_1, J_2, appendages of median scales; K, cupule margin; L, female receptacle from side; M, female receptacle from above; N, c/s of female stalk; O_1, O_2, scales from foot of female stalk; P_1–P_3, scales from along female stalk; Q_1, Q_2, scales from female receptacle; R, margin of involucre. A, E_1, E_2, G, I, J_1, J_2, *Rankin 206*; B–D, F, H_1, H_2, K, *Perold 3264*; L–R, *C. Tavares LISU P 66716*. Scale bars: A, B, L, M, 2 mm; C, 1 mm; D–G, 50 µm; H–K, N–R, 250 µm. Drawings by M. Steyn.

small, median projection dorsally, or not, shortly divided into 9–11 rather flat, short lobes, sometimes basally narrow, widening slightly toward truncate apex. *Stalks* of gametangiophores basally surrounded by quite large scales. *Involucre* margins shortly to longly ciliate. *Spores* 20–30 µm diam.; distal face ornamented with wide, irregular, smooth ridges forming incomplete alveoli filled with nodules; proximal face entirely covered with nodules.

Of the southern African taxa, only *M. pappeana* belongs in this section. The ornamentation of its spores is referred to as the *chenopoda*-type; there are, however, two other spore coat ornamentation types in the section (Bischler-Causse 1989a). The section is distinct in the shape of the female receptacle and in the ciliate margins of the involucres and cupules.

4. **Marchantia pappeana** *Lehm.*, Novarum et minus cognitarum stirpium, pugillus X: 21 (1857); Bischl.: 76 (1993); Perold: 197 (1995c). Type: South Africa, 'In Prom. B.S. leg. *Pappe*', ex herb. Lehmann (RO, holo.?; G! ex herb. Univ. di Roma).

M. planiloba Steph.: 90 (1886a); Steph.: 181–182 '153–154' (1886b). Type: São Tomé, Cachoeira do Rio Manuel Jorge, circa S. Nicolau, 800 m, 1885, *Moller 32* [G, lecto. fide Vanden Berghen: 52 (1960)].

M. wilmsii Steph.: 126 (1892). Type: South Africa, Transvaal, McLea in Rehmann Hep. austro-afr. exs. 1 [PC, lecto. fide Vanden Berghen: 44 (1954); BM!, G, NY, S, isolecto. fide Bischl.: 84 (1993)].

M. parviloba Steph.: 305 (1895b); Vanden Berghen: 46 (1954); S.W.Arnell: 56 (1963a). Type: Uganda, Runssoro, um 2 800 m, 10 Juli 1891, *Stuhlmann 2368a* [G, lecto. fide Vanden Berghen: 46 (1954); BM, isolecto. fide Bischl.: 82 (1993)].

M. planiloba Steph. var. *walteri* Burgeff: 276 (1943). Type: Tanzania, 'Nderema in Ost-Usambara, etwa 1 000 m, leg. *H. Walter*', syn. fide Bischl.: 83 (1993).

M. flavescens Steph. in Bonner: 107 (1953). Type: Fernando Pó, 1911 *Mildbraed 6275* (G).

M. winkleri Steph. in Bonner: 112 (1953). Type: Cameroon, *Winkler 270* (G).

M. stephanii Vanden Berghen: 50 (1954) [= *M. umbellata* Steph.: 305 (1895b), nom. illegit.]. Type: Tanzania, Usambara, *Holst 692* (FH, G), syn. fide Bischl.: 83 (1993).

M. pappeana Lehm. subsp. *pappeana*, Bischl.: 82 (1993); Perold: 199 (1995c).

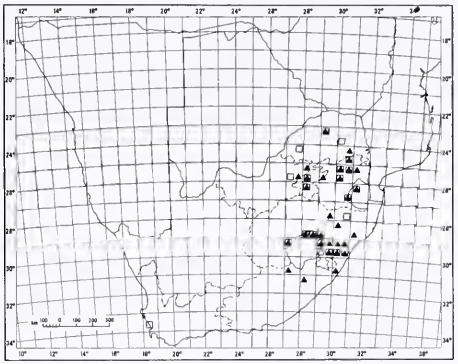
Thalli medium-sized to large, in densely crowded mats; light green to yellowish green, without dark median band, areolate, flecked with whitish oil cells, air pores quite large, margins usually hyaline, occasionally purple, undulate, scalloped, mostly crisped, entire; when dry, margins rarely raised, not incurved. *Branches* rather distantly and irregularly furcate, not ribbon-like or flat, terminal segments oblong to obovate, 10–15 mm long, (6.0–)7.0–8.5(–10.0) mm wide, 740–925 µm thick medianly, in section ± 9 times wider than thick, apex notched, median scale appendages recurved over edge; groove absent, thallus margins acute; flanks sloping obliquely; ventral face medianly keeled. *Scales* in 4 ventral rows, extending over $^2/_5$–$^3/_4$ of thallus width: *median scales* with body obliquely triangular, purple, 800–1125 µm long, base arched, 1430–1875 µm wide, margins sometimes with protruding papillae, narrowing upwards and deeply constricted where joined with appendage, scattered oil cells present, appendage of median scales ovate to orbicular or broadly triangular, purple-brown or reddish, 520–550 × 375–530 µm, apex mostly acute, sometimes shortly apiculate, basally rounded or cordate, margins entire or sometimes bluntly toothed, marginal cells only slightly smaller than large inner cells, oil cells solitary, rarely more numerous; *laminal scales* lateral to median scales, mauve with hyaline base, obtusely triangular, (750–)980–1125 µm long, base (360–)630–1075 µm wide, longer than wide, margins often with protruding papillae, oil cells scattered throughout.

Dorsal epidermal cells mostly unistratose, hyaline, 5- or 6-sided, 42.5–80.0(–105.0) × 22.5–37.5 µm, thin-walled; air pores raised, compound, (65–)90–105 × 70–100 µm, sur-

rounded by 6 or 7 concentric rings of cells, 3 or 4 above epidermis and 2 or 3 projecting into air chambers, inner opening with 4 or 5(6) cells, inside walls convex or almost straight. *Assimilation tissue* 60–90 µm thick, air chambers in single storey, crowded with chlorophyllose filaments, bounding walls 2 or 3 cells high; storage tissue occupying most of ventral part of thallus medianly, decreasing laterally, sclerotic cells present or absent, mucilage openings few or absent; oil cells scattered throughout tissues.

Cupule margins with cilia up to 6(7) cells long, exterior occasionally also ciliate.

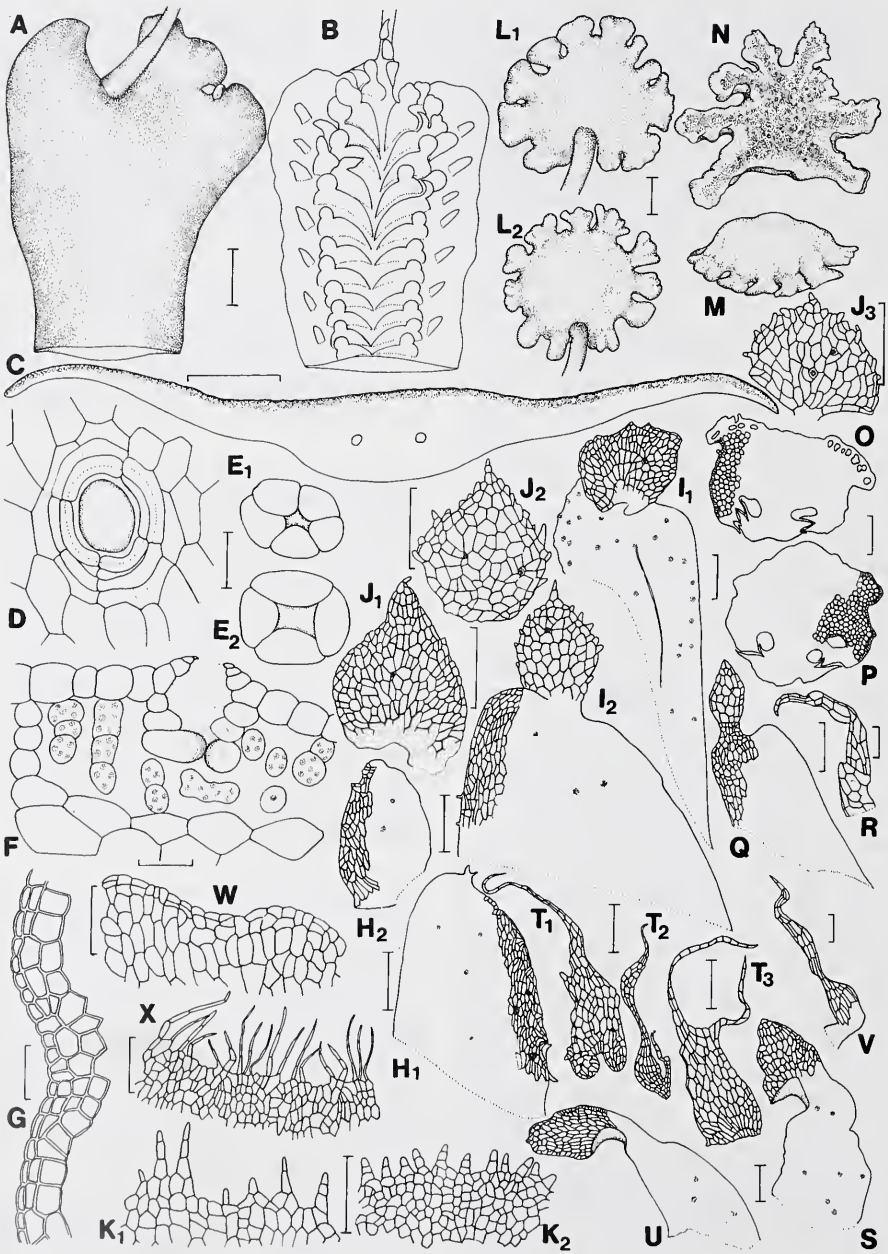
Dioicous. *Antheridiophore* arising from apex of terminal segment of main branch, raised on stalk; receptacle 9–14 mm diam., palmate, dissected into 6–8 rays, 1.7–3.4 mm long, ± 3.5 mm wide, basal sinus 120–140°, ray margins reddish, undulating, entire; *median scales* on ventral side of rays brownish, obtusely triangular, body ± 750 × 500 µm, appendage tapering to acute apex, 350–375 × 125–250 µm. *Stalk* 9–18(–32) mm long, 775–925 µm diam., with 2(3) rhizoid furrows, air chambers absent; *scales at base of stalk* 1 or 2, hyaline, broadly triangular, 1000–1150 × 550–750 µm, sometimes with appendage, ± 675 × 500 µm, partly or not constricted at base; *scales along length of stalk* narrowly triangular and tapering toward apex, up to 1300 µm long, base ± 175 µm wide. *Archegoniophore* arising from apex of terminal segment of main branch, raised on stalk; carpocephalum (6.5–)8.0–11.0 mm diam., with small, rounded, median projection dorsally, shortly and ± symmetrically divided into 9–11 lobes (occasionally 1 or 2 lobes replaced by male rays), 1.4–1.7 mm long, base narrow, widening toward truncate apex, basal sinus ± 30°; *scales of carpocephalum* mauve or hyaline, tapering toward apex, occasionally forked, up to 3250 × 250 µm, apices filamentous, ± 450 µm long, papillate marginally, several oil cells present. *Stalk* 16–32(–60) mm long, 850–1250 µm diam., with 2 separate and opposite bands of air chambers and 2 rhizoid furrows; *scales at base of stalk*, 1 or 2, shape irregular, ± 1350 × 850 µm, often with triangular appendage, 750–900 × 500–550 µm; *scales along length of stalk* tapering, apically with filamentous, hyaline strands. *Involucre* with margins hyaline, delicately ciliate, cilia sometimes collapsed, 187.5–200.0 µm long. Figure 22. *Spores* 22.5–30.0 µm diam., triangular-globular, yellow-brown; distal face with irregular, ± smooth ridges, forming incomplete alveoli filled with nodules; proximal face with faint triradiate ridge, each facet densely covered with nodules, some discrete, others confluent, narrowly winged, margin entire. *Elaters* yellow-brown, up to 825 µm long, 7.5 µm wide, tapering toward ends, 5.0 µm wide, bispiral. *Chromosome number*: n = 18 (Bischler-Causse 1993). Plate 9E, F.



MAP 9.—❑ **Marchantia pappeana** subsp. **pappeana**
▲ **M. debilis**

Marchantia pappeana is widely distributed in tropical Africa, Bischler-Causse (1993) reporting it from the Cape Verde Islands to Ethiopia and south to southern Africa, generally at an altitudinal range of 1 000–2 500 m. In southern Africa it is known from North-West, Northern Province, Gauteng, Mpumalanga, Swaziland, Free State, KwaZulu-Natal and Lesotho. It has also been collected at Kirstenbosch Botanical Garden, Western Cape, a number of times and the type specimen is from Promontorium Bonae Spei. Map 9.

Marchantia pappeana often grows in the same localities as *M. debilis*, on vertical soil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banks of streams, at waterfalls, at sluice canals, very rarely on rotting wood or on rocks, in open grassland or in forests, sometimes in deep shade.

Generally, the species can be distinguished by being larger than *M. debilis* and by lacking a dark median line on the dorsal surface of the thallus; its median scale appendages are large and often marginally toothed, with the inner cells large, presenting a 'loose' appearance; its cupules have longer cilia; the female receptacle is shortly divided into rays and the involucral margin is ciliate; androgynous branches in the female receptacle are sometimes present.

M. pappeana subsp. *pappeana* differs from *M. pappeana* subsp. *robusta* (Steph.) Bischl., a close relative in South India and Sri Lanka, by the latter having numerous sclerotic cells and mucilage cavities in the thallus; oil bodies in the median scale appendages are, however, absent.

Vouchers: *Bottomley CH1335; Burgoyne 2068; Hilliard & Burtt 15460* (BOL); *Perold & Koekemoer 2841; Scheepers 562.*

Subgenus **Chlamidium** section **Papillatae** *Bischl.* in Cryptogamie, Bryologie et Lichénologie 10: 69 (1989b); Bischl.: 99 (1993). Type: *M. papillata* Raddi [PI, lecto., Bischl.: 95 (1984)].

Thalli with branches rather narrow, (2.1–)4.5–7.3 mm wide, ribbon-like, often quite regularly spaced, moderately to widely divergent; *median scales* with appendage orbicular or ovate, apically acute or apiculate, seldom obtuse, basally rounded, width across widest part 275–340 µm, margins toothed, oil cells absent.

Dorsal epidermis without papillae; air pores with inner opening bordered by cells, their inside walls convex or straight.

Cupule margins with short cilia, 3(4) cells long and 1 or 2 cells wide basally, externally without papillae.

Dioicous. *Antheridiophore* with receptacle smallish, palmate, asymmetric and deeply divided into (4)5–7 rays, dorsal surface without papillae. *Archegoniophore* with carpocephalum smallish, dorsally bearing a rounded median projection and deeply divided into 8–10 lobes, these basally convex and costate, apically broadened. *Stalks* of gametangiophores basally surrounded by smaller, narrowly triangular scales. *Involucre* margins entire or crenulate. *Spores* 25–32 µm diam.; distal face ornamented with irregular ridges, forming incomplete alveoli filled with granules; proximal face densely verruculose.

Only *M. debilis* of the southern African taxa belongs to this section. Bischler-Causse (1993) states that it is closest to the Asiatic species, *M. emarginata* subsp. *tosana*. The ornamentation of the spores is of the *papillata* type. The section differs from sect. *Paleaceae* and sect. *Chlamidium* in the shape of the female receptacle, with the lobes costate basally and broadened apically.

FIGURE 22.—**Marchantia pappeana** subsp. **pappeana**. A–C, thallus: A, dorsal face; B, ventral face; C, cross section. D–F, air pore: D, from above; E_1, E_2, from below; F, c/s with dorsal epidermal cells and part of air chamber. G, margin of thallus; H_1, H_2, laminal scales; I_1, I_2, median scales; J_1–J_3, appendages of median scales; K_1, K_2, margins of cupules; L_1, L_2, female receptacles from above; M, female receptacle from side; N, male receptacle; O, c/s of female stalk; P, c/s of male stalk; Q, median scale of male receptacle; R, scale from along male stalk; S, scale from foot of male stalk; T_1–T_3, scales from female receptacle; U, scale from foot of female stalk; V, scale from along female stalk; W, margin of male ray; X, margin of involucre. A, G, H_1, I_2, J_2, K_1, L_1, L_2, M, T_1–T_3, X, *Koekemoer 1050*; B, C, F, J_3, K_2, N, *Perold & Koekemoer 2918*; D, O, V, *Burgoyne 2068*; E_1, S, *H. Anderson 1261*; E_2, I_1, J_1, H_2, *Perold & Koekemoer 2841*; P–R, W, *Hilliard & Burtt 15460*; U, *H. Anderson CH13278*. Scale bars: A, B, L–M, 2 mm; C, 1 mm; D–G, 50 µm; H–V, X, 250 µm; W, 100 µm. Drawings by M. Steyn.

5. **Marchantia debilis** *K.I.Goebel* in Organographie der Pflanzen. 1. Bryophyten 2, edn 2: 901 (1915); Bischl.: 100 (1993); Perold: 201 (1995c). Type: Cameroon, Urwaldgebiet von Bipindi, *Zenker*, *Flora von Kamerun exs. 1339* (BM!, BR, E, F, G!, GOET, M, S, iso.).

M. chevalieri Steph. in Bonner: 103 (1953). Type: Ivory Coast, Haute Côte d'Ivoire, pays Dijola, environs de Ona, 4-1909, *Chevalier s.n.* (G, PC).

Thalli smallish to medium-sized, in crowded patches, rarely in partial rosettes; green, occasionally purplish all over, medianly with broken, dark, narrow, longitudinal band, areolate, air pores quite small, margins narrowly reddish purple or hyaline, entire, occasionally slightly crisped; when dry, margins not raised or incurved. *Branches* repeatedly pseudodichotomously furcate, sometimes quite regularly so, ribbon-like, rather flat, apical segments oblong or broadly lingulate, 5–12 mm long, 4.5–7.3 mm wide, 675–850 µm thick medianly, in section 7 or 8 times wider than thick, apex notched, with median scale appendages recurved over edge; groove absent, thallus margins acute, thin; flanks sloping obliquely; ventral face medianly keeled, purplish. *Scales* in 4 ventral rows, extending over $^{7}/_{10}$ or more of thallus width: *median scales* with body ± obliquely triangular, brownish or purplish, upper margins serrate, up to 625 µm long, base slightly arched, up to 3000 µm wide, narrowing upwards and constricted where joined with appendage, scattered oil cells present throughout, appendage of median scales orbicular or ovate, reddish brown or mauve, 350–375 × 275–340 µm, apex acute or apiculate, rarely rounded, basally narrowed, margins toothed, cells smaller than inner cells, oil cells absent; *laminal scales* lateral to median scales, brownish, ± ovate, 450–560 µm long, base 430–670(–900) µm wide, wider than long, margins sometimes ± papillate, oil cells rare or absent.

Dorsal epidermal cells mostly unistratose, generally hyaline, polygonal, (4)5–7-sided, 37.0–62.5 × 22.0–32.0 µm, thin-walled; air pores raised, compound, 37.5–62.5 × 40.0–52.5 µm, surrounded by 4(5) or 6 concentric rings of cells, 2 or 3 above epidermis and 2 or 3 projecting into air chambers, inner opening with 4 or 5 cells, inside walls ± convex or nearly straight. *Assimilation tissue* up to 150 µm thick, air chambers in single storey, crowded with chlorophyllose filaments, bounding walls 2 or 3 cells high; storage tissue occupying most of ventral part of thallus medianly, decreasing laterally, sclerotic cells and mucilage cavities usually absent; oil cells scattered throughout tissues.

Cupule margins with short cilia, 1–3 cells long.

Dioicous. *Antheridiophore* arising from apex of terminal segment of main branch or of short lateral branch, raised on stalk; receptacle 7.5–9.0 mm diam., asymmetric, dissected into (4)5–7 rays, 1.5–3.0 mm long, ± 1.2 mm wide at base, narrowing slightly to tip, basal sinus ± 130°, ray margins hyaline, undulating, entire; *median scales* on ventral side of rays, hyaline or mauve, obtusely triangular, up to 1000 × 670 µm, margin with some papillae, sometimes with apical appendage, which is basally constricted or not, narrowly to broadly triangular, 300–430 × 100–200 µm, brownish with mauve cell walls. *Stalk* (2.5–)7.0–16.0 mm long, 625–700 µm diam., with 2 rhizoid furrows, reduced air chambers in single band; *scales at base of stalk*, narrowly triangular, 750–1250 µm long, 150–500 µm wide at base, margins with few papillae, sometimes ± midway divided into (2)3 tapering segments, apices filamentous; *scales along length of stalk* filiform, up to 1100 × 50 µm, 2 or 3 cells wide, apical cells uniseriate. *Archegoniophore* arising from apex of terminal segment of main or short lateral branch, raised on stalk; carpocephalum (3.5–)4.5–7.0(–9.0) mm diam., with small rounded projection medianly, deeply dissected into 8–10 lobes, 0.8–1.25 mm long, narrower at base, widening toward apex, basal sinus 40–60°; *scales of carpocephalum* hyaline or yellow-brown or purple, irregularly shaped, tapering toward apex, 800–1000 × 330–370 µm. *Stalk* 9–16 mm long, 400–550 µm diam., with 2 rhizoid furrows, and generally a single band of air chambers, rarely 2 bands; *scale(s) at base of stalk* brownish, ± triangular, 900–1000 × 400–450 µm, apex fili-

form with 3 or 4 single cells in a row; *scales along length of stalk* scattered, ± 700 × 112 µm, tapering upwards, ± 35 µm wide. *Involucre* with margins hyaline, entire or crenulate. Figure 23. *Spores* 25.0–32.5 µm diam., faintly triangular-globular, brown; distal face with irregular, coarse ridges, forming incomplete alveoli, spaces in between filled with granules; proximal face with triradiate mark hardly visible, facets densely verruculose. *Elaters* brown, up to 295 µm long, ± 7.5 µm wide, bispiral. *Chromosome number*: unknown. Plate 10A, B.

Marchantia debilis is widely distributed in Africa and occurs from Morocco to southern Africa, as well as on Réunion and in the eastern part of Madagascar. In the *FSA* region it occurs in the summer rainfall areas of Northern Province, Gauteng, Mpumalanga, Swaziland, Free State, KwaZulu-Natal, Lesotho and Eastern Cape. Map 9.

The species generally grows on damp soil on vertical stream banks or waterfalls, on mud (or occasionally on stones) of stream beds, at weirs, or sluice canals, on stone dam walls kept wet by spray, and on soil overlying sandstone or granite, in open grassland or in forests, sometimes in partial shade.

Sterile plants of *M. debilis* can be distinguished from *M. pappeana*, the species it has frequently been confused with, by the smaller size of the rather ribbon-like thallus branches, the dark median line on the dorsal face of the thallus, the smaller appendages of the median scales and by the shortly ciliate or almost entire margins of the cupules. Fertile plants should not be difficult to identify as the smallish male and female receptacles, the latter with deeply divided lobes, are quite distinctive and the margin of the involucre is entire.

Bischler-Causse (1993) states that this species, which is confined to Africa, had not been mentioned since its description by Goebel (1915) and that it occurs in various herbaria under 14 different names, but most commonly under *M. wilmsii, M. planiloba* and *M. chevalieri*. She was able to resolve the taxonomy of this species. In Stephani's herbarium, she found that 13 of the 16 '*M. wilmsii*' specimens belong to *M. pappeana* and only three to *M. debilis*. She concluded that Stephani probably had *M. pappeana* in mind, and not *M. debilis*, since he clearly described *M. pappeana* under the epithet *M. wilmsii*.

Vouchers*: Bester 2544; Dieterlen 850; Glen 1690; Koekemoer 1049; Perold 3261; Van Rooy 1012.*

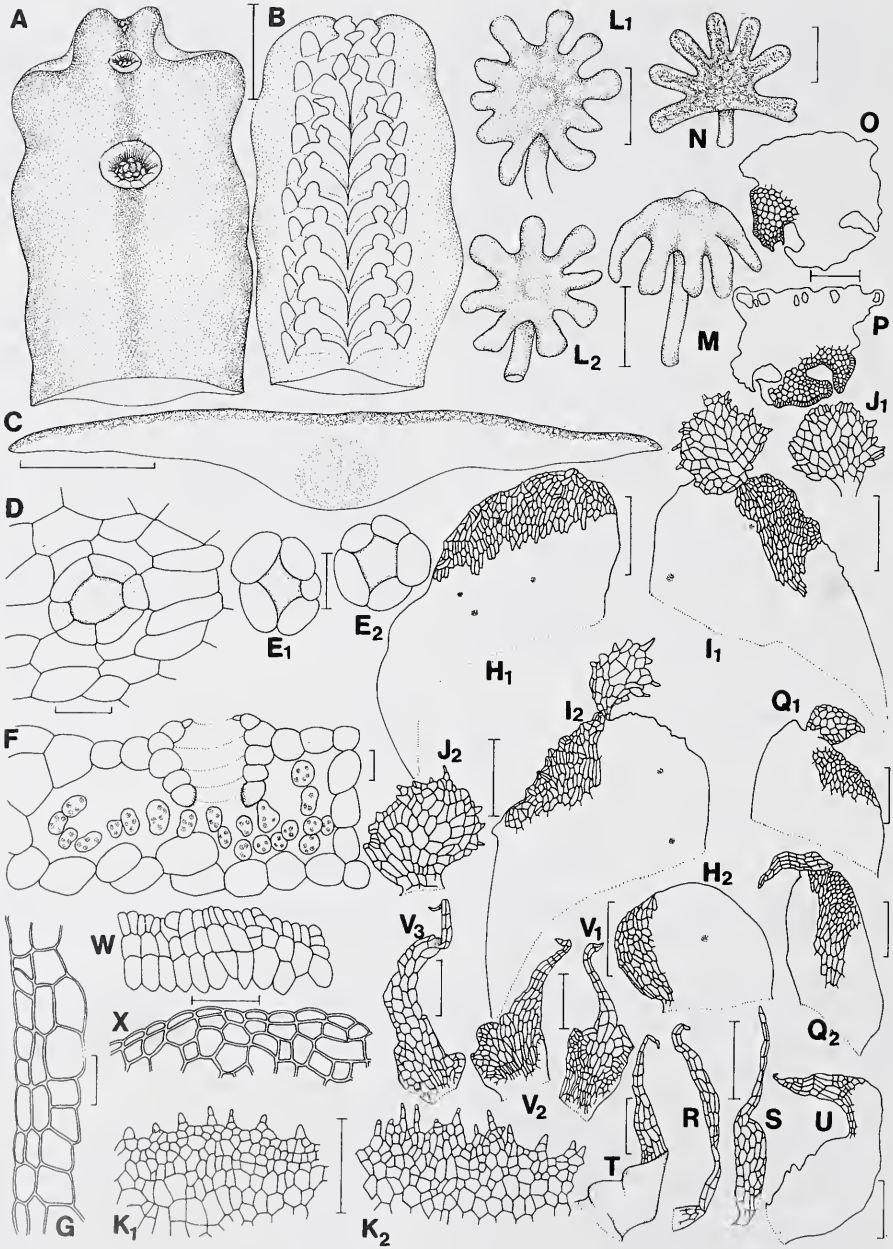
Subfamily **DUMORTIEROIDEAE**

Dumortieroideae *R.M.Schust.* in Phytologia 56: 71 (1984a); R.M.Schust.: 375 (1992c). Type: *Dumortiera* Nees ex Reinw.

Thalli large, in extensive mats or sheets; dark green, thin, translucent. *Branches* broadly and rather irregularly strap-shaped, pseudodichotomously furcate, occasionally articulate, with apical and/or ventrolateral innovations, apex notched; groove absent, thallus dorsally flat, margins thin, undulate, to nearly flat, occasionally scalloped, sparsely hirsute; flanks sloping very obliquely; ventral face medianly keeled. *Scales* vestigial, without appendages, evanescent.

Dorsal epidermis, air pores and assimilation tissue absent, dorsally ± smooth, but sometimes with vestigial and ephemeral faint ridges delimiting polygonal areas of open air chambers, cells in 'floor' of air chambers small, chlorophyllose; storage tissue with large, hyaline cells often containing starch grains; oil cells rare.

Asexual reproduction absent.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Monoicous or ?dioicous. *Antheridiophore* subsessile, on very short stalk with 2 rhizoid furrows, arising apically; receptacle disciform, antheridia dorsally sunken, margins fringed with hairs, underneath with filiform scales. *Gynoecial receptacle* raised on stalk arising from apical notch of thallus; carpocephalum disciform, radially grooved above by sinuses, mostly lacking air pores and air chambers, but with scattered, bristle-like hairs, ventrally 6–8(–10)-lobed. *Stalk* ± 4 mm long, with 2 rhizoid furrows, at apex with filiform, hyaline scales. *Involucres* fleshy, saccate, apices with narrow, slit-like openings. *Pseudoperianth* absent. *Sporophyte* with foot, longish seta and ellipsoid capsule, wall unistratose, with annular or semi-annular thickenings, dehiscing by 4 irregular valves. *Spores* small; distal face rounded; proximal face ± flat, ornamented with numerous nodules. *Elaters* tapering at ends, bispiral. *Chromosome numbers*: n = 9, 18, 27.

The subfamily Dumortieroideae is monotypic with the only genus *Dumortiera* placed here.

DUMORTIERA

Dumortiera *Nees* in Nova acta academiae caesareae Leopoldino-Carolinae germanicae naturae curiosorum XII: 410 (1824); Gottsche et al.: 542 (1844–1847); Schiffn.: 35 (1893); Steph.: 222 (1899); Sim: 25 (1926); Müll.Frib.: 394 (1951–1958); S.W.Arnell: 52 (1963a); Hässel de Menéndez: 182 (1963); R.M.Schust.: 377 (1992c); Perold: 49 (1993a).

Synonymy according to Nelson & Parnell: 35 (1992).

Hygropyla Taylor: 390 (1836).

Hygrophila Taylor (orth. var.) in J.Mackay: 53 (1836) non R.Br. (1810).

Hygrophyla Taylor (orth. var.) in J.Mackay: X (1836).

Hygropila Taylor (orth. var.) in Hook.f. & Taylor: 576 (1844).

Askepos Griff.: 340 (1849).

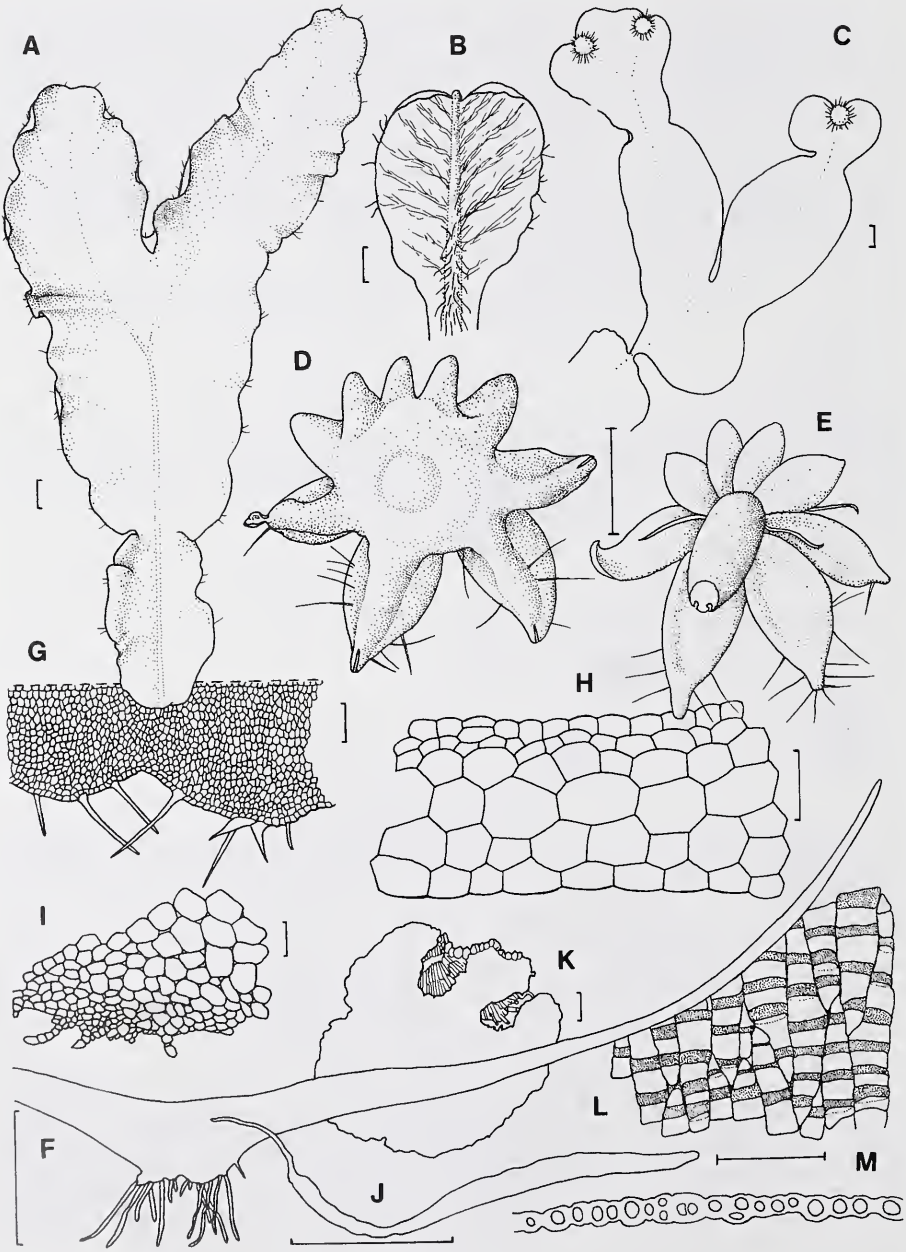
The generic diagnosis is contained in the diagnosis of the subfamily.

Dumortiera hirsuta *(Sw.) Nees* in Nova acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum XII: 410 (1824); Gottsche et al.: 542 (1844–1847); Spruce: 566 (1885); Steph.: 224 (1899); Macvicar: 41 (1926); Sim: 25 (1926); Müll.Frib.: 396 (1951–1958); S.W.Arnell: 52 (1963a); Hässel de Menéndez: 182 (1963); R.M.Schust.: 383 (1992c); Perold: 49 (1993a). Type: Jamaica, leg. *Swartz s.n.* [S, holo.!; MW, iso., *Hb. Hoffm. No. 8497*; UPS, fide Grolle (1976)].

Marchantia hirsuta Sw.: 145 (1788).

M. irrigua Wilson in Hook. (1833) and in Sm.: 106 (1833). *Hygropyla irrigua* (Wilson in Hook.) Taylor: 390 (1836); J.Mackay: 54 (1836); Steph.: 150 (1899). *Dumortiera irri-*

FIGURE 23.—**Marchantia debilis**. A–C, thallus: A, dorsal face with cupules; B, ventral face; C, cross section. D–F, air pore: D, from above; E_1, E_2, from below; F, c/s with dorsal epidermal cells and air chamber. G, margin of thallus; H_1, H_2, laminal scales; I_1, I_2, median scales; J_1, J_2, appendages of median scales; K_1, K_2, margins of cupules; L_1, L_2, female receptacles from above; M, female receptacle from side; N, male receptacle; O, c/s of male stalk; P, c/s of female stalk; Q_1, Q_2, median scales of male ray; R, scale from along male stalk; S, scale from along female stalk; T, scale from base of female stalk; U, scale from base of male stalk; V_1–V_3, scales from female receptacle; W, margin of male ray; X, margin of involucre. A, *H. Anderson CH1223*; B, R, U, W, X, *Mogg 6172*; C–G, H_2, J_1, K_1, *Condy 90*; H_1, I_1, I_2, K_2, *Bester 2544*; J_2, *Glen 1940*; L_1, L_2, M, P, S, T, *Dieterlen 850*; N, *Sim CH1345*; O, *Perold 2891*; Q_1, Q_2, V_1–V_3, *Perold 3048*. Scale bars: A–B, L–N, 2 mm; C, 1 mm; D–G, 50 µm; H–K_2, O–V_3, 250 µm; W, X, 100 µm. Drawings by M. Steyn.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gua (Wilson in Hook.) Nees: 159 (1838). *D. hirsuta* Sw. var. *irrigua* (Wilson in Hook.) Spruce: 566 (1885). Type: Ireland, Turk Cascade, near Killarney, *Mr Wilson*.

D. hirsuta Sw. var. *angustior* Gottsche et al.: 544 (1844–1847).

D. hirsuta Sw. var. *intermedia* Gottsche et al.: 544 (1844–1847).

D. velutina Schiffn.: 156 (1898).

Askepos brevipes Griff.: 340 (1849). Type: India, in sylvis umbrosis Tingrei agri, II-1836.

Thalli very large, in extensive mats or sheets; uniformly dark green, hygrophylous, thin, translucent, from above mostly smooth, rarely with vestigial and ephemeral polygonal ridges; pores absent, margins undulate, occasionally scalloped, sparsely hirsute; when dry, crisped and shrivelled, dull, margins not raised. *Branches* creeping, once to several times pseudodichotomously furcate, occasionally articulate with ventrolateral or apical innovations, apical segments broadly and irregularly strap-shaped, 50–95(–200) mm long, 8–13(–22) mm wide, ± 500 µm thick medianly, in section 16–26 times wider than thick, apex notched, without scale tips; groove absent, thallus dorsally flat, margins acute, thin, sparsely hirsute; flanks sloping very obliquely; ventral face medianly keeled. *Scales* in 2 ventral rows, only toward apex, hyaline, vestigial, without appendages, evanescent, marginally with slime papillae.

Dorsal epidermis, air pores and assimilation tissue absent; surface cells of thallus unistratose, thin-walled, chlorophyllose; margins with sparse hairs, ± 250 µm long, tapering slightly to somewhat blunt tip; storage tissue with ± 18 cell rows medianly, cells larger, angular in upper 3 rows, walls wavy, with scattered chloroplasts, lower down cells smaller, lacking chloroplasts, cell rows decreasing in number laterally; oil cells quite rare, mostly confined to keel.

Asexual reproduction absent.

Monoicous or ?dioicous. *Androecial receptacle* subsessile, disciform, ± 2.8 mm diam., antheridia sunken, bristle-like hairs, 600–1100 µm long, dorsally scattered, densely fringing margins, underneath with filiform, hyaline paleae. *Stalk* arising from apical notch of thallus, very short, with 2 rhizoid furrows, air chambers absent. *Gynoecial receptacle* arising at apical notch of thallus between overlapping sides; carpocephalum disciform, ± 3.8 mm diam., centrally convex above, mostly lacking air pores and chambers, radially grooved by sinuses, ventrally with 6–8(–10) lobes in radiating rows, almost star-shaped, sparsely bristled. *Stalk* ± 4 mm long, 925 µm wide, with 2 rhizoid furrows, air chambers absent, summit encircled by numerous, filiform or lanceolate, hyaline paleae, up to 3750 µm long, 300 µm wide at base, oil cells absent. *Involucres* green when young, fleshy, saccate, apices with narrow, slit-like openings, through which long archegonial necks protrude, at maturity generally only one sporophyte in each involucre, rarely 2, sometimes none. *Pseudoperianth* absent. *Sporophyte* with longish seta, capsule ellipsoid, wall unistratose, with annular or semi-annular thickenings, dehiscing irregularly by 4 valves. Figure 24. *Spores* 25–30 µm diam., ± hemispherical, golden brown, semitransparent, ornamented with numerous nodules or tubercles, irregular in size and shape; distal face rounded; proximal face ± flat to slightly peaked in centre, triradiate mark indistinct. *Elaters* yellow-brown or orange-brown, 225–470 µm long, 7.5–10.0 µm wide in centre and 3.5 µm wide at tapered ends, bispiral. *Chromosome number* n = 9. Plate 10C, D.

Dumortiera hirsuta is subcosmopolitan and is widespread and common in tropical and temperate regions, but rare in the British Isles and Europe and seemingly absent from southern

FIGURE 24.—**Dumortiera hirsuta**. A–C, F–H, thallus: A, dorsal face; B, ventral face; C, male with disciform receptacles at apices; F, cross section; G, margin with hairs; H, c/s, much enlarged. D, E, young female receptacle: D, from above; E, from below. I, c/s of lower cells of costa and vestigial scales; J, filiform palea from top of stalk; K, c/s of stalk with two rhizoid furrows. L, M, capsule wall: L, cells with thickenings; M, cross section. A, F–H, *Perold 2694*; B, *Perold 2634*; C, *Nicholas 1176*; D, E, I, *H. Anderson CH13495*; J–L, *Doidge CH3581*. Scale bars: A–C, 2 mm; D–F, J, 1 mm; G, K, 100 µm; H, I, L, M, 50 µm. Drawings by G. Condy.

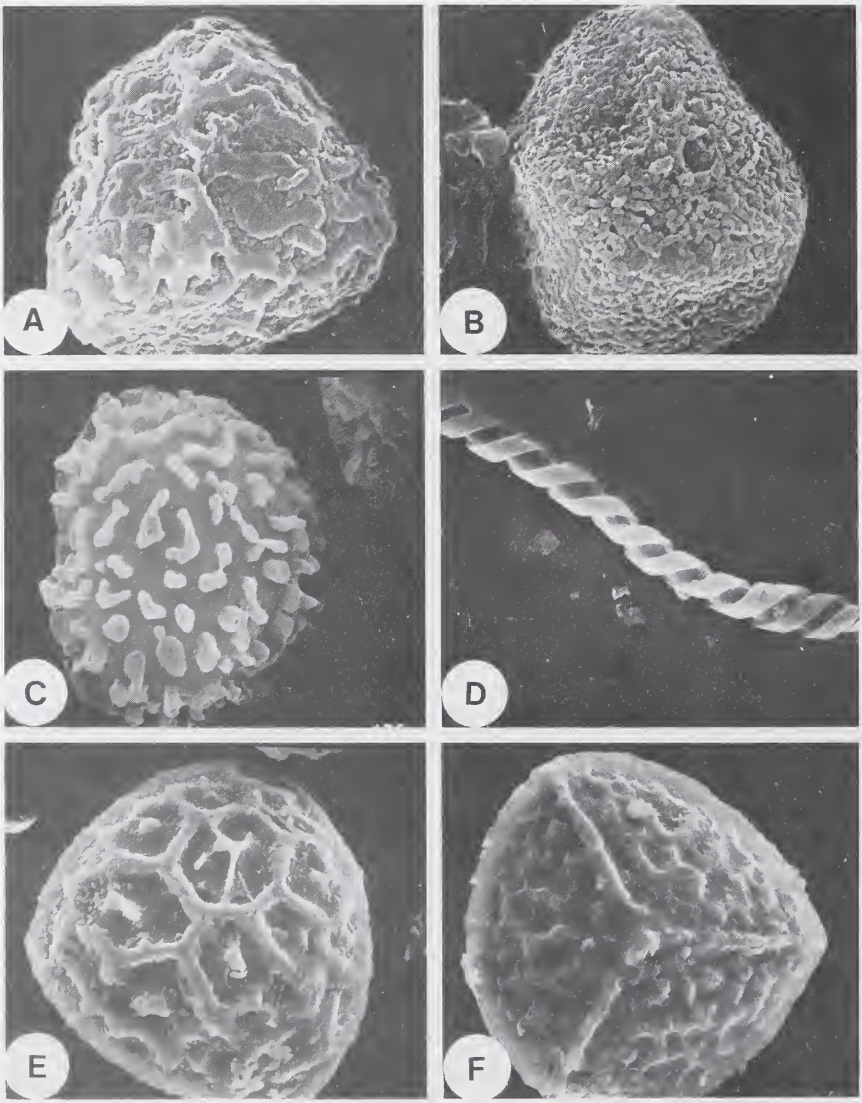
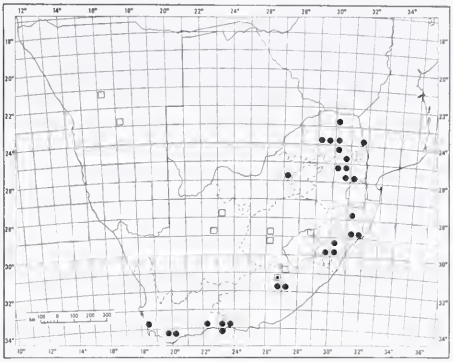


PLATE 10.—Spores and elater. A, B, **Marchantia debilis**: A, distal face; B, proximal face. C, D, **Dumortiera hirsuta**: C, distal face; D, elater. E, F, **Oxymitra cristata**: E, distal face; F, proximal face. A, B, *Preuss s.n.*; C, D, *H. Anderson CH4527*, E, F, *Volk 00906*. A, × 1810; B, × 1760; C, × 2280; D, × 310; E, F, × 420.

South America and Australasia. In southern Africa it is known from the North-West, Northern Province, Mpumalanga, Swaziland, KwaZulu-Natal, Western and Eastern Cape. Map 10. It generally grows in sheltered, wooded, shaded and damp areas, on soil or on rock.

Specimens of *D. hirsuta* are easily recognized even when sterile, by the large, thin and translucent, dark green thalli lacking a dorsal epidermis, air pores and air chambers, as well as by the sparsely hirsute margins.

All southern African specimens have been identified as belonging to *D. hirsuta*; *D. nepalensis* (with 18 chromosomes) is absent from Europe and Africa; a Japanese species, *D. hiroshima*, is said to have 27 chromosomes (Schuster 1992c).



MAP 10.—● **Dumortiera hirsuta**
❑ **Oxymitra cristata**

Vouchers: *Bosman 3318; Gerstner 4386; Glen 2881; Koekemoer 972; Perold & Koekemoer 2864; Stirton 9648.*

SUBORDER **RICCIINEAE**

Ricciineae *H.Buch*, Suomen Maksasammalet: 39, 107 (1936); R.M.Schust.: 622 (1953); R.M.Schust.: 394 (1992c); Müll.Frib.: 409 (1951–1958); S.W.Arnell: 276 (1956a); S.W.Arnell: 10 (1963a).

Thalli small to large, in gregarious patches or scattered or in partial to complete rosettes; light green to yellow green to deep green; terricolous, rarely aquatic. *Branches* once to several times pseudodichotomously furcate, oblong or ovate or obovate, occasionally linear, apex truncate to rounded, emarginate; groove median along dorsal face, sometimes only present toward apex, thallus margins acute to obtuse, glabrous, occasionally ciliated; flanks sloping obliquely or steep; ventral face rounded to flat. *Scales* lacking distinct appendages, often large, lateral, imbricate, hyaline or variously coloured, purple, red or black, sometimes ventral and in a single (or split) median, transversely inserted, well-spaced row, rarely absent.

Dorsal epidermis chlorophyllose or hyaline, cells in 1 or 2 storeys or in free uniseriate multicellular pillars; air pores simple, spaced, surrounded by one ring of 4–6 differentiated cells, with radial walls thickened in *Oxymitra*, or surrounding cells undifferentiated or pores not defined, numerous, small regular openings in Ricciaceae. *Assimilation tissue* either spongy, with unistratose cell walls enclosing wide, empty, polyhedral air chambers in one to several storeys, or compact, with cell columns enclosing narrow, vertical air canals; storage tissue occupying ventral part of thallus, compact; oil cells only present in *Ricciocarpus*; rhizoids dimorphic, numerous in terrestrial plants, absent in aquatic forms.

Asexual reproduction sometimes by tubers or bulbils or perennation, rarely by ventral stolons.

Monoicous or dioicous. *Gametangia* on or below dorsal surface of thallus and then embedded, with only necks projecting, in defined groups in *Oxymitra*, otherwise median along groove or scattered. *Sporophytes* in groups enclosed above by continuous crest-like involucre in *Oxymitra* or in Ricciaceae surrounded by unspecialized thallus tissue, foot and seta lacking, calyptra wall unistratose, capsule globose, its wall also mostly unistratose, without thickening bands, resorbed during spore maturation, cleistocarpous, spores freed by rupture of dorsal or ventral thallus tissue. *Spores* generally large, separating at maturity, rarely remaining in tetrads, triangular-globular or subglobular, ornamentation mostly reticulate. *Elaters* absent. *Chromosome number*: n = 9, 18 in Oxymitraceae; 8, sometimes multiples of 8 (or other) in Ricciaceae.

Two families are placed in the suborder Ricciineae: Oxymitraceae and Ricciaceae.

Key to families of Ricciineae

Assimilation tissue with tall air chambers, in one storey, subvertical, rather narrow, 4–7-sided; air pores simple, stellate, with thickened radial walls; gametangia on dorsal surface of thallus in defined groups; sporangia in groups enclosed above by a continuous, crest-like involucre (or in extra-southern African species individually enclosed in separate, pyriform involucres) ..... Oxymitraceae

Assimilation tissue with wide air chambers, in one or more storeys, or with narrow, vertical, canal-like air spaces; air pores simple, surrounded by undifferentiated cells, or mere exits of air canals; gametangia sunken within thallus; sporangia ripening internally, lacking an involucre ..... Ricciaceae

Schier (1974), on the basis of biochemical studies, segregated the Oxymitraceae from the Ricciineae in a distinct suborder, the Oxymitrineae, but this has not been followed here.

OXYMITRACEAE

Oxymitraceae *Müll.Frib.* in Dr L. Rabenhorst's Kryptogamen-Flora 6,2: 286 (1940b); Müll.Frib.: 410 (1951–1958); Grolle: 215 (1972); R.M.Schust.: 399 (1992c).

Thalli medium-sized, in gregarious or rosette-like patches; pale green to deep green. *Branches* simple or once/twice furcate, broadly ovate or oblong, apex emarginate; groove medianly sharp and deep, thallus margins acute; flanks sloping obliquely; ventral face rounded to flat. *Scales* lateral, projecting far above thallus margins, obliquely triangular, dark red to almost black in local species.

Dorsal epidermis hyaline, persistent; air pores tiny, simple, stellate, radial walls of surrounding cells thickened. *Assimilation tissue* with one storey of empty, tall, narrow, subvertical or polygonal air chambers, bounded by unistratose walls of chlorophyllose cells; storage tissue compact, occupying ventral part of thallus.

Asexual reproduction reputed to be by tuber formation.

Monoicous or dioicous. *Antheridia* in median groups, proximal to archegonia, immersed in thallus. *Archegonia* in median groups enclosed in flask-shaped cavities, partly sunken into thallus. *Involucre* covering archegonia fleshy, continuous, crest-like (in local species). *Sporophyte* without

stalk or foot, capsule globose, wall hyaline, unistratose or locally bistratose, lacking thickening bands. *Spores* triangular-globular; distal face with several large alveoli, each containing a central nodule; proximal face with or without distinct triradiate mark, irregularly reticulate. *Elaters* absent. *Chromosome number*: n = 18 or 9.

The family contains a single genus, *Oxymitra*, with only two species, the type species, *O. incrassata* (Brot.) Sérgio & Sim-Sim (better known as *O. paleacea* Bisch. ex Lindenb.) from the northern hemisphere as well as South America, and the southern African *O. cristata*. *O. incrassata* differs from *O. cristata*, by individual, not fused involucres, by hyaline, not purple scales, by the absence of a central nodule in the alveoli on the distal spore face, and by the smooth, not irregularly reticulate proximal face.

OXYMITRA

Oxymitra *Bisch. ex Lindenb.* in Nova acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum, Suppl. 14: 124 (1829); Gottsche et al.: 597 (1844–1847); Frye & L.Clark: 40 (1937); Müll.Frib.: 410 (1951–1958); S.W.Arnell: 11 (1963a); Hässel de Menéndez: 200 (1963); Perold: 210 (1993b). Lectotype: *O. incrassata* (Brot.) Sérgio & Sim-Sim (1989).

Pycnoscenus Lindb.: 606 (1863), nom. illegit.

Tessellina auct. non Dumort.: 78 (1822).

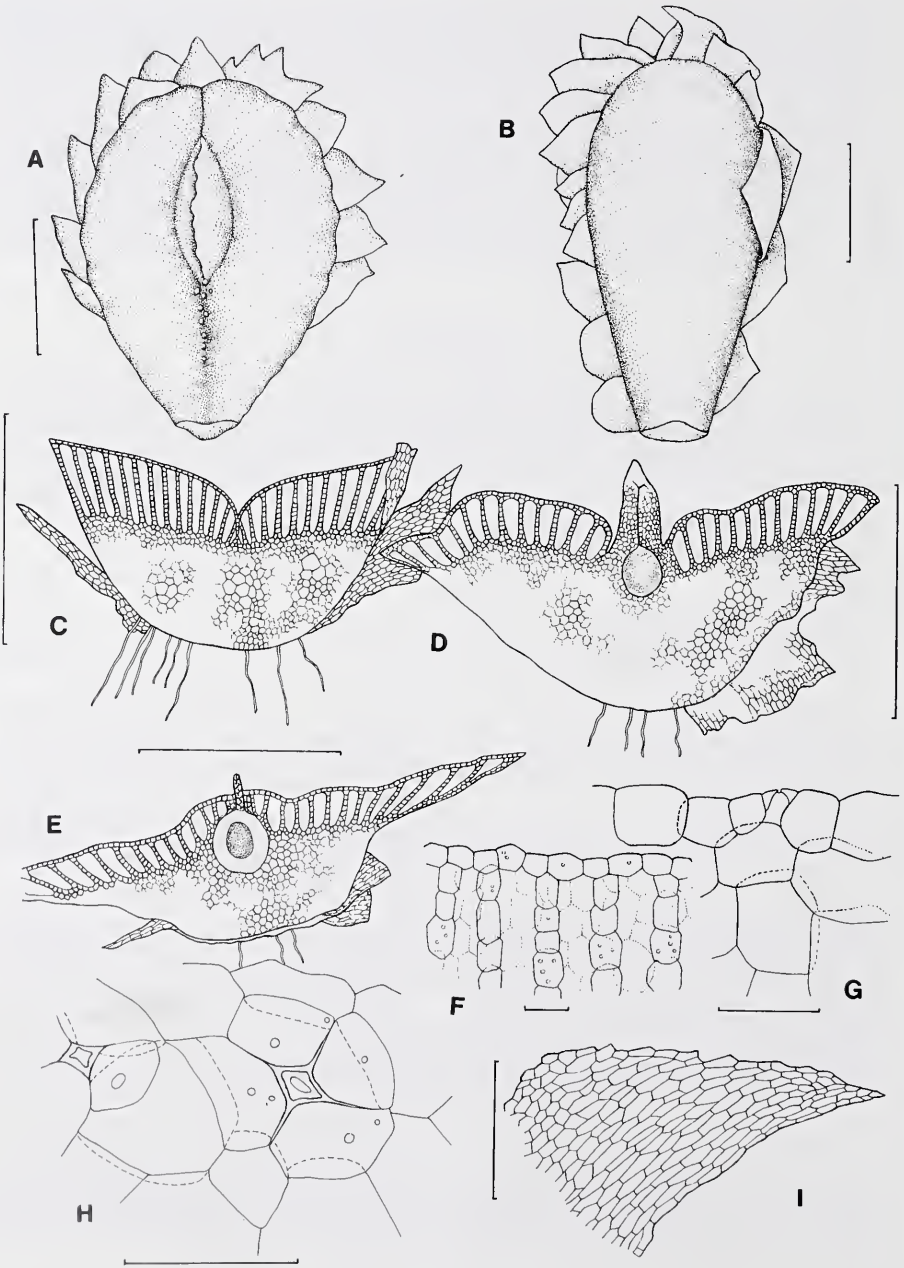
With characters of the family.

Oxymitra cristata *Garside ex Perold* in Bothalia 23: 211 (1993b). Type: Cape, near Bredby Mine (25 miles S of Kuruman), *Schelpe 5900* (BOL, holo.!).

Oxymitra cristata Garside: 83, 174a (1958). Types: *Schelpe 5900; Duthie 5531* (BOL), holo. not designated, hence invalidly published.

Thalli smallish to medium-sized, in crowded, overlying patches; bright green to deep green, areolate, air pores tiny, margins dark red, scalloped or undulating; when dry, thallus margins incurved or raised and clasped together. *Branches* simple or once/twice pseudodichotomously furcate, narrowly to moderately divergent, broadly ovate or oblong, (3–)5–10(–12) mm long, 2.5–4.8 mm wide, 1100–2000 µm thick medianly, in section ± twice wider than thick, apex emarginate; groove deep along entire midline, except where interrupted by gametangia, thallus margins rather obtuse to acute; flanks steep to sloping obliquely, deep purple; ventral face rounded to flattish, green. *Scales* lateral, covering flanks, obliquely triangular, dark red, to almost black, shiny, in apical scales basal part hyaline, closely imbricate, 1250–1375 µm long, margins entire, sometimes crenate or shortly toothed toward base of distal side, 1075–1200 µm wide across base, apex projecting up to 375 µm above thallus margins, oil cells absent.

Dorsal epidermal cells unistratose, hyaline, polygonal, (22.5–)37.5–45.0(–52.0) × 27.5–37.5 (–47.5) µm; air pores slightly raised, small, simple, 5–10 µm wide, 4- or 5(6)-sided, stellate, surrounded by one ring of 4 or 5, rarely 6, small, bluntly wedge-shaped cells, radial walls slightly thickened, partly overlying, or occasionally adjoining larger polygonal cells. *Assimilation tissue* 400–600 µm thick, air chambers empty, in one storey, bounding walls chlorophyllose, unistratose; storage tissue occupying ventral part of thallus, composed of rounded or angular cells, ± 50 µm wide; oil cells absent.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Monoicous. *Antheridia* in row along midline, proximal to archegonia, immersed, necks hyaline, cylindrical, protruding above dorsal surface of thallus. *Archegonia* in median row, in flask-shaped cavities, partly sunken into thallus. *Involucre* ridged, enclosing archegonial groups, ± 600 µm high, irregular, fleshy, crest-like, tinged reddish on top around openings of archegonial necks, these long and turning purple with age. Figure 25. *Sporophytes* ventrally partly sunken into thallus, dorsally bulging on either side of central crest, capsule globose, wall thin, delicate, lacking thickening bands. *Spores* (108–)110–115 (–125) µm diam., triangular-globular, black, opaque, anisopolar, with ornamentation different on two faces; distal face with 6 or 7 large, central alveoli, up to 30 µm wide, smaller toward margin, generally with a nodule and thin radiating ridges in middle of each, alveolar walls thick; proximal face with triradiate mark distinct, 3 facets with incomplete alveoli, walls irregular, sometimes rather indistinct, wing ± 5 µm wide, entire. *Chromosome number*: n = 18 (Baudoin 1976). Plate 10E, F.

Oxymitra cristata is endemic to southern Africa, and very rarely collected. It is known from Namibia, Free State, Northern and Eastern Cape. Map 10. It has been found mainly on substrates derived from ironstone, and it occasionally grows in association with *Plagiochasma* spp. and *Riccia* spp.

Oxymitra cristata is distinguished by its large, obliquely triangular, shiny, dark red scales and by the row of archegonia enclosed in an irregular, but continuous, crest-like, fleshy ridge of tissue.

Vouchers: *Burrows 2523; Cooke s.n.; Koekemoer 1024; Volk 5050* (herb. Volk); *Zietsman 943.*

RICCIACEAE

Ricciaceae *Rchb.*, Botanik für Damen, Künstler und Freunde: 255 (1828); Jovet-Ast: 291 (1986); Perold: 17 (1991c).

Thalli small to large, scattered or in gregarious patches or in rosettes; green; terricolous, rarely aquatic. *Branches* 2 or 3 times pseudodichotomously furcate, linear to obovate, apex truncate to rounded, emarginate; groove often present, median along dorsal face, thallus margins acute to obtuse, glabrous or occasionally ciliate; flanks sloping obliquely or steep; ventral face rounded to flat. *Scales* lateral or ventral, small to large, rarely absent, generally imbricate, hyaline or variously coloured, purple, red or black.

Dorsal covering either an *epidermis*, chlorophyllose, generally unistratose with air pores simple, scattered and delimited, often enlarging and becoming lacunose; otherwise dorsal covering an *epithelium*, hyaline, echlorophyllose, cells uni- or bistratose, or in free uniseriate, multicellular pillars with air pores not defined, numerous, small, regular spaces. *Assimilation tissue* spongy, with mostly unistratose cell walls bounding wide polyhedral air chambers, or else compact, with cell columns enclosing narrow vertical air canals; storage tissue occupying ventral $^1/_2$ or less of thallus. *Rhizoids* long, unicellular, dimorphic, smooth or pegged, arising from ventral epidermis.

Asexual reproduction rare, sometimes by bulbils, perennation occasionally by ventral stolons.

FIGURE 25.—**Oxymitra cristata**. A–E, thallus: A, dorsal face with crest-like involucre and proximally, row of antheridia; B, ventral face; C, c/s showing median dorsal groove; D, c/s through involucre with archegonium; E, c/s through antheridium. F, c/s of dorsal cells and air chambers. G, H, air pore(s): G, c/s with dorsal epidermal cells; H, from above. I, ventral scale. A, B, D, *Volk 00906*; C, F–I, *Volk 81/050*; E, *Volk 00957*. Scale bars: A–E, 2 mm; F–H, 50 µm; I, 500 µm. Drawings by A. Pienaar.

Monoicous or dioicous. *Gametangia* acropetally arranged, embedded, only necks projecting, median along groove or scattered. *Sporophyte* without stalk or foot, capsule globose, the unistratose wall resorbed during spore maturation, surrounding venter wall soon disintegrating to liberate spores. *Spores* generally large, separating at maturity, rarely remaining adherent in tetrads, triangular-globular or subglobular, ornamentation mostly reticulate, often specific. *Elaters* absent. *Chromosome number*: n = 8 usually, sometimes multiples of 8, or rarely 9, 10, 12, 15, 17 or 20.

The family comprises two genera: the monotypic, cosmopolitan genus *Ricciocarpos,* and the species-rich genus *Riccia,* with up to ± 200 species worldwide, and particularly well represented in southern Africa.

Key to genera of Ricciaceae

Thalli floating or temporarily terricolous; assimilation tissue with large air chambers in several storeys; scales long, pendant, purple ribbons, but small in land form, margins dentate; oil cells present; gametangia only along deep central groove ..... *Ricciocarpos*

Thalli with very rare exceptions terricolous; assimilation tissue spongy, with air chambers, or else compact, with cell columns enclosing narrow vertical air canals; scales small to large, imbricate, mostly rounded, margins smooth, rarely denticulate; oil cells absent; gametangia along groove or scattered ..... *Riccia*

RICCIOCARPOS

Ricciocarpos *Corda* in Opiz, Beiträge zur Naturgeschichte 12: 651 (1829) [orth. var.: *Ricciocarpon* Corda (1829); *Ricciocarpus* Corda mut. Dumort. (1874)]; M.Howe: 26 (1899); Müll.Frib.: 44 (1951–1958); Hässel de Menéndez: 205 (1963); S.W.Arnell: 12 (1963a); Perold: 72 (1991c); R.M.Schust.: 415 (1992c). Type: *R. natans* (L.) Corda.

Hemiseuma Bisch.: 1040, 1071 (1835).

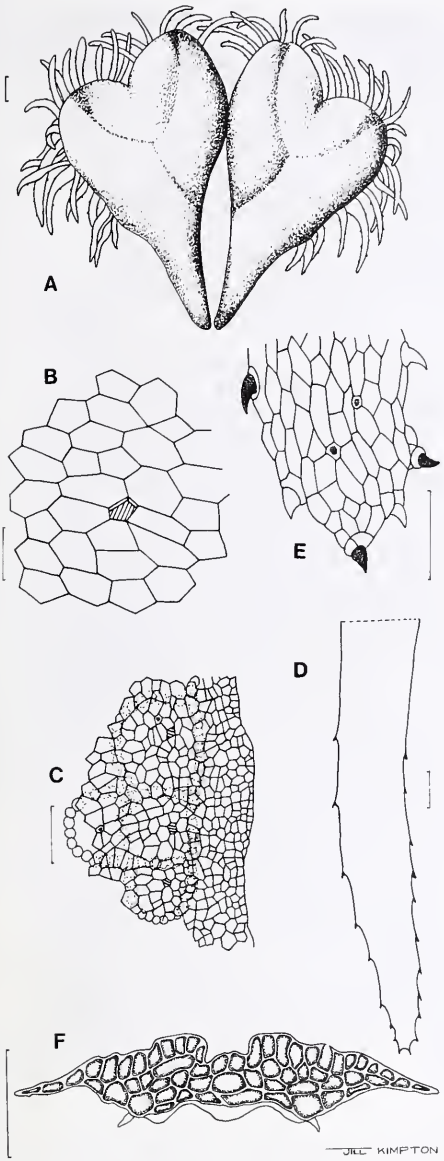
Hemiseumata Bisch. ex Lindl.: 57 (1847).

Thalli large, gregarious or in partial rosettes; olive-green to yellowish green; aquatic or temporarily terricolous. *Branches* 2–3 times symmetrically furcate, hardly divergent, up to 14 mm long, 3–7 mm wide, less than 1 mm thick, in section 4–8 times wider than thick, apex rounded, emarginate; groove very pronounced throughout, dividing near apex, its sides obscuring central ridge. *Scales* ventral, conspicuous, in dense, purple ribbons, margins dentate, pendant in water form, small in land form.

Dorsal epidermis covering air chambers persistent, interrupted by simple air pores. *Assimilation tissue* with several storeys of large, superimposed, polyhedral air chambers; storage tissue reduced to only 3 or 4 layers of cells; oil cells present. *Rhizoids* mostly absent in aquatic form, smooth and tuberculate in land form.

Monoicous. *Sporangia* rare, immersed in ridge along groove toward base. *Spores* smallish, triangular-globular, polar, black, opaque, granulate-alveolate, ornamentation poorly defined.

Ricciocarpos is a monotypic genus and worldwide in its distribution. In southern Africa it is infrequently collected in stagnant pans or still pools in forested regions, and in swamps or vleis.



Ricciocarpos natans *(L.) Corda* in Opiz, Beiträge zur Naturgeschichte 12: 651 (1829); Steph.: 51 (1898); M. Howe: 33 (1899); Schiffn.: 15 (1893); C.Massal.: 831 (1912); Casares-Gil: 235 (1919); Macvicar: 30 (1926); Frye & L.Clark: 39 (1937); Müll.Frib.: 414 (1951–1958); Hässel de Menéndez: 205 (1963); S.W.Arnell: 12 (1963a); Vanden Berghen: 183 (1972); E.O.Campb.: 121 (1975); Perold: 72 (1991c); R.M.Schust.: 415 (1992c). Type: Britain, Suffolk, 'in stagnis, circa Hadley', leg. *Buddle* [OXF, holo. fide Grolle 87: 229 (1976); H-SOL, iso. fide Isov. 89: 23 (1970) xerox copy! Lichen no. 18, tab. 78, fig. 18, Dill.: 536 (1741)].

Riccia natans L.: 1339 (1753); Lindenb.: 121 (1829); Nees: 319, 419 (1838); Gottsche et al.: 607 (1844–1847); Sim: 15 (1926).

R. capillata Schmidel: 276 (1793).

R. velutina Wilson: t. 249 (1839).

Ricciocarpus velutinus Steph.: 758 (1898); Ladyz.: 3 (1943).

Thalli large, gregarious, occasionally in dense mats or in partial rosettes, 20–30 mm across; olive-green to yellowish green, margins tinged with purple, firm and somewhat leathery, convex above and areolate; when dry, deflated, otherwise little altered, sides not inflexed. *Branches* 2–3 times pseudodichotomously furcate, shortly to deeply divided, hardly divergent, broadly obcordate, narrow at base, 8–14 × 3–7 mm, less than 1 mm thick medianly, rapidly thinning toward margins, in section 4–8 times wider than thick, apex rounded, emarginate; groove very pronounced throughout, dividing near apex, containing centrally raised ridge, obscured by highly convex sides of groove that almost meet above it, thallus margins thin and very acute in aquatic form, fleshy and rather obtuse in land form; flanks sloping very obliquely to almost flat; ventral face flat, violet to brown. *Scales* ventral, small in land form, in aquatic form up to 10 mm long, 375–600 µm wide, in several rows, in dense bunches of

FIGURE 26.—**Ricciocarpos natans**. A, dorsal face of thallus of aquatic form. B, C, dorsal epidermis with air pores (hatched); C, with oil cells (solid specks), overlying air chambers left, thin marginal area right. D, E, scale: E, enlarged tip, oil cells (solid specks) and toothed margin. F, c/s thallus. A–F, *Ward s.n.* Scale bars: A, F, 1 mm; B, E, 50 µm; C, D, 100 µm.

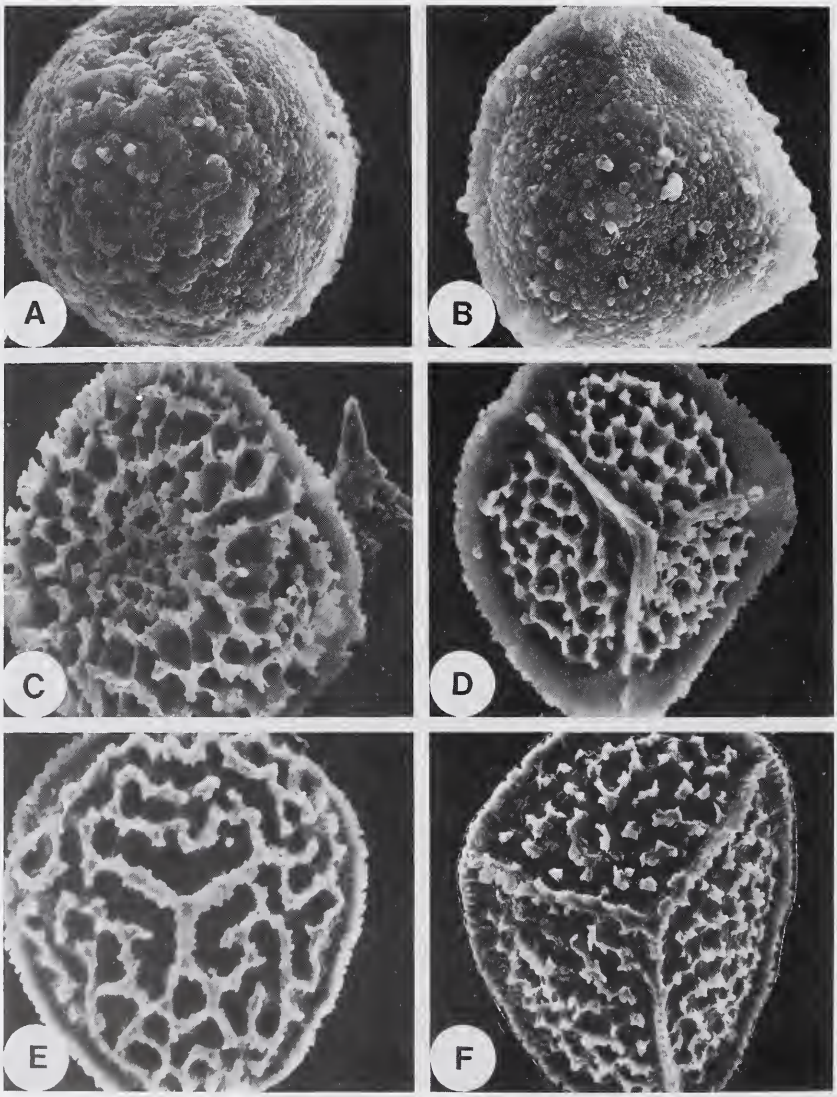


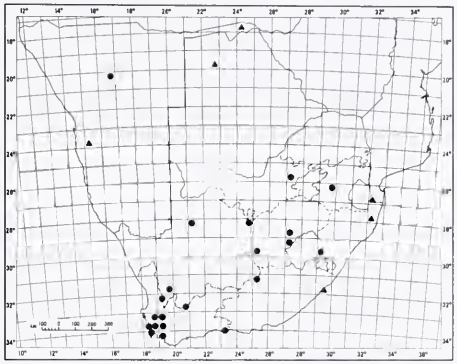
PLATE 11.—Spores. A, B, **Ricciocarpos natans**. A, distal face; B, proximal face. C, D, **Riccia crystallina**: C, distal face; D, proximal face. E, F, **R. cavernosa**: E, distal face; F, proximal face. A, B, *Ward s.n.*; C, *Duthie & Garside 5529* (BOL); D, *Arnell 150* (BOL); E, *F. van der Merwe CH3595*; F, *Koch 14934*. A, B, × 800; C, D, × 1000, E, F, × 700.

pendant ribbons, violet to reddish black, linear-lanceolate to tapering, margins toothed, with dark, projecting conical cells, oil cells occasional, small, scattered.

Dorsal epidermis covering air chambers persistent, cells hexagonal to polygonal, 25–50 × 15–27 µm; air pores 5- or 6-sided, ± 17.5 µm wide, 5–8 surrounding cells slightly thicker-walled. *Assimilation tissue* occupying most of thickness of thallus, air chambers in several storeys, superimposed, polyhedral, bounded by unistratose cell walls; storage tissue only 3 or 4 layers of cells ventrally; occasionally with scattered oil cells. Figure 26.

Monoicous. *Antheridia* along ridge in central groove, hyaline necks ± 100 µm long. *Archegonia* also along groove, but not together with antheridia. *Sporangia* infrequent, single or up to 3 in sequence, immersed, the position marked by a slight elevation. *Spores* (55–)60–67(–75) µm diam., triangular-globular, polar, black, opaque; wing narrow, margin crenulate; ornamentation granulate-alveolate; distal face with 6–8 poorly defined alveoli across diam. of spore, entire surface thickly covered with granules; proximal face without defined triradiate mark, alveoli absent, sprinkled with granules and papillae. *Chromosome number*: n = 9 (Siler 1934; Müll.Frib. 1951–1958; Jovet-Ast 1974; Bornefeld 1987). Plate 11A, B.

Ricciocarpos natans is cosmopolitan and although rare, is found in all parts of the world,



MAP 11.—▲ **Ricciocarpos natans**
● **Riccia crystallina**

even in Alaska. In the *FSA* area *Ricciocarpos natans* is known from Namibia, (East Caprivi), Botswana, KwaZulu-Natal, including Zululand and Eastern Cape. It floats on still water, often in association with *Lemna* and *Azolla*, or becomes stranded on mud at the margins of pools or vleis. Map 11.

It is distinguished by its somewhat leathery appearance, conspicuous, pendant, marginally serrate scales, and by occasional oil cells.

Vouchers: *Pienaar & Vahrmeyer 474* (PRE); *Smith 1441* (PRE); *Tinley 418* (PRE); *Wager 55* (PRE).

RICCIA

Riccia *L.*, Species plantarum: 1138 (1753); Steph.: 314 (1898); Sim: 8 (1926); Müll.Frib.: 416 (1951–1958); S.W.Arnell: 13 (1963a); Hässel de Menéndez: 208 (1963); Na-Thalang: 71 (1980); Jovet-Ast: 291 (1986); Jovet-Ast: 214 (1991); Perold: 19 (1991c); R.M.Schust.: 421 (1992b). Lectotype: *R. glauca* L., fide Hässel de Menéndez: 208 (1963).

Euriccia Lindb. ex Lacout.: 23 (1905).

Ricciella A.Braun: 756 (1821).

Lichenoides (Bisch.) Lindl.: 57 (1847).

Cryptocarpus Austin: 231 (1870) nom. illegit.

Thallocarpus Lindb.: 377 (1874).

Angiocarpus Trevis.: 444 (1877).

Riccinia Trab. in Douin & Trab.: 326 (1916).

Fysonia Kashyap in Kashyap & Sethi: 203 (1923).

Pteroriccia R.M.Schust.: 72 (1984a).

Thalli small to large, in gregarious patches or frequently in rosettes; terricolous, very rarely aquatic. *Branches* once to several times symmetrically or asymmetrically furcate; groove median, deep or shallow, along length of branches or only apical. *Scales* lateral or ventral, vestigial to conspicuous, usually imbricate, rounded, very rarely triangular, hyaline or variously coloured.

Dorsal epidermis chlorophyllose, unistratose (rarely not so); air pores simple, scattered, stomata delimited, becoming lacunose, or else if present, *dorsal epithelium* hyaline, echlorophyllose, cells uni- or bistratose or in free, uniseriate, multicellular pillars; air pores small, regular spaces. *Assimilation tissue* generally $^1/_2$ (or more) the thickness of thallus, spongy, with wide polyhedral air chambers; otherwise compact, in vertical cell columns, enclosing narrow air canals; storage tissue occupying ventral $^1/_2$ or less of thallus, cells rounded, often containing starch granules; oil cells absent. Rhizoids arising from ventral epidermis and sometimes from base of scales, some smooth, others tuberculate, 15–25 µm wide.

Monoicous or dioicous. *Antheridia* sunken along groove, with protruding hyaline necks. *Archegonia* also sunken, with protruding purple necks. *Sporangia* bulging dorsally or not, rarely bulging conspicuously ventrally, usually containing several hundred spores, released by decay of surrounding tissue. *Spores* in tetrads separating at maturity, rarely remaining adherent in tetrads, mostly 80–110 µm diam., triangular-globular or subglobose; ornamentation on distal face generally reticulate, alveoli small to large, otherwise papillate, verruculose or vermiculate; proximal face divided into 3 facets by distinct or faint triradiate mark. *Chromosome* number: n = 8 usually, sometimes multiples of 8 or rarely 9, 10, 12, 15, 17 or 20.

The genus *Riccia* comprises up to ± 200 currently recognized species and has a worldwide distribution. It is primarily distributed in the temperate zones and tropics, but is also known from cold climates. The greatest concentration of species is undoubtedly in southern Africa with more than 50 now known. Namaqualand in the northwestern Northern Cape has yielded several new, unusual species. *Riccia* species frequently grow on soil at the margin of flat rock outcrops, at streambanks or at seepages.

Key to the subgenera, sections, groups and species of *Riccia*

1a (1b: p. 118) Thalli covered by epidermis of mostly thin-walled, generally chlorophyllose cells, very rarely bearing vertical, cellular outgrowths dorsally; air pores mostly delimited, often ringed by smaller cells, well spaced, fewer in number than in subgenus *Riccia*, frequently enlarging and becoming lacunose; assimilation tissue loosely arranged, spongy, unistratose cell walls enclosing large polyhedral air chambers; scales small and evanescent to occasionally large and persistent; spore tetrads separating at maturity or very rarely remaining in tetrads; habitat mostly mesic, rarely xeric or aquatic:

2a (2b: p. 118) Dorsal epidermis a single layer of thin-walled, closely joined, flattened cells (rarely globose, and then somewhat loosely connected), interrupted by air pores, becoming lacunose over air chambers or not; scales ventral, mostly hyaline and inconspicuous, evanescent:

3a Spores remaining in tetrads . . . B. subgenus **Thallocarpus**:
4a Thalli in complete or incomplete rosettes, 10 mm or more across; heterothallic; spores joined together by narrow band or ridge into tetrahedral tetrads; ornamentation with slender spinules up to 5 µm long (Plate 15E, F) . . . . . 11. *R. curtisii*
4b Thalli reportedly in rosettes up to 11 mm across; heterothallic; spores joined together by wide band into rhomboidal tetrads; ornamentation with stout spines 10–15 µm long (Plate 16A, B) . . . . . 12. *R. perssonii*
3b Spore tetrads separating at maturity . . . A. subgenus **Ricciella**:
5a Thalli generally annual; not in rosettes; branches linear, strap-shaped or 'ribbon-like', up to 15–20 × 0.5–2.0 mm; not lacunose dorsally; sporangia bulging markedly ventrally . . . A2. section *Ricciella*:
6a Thalli monoicous; sometimes aquatic; sporangia obliquely borne (Figure 34D); distal spore face with alveolar walls thick and prominent; at times forming apical stolons; widespread in mostly summer rainfall areas . . . . . 9. *R. stricta*
6b Thalli dioicous; thin and lax; strictly terrestrial; sporangia vertically borne; distal spore face with alveolar walls thin; at times forming apical stolons; distribution restricted to winter rainfall areas of the southwestern Northern Cape and the southwestern and southeastern parts of Western Cape . . . . . 10. *R. purpurascens*
5b Thalli annual or perennial; sometimes in rosettes; branches not strap-shaped, 2–15 × (1–)3–6(–8) mm; dorsally lacunose to markedly lacunose; monoicous or dioicous; sporangia deeply imbedded or bulging somewhat above or below . . . A1. section *Spongodes*:
7a Thalli finely to coarsely spongiose; dorsally not deeply grooved; often in rosettes; glaucous-green to yellow-green, sometimes tinged with red . . . A1.1. group Crystallina:
8a Thalli dioicous; markedly heterothallic with small male gametophytes (Figure 29); bright green to yellowish green; from above, air chamber walls visible or dorsal epidermis lacunose; spores foveolate, triradiate mark pronounced (Plate 12D) . . . . . 4. *R. cupulifera*
8b Thalli monoicous; from above, air chamber walls visible or not; spores completely or incompletely reticulate:
9a Thalli green to yellow-green, faintly red at margins; from above, walls of large air chambers visible or dorsally lacunose (cavernose); spores 85–115 µm diam.; red-brown to black, distal face centrally with thicker, irregularly bi- or trichotomously branching ridges (Plate 11E) . . . . . 2. *R. cavernosa*
9b Thalli blue-green, dorsally crystalline, with rounded cells, in tiers or not; scales present or absent; spores 65–85 µm diam.; light brown; ornamentation on proximal and distal faces similar or dissimilar:
10a Thalli dorsally crystalline and glistening, with rounded cells in loose, double tiers; scales absent or evanescent; ornamentation on 2 spore faces similar, alveoli regular and complete, walls thin, triradiate mark on proximal face distinct (Plate 11C, D) . . . . . 1. *R. crystallina*
10b Thalli dorsally finely areolate; scales present, purple or hyaline; spores with 2 faces dissimilar, proximal face with numerous small, shallow alveoli and triradiate mark absent, distal face with 8–10 alveoli across width (Plate 12A, B) . . . . . 3. *R. moenkemeyeri*
7b Thalli swollen to rather flat; usually markedly lacunose; dorsally deeply grooved along entire length or only apically; rarely in rosettes; green to straw-coloured or whitish, very rarely tinged with purple . . . A1.2. group Vesiculosa:

11a Thalli large and very wide, 5–15 × 3.5–5.5(–8) mm; when dry, yellowish to straw-coloured or white; spores 100–150(–160) µm diam., with 8–12 alveoli across distal face, wing thin, ± 10 µm wide:
12a Thalli straw-coloured when dry; deeply grooved along entire length; pitted in older parts only; spores with alveoli on distal face 10–15 µm wide . . 5. *R. bullosa*
12b Thalli white when dry; mostly only apically grooved; honeycomb-pitted dorsally; spores with alveoli on both faces larger, up to 20 µm wide . . . 6. *R. garsidei*
11b Thalli narrower, up to 12 × 2.5–3.0 mm; when dry, greyish white to yellowish; spores 88–112 µm diam., with 5–8 alveoli across distal face, wing narrow, width 3–5 µm:
13a Thalli rarely in rosettes; antheridial necks inconspicuous, hyaline; apical stolons not formed; widespread in summer rainfall areas . . . . . 7. *R. volkii*
13b Thalli not in rosettes, somewhat linear; antheridia with conspicuous purple necks (Figure 33B); apical stolons formed; very rare, only known from Knysna Dist. . . . . 8. *R. rubricollis*
2b Dorsal epidermis other than thin-walled, single-layered flat cells interrupted by air pores:
14a Dorsal epidermis with thick-walled cells, lacking chlorophyll; air pores surrounded by superimposed ring of smaller, thin-walled cells; thallus narrowly grooved, acutely winged; scales rounded, persistent, large, reaching thallus margins; spores single . . . D. subgenus **Chartacea**: . . . . . 14. *R. schelpei*
14b Dorsal epidermis with cellular outgrowths of very tall, hair-like pillars; air pores surrounded by radially arranged wedge-shaped cells; thallus broadly grooved, obtusely winged; scales triangular, persistent, large, filamentous apices extending beyond thallus margins; spores remaining in globular to tetrahedral tetrads (Plate 16C, D) . . . C. subgenus **Pannosae**: . . . . . 13. *R. tomentosa*
1b Thalli covered by dorsal 'epithelium' of echlorophyllose cells in 1 or several strata; air pores numerous, small, regular intercellular spaces; assimilation tissue compact, in vertical rows of chlorophyllose cells separated by mostly very narrow interstitial air canals; scales small to large; spore tetrads separating at maturity; habitat often xeric, sometimes mesic . . . E. subgenus **Riccia**:
15a (15b: p. 121) Epithelial cells closely associated, in one or two layers, top cells globose, mammillose or pyriform, outer walls (or cells) often collapsing, generally orientated egularly and in parallel rows running from median groove across to margin; scales small to large, rounded . . . E1. section *Riccia*:
16a Thalli with cilia along margins, occasionally also present over sporangia; ventral scales not conspicuous; sometimes flanks dark purple . . . E1.1. group Ciliatae:
17a Thalli medium-sized to large, branches up to 12 × 4 mm; cilia white when dry, 300(–400) µm long, finely granular (Figure 43C), absent over sporangia; spores straw-coloured, with wing 10 µm wide, slightly undulating . . . . . 18. *R. natalensis*
17b Thalli smaller, less than 8.0 × 1.5 mm; cilia hyaline, dry or wet, long or short; spores brown to black, with or without wing:
18a Cilia generally quite sparse, 250(–400) µm long, finely granular, absent over sporangia; scales small, purple; flanks green; spores with wing ± 7.5 µm wide; distribution in *FSA* area restricted to winter rainfall region of southwestern Western Cape . . . . . 16. *R. crozalsii*
18b Cilia crowded, dense, variously long, not granular, present over sporangia; flanks dark purple; spores mostly wingless; widespread in summer rainfall areas:
19a Thalli 5–6 × 0.9–1.5 mm; cilia straight to slightly flexuose, up to 950 µm long, smooth; spores 100–120 µm diam., ornamentation reticulate, alveolar walls heavily encrusted with papillae (Plate 17A, B) . . . . . 15. *R. trichocarpa*

19b Thalli small, 1–4 × 0.6–0.8 mm; cilia arched (Figure 42C), up to 300 μm long, channelled and finely striate; spores 80–90 μm diam., ornamentation reticulate, alveolar walls mostly smooth . . . . . 17. *R. microciliata*

16b Thallus margins not ciliate, marginal cells enlarged or not; ventral scales small to large . . . E1.2. group Mammillatae:

20a Thallus margins apically with row of mammillate cells (Figure 43K) up to 150 μm long; scales small, not extending to thallus margins, violet to hyaline . . 19. *R. mammifera*

20b Thallus margins glabrous; scales larger, extending to margins or projecting above, hyaline or variously pigmented . . . E1.3. group Squamatae:

21a Scales not conspicuous, hyaline or partly hyaline; thallus margins hyaline; groove narrow and deep along entire length of thallus; dorsal epithelium generally with some cell walls thickened:

22a Dorsal epithelial and subepithelial cells always with markedly thicker walls (Figure 44E); thalli light green, appearing almost waxy; flanks green; spores polar, dark reddish brown to black, proximal face densely granulate (Plate 19F); widespread (nearly cosmopolitan), but rare in *FSA* area . . . . . 20. *R. sorocarpa*

22b Dorsal epithelial cells with walls sometimes thicker; thalli glaucous-green to silvery grey-green; flanks dark red-brown; spores almost apolar, subglobular, dull dark brown to nearly black, reticulate; endemic and common in summer rainfall areas . . . . . 21. *R. atropurpurea*

21b Scales large and conspicuous, pigmented, with or without hyaline border or entirely hyaline to white; groove various; dorsal epithelial cell walls not thickened:

23a Scales dark, black or reddish black to deep violet, shiny; thallus size variable; dorsally glaucous-green to green or purplish, rarely brown:

24a Thalli smallish to medium-sized; in section once to twice wider than thick; flanks steeply rising:

25a Thalli medium-sized; dorsally entirely glaucous-green; scales with crenate edges, projecting above thallus margins (Figure 46H); when dry, rather dull black; pores golden brown, wingless, densely papillate . . . . . 22. *R. okahandjana*

25b Thalli smallish; glaucous-green, rust-brown along margins and proximally; scales with entire edges appressed, not projecting above thallus margins, shiny when dry or wet; spores light brown to dark brown, winged, incompletely reticulate . . . . . 26. *R. nigrella*

24b Thalli medium-sized to large; in section 2.5–5.0 times wider than thick; flanks sloping obliquely:

26a Thalli large, up to 15 × 5 mm; margins winged, overhanging; spores subglobular, apolar, ornamentation reticulate with thin, high alveolar walls . . . . . 23. *R. congoana*

26b Thalli medium-sized to large, up to 15 × 3(–4) mm; margins attenuate, not overhanging; spores triangular-globular, polar, alveolar walls thick, low:

27a Thalli quite fleshy; scales imbricate, clasped together along midline when dry (Figure 48A); spores 90–125 μm diam., distal face with short spiralling ridges, proximal face almost smooth, with scattered pores; distribution in *FSA* area restricted to winter rainfall regions of Cape . . . . . 24. *R. limbata*

27b Thalli mostly thinner; scales imbricate to proximally more widely spaced; when dry, opposite scales meeting or not, never clasped together; spores 72–82 μm diam.; distal face with alveoli in more or less concentric rings; proximal face completely or incompletely reticulate; widespread in summer rainfall regions, but not common . . . . . 25. *R. angolensis*

23b Scales other than black, variously coloured or white; thalli small to medium-sized; dorsally green to yellow-green, white or brownish:

28a Scales brown or various shades of pink to red:

29a Thallus margins and scales brownish yellow; idioblasts (enlarged cells with brown contents) present throughout thalli (Figure 50K); spores vermiculate; species very rare in *FSA* area . . . . . 27. *R. macrocarpa*

29b Thallus margins not brown; scales pink to dark red; idioblasts absent; spores reticulate:

30a Thalli very small, 1.5–2.5(–3) × 0.7–1.0 mm; bottle-green, tumid; scales regular, appressed, dark red, white-bordered; spores 60–78 µm diam., triangular-globular, polar; distribution restricted . . . . . 28. *R. pottsiana*

30b Thalli medium-sized; bright green or light green to whitish; scales wine-red or rose-pink; spores 80–105 µm diam., globular to subglobular, apolar; distribution widespread:

31a Thalli 7–9 × 1.2–1.6 mm; bright green, turning grey-green; scales dark red, shiny, with narrow hyaline border; monoicous; spores red to black, subglobular, periphery with prominent projections, cogwheel-like in profile . . . . . 29. *R. runssorensis*

31b Thalli up to 12 × 1.0–2.5 mm; pale green but white along margins; scales wavy, rose-pink with wide hyaline border; dioicous; spores rare, light brown, periphery with low projections . . . . . 30. *R. rosea*

28b Scales predominantly white or hyaline, often encrusted with calcium deposits, wavy or appressed:

32a Scales large, up to 1250 × 750 µm, irregularly wavy to frilly, closely imbricate; thalli mostly 8–9 (rarely up to 12) × 1.5–2.0(–4) mm; apically grooved; dorsally green, turning white and spongy over sporangia:

33a Thalli in rosettes or gregarious; spores with 10–12 round to angular alveoli across diam. of distal face; widespread and quite common . . . . 31. *R. albolimbata*

33b Thalli not in rosettes; spores with 14–20 small, deep alveoli across diam. of distal face; quite rare, distribution apparently restricted to Northern, Western and northern part of Eastern Cape . . . . . 33. *R. albornata*

32b Scales smaller, up to 850 × 500 µm, mostly appressed and regular, imbricate; thalli generally rather smaller, 7–8 × 0.7–2.0(–4) mm; grooved apically or along almost entire length; dorsally mat or shiny:

34a Thalli deeply grooved along most of length; dioicous; spores apolar or polar:

35a Dorsally mat, grey-green; compact; dorsal epithelial cells thick-walled, collapsed, in regular honeycomb pattern; scales tightly appressed (Figure 55B), base silvery purple-grey; spores apolar, wingless; fairly widespread . . . . . 32. *R. argenteolimbata*

35b Dorsally glistening, light green to green; finely spongy; dorsal epithelial cells thin-walled, not in regular pattern; scales apically wavy, soon appressed; spores polar, winged; distribution restricted to eastern mountainous regions . . . . . 34. *R. montana*

34b Thalli only apically grooved; monoicous; spores polar:

36a Thalli with wide, shallow groove; 8 × 4 mm; dorsally very heavily encrusted with calcium deposits; air pores large, regular; scales white; spores finely reticulate . . . . . 35. *R. alboporosa*

36b Thalli narrowly grooved; up to 5 × 1–2 mm; dorsally with fine calcium deposits; air pores small to large, irregular; scales bicoloured, with deep purple base; spores more coarsely reticulate . . . . . 36. *R. bicolorata*

15b Epithelial cells in free-standing 2–5(–6)-celled, uniseriate pillars not regularly orientated, top cells variously shaped, soon collapsing; scales small to large, mostly rounded and smooth-margined, rarely triangular and dentate or apically filiform . . . E2. section *Pilifer*:

37a Dorsal pillars short, often shorter than 200 µm, consisting of 2 or 3(4) cells, mostly wider than long, tapering or not tapering:

38a Dorsal pillars tapering; air canals rather wide, width up to 100 µm:

39a Spores narrowly winged, wing ± 5 µm wide; ornamentation on distal face not elaborate, especially not on proximal face where often reduced to simple projections and stipplings; widespread . . . . . 44. *R. albovestita*

39b Spores wide-winged, wing up to 10 µm wide; distal face elaborately ornamented; very rarely found:

40a Thalli large, up to 10.0 × 2.5–3.8 mm; scales hyaline . . . . . 42. *R. hantamensis*

40b Thalli small, 3.5–5.0 × 0.9–1.5(–2) mm; scales red . . . . . 41. *R. alatospora*

38b Dorsal pillars not tapering; air canals narrow:

41a Thalli quite large, 6–10 × 3–4 mm; broadly ovate to obovate; in section 3–4 times wider than thick; flanks sloping obliquely; distal spore face with 10–14 alveoli across diam., sometimes with central papilla or short radiating ridges . . 46. *R. concava*

41b Thalli smaller, up to 8 × 1–2 mm, ligulate to ovate; in section as wide as, to twice wider than thick; flanks steep; spores variously ornamented:

42a Branches frequently simple, long and narrow; spore distal face with 5–7 large, incomplete alveoli across diam., often with central boss . . . . . 39. *R. elongata*

42b Branches mostly several times furcate; spore distal face with more than 7 smaller alveoli across diam., lacking central boss:

43a Branches apically rounded, margins not tumid; dorsal cell pillars only 70–105 µm long; proximal spore face granulate . . . . . 37. *R. pulveracea*

43b Branches apically keeled to wedge-shaped, margins somewhat tumid; dorsal cell pillars up to 180 µm long; proximal spore face reticulate:

44a Dorsal pillars with top cell mammillose; distal spore face with ridges generally forming a central cross (Plate 25E); distribution restricted to southeastern Northern and northern and north-central Western Cape . . . . . 38. *R. furfuracea*

44b Dorsal pillars with top cell globose; distal spore face with ± 8 angular, irregular alveoli across diam.; distribution apparently restricted to Lesotho . . . . . 40. *R. trachyglossum*

37b Dorsal pillars tall, more than 200 µm and up to ± 450 µm (rarely 1000 µm) long, consisting of (3–)4–6 narrow, elongated cells (1.5–)2–3 (or more) times longer than wide:

45a Dorsal surface of thalli generally somewhat velvety or furry when fresh; emerald-green to lighter green; cell pillars gradually tapering to narrower apical cell:

46a Scales rounded, wavy, large, ± 1500 × 600–900 µm, margin entire; thalli emerald-green; basal cells of pillars almost equally long, walls somewhat thickened; spores polar, ornamentation finely or coarsely reticulate . . . . . 52. *R. simii*

46b Scales triangular, very large, up to 1800 µm long; basal cells of pillars variably long, walls not thickened; spores variously ornamented:

47a Triangular scales with dentate margins (Figure 71E); dorsal pillars up to 450 µm long; spores papillose; not rare, but distribution restricted to western Northern Cape and Western and Eastern Cape . . . . . 50. *R. villosa*

47b Triangular scales with filamentous apices (Figure 72G); dorsal pillars up to 1000 µm long; spore ornamentation incompletely reticulate; very rare ..... 51. *R. hirsuta*

45b Dorsal surface of thalli rarely velvety or furry; steel-grey to bright green or olivaceous green; cell pillars not, or hardly tapering:

48a Thalli dorsally steel-grey; tall cell pillars (up to 450 µm long) like slivers of glass, often interlocking over groove; branches up to 9 mm long; scales large and billowing, basal cell walls appearing 'stretched'; distal spore face with a few short, well-spaced, radiating, central ridges; proximal spore face incompletely reticulate and granulate ..... 49. *R. vitrea*

48b Thalli dorsally olivaceous green or crystalline; cell pillars shorter (mostly less than 350 µm long), not interlocking, or if so, only temporarily toward apex; branches mostly less than 8 mm long; scales smaller and not billowing; spore ornamentation on distal face reticulate or with several, long, thick, radiating ridges; on proximal face, not granulate:

49a Dried thalli with brown, parchment-like flanks, proximally almost denuded of scales; wet thalli velvety, olivaceous green; distal spore face with thick radiating ridges ..... 47. *R. albomarginata*

49b Dried thalli frequently with somewhat purple flanks; wet thalli rather crystalline, bright green or purplish green:

50a Thalli in section 1.5 times to nearly twice wider than thick; sides tightly inflexed when dry ..... 48. *R. namaquensis*

50b Thalli in section 2–4 times wider than thick; sides incurved when dry:

51a Cells in dorsal pillars mostly somewhat constricted in the middle, ampulla-shaped; spores 90–95(–105) µm diam.; distal face with several radiating ridges; distribution restricted to eastern mountains ..... 45. *R. ampullacea*

51b Cells in dorsal pillars not constricted; spores 70–80(–90) µm diam.; ornamentation with numerous small alveoli; distribution restricted to western and northern Western Cape ..... 43. *R. parvo-areolata*

A. Subgenus **Ricciella**

Ricciella *(A.Braun) Rchb.*, Der Deutsche Botaniker, Vol. 1. Das Herbarienbuch: 23 (1841), fide Grolle: 426 (1983b). Lectotype: *R. fluitans* L.

Spongodes (Nees) O.H.Volk: 456 (1983). Type: not designated.

Thalli smallish to large; terricolous, rarely aquatic. *Scales* ventral, small, mostly evanescent.

Dorsal epidermis chlorophyllose; air pores scattered, soon enlarging, often becoming lacunose. *Assimilation tissue* with large, polyhedral to irregular air chambers.

Sporangia immersed or bulging ventrally; vertical or rarely oblique. *Spores* smallish to medium-sized to large; tetrads separating at maturity.

A1. Section **Spongodes** *Nees*, Naturgeschichte der Europäischen Lebermoose 4: 391 (1838). Lectotype: *R. crystallina* L. emend. Raddi, fide Grolle: 248 (1976).

Thalli medium-sized to large, rarely heterothallic with small male gametophytes; terricolous. *Scales* ventral, small, evanescent.

Dorsal epidermis chlorophyllose; air pores soon large, lacunose. *Assimilation tissue* with large polyhedral air chambers.

Sporangia mostly immersed, sometimes bulging somewhat ventrally or dorsally. *Spores* medium-sized to large; separating at maturity.

Two groups are recognized within this section: Group Crystallina and Group Vesiculosa.

Al.1. Group **Crystallina**

Thalli mostly in rosettes or partial rosettes; dorsally becoming lacunose.

1. **Riccia crystallina** *L. emend. Raddi* in Opuscoli Scientifici. Bologna 2: 351, 353 (1818); Steph.: 369 (1898); Sim: 14 (1926); Jovet-Ast: 459 (1964); Jovet-Ast: 82 (1966); Na-Thalang: 107 (1980); Jovet-Ast: 340 (1986); Perold: 58 (1991c); R.M.Schust.: 494 (1992b); Jovet-Ast: 229 (1993). Type: Micheli, P.A. 1729. Nova plantarum genera, tab. 57, fig. 3, lecto., *Riccia* 0:2.n:1 (FI, typo.) fide Perold (1992b).

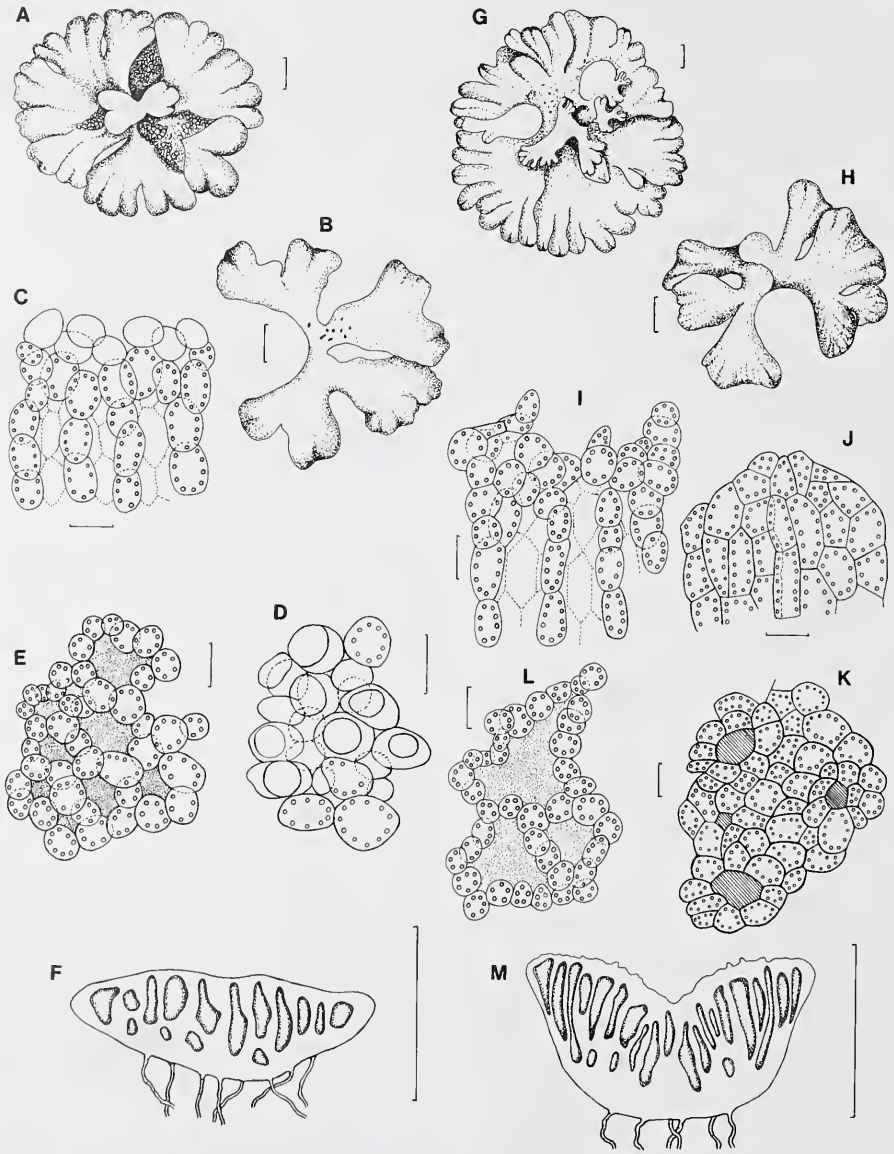
R. plana Taylor: 414 (1846); Steph.: 368 (1898); A.V.Duthie & Garside: 111 (1937); Hässel de Menéndez: 223 (1963); S.W.Arnell: 40 (1963a). Type: Australia, Swan River, *Drummond s.n.*, 1843 (K, holo.; MEL, iso.).

Thalli medium-sized, isolated or crowded, or in incomplete or complete compact rosettes, 15–20(–25) mm across; glaucous-green or greyish green, crystalline, not pitted apically, only more proximally becoming slightly spongy; when dry, bluish grey, finely spongy, margins raised, not inflexed. *Branches* 2 or 3 times furcate, shortly to rather more deeply divided, often crowded and overlapping laterally to moderately divergent, obcuneate, 5–7 × (2–)3–4 mm, 0.6–0.8(–1.0) mm thick, in section 3–5 times wider than thick, apex rounded, truncate or shortly emarginate; groove only present distally, shallow, thallus margins rounded, obtuse; flanks sloping obliquely, green; ventral face gently rounded to flat, green. *Scales* ventrally present near apex only, minute, difficult to detect, hyaline.

Dorsal epidermis not areolate, cells when turgid, almost globular, shiny, single or tiered in pairs, laterally rather loosely connected, 37.5–50.0 × 50–60 µm; air pores apically small and obscured, soon widening as air chambers enlarge, eventually leaving them more exposed. *Assimilation tissue* 400–600 µm thick, air chambers apically narrow, slit-like, wide toward base, polygonal, bounded by unistratose walls of chlorophyllose cells; storage tissue occupying ± 4 ventral cell layers of thallus. Figure 27A–F.

Monoicous. *Antheridia* sunken in rows along dorsal face of lobes, necks colourless, ± 200 µm long. *Archegonia* embedded along middle of lobes, necks purple-brown, ± 250 µm long. *Sporangia* abundant, bulging slightly ventrally, crowded. *Spores* 65–80(–85) µm diam., triangular-globular, polar, pale yellow to light brown, semitransparent; wing up to 7.5 µm wide, usually broader at marginal angles, notched or with a round pore, 5 µm across, margin finely crenulate, sometimes erose; ornamentation regularly reticulate, similar on 2 spore faces; distal face highly convex, with 8–10 usually complete, round or oval alveoli across diam. of spore, 7.5–10.0 µm wide, alveolar walls thin and low, raised at nodes into spinous or truncate processes, ± 7.5 µm high, tips often bifid or even trifid; proximal face with triradiate mark distinct, its arms ± 5 µm high, often interrupted for short sections, dotted with granules, each of 3 facets with ± 20 rounded or angular alveoli, 5.0–7.5 µm wide, walls thin and low, raised at nodes into spinous processes, granular or divided at tips. *Chromosome number*: n = 8 (Mehra 1977; Jovet-Ast 1986; Bornefeld 1989). Plate 11C, D; Perold (1989e: fig. 36.1–6).

Although Micheli (1729) had clearly distinguished between two species, Linnaeus (1753)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united into one species '*Riccia minima et minor*' and named the combination *R. crystallina*. Years of confusion followed until Jovet-Ast (1964, 1966) distinctly defined *R. crystallina* and *R. cavernosa*.

Riccia crystallina is a subcosmopolitan species. It is widely distributed in southern Africa, but has been fairly rarely collected, except in the southwestern part of Western Cape, where it is relatively common. It is found on damp, sandy or clayey soils or on mud, at the edges of ponds, at streambanks, on cultivated ground in gardens and along footpaths. Map 11.

This species can be distinguished from *R. cavernosa* (no. 2) by the finer, compact texture of the thallus, its crystalline appearance and glaucous-green colour. The spores are highly ornamented, somewhat 'prickly' in appearance, and have eroded wing margins. It is, however, uncertain what Sim's (1926) concept of the species was. Duthie & Garside (1937) remarked that Sim's illustration of *R. crystallina*, fig. A, is of *R. cupulifera* and that the spore depicted in fig. D is of *R. curtisii*, since it is in a tetrad. Duthie's note enclosed with the specimen, *Garside 6*, a bequest from Sim's herbarium and identified by him as *R. crystallina*, reads: 'Possibly a mixture of *R. crystallina*? and *R. curtisii*. The only spores seen adhered in tetrads and is characteristic of *R. curtisii*'. *Riccia plana* was placed in synonymy under *R. crystallina* by Jovet-Ast (1966); their relationship according to Arnell (1953), had also been pointed out by Garside, yet he (Arnell 1963a) described both.

Vouchers: *S.W. Arnell 189* (BOL); *Duthie 5006* (BOL); *Koekemoer 103a* (PRE); *Morley 308* (PRE); *S.M. Perold 455* (PRE).

2. **Riccia cavernosa** *Hoffm. emend. Raddi* in Opuscoli Scientifici. Bologna 2: 353 (1818); Jovet-Ast: 459 (1964); Jovet-Ast: 82 (1966); Jovet-Ast: 342 (1986); Na-Thalang: 108 (1980); Vianna: 71 (1981); Perold: 59 (1991c); R.M. Schust.: 487 (1992b); Jovet-Ast: 231 (1993). Type: Allemagne. In terra limosa, ad piscinas. [Herb. Hoffm., not at MW, fide Jovet-Ast: 342 (1986)].

R. cavernosa Hoffm.: 95 (1795).

Ricciella rautanenii Steph.: 374 (1895a); A.V.Duthie & Garside: 20 (1939); S.W.Arnell: 40 (1963a). Type: Hereroland, Tsoachaub River, *Rautanen* (G).

Thalli medium-sized to large, in complete, regular rosettes up to 30 mm across; bright grass-green to yellowish green, often becoming tinged with red along margins, older parts lacunose (cavernose); when dry, margins not inflexed, yellowish, spongy. *Branches* repeatedly furcate, shortly to deeply divided, nearly parallel or crowded and overlapping, oblong-obovate or obcuneate, (2–)4–8 × 1.5–2.5(–4) mm, up to 1 mm thick, in section 1.5–2.5(–4) times wider than thick, apex obtusely rounded, shortly emarginate; groove generally only distally present, shallow, thallus margins rounded, obtuse; flanks obliquely sloping; ventral face rounded, green. *Scales* absent or evanescent.

Dorsal epidermis areolate, gently domed over each air chamber, cells 4- or 5(6)-sided, walls slightly bulging, up to 80–105 × 50–55 µm, in between some scattered conical cells projecting vertically, 50–60 × 37.0–47.5 µm; air pores when young, generally somewhat obscured, with radially arranged surrounding cells soon enlarging and becoming lacunose (cavernose). *Assimilation tissue* up to 800 µm thick, air chambers generally in a single storey, appearing to be several storeys in section, because of obliquely sloping cavities, bounded by unistratose walls of chlorophyllose cells; storage tissue occupying ventral part of thallus. Figure 27G–M.

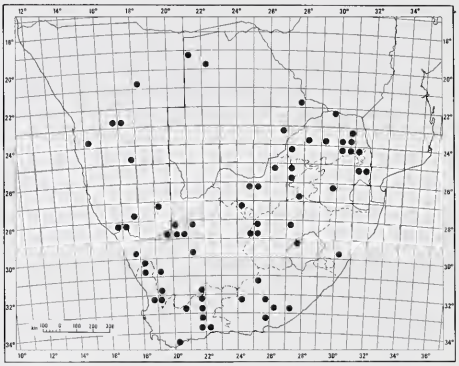
FIGURE 27.—A–F, **Riccia crystallina**: A, complete rosette; B, partial rosette; C, c/s epidermal cells and assimilation tissue; D, epidermal cells from above; E, h/s assimilation tissue, air canals (stippled); F, c/s branch. G–M, **R. cavernosa**: G, complete rosette; H, partial rosette; I, c/s epidermal cells and assimilation tissue; J, dorsal epidermis forming 'dome' over larger air chamber; K, several epidermal 'domes' and air pores (hatched) from above; L, h/s through air chambers (stippled); M, c/s thallus. A, D–F, *Koekemoer 103*; B, *S.M. Perold 2428*; C, *S.M. Perold 455*; G–I, L, *Arnold 4323*; J, K, M, *S.M. Perold 453*. Scale bars: A, B, F–H, M, 1 mm; C–E, I–L, 50 µm. Artist: J. Kimpton.

Monoicous. *Antheridia* sunken in a row along length of thallus, with colourless necks projecting from pits in the surface. *Archegonia* in deeply embedded rows, with purple necks not prominent. *Sporangia* protruding somewhat ventrally as dark bulges, numerous, crowded. *Spores* 85–110(–115) µm diam., triangular-globular, polar, reddish brown or almost black, semitransparent to opaque; wing 5 µm wide, somewhat broader at marginal angles, sometimes notched or porate, margin finely crenulate or serrulate, occasionally erose; ornamentation with irregular ridges, complete alveoli rare, dissimilar on 2 spore faces; distal face convex, centre prominently ridged, irregularly 2 or 3 times branched, ridges short and low toward margin; proximal face with triradiate mark and apex distinct, simple or branching or anastomosing ridges occasionally uniting to form mostly incomplete alveoli, quite variable. *Chromosome number*: n = 8 (Na-Thalang 1980; Jovet-Ast 1986; Bornefeld 1989). Plate 11E, F; Perold (1989e: fig. 37.1–6).

Riccia cavernosa is an almost cosmopolitan species. It is also widely distributed in southern Africa, where it is found on alluvial mud or on damp, sandy soil in Namibia, Botswana, Northern Province, North-West, Mpumalanga, Free State, KwaZulu-Natal, Lesotho, and Northern, Western and Eastern Cape. Map 12.

The species can be recognized by the large, mostly regular, yellowish green rosettes, often tinged with red along the thallus margins; the spores are characteristically bi- or trichotomously ridged on the distal face.

The type specimen of *R. cavernosa* was not seen, but Jovet-Ast's (1964, 1966) detailed descriptions, illustrations and measurements of the thalli and the various patterns which the sculpturing of the spores can assume, leave no doubt that the southern African specimens have been correctly referred here. *Riccia rautanenii* Steph. was placed in synonymy under *R. cavernosa* by Jovet-Ast (1964) and southern African specimens were seen by her. The *R. chrystallina* (sic) spores illustrated by Arnell (1963a) indicate that he was describing *R. cavernosa*, a mistake commonly made until Jovet-Ast's (1964, 1966) thorough investigations clarified the matter.



MAP 12.—● **Riccia cavernosa**

Vouchers: *Acocks CH3602* (PRE); *Kock 934* (PRE); *S.M. Perold 363* (PRE); *Schelpe 3907* (PRE); *Volk 81/228* (M, PRE).

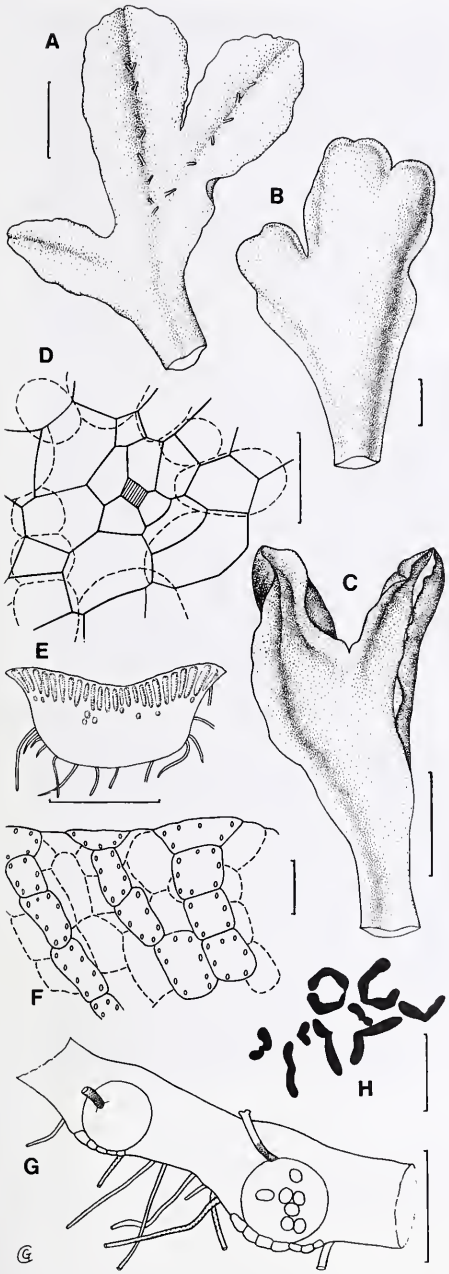
3. **Riccia moenkemeyeri** *Steph.*, in Botanische Jahrbücher 8: 95 (1886b); Steph.: 372 (1898); E.W.Jones: 211 (1957); Vanden Berghen: 189 (1972); Perold: 19 (1992a). Type: Niger Gebiet, Alt Calabar in terra, leg. *Moenkemeyer N3*, 11-10-1884 (*G024384*, holo.!; S, iso.).

R. abnormis Steph.: 213 (1891); Steph.: 364 (1898). Type: Kamerun, Bateki, leg. *P. Dusén 125*, 17 Oct. 1890 (G).

?R. chevalieri Steph.: 116 (1912); Steph.: 1 (1917). Type: Central African Republic, Haut-Oubangui, Plateau des Ungourras, 650 m, Nov. 1902, leg. *Chevalier*, ex Herb. Corbière.

Ricciella undulata S.W.Arnell: 105 (1952). Type: Africa occidentalis, Sierra Leone, Freetown, stream-side above Calabar Point, *S.W. Arnell 2252* (S).

Thalli medium-sized to fairly large, in crowded and often overlapping, gregarious patches; glaucous-green, turning white over older parts and along undulating margins, sometimes with purple-red band on inner side, only becoming pitted towards margins and



proximally; when dry, concave dorsally, margins apically incurved to inflexed or somewhat recurved. *Branches* once to several times furcate, closely to moderately divergent, oblong to ovate, 9–10(–12) × 1.6–2.4 mm, 0.8 mm thick medianly, thinner toward margins, in section 2–3 times wider than thick, apex rounded to subacute, emarginate; groove distally deep, becoming shallow to flat or concave proximally, thallus margins rapidly thinning, acute, winged and attenuate, ultimately consisting of a single row of echlorophyllose cells; flanks green to purple-red below, rather steep, then abruptly sloping obliquely, becoming white toward margins; ventral face rounded, green. *Scales* mostly quite firmly attached to flanks and difficult to detach, not extending to thallus margins, rather distant, dark wine-red and shiny or hyaline.

Dorsal epidermis with numerous small, slightly domed to flat areolae over individual air chambers, enlarging toward margins and proximally, sometimes rupturing, cells polygonal, 42–55 × 20–37 µm; air pores encircled by smaller companion cells. *Assimilation tissue* 350– 400 µm thick, air chambers in one storey, but often appearing to be secondarily partitioned, bounded by unistratose walls of chlorophyllose cells; storage tissue occupying ventral part of thallus, cells with small spaces wedged in between. Figure 28.

Monoicous. *Antheridia* sunken in a row along groove, hyaline necks emerging from small depressions. *Archegonia* deeply embedded along groove, necks sloping toward apex of thallus, difficult to detect from above. *Sporangia* obliquely orientated and protruding ventrally, single or 2 adjacent or serially arranged, subspherical. *Spores* (65–)68–75 (–85) µm diam.,

FIGURE 28.—**Riccia moenkemeyeri.** A–C, thallus: A, dorsal face, with rows of antheridial necks; B, ventral face; C, when dry. D, air pore (hatched), dorsal and subdorsal cells (stippled lines) enclosing air chamber; E, c/s branch; F, c/s showing air chambers; G, l/s sporangium with forward-sloping archegonial neck; H, chromosomes. A–H, *S.M. Perold 2603*. Scale bars: A–C, E, G, 1 mm; D, F, 50 µm; H, 1 µm. Drawings by G. Condy; karyotype by T. Bornefeld (pers. comm.).

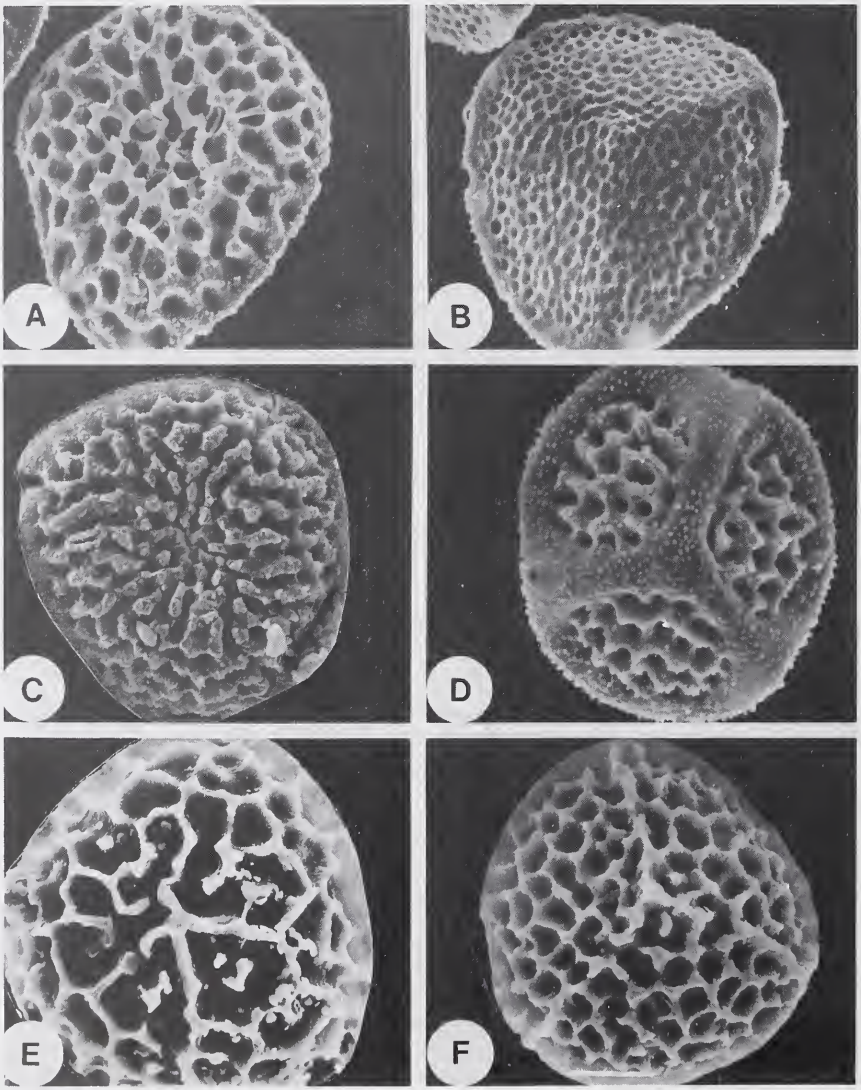


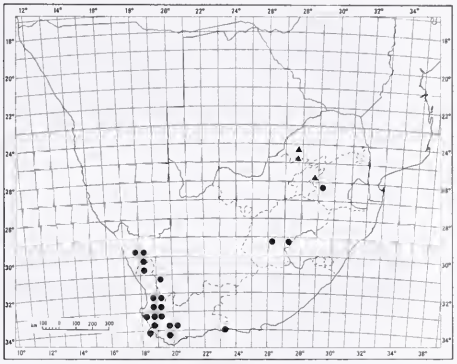
PLATE 12.—Spores. A, B, **Riccia moenkemeyeri**: A, distal face; B, proximal face. C, D, **R. cupulifera**: C, distal face; D, proximal face. E, F, **R. bullosa**: E, distal face; F, proximal face. A, B, *Sim 9072*; C, *S.M. Perold 2371*; D, *Schelpe 7787* (BOL); E, F, *S.M. Perold 467*. A, B, D, × 700; C, E, × 600; F, × 500.

triangular-globular, polar, light tan to yellowish brown, semitransparent; wing ± 5 µm wide, somewhat broader at generally perforated marginal angles, margin finely crenulate; ornamentation reticulate, but completely dissimilar on 2 spore faces; distal face convex, with (8)9 or 10 alveoli across diam., 8–10(– 12) µm wide, occasionally incompletely separated, walls low, covered with fine granules and slightly raised into papillae at nodes; proximal face lacking a triradiate mark, each of 3 facets with up to ± 100 tiny, mostly less than 2.5 µm wide, shallow, but clearly defined alveoli, the walls forming a fine network. *Chromosome number*: n = 9 (Bornefeld pers. comm. on *S.M. Perold 2603*); n = 8 (Jovet-Ast 1969) Plate 12A, B.

Riccia moenkemeyeri is a tropical African species, known from Sierra Leone (as *R. undulata*), Angola, Cameroon, the Congo Basin [Région du Lac Moero (Vanden Berghen 1972)], Gambia, Ghana, Ivory Coast, Malawi, Niger, Rwanda, Tanzania, Zimbabwe, and now also with outliers into the Northern Province and Gauteng, southern Africa (Map 13). Its presence on Fernando Po, as reported by Stephani (1887) for the type specimen, *Moenkemeyer 3*, must have been a mistake, as the locality given on the label is Calabar, Niger, which is confirmed in *Species hepaticarum* (Stephani 1989).

The species grows in damp places, on rich loamy soil, mostly near streams and in association with other *Riccia* species (in southern Africa) such as *R. stricta*, *R. atropurpurea* and with *Exormotheca pustulosa*.

Riccia moenkemeyeri is characterized by a more or less persistent dorsal epidermis which is marked out into small areolae, each with a small central air pore; by numerous narrow air chambers, appearing to be in more than one storey; by undulating thallus margins which terminate in a single row of hyaline cells; by obliquely orientated sporangia and a highly distinctive spore ornamentation with 8–10 large alveoli on the distal face and numerous tiny alveoli on the proximal face, which lack a triradiate mark.



MAP 13.—▲ **Riccia moenkemeyeri**
● **R. cupulifera**

Vouchers: *Condy 22, 23*; *S.M. Perold 2603*.

4. **Riccia cupulifera** *A.V.Duthie* in Transactions of the Royal Society of South Africa 24: 116 (1937); S.W.Arnell: 39 (1963a): Perold: 60 (1991c). Type: Cape, Stellenbosch, *A.V. Duthie 5007* (BOL, syn.!).

Plants heterothallic, *male thalli* very small, simple or furcate; rather light green to yellow-green; *female thalli* smallish to medium-sized, crowded or in incomplete to complete rosettes, 20–25 mm across, or scattered and in so-called 'butterfly' shapes; bright green to yellowish green, soon becoming pitted and basally lacunose; when dry, greenish yellow and slightly wrinkled, spongy, margins not inflexed. *Branches* in female thalli, 2 or 3 times furcate, shortly to deeply divided, almost overlapping or closely to moderately divergent, oblong to obcuneate, up to 7 × 2.0–3.5 mm, 0.7–1.0(–1.5) mm thick, in section ± 3 times wider than thick, apex rounded, truncate or emarginate; groove distally short and shallow, otherwise flat, thallus margins obtuse, rounded; flanks slightly bulging to somewhat obliquely sloping; ventral face rounded to flat, green. *Scales* ventral toward apex, minute, evanescent, rarely observed. Plate 13A.

Dorsal epidermis areolate, slightly domed over each air chamber, cells polygonal, variable

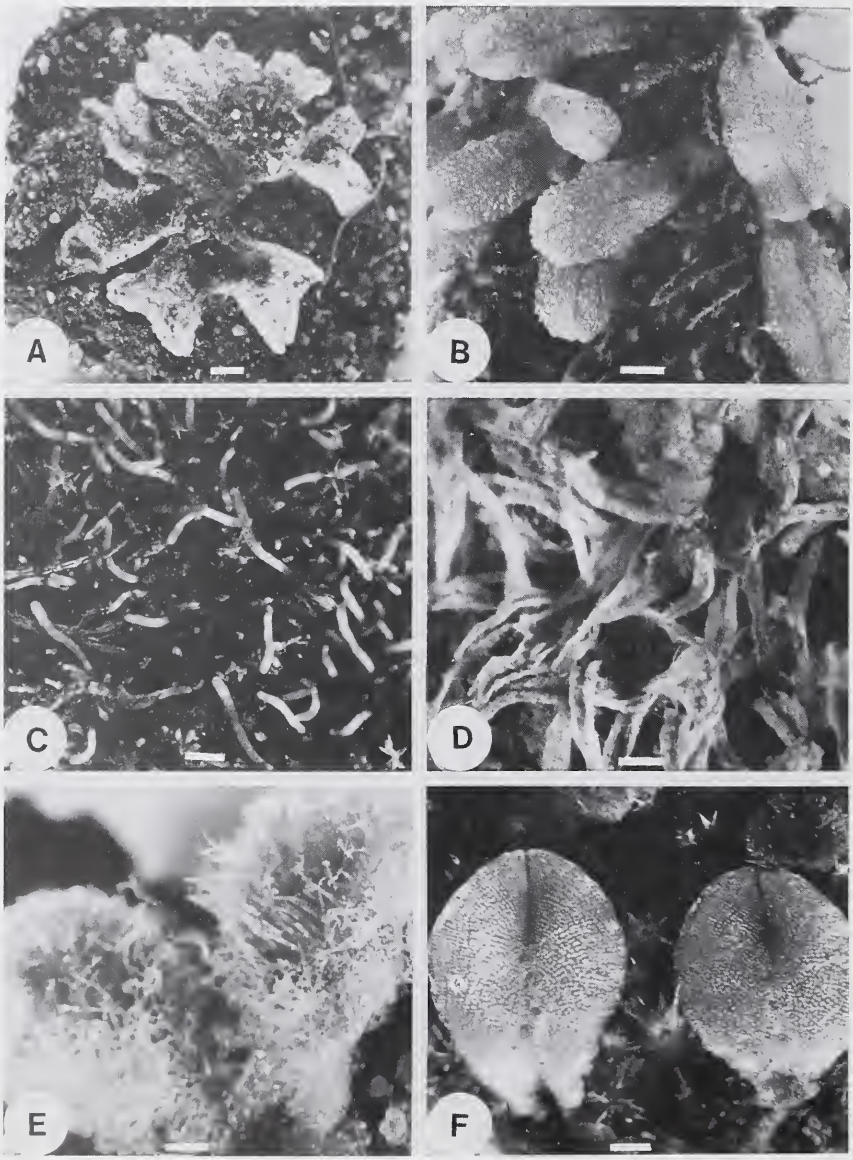
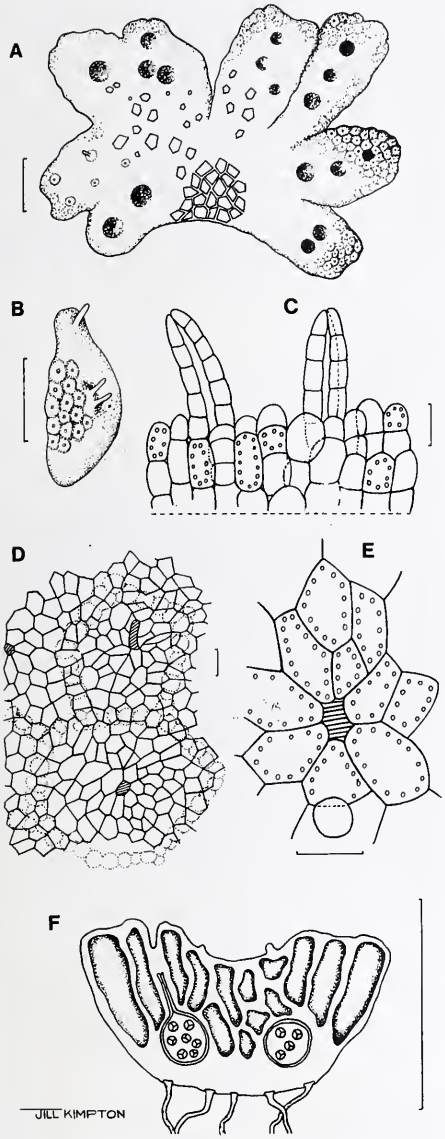


PLATE 13.—Thalli. A, **Riccia cupulifera**, rosette; B, **R. volkii**, crowded branches; C, **R. stricta**, overlapping branches; D, **R. purpurascens**, overlapping branches; E, **R. tomentosa**, hairy branches. F, **R. schelpei,** deeply grooved branches. A, *S.M. Perold 2395*; B, *S.M. Perold 2472*; C, *S.M. Perold 2524*; D, *S.M. Perold 2386*, E, *S.M. Perold & M.J.A.W. Crosby 2157*; F, *S.M. Perold 1422*. Scale bars: A–F, 1 mm.



in size, 60–130 × 50–75 µm, in between with scattered, erect, rounded cells, mostly ± 40 µm long, more numerous toward apex and around bases of antheridial and archegonial necks; air pores small at apex, rapidly enlarging by rupture of surrounding, radially arranged cells, proximally becoming as wide as air chambers. *Assimilation tissue* 500–800 µm thick, air chambers polyhedral, in one storey, narrow in younger parts of thallus, wider proximally, bounded by unistratose walls of chlorophyllose cells; storage tissue occupying ventral 3 or 4(5) cell layers of thallus. Figure 29.

Dioicous. *Antheridia* very numerous, sunken in a row along middle of mostly small male thalli, necks hyaline, ± 200 µm long. *Archegonia* scattered along median area of female plants, necks purple. *Sporangia* bulging dorsally, from above dark spore mass visible through overlying tissue, which gradually shrinks away, exposing cup-like hollows, becoming confluent along middle of older thalli and containing large numbers of liberated spores. *Spores* 90–115(–122) µm diam., triangular-globular, polar, light brown to darker brown, semitransparent; wing thick, up to 7.5 µm wide, notched or perforated at marginal angles, margin finely crenulate, with row of granules along edge; ornamentation foveolate, with deep-set, rounded alveoli on both spore faces, similar to rather dissimilar; distal face often highly convex, with 12–13 small alveoli or fovea across diam., 2.5–5.0 µm wide, walls high, up to 5 µm wide, warty or knobbly, raised into truncate processes at nodes, borders often joining to form short, undulating or radiating ridges; proximal face with triradiate mark very prominent, its arms up to 7.5 µm wide, even wider at join with wing, dotted with fine granules, each of 3 facets with ± 35 small, deep, rounded alveoli, less than 5 µm wide, sometimes adjacent ones confluent, walls thickened and raised, especially at nodes, granulate to papillate. *Chromosome number*: n = 8 (Borne-

FIGURE 29.—**Riccia cupulifera**. A, B, thallus: A, female in partial rosette; B, small male. C, l/s of 2 antheridial necks; D, epidermal cells and air pores (hatched) overlying air chambers seen from above; E, air pore (hatched) with surrounding cells, only one of scattered, rounded cells shown, from above; F, c/s branch. A–C, *S.M. Perold 2395*; D–F, *Oliver 8043*. Scale bars: A, B, F, 1 mm; C, E, 50 µm; D, 100 µm. Artist: J. Kimpton.

feld 1989). Plate 12C, D; Perold (1989e: fig. 38.1–6).

Riccia cupulifera is endemic to southern Africa, and widespread in the shrublands of the western parts of Northern and Western Cape, rare in the Free State and only found once in Mpumalanga. Map 13.

The species grows on damp, sandy soil or on mud, and can be distinguished from *R. crystallina* (no. 1) and *R. cavernosa* (no. 2), the other two rather similar species with spongy thalli, by being dioicous and heterothallic, by the characteristic 'butterfly' shape of young thalli, and by never developing a reddish or purple tint on exposure to the sun, as in *R. cavernosa*. The spores can be recognized by the very prominent arms of the triradiate mark on the proximal face, the thick wing and foveolate ornamentation.

Vouchers: *S.W. Arnell 303* (PRE); *Duthie 5488* (BOL); *Oliver 8053* (PRE); *S.M. Perold 591* (PRE); *Schelpe 7787* (BOL).

A1.2. Group **Vesiculosa**

Thalli rarely in rosettes; mostly large and succulent.

5. **Riccia bullosa** *Link ex Lindenb.* in Nova acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum, Supplement 14: 119 (1829); Lehm.: 371 (1829); Lindenb.: 441 (1836); Nees: 391, 433 (1838); Gottsche et al.: 609 (1844–1847); Steph.: 377 (1898); Sim: 13 (1926); S.W.Arnell: 42 (1963a); Perold: 131 (1991b); Perold: 61 (1991c). Type: Cape, terrestris, ad montem tabularem versus montum Leonio, *Ecklon s.n.* (STR, lecto.!).

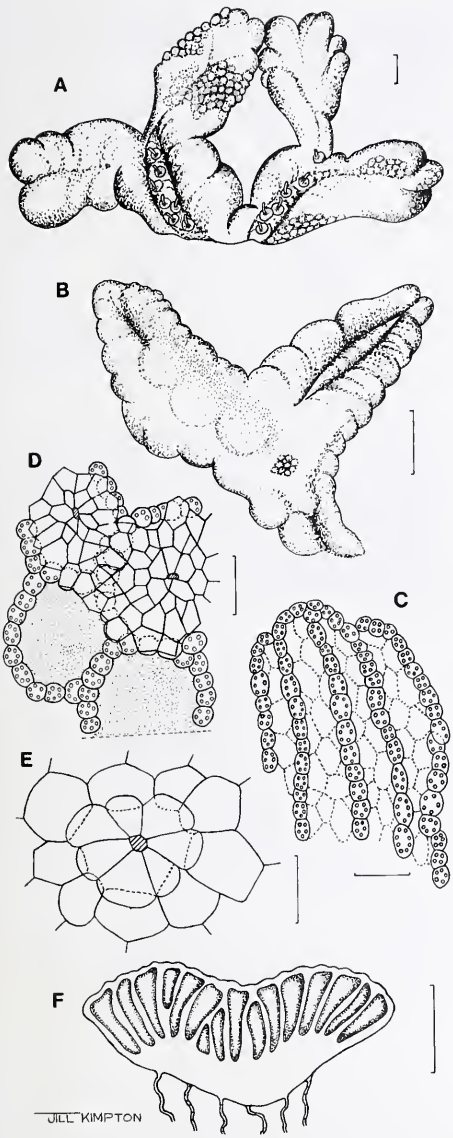
R. crassa Nees ex Lindenb.: 119 (1829) nom. inval.

R. montaguensis S.W.Arnell: 308 (1952); S.W.Arnell: 44 (1963a). Types: Cape Province, Montagu, Bath Kloof, near the caves, *S.W. Arnell 714* (BOL!; PRE!), *741* (BOL!).

Thalli medium-sized to large, in crowded, gregarious patches or scattered; apically light green, soon turning straw-coloured, medianly deeply grooved, laterally swollen to bloated, with small, polygonal, domed alveoli, transversely wrinkled, becoming proximally pitted and spongy; when dry, rather deflated and with folds across, sides not inflexed, margins scalloped. *Branches* once, occasionally twice furcate, sometimes simple, shortly to deeply divided, moderately to widely divergent, broadly ovate to oblong, 5–15 × 3.5–5.5 mm, 1.5–2.5 mm thick, in section 2.0–2.5 times wider than thick, apex obtuse to truncate, emarginate; groove deep and narrow, sometimes split into two by raised wedge of tissue, disappearing toward base or at sporangia, thallus margins obtuse, rounded, often overhanging; flanks sloping obliquely; ventral face rounded to keeled, green. *Scales* ventral, toward apex only, vestigial, hyaline, in pairs.

Dorsal epidermis forming a domed roof over each air chamber, cells 4–6-sided, 62–75 × 35–40 µm; air pores surrounded by 6 or 7 wedge-shaped, smaller and often thinner-walled cells, breaking down with age and exposing air chambers. *Assimilation tissue* 1000–1500 µm thick, air chambers tall, mostly in one storey, vertical or sloping obliquely, narrower toward centre and apex, bounded by unistratose, chlorophyllose cell walls; storage tissue occupying ventral part of thallus, cells angular, closely packed, containing starch granules. Figure 30.

Dioicous. *Antheridia* sunken in 1 or 2 crowded rows along slightly raised central ridge in groove, hyaline necks protruding from small pits, up to 500 µm long. *Archegonia* embedded in a row along groove, purple necks ± 300 µm long. *Sporangia* crowded together, bulging dorsally, overlying tissue thinning and disintegrat-



ing. *Spores* (100–)130–150(–160) µm diam., triangular-globular, polar, yellow-brown, becoming darker with age, semitransparent; wing thin, undulating, up to 10 µm wide, often perforated at marginal angles, margin finely crenulate, occasionally partly erose; ornamentation reticulate, rather similar on two spore faces; distal face with 10–12 rounded alveoli across diam., 10–15 µm wide, sometimes larger and incompletely separated by low, fragmentary ridges radiating from central pillar, alveolar walls finely granular, 5 µm high, thin, generally becoming higher and thicker over centre, raised at nodes and often extending onto wing; proximal face with triradiate mark consisting of thin ridges up to 7.5 µm high, frequently joined by alveolar walls, each of three facets with 13–18(–25) rounded alveoli, 10–15 µm wide, often incompletely separated and adjoining ones confluent. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 12E, F; Perold (1989e: fig. 39.1–6).

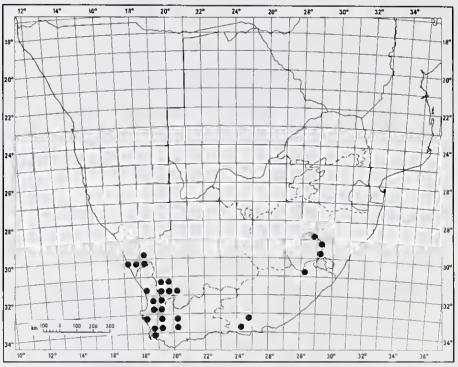
Riccia bullosa is endemic to southern Africa and is found at seepages or on damp sandy soil under brush or at granite, basalt or sandstone outcrops in the western parts of Northern and Western Cape, the southern Eastern Cape, as well as the Drakensberg Mountain Range of KwaZulu-Natal and Lesotho. Map 14.

The species can be distinguished from others in the subgenus by its large, rather bloated, straw-coloured or yellow-green thalli. *Riccia garsidei* (no. 6), although closely related, is often larger, almost white when dry, with many exposed air chambers; its spores have fewer and larger alveoli. *Riccia volkii* (no. 7) (see note under that species) is less robust and swollen, with narrowly winged, smaller spores and its distribution is restricted to the summer rainfall areas.

Riccia bullosa was originally supposed to also grow in Portugal (Nees 1838), not Spain as men-

FIGURE 30.—**Riccia bullosa**. A, B, thallus: A, male; B, female. C, c/s epidermis and assimilation tissue; D, epidermal cells and air pores (hatched), overlying air chambers, some partly exposed, others covered (cells stippled); E, air pore (hatched) and surrounding cells seen from above; F, c/s branch. A, B, *S.M. Perold 467*; C–F, *Van Rooy 3541*. Scale bars: A, B, F, 1 mm; C, D, 100 µm; E, 50 µm. Artist: J. Kimpton.

tioned by Duthie & Garside (1937), but as explained by them, the collection by Link was subsequently shown to be a species of *Exormotheca*. Stephani (1898) also stated that it was not a *Riccia* and later (Stephani 1899) referred it to *Exormotheca welwitschii*. Although Lindenberg (1836) cited both collections, Link's from Portugal and Ecklon's from the Cape, his illustration (XXIII, fig. 1) is clearly that of *R. bullosa* and so are his references to its colour, groove, air chambers and pores. Müller's (1947) selection of Link's specimen as the lectotype of *Exormotheca bullosa*, thus leaving the *Riccia* element without a correct name, is therefore not accepted here; *R. bullosa* is regarded as the correct name for this species (Perold 1991b).



MAP 14.—● **Riccia bullosa**

Sim's (1926: 13) note under *R. bullosa*, that *R. capensis* (the type specimen *Brunnthaler s.n.*) (see comment under *R. limbata*, no. 24) 'appears to be a young sterile condition of this', is inexplicable, as they are completely different species, even belonging in different subgenera! The Giffen collection, (Herb. Sim, PRE) from O'Kiep, Namaqualand, which Sim cites, has been placed under *R. schelpei* (no. 14), but the Pole Evans collection from Premier Mine, Gauteng has not been traced. Judging by its distribution it is most probably a specimen of *R. volkii* (no. 7).

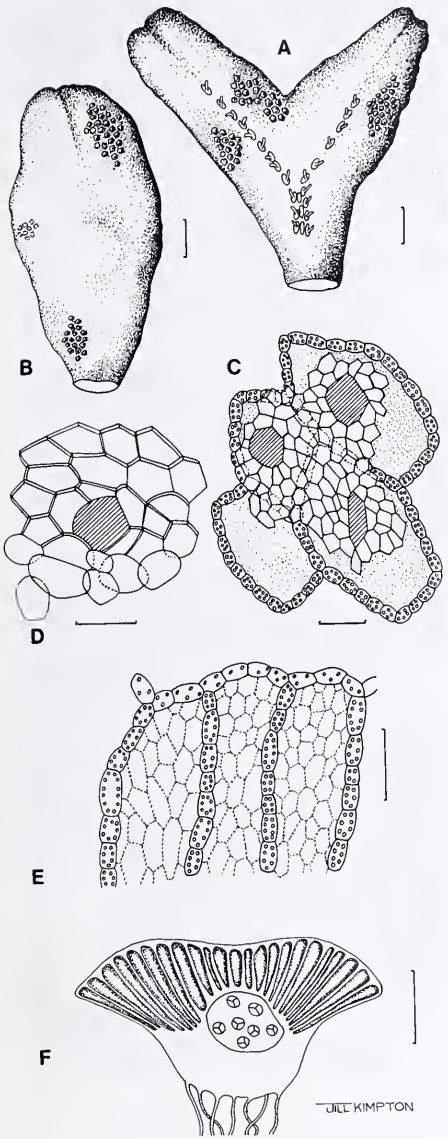
Vouchers: *Magill PRE-CH4509* (PRE); *Morley 272* (PRE); *Oliver 8777* (PRE); *S.M. Perold 467* (PRE); *Van Rooy 3541* (PRE).

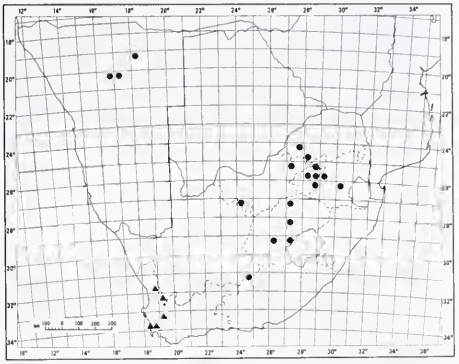
6. **Riccia garsidei** *Sim*, The Bryophyta of South Africa: 13 (1926); S.W.Arnell: 41 (1963a): Perold: 62 (1991c). Type: Cape, Stellenbosch Flats, *Garside 2* (*CH1059*) (PRE, holo.!).

Thalli medium-sized to large or very large, in gregarious patches or scattered; glaucous to pale olive or buff, very bloated; when dry, light smokey grey to white, honeycomb-pitted, sides not inflexed. *Branches* simple or once symmetrically furcate, mostly shortly divided, moderately to widely divergent, elliptical-oblong to broadly ovate, 10–12(–15) × (4–)6(–8) mm, 2.5–2.7 mm thick, in section 2–3 times wider than thick, apex gradually or abruptly tapered, shortly emarginate; groove deep and narrow distally, proximally rather flat, thallus margins obtuse, rounded, sometimes overhanging; flanks vertical to sloping obliquely; ventral face rounded or broadly keeled, glaucous to greyish green. *Scales* absent.

Dorsal epidermis forming a slightly domed to flat roof over each air chamber, cells variable in shape and size, some rectangular, others hexagonal, 30–85 × 15–35 µm; air pores surrounded by 6 or 7 smaller cells, variable in shape, 20–25 × ± 12 µm, soon rupturing, completely exposing air chambers below. *Assimilation tissue* up to 1800 µm thick, air chambers very tall, mostly in one storey, vertical to obliquely sloping laterally, gradually widening upward, shape mostly hexagonal when viewed from above, bounded by unistratose, chlorophyllose cell walls; storage tissue occupying ventral part of thallus, cells angular, closely packed. Figure 31.

Dioicous. *Antheridia* sunken in 1 (or 2) rows, along centre of branches, hyaline necks protruding individually from quite large hollows. *Archegonia* serially arranged, thin, purple necks obscured. *Sporangia* quite deeply embedded below midline, mostly crowded together. *Spores* (118–)120–130(–135) µm diam., triangular-globular, polar, golden brown





MAP 15.—▲ **Riccia garsidei**
● **R. volkii**

to tan-brown, semitransparent; wing thin, wavy up to 10 µm wide, marginal angles perforated, margin finely crenulate, sometimes with one or two notches; ornamentation reticulate and similar on two spore faces; distal face with 8–10 large, shallow, roundish or angular alveoli across diam., 12.5–20.0 µm wide, alveolar walls thin, faintly granular, 2.5–5.0 µm high, usually raised at nodes and extending across wing; proximal face with triradiate mark often not distinct and interrupted, each of three facets with ± 18 alveoli, usually more than 15 µm wide, adjacent ones sometimes confluent, alveolar walls up to 5 µm high, some meeting along arms of triradiate mark and marginally extending across wing. *Chromosome number*: not known. Plate 14A, B; Perold (1989e: fig. 40.1–6).

This species is endemic to southern Africa and has been collected in Western Cape on gravelly or clayey soil. Map 15.

Riccia garsidei is closely related to *R. bullosa* (no. 5), but can be distinguished from it by its almost white colour when dry, the larger size

FIGURE 31.—**Riccia garsidei**. A, B, thallus: A, male; B, female. C, epidermal cells and air pores (hatched) overlying air chambers, seen from above; D, air pore (hatched) with surrounding cells; E, c/s thallus through air chambers; F, c/s branch. A–F, *Duthie s.n.*, 15-11-1937. Scale bars: A, B, F, 1 mm; C, E, 100 µm; D, 50 µm. Artist: J. Kimpton.

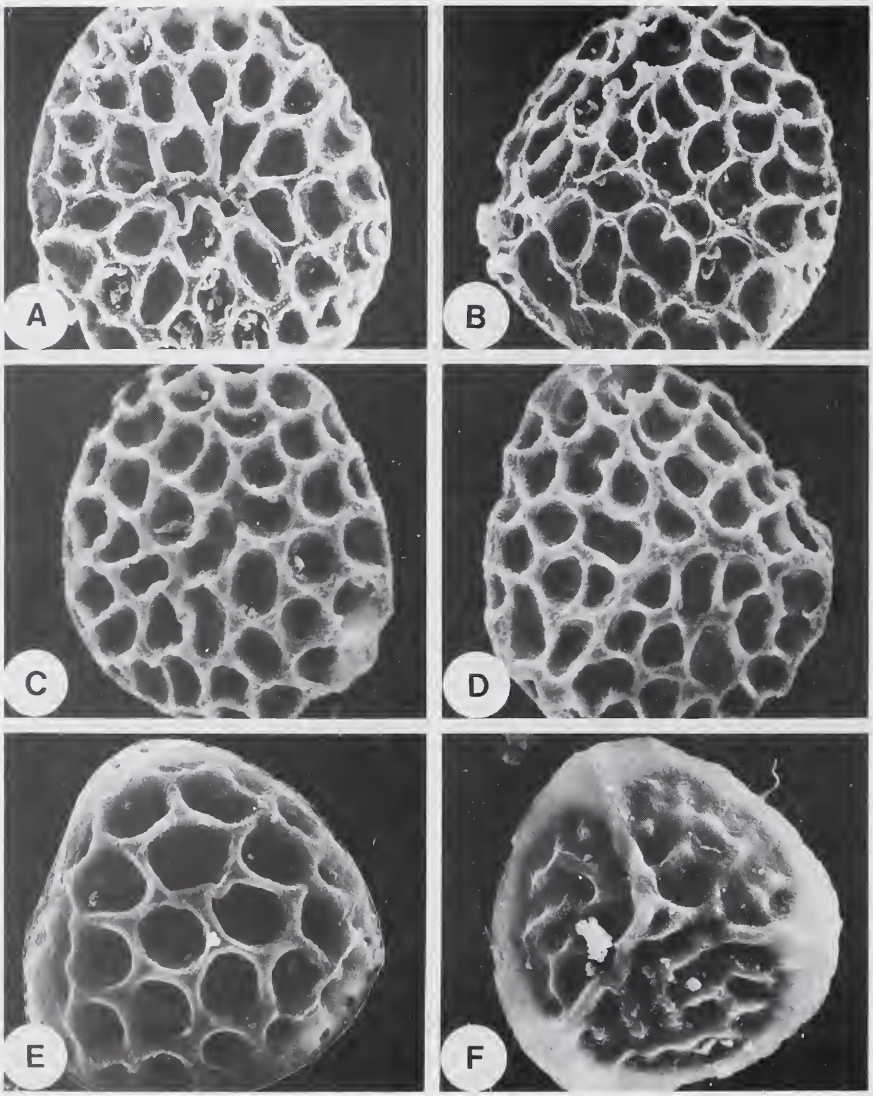


PLATE 14.—Spores. A, B, **Riccia garsidei**. A, distal face; B, proximal face. C, D, **R. volkii**: C, distal face; D, proximal face. E, F, **R. rubricollis**. E, distal face; F, proximal face. A, B, *Garside 2*; C, D, *Volk 81/230*; E, F, *Duthie 5014*. A, B, E, F, × 600; C, D, × 700.

of the thalli, the less pronounced and generally shorter groove and the many exposed, hexagonal air chambers. There is a good deal of overlap in the size of the spores of the two species, but in *R. garsidei* there are generally fewer and larger alveoli.

Vouchers: *Duthie 5002, 5075, 5475* (BOL); *Marais 5464a* (BOL); *Wilman 663* (BOL).

7. **Riccia volkii** *S.W.Arnell* in Mitteilungen der Botanischen Staatssammlung, München 16: 271 (1957); S.W.Arnell: 42 (1963a); Perold: 63 (1991c). Type: SWA/ Namibia, Otjiwarongo: Kleiner Waterberg, am Rand der Wannen im roten Sandstein, Boden kalkfrei, *Volk 1029* (M, holo.; PRE, iso.!).

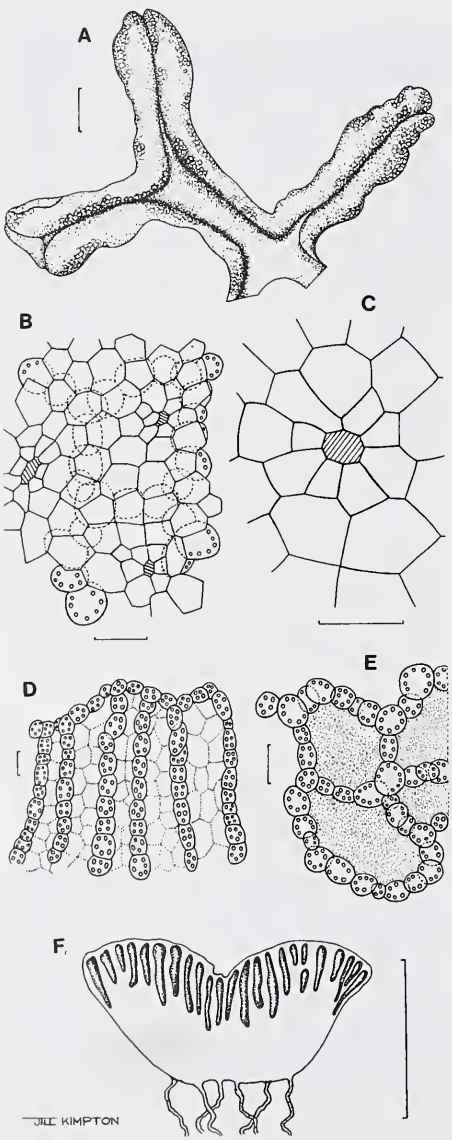
Thalli medium-sized, in crowded, gregarious patches or scattered, occasionally in rosettes, up to 20 mm across; pale green to lime-green, deeply grooved, laterally tumid and swollen, spongy toward base; when dry, yellowish to greyish white, sides transversely wrinkled, not inflexed. *Branches* once to several times furcate, shortly to deeply divided, moderately to widely divergent, broadly ligulate to lingulate, up to 9 mm long, segments 2–6 × 2.5–3.5 mm, 1.0–1.2 mm thick, in section 2–3 times wider than thick, apex obtusely rounded, emarginate; groove deep and narrow apically, becoming wider and concave proximally, thallus margins obtuse, rounded; flanks sloping obliquely, ventral face gently rounded, green. *Scales* ventral, vestigial or absent, hyaline. Plate 13B.

Dorsal epidermis areolate, forming a slightly domed to flat roof over each air chamber, partly chlorophyllose, cells 5- or 6-sided, 47.5–60.0 × 25–40 µm; air pores small, surrounded by 6 or 7(8) radially arranged, smaller cells, enlarging by rupture of cells as air chambers increase in size. *Assimilation tissue* ± 650 µm thick, consisting of one storey of almost vertical air chambers, bounded by unistratose, chlorophyllose walls of cells; storage tissue occupying ventral part of thallus, cells angular, closely packed. Figure 32.

Dioicous. *Antheridia* in 1 or 2 rows along groove, hyaline necks emerging from small pits. *Archegonia* embedded, purple necks up to 250 µm long, median. *Sporangia* bulging dorsally, 2 or 3 linearly arranged toward base, overlying tissue disintegrating. *Spores* (88–)90–100(–112) µm diam., triangular-globular, polar, yellow-brown to tan, semitransparent; wing thin, narrow, 3 µm wide, slightly undulating, pores occasionally present at marginal angles, margin finely crenulate; ornamentation reticulate, similar on 2 spore faces; distal face with 7 or 8 deep, round or oval alveoli across diam., 10–15 µm wide, sometimes 2 adjacent alveoli confluent, with slight constriction where cross wall failed to develop, alveolar walls rounded, smooth or finely granular, 3–5 µm high, ± 2.5 µm wide, at nodes slightly wider, scarcely raised, extending onto wing; proximal face with triradiate mark not well defined, faintly granular, each facet with ± 15 rounded alveoli, up to 10 µm wide, sometimes confluent or with slight constriction. *Chromosome number*: n = 8 (Bornefeld 1984, 1989). Plate 14C, D; Perold (1989e: fig. 42.1–6).

Riccia volkii is a southern African endemic species and is quite rarely collected in the savanna and grassland summer rainfall areas of the region. It is found on damp, gravelly or sandy soil, overlying quartzite, basalt or red sandstone rock outcrops in Namibia, Northern Province, North-West, Gauteng, Mpumalanga, Free State and southeastern Northern Cape. Map 15.

The species can be recognized by the smallish, hardly robust, lingulate branches of the lime-green to yellowish thalli. In some respects it is rather similar to small plants of *R. bullosa* (no. 5) and of *R. garsidei* (no. 6), but the branches are narrower and more delicate, sometimes forming a rosette. The smaller, narrow-winged spores with poorly defined, triradiate mark and rounded alveoli with distinctly wider walls, scarcely raised at the nodes, also differ from those of *R. bullosa* and of *R. garsidei* (see notes under those species).



Vouchers: *S.M. Perold 195, 433* (PRE); *J.M. Perold 38c* (PRE); *Volk 81/133, 81/230* (M, PRE).

8. **Riccia rubricollis** *Garside & A.V.Duthie ex Perold* in Bothalia 21: 51 (1991a); S.W.Arnell: 35 (1963a); Perold: 64 (1991c). Type: Cape, Knysna, Belvidere, on turf in shady places, not far from lagoon, Sept./Oct. 1929, *Duthie 5014* (BOL, lecto.!; PRE, isolecto.!).

Thalli medium-sized to large, in gregarious patches, sometimes with branches overlying, or scattered, not in rosettes; yellowish green, occasionally with some purple blotches; when dry, straw-coloured to light brown, margins not inflexed, somewhat raised, dorsally pitted in older parts. *Branches* rarely simple, mostly once or twice symmetrically or asymmetrically furcate, moderately to widely divergent, oblong or somewhat linear, up to 12 mm long, segments 2.5–6.0 × 2.8–3.0 mm, 0.7–1.0 mm thick medianly, in section 2–4 times wider than thick, apex tapered, ventrally keeled; groove only distally deep, soon shallow and wide, thallus margins subacute, rather irregularly undulating, winged; flanks sloping obliquely to very obliquely, yellowish; ventral face rounded or keeled medianly. *Scales* toward apex only, ventral, small, hyaline.

Dorsal epidermis forming slightly domed to flat roof over large air chambers, cells oblong-hexagonal or 5-sided, 62–80 × 50 µm; air pores apically small, surrounded by slightly curved, narrow, elongated cells, soon disintegrating and air pores rapidly enlarged, leaving air chambers exposed. *Assimilation tissue* 400–750 µm thick, air chambers 5- or 6-sided, elongated, mostly in one storey, generally 12 across width of thallus, sloping laterally and widening toward top, bounded by unistratose, chlorophyllose cell

FIGURE 32.—**Riccia volkii.** A, thallus; B, epidermal cells and air pores (hatched), overlying air chambers, seen from above; C, air pore (hatched) and surrounding cells from above; D, c/s epidermis and assimilation tissue; E, h/s air chambers (stippled); F, c/s branch. A, *S.M. Perold 433*; B–F, *S.M. Perold 2472*. Scale bars: A, F, 1 mm; B, D, E, 100 µm; C, 50 µm. Artist: J. Kimpton.

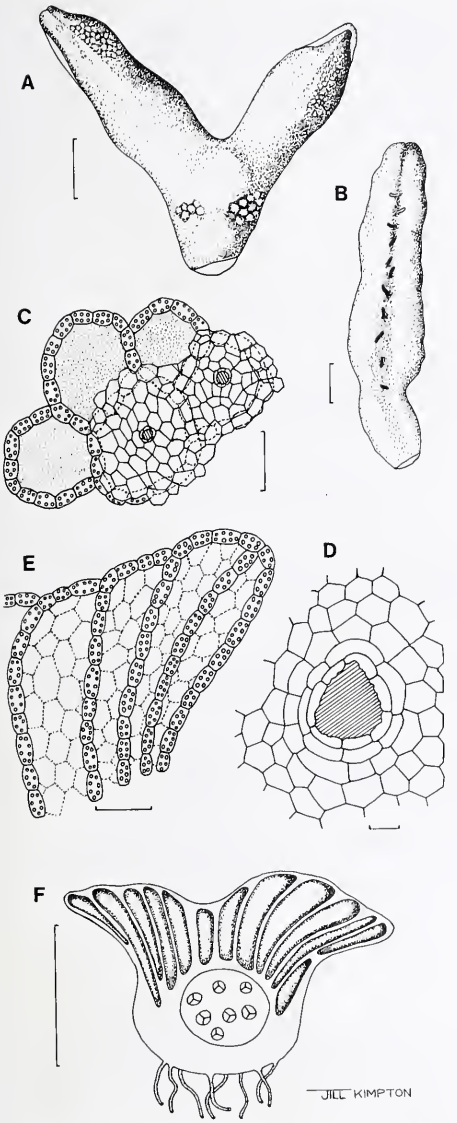


FIGURE 33.—**Riccia rubricollis**. A, B, thallus: A, male; B, female. C, epidermal cells and air pores (hatched), overlying air chambers seen from above; D, air pore (hatched) with surrounding cells; E, c/s showing air chambers; F, c/s female branch. A–F, *Duthie 5014*. Scale bars: A, B, F, 1 mm; C, E, 100 µm; D, 50 µm. Artist: J. Kimpton.

walls; storage tissue occupying ventral part of thallus, cells empty, angular. Figure 33.

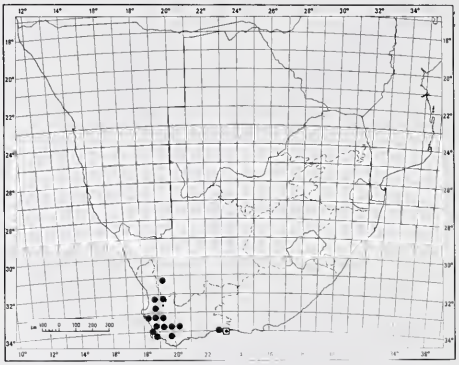
Stolons confined to the thickened, perennating tips of some branches.

Dioicous. *Antheridia* sunken in a row along midline of branches, when mature bulging dorsally, with conspicuous, mostly dark purple necks, up to 300 µm long. *Archegonia* 3 or 4 serially arranged toward base, necks purple, thin, hidden. *Sporangia* deeply imbedded, not bulging dorsally or protruding ventrally, but eventually opening to upper surface. *Spores* 92–100(–105) µm diam., triangular-globular, polar, reddish brown to deep russet-brown, semitransparent to opaque; wing 5 µm wide, at marginal angles wider, perforated and often elsewhere too, margin finely crenulate, slightly undulating; ornamentation completely or incompletely reticulate, rather different on 2 spore faces; distal face with 5 or 6 alveoli across diam., central ones larger, 20–25 µm wide, smaller toward margin, ± 10 µm wide, walls 4 µm thick and 6 µm deep, shallower laterally, not raised at nodes; proximal face with triradiate mark prominent, widening toward marginal angles at juncture with wing, alveoli up to 12 µm wide, mostly incomplete, walls slightly raised at nodes. *Chromosome number*: not known, as living material not available. Plate 14E, F.

Riccia rubricollis is only known from Knysna in the southeastern Western Cape, where it was collected on a few occasions by Duthie. It has so far not been found elsewhere in southern Africa. It grows in damp, shady places, on dark grey, somewhat gravelly turf, in association with *R. purpurascens* (no. 10), *Fossombronia* sp. and *Pleuridium* sp. Map 16.

The species is easily recognized by the single conspicuous row of deep purple antheridial necks along the midline of the ± linear, apically tapering branches of the male plants. The specific epithet, *R. rubraosteolata* in Duthie's handwriting, appears on one of her collections,

which she kept in cultivation at Stellenbosch. Unfortunately, she and Garside did not publish a description of this rare, endemic species. Later on, S.W. Arnell (1963a) described it under the name *R. rubricollis*, but without providing a Latin description or citing a type specimen. This has now been done (Perold 1991a), after Duthie's specimens, following an extended search, were relocated at BOL. Although more robust and fleshy, *R. rubricollis* is clearly related to *R. purpurascens* (no. 10), because of its somewhat linear habit, but it is not classified together with *R. purpurascens* and *R. stricta* (no. 9) in section *Ricciella*, as the sporangia do not conspicuously bulge ventrally. Na-Thalang (1980) regards the Australian species, *R. collata*, as having the closest affinity to *R. rubricollis*, although the latter plant is larger and the alveoli on the distal face of the spores are wider.



MAP 16.—❑ **Riccia rubricollis**
● **R. purpurascens**

Voucher: *Duthie 5406* (BOL).

A2. Section **Ricciella** *(A.Braun,* pro gen.*) Bisch.*, Nova acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum 17: 1068 (1835). Lectotype: *R. fluitans* L. fide Grolle: 248 (1976).

Thalli smallish to rather large; terricolous or aquatic. *Branches* linear, quite firm or lax, 10–15 mm long, sparsely furcate. *Scales* ventral, mostly only toward apex, very small to small, single or split, without central appendage.

Dorsal epidermis chlorophyllose; air pores small, surrounded by smaller companion cells, not becoming lacunose. *Assimilation tissue* with polyhedral air chambers enclosed by unistratose walls.

Sporangia bulging and opening ventrally; vertical or oblique. *Spores* smallish, alveolar walls thick or partly thick.

9. **Riccia stricta** *(Lindenb.) Perold* in Bothalia 20: 197 (1990f); Perold: 65 (1991c). Type: Cape, Philipstown, ad arborum truncos (!?), *Ecklon s.n.* (BM, lecto.!).

R. fluitans L. var. δ *stricta* Lindenb.: 85 (1836).

R. fluitans L. var. δ *stricta* Nees: 440 (1838).

R. fluitans L. var. ?ε *stricta* Gottsche et al.: 610 (1844–1847). Type: Cape, Philipstown, *Ecklon s.n.* (BM!).

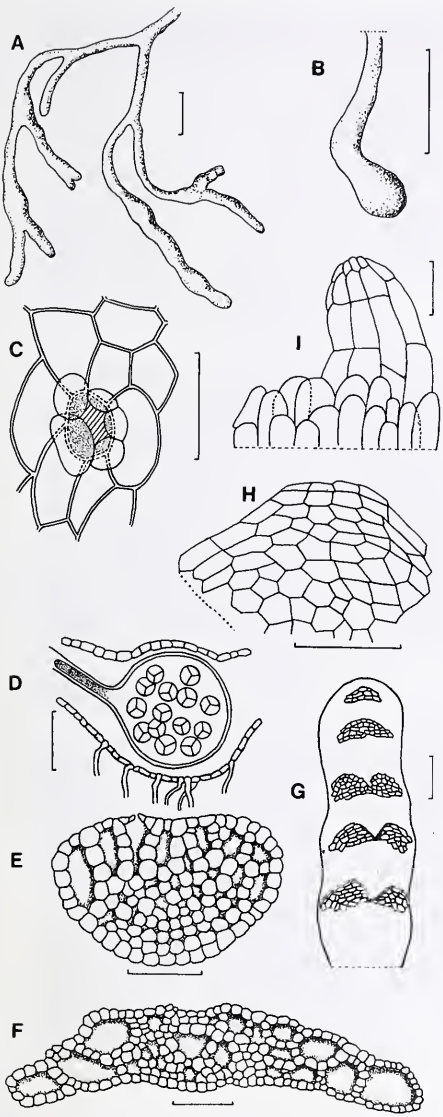
Invalidly published or unpublished synonyms

R. tenerrima Steph. Icones ined. Type: Natal, Dist. Alexandra, Sta. Dumisa, leg. *Rudatis* (M).

R. stricta A.V.Duthie ined. fide S.W.Arnell: 37 (1963a).

? *Ricciella stricta* (Gottsche et al.) Trevis.: 62 (1877).

Thalli small to medium-sized, in dense, tangled masses; bright green, often with purple streaks along margins; when dry, flattened to almost unchanged. *Branches* repeatedly symmetrically or asymmetrically furcate, moderately to widely divergent, linear or strap-shaped, 15–20 mm long, segments 5 mm or more long, (0.3–)0.5–0.8(–1.2) mm wide, 0.25–0.35(–0.5) mm thick, in section 1–3(–4) times wider than thick, apex slightly narrowed, somewhat taper-



ing, occasionally bulbous; groove only visible distally in living plants, thallus margins rounded, obtuse to subacute; flanks vertical to sloping obliquely to almost flat; ventral face gently rounded to flat, green. *Scales* under apex and spaced at short or rather longer intervals along ventral face of terminal segments, small, up to 250–500 × 150–400 µm, apically single, soon splitting into two halves, obtusely triangular, concave, hyaline, occasionally somewhat purple. Plate 13C.

Dorsal epidermis not distinctly areolate, forming a rather smooth cover over elongated air chambers, cells long-hexagonal, 42–65 × 25–50 µm, smaller and isodiametric at margins, ± 25 × 25 µm; air pores small, surrounded by ring of 5 or 6 smaller companion cells, partly overlying slightly thicker-walled epidermal cells. *Assimilation tissue* 100–500 µm thick, air chambers in 1 or 2 storeys medianly, uniseriate laterally, bounded by unistratose chlorophyllose cell walls; storage tissue occupying ventral part of thallus, cells rounded. Figure 34.

Perennation by apical bulbils or by ventral stolons.

Monoicous. *Antheridia* near apex and more proximally, at intervals medianly along branches, necks hyaline, conspicuous, 150–200 µm long, basally surrounded by low, hyaline, conical cells. *Archegonia* median, up to 3 per segment, serially arranged, sometimes interspersed between antheridia, obliquely orientated, necks purple, 100–250 µm long, sloping at an angle toward, and opening into shallow, apically directed furrow, the 'blind' end fringed with erect, hyaline, conical cells. *Sporangia* at generally wider and always thicker sites along thallus, oblique and protruding conspicuously ventrally, covering tissue abundantly supplied with

FIGURE 34.—**Riccia stricta**. A, thallus; B, ventral stolon; C, air pore (hatched) with thin-walled surrounding cells and thicker-walled epidermal cells, part of air chamber stippled; D, l/s sporangium; E, c/s narrow branch from drier habitat; F, c/s thin, wide branch from wet habitat; G, ventral face with scales, apically single, others split into two; H, single scale; I, antheridial neck with basal collar of conical cells. A, *Van Rooy 3539*; B, *Van Zinderen-Bakker 7472*; C, *S.M. Perold 861*; D, *S.M. Perold 365*; E, G, *S.M. Perold 354*; F, *Magill 6592*; H, *T.R. Sim PRE-CH1119*; I, *S.M. Perold 842*. Scale bars: A, B, 1 mm; C, I, 50 µm; D, F, G, 200 µm; E, H, 100 µm. Artist: J. Kimpton.

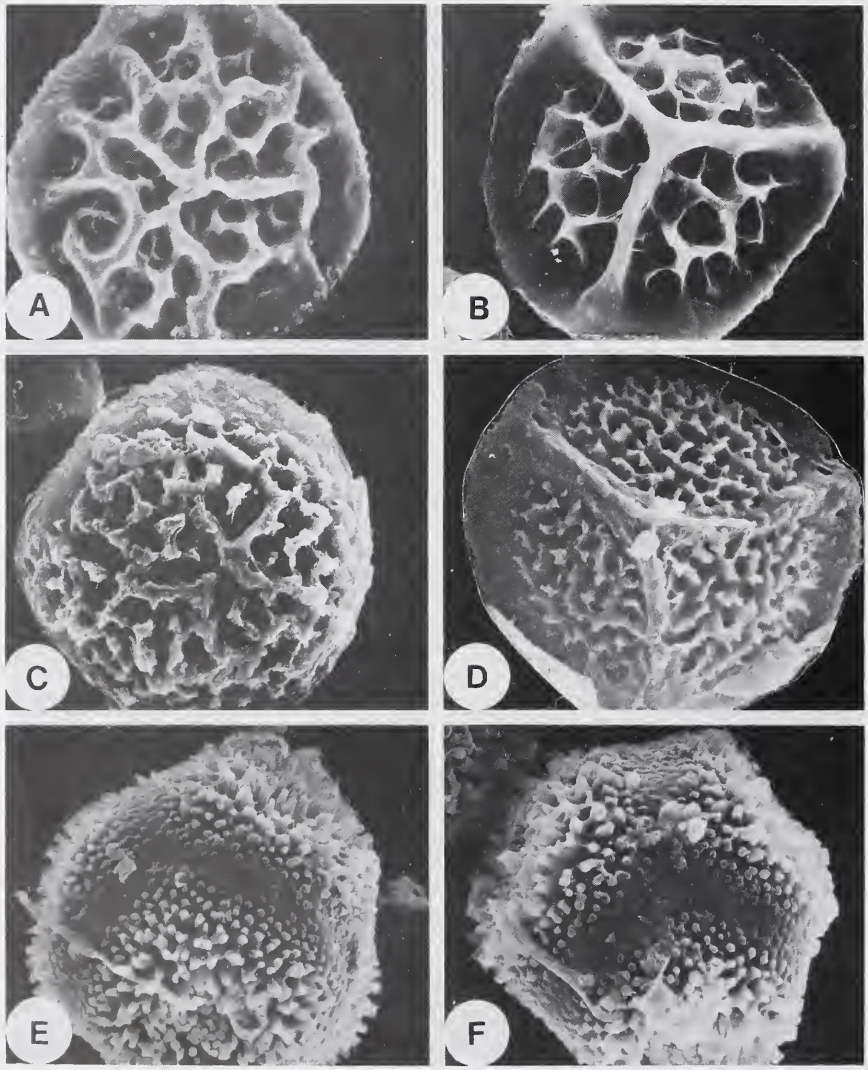
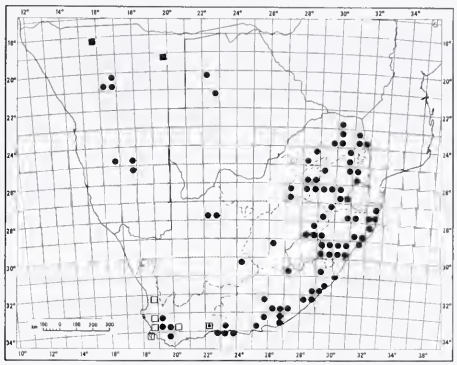


PLATE 15.—Spores. A, B, **Riccia stricta**. A, distal face; B, proximal face. C, D, **R. purpurascens**: C, distal face; D, proximal face. E, F, **R. curtisii**: spore tetrads. A, *R.J. Ward 5354*; B, *Wells 57*, C, *S.M. Perold 587*; D, *Garside 7*; E, F, *S.M. Perold 2059*. A, × 1000; B, D, × 800; C, × 740; E, F, × 600.

rhizoids. *Spores* (50–)62–70(–75) µm diam., triangular-globular, polar, light brown, semi-transparent; wing thick, 7.5 µm wide, wider at perforated or notched marginal angles, with a row of fine granules along edge, margin crenulate; ornamentation reticulate, different on 2 spore faces; distal face highly convex, with (4–)5 or 6 large, deep alveoli across diam. of spore, 17–20 µm wide, in centre a pillar or boss, from which several low ridges radiate outward, sometimes forming a network, alveolar walls rounded, 3–4 µm wide and up to 7.5 µm high, sometimes sparsely granulate; proximal face with triradiate mark very prominent, up to 5 µm high, as wide (or wider) toward marginal angles at join with wing, each facet with 6–10 alveoli, some incomplete, often subdivided by faint radiating ridges, walls thin, raised at nodes. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 15A, B; Perold (1989e: fig. 34.1–6).

Riccia stricta is known from Angola, Burundi, Cameroon, Ethiopia, Ghana, Ivory Coast, Kenya, Malawi, Mozambique, Niger, Nigeria, Rwanda, Sudan, Tanzania, Togo, Uganda, Zaïre, Zambia, Zimbabwe and southern Africa (Perold 1995b). In the *FSA* area it is widely distributed in the summer rainfall areas especially, and is one of the most commonly collected *Riccia* species in the region. It is either terrestrial, growing on mud or damp soil, or aquatic, when it floats on, or is submerged in fresh or stagnant water. It is recorded from Namibia, Botswana, Northern Province, North-West, Gauteng, Mpumalanga, Free State, KwaZulu-Natal, Lesotho, Northern, Western and Eastern Cape. Map 17.

Species in the *R. fluitans* complex are difficult to distinguish, as the gametophytes are highly sensitive to different environmental conditions and the habitat can vary from terrestrial to aquatic. Nevertheless, *R. stricta* can generally be recognized by its mostly smooth dorsal surface, through which the large air chambers are faintly to fairly clearly visible, by small ventral scales and by smallish spores with large, deep-walled alveoli containing a central boss on the distal face and, on the proximal face, a prominent triradiate mark.



MAP 17.—● **Riccia stricta**
❑ **R. curtisii**
■ **R. perssonii**

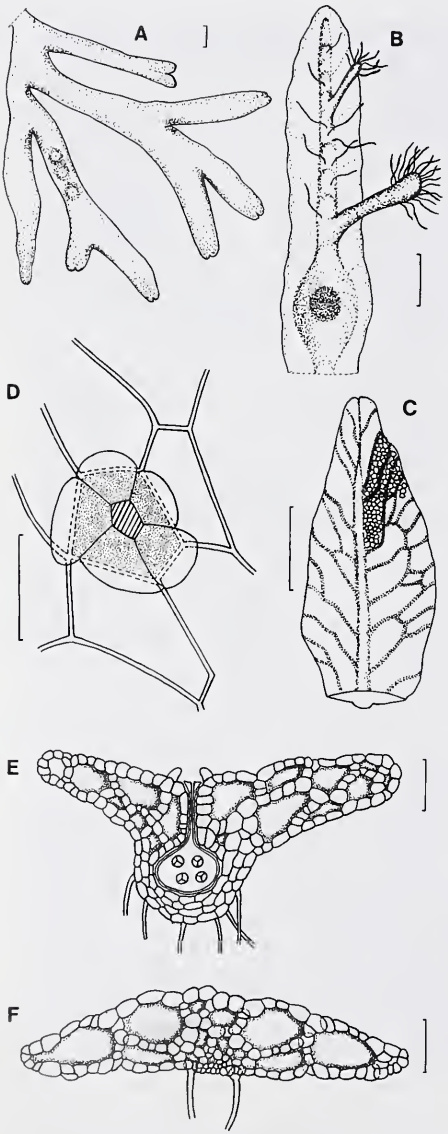
R. fluitans L. *sensu stricto* is thought not to occur naturally in southern Africa (Perold 1990f) and very rarely produces spores wherever it grows.

Vouchers: *Glen 1832* (PRE); *Magill 5039* (PRE); *Mauve & Venter 5077* (PRE); *S.M. Perold 2455* (PRE); *Van Zinderen-Bakker 7472* (BOL).

10. **Riccia purpurascens** *Lehm.* in Linnaea 4: 371 (1829); Lindenb.: 451 (1836); Gottsche et al.: 611 (1844–1847); Steph.: 363 (1898); Sim: 15 (1926); S.W.Arnell: 36 (1963a); Perold: 203 (1990f); Perold: 66 (1991c). Type: Cape, crescit humi in sylvula quercina ad latus boreale et ad radicem montis Tafelberg in Promont. Bonae Spei, *Ecklon s.n.* (S, holo.!; G, iso.!).

Ricciella purpurascens (Lehm.) Lehm.: 23 (1832); Trevis.: 62 (1877).

Thalli medium-sized to fairly large, in thin, creeping strands or ribbons, frequently overlapping and becoming quite densely massed; light green, occasionally purple along margins and over gametangia; when dry, yellowish green, flaccid and rather flat. *Branches* repeatedly and irregularly furcate, narrowly to moderately divergent, linear, 9–17 mm long, segments 1–5



× 1.5–2.0 mm, 0.4–0.6 mm thick medianly over keeled ventral part, wings thinner, in section 3–5(–7) times wider than thick, apex narrowed, shortly emarginate; groove distinct distally, soon becoming wide and shallow, thallus margins subacute, rather irregularly undulating, winged or attenuate; flanks sloping obliquely to almost flat, green; ventral face flat to narrowly keeled medianly. *Scales* toward apex only, ventral, difficult to detect, spaced and split into 2 halves, up to 3 pairs, hyaline. Plate 13D.

Dorsal epidermis areolate, forming flat cover over large air chambers, cells oblong-hexagonal or 5-sided, 87.5–110.0 × 60–75 µm, at apical margin rectangular, smaller, ± 45 × 30 µm; air pores small, surrounded by 4 or 5 radially arranged, thin-walled cells, partly overlying slightly thicker-walled epidermal cells. *Assimilation tissue* 300–400 µm thick, occupying most of thickness of thallus, air chambers polyhedral, in 2 storeys medianly, uniseriate laterally, bounded by unistratose chlorophyllose walls; storage tissue confined to central keeled part, mostly only 1–4 layers of angular cells. Figure 35.

Perennation by ventral stolons.

Dioicous. *Antheridia* serially arranged in groups of 2 or 3, with sterile areas in between, along middle of thallus, bulging above and below, necks up to 200 µm long, bases encircled by hyaline, conical cells. *Archegonia* single or in pairs, sometimes adjacent, median, vertically orientated, necks short, brownish purple with hyaline tips, opening into a depression, base surrounded by conical cells. *Sporangia* causing thallus to widen laterally and to bulge ventrally. *Spores* (65–)70–80(–88) µm diam., triangular-globular, polar, yellow to bright brown, semi-transparent; wing thick, up to 7.5 µm wide, at marginal angles 2 small pores, one on either side of each arm of triradiate mark, margin fine-

FIGURE 35.—**Riccia purpurascens.** A, thallus; B, ventral face with stolons and sporangium; C, dorsal face with air chambers and epidermal cells partly drawn in; D, air pore (hatched), with thin-walled surrounding cells and thicker-walled epidermal cells, part of air chamber stippled; E, c/s branch at sporangium; F, c/s sterile part of branch. A, B, F, *Morley 291*; C, *S.M. Perold 1941*; D, E, *S.M. Perold 1170*. Scale bars: A–B, C, 1 mm; D, 50 µm; E, F, 200 µm. Artist: J. Kimpton.

ly crenulate; ornamentation incompletely reticulate, different on 2 spore faces; distal face with 4–6 large, angular, mostly incomplete alveoli across diam., ± 20 µm wide, usually subdivided into smaller alveoli by secondary ridges or a central pillar, toward margin often reduced to short ridges only, walls 5 µm high, densely fringed with granules, slightly raised at nodes; proximal face with triradiate mark prominent, 2.5 µm wide, becoming wider toward marginal angles at juncture with wing, row of superimposed papillae running along arms, on each of 3 facets rarely any complete alveoli, mostly short broken walls, straight or curved, edged with tall, uneven spines, warty papillae or low granules. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 15C, D; Perold (1989e: fig. 35.1–6).

Endemic to southern Africa, *R. purpurascens* has been collected in the western part of Northern Cape and Western Cape, which are winter rainfall areas (Map 16). It grows on damp, sandy soil or on mud. It is not nearly as widespread as *R. stricta* (no. 9), which occurs mostly in summer rainfall regions; only in the southern parts of Western Cape do their distribution areas overlap. Arnell (1963a) also reported *R. purpurascens* from Victoria Falls, Zimbabwe, but this specimen, *T.R. Sim 9066*, had been misidentified and actually is *R. stricta*, as is the specimen *Eyles 1237*, cited by Best (1990) from Zimbabwe.

Riccia purpurascens can be recognized by its long, thin, rather lax, linear branches, frequently tinged with purple and keeled ventral face, from which stolons arise. The ventrally protruding sporangia are vertically orientated and not oblique as in *R. stricta*; the archegonial necks are shorter, the spores are generally slightly larger than those of *R. stricta* (no. 9), and the ornamentation is different.

Vouchers: *S.W. Arnell 332* (BOL); *McLaughlin PRE-CH4197*; *S.M. Perold 634a, 1770* (PRE).

B. Subgenus **Thallocarpus**

Thallocarpus *(Lindb.) Jovet-Ast*, Revue bryologique et lichénologique 41: 452 (1976). R.M.Schust.: 413 (1985); Perold: 67 (1991c); Jovet-Ast: 220 (1993). Type: *R. curtisii* (James ex Austin) Austin.

Cryptocarpus sensu Austin: 231 (1870) not of Kunth: 187 (1817). *Thallocarpus* Lindb.: 377 (1874). *Angiocarpus* Trevis.: 444 (1877).

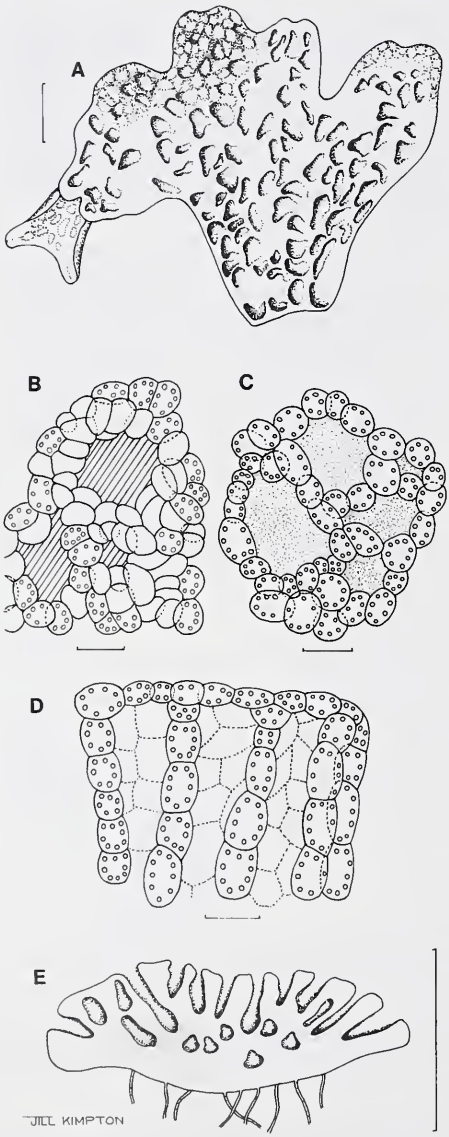
Riccia section *Thallocarpus* Austin: 305 (1879).

Plants heterothallic; terricolous. *Scales* absent.

Dorsal epidermis chlorophyllose, unistratose, lacunose. *Assimilation tissue* with polyhedral air chambers.

Sporangia immersed. *Spores* remaining adherent in tetrads, ornamentation with slender spinules or stout spines.

11. **Riccia curtisii** *(James ex Austin) Austin* in Bulletin of the Torrey Botanical Club 6: 305 (1879); Steph.: 369 (1898); Haynes: 284 (1920); A.V.Duthie & Garside: 122 (1937); Frye & L.Clark: 32 (1937); Hässel de Menéndez: 218 (1963); S.W. Arnell: 36 (1963a); Jovet-Ast: 452 (1976); Vianna: 76 (1981); Perold: 67 (1991c); R.M.Schust.: 509 (1992b); Jovet-Ast: 221 (1993). Type: North Carolina, Society Hill, leg. *Curtis s.n.*, 1853; on moist ground, South Carolina, Ravenel, leg. *Curtis s.n.*, 1849 (Hb. Sull.).



Cryptocarpus curtisii Austin: 231 ('Dec. 1869', 1870) nom. illeg. *Angiocarpus curtisii* (Austin) Trevis.: 444 (1877). *Thallocarpus curtisii* (Austin) Lindb.: 377 (1874); Austin: 21 (1875); McAllister: 117 (1916).

For further synonymy see Jovet-Ast (1993).

Riccia spongosa S.W.Arnell: 310 (1952); S.W.Arnell: 38 (1963a). Type: Cape, George, Wilderness, forest path $^1/_2$ mile east of the hotel, *S.W. Arnell 1393* (BOL, holo.!).

Plants heterothallic, *male thalli* very small, frequently partly overgrown by female thalli; yellowish to reddish brown in some areas, often with some purple colouration; *female thalli* smallish to medium-sized, scattered or crowded, in complete or incomplete rosettes, up to 10 mm, rarely to 20 mm across; light green to yellowish green, dorsally intact toward apex, soon becoming pitted and spongy; when dry, margins not inflexed, dull green, lacunose. *Branches* in female plants once to several times pseudodichotomously furcate, shortly to deeply divided, almost overlapping to narrowly divergent, oblong or quite variable, 2–8 × 2–4 mm, up to 1 mm thick, in section 2–4 or more times wider than thick, apex truncate to rounded, emarginate; groove indistinct, thallus margins obtuse, rounded; flanks sloping obliquely to nearly flat; ventral face slightly rounded to flat, green. *Scales* absent.

Dorsal epidermis slightly domed over each air chamber, soon disintegrating, cells 100–150 × 75–80 µm, but quite variable in size and shape; air pores surrounded by rather smaller, unmodified and regularly arranged cells, at apex small and inconspicuous, rapidly enlarging, becoming almost as wide as air chambers, irregularly polygonal to oblong. *Assimilation tissue* up to 750 µm thick, air chambers polyhedral, sloping, much enlarged proximally, enclosed by unistratose, chlorophyllose cell walls; storage tissue restricted to 3–5 ventral cell rows. Figure 36.

FIGURE 36.—**Riccia curtisii**. A, female thallus with small male thallus protruding from underneath on left side; B, epidermal cells and air pores (hatched) from above; C, h/s assimilation tissue, air chambers stippled; D, c/s epidermis and assimilation tissue; E, c/s branch. A, *S.M. Perold 641*; B–E, *S.M. Perold 2395a*. Scale bars: A, E, 1 mm; B–D, 100 µm. Artist: J. Kimpton.

Dioicous. *Antheridia* with numerous and conspicuous necks in one or two rows along middle of small male plants, hyaline, up to 200 µm long, basally surrounded by conical cells. *Archegonia* scattered, necks ± 200 µm long, base purple. *Sporangia* several, crowded together. *Spores* in tetrads, (100–)105–115(–125) µm diam., yellow-brown to tan-brown, semi-transparent; wingless; usually only three spores of tetrad visible, occasionally all 4, joined by narrow band or ridge; ornamentation reticulate, variously developed, with small, deep, round alveoli or fovea, 2.5–3.5 µm wide, extending to connecting band, alveolar walls low and thin, raised at nodes into stout, conspicuous, truncate processes, up to 5 µm long in centre of convex face, lower toward sides, tips of processes crowned with numerous granules. *Chromosome number*: n = 8 (Siler 1934; Jovet-Ast 1975; Bornefeld 1989). Plate 15E, F; Perold (1989e: fig. 45.1–6).

The species is quite widely distributed and is known from North, Central and South America, India, North Africa (Chad) and southern Africa.

In the *FSA* area, *R. curtisii* is fairly rare; it has been collected at seepages on soil derived from granitic rock in the shrublands of western Northern Cape, on cultivated soil in a wheatfield and on garden paths in the southern part of Western Cape. Map 17.

Riccia curtisii can be distinguished from other *Riccia* species by the generally very loosely reticulate composition of its thalli, and the spores which adhere permanently in tetrahedral tetrads.

Riccia spongosa is regarded as a synonym of *R. curtisii* (Perold 1991c); its spore tetrads appear to be rather young and therefore, misleading in their so-called differences.

Duthie & Garside (1939) described a closely related species, *R. compacta*, which they distinguished from *R. curtisii* by the firmer composition of its thalli and by the more compact nature of its air chambers, by well-marked tuberculate rhizoids and by characteristic spore markings. They dismissed the possibility that *R. compacta* could be a growth form of *R. curtisii*. Very few collections of *R. compacta* were available for study. Herbarium specimens proved to be unsuitable for the critical examination necessary to verify the differences between the thalli of *R. curtisii* and *R. compacta*, and culture experiments with fresh material were unsuccessful. Whether to accept or reject *R. compacta* as a distinct species, remains unresolved.

Vouchers: *S.W. Arnell 12* (BOL); *Duthie 5018, 5486* (BOL); *S.M. Perold 474, 479* (PRE).

12. **Riccia perssonii** *S.A.Kahn* in Svensk botanisk tidskrift 49: 433 (1955); S.W.Arnell: 37 (1963a); Jovet-Ast: 149 (1967); Jovet-Ast: 449 (1976); Perold: 68 (1991c). Type: Bangladesh (= East Pakistan), Dacca, growing on shaded soft mud along the edge of a pond, *Kahn 1* (Dacca Univ.).

Plants heterothallic, *male thalli* very small, once pseudodichotomously furcate; *female thalli* small to medium-sized, scattered, reported to form rosettes up to 11 mm across; light green, dorsally spongy. *Branches* once or twice, sometimes up to 3 times pseudodichotomously furcate, shortly to deeply divided, moderately divergent, oblong, 2–4 × 0.5–1.3 mm, ± 0.3 mm thick, in section 2–4 times wider than thick, apex rounded to acute; groove not observed, thallus margins acute; flanks sloping obliquely to almost flat; ventral face slightly rounded to flat, green. *Scales* absent.

Dorsal epidermis pitted by numerous small to large air pores, irregularly shaped. *Assimilation tissue* occupying most of thickness of thallus, air chambers polyhedral, bounded by chlorophyllose, unistratose cell walls; storage tissue consisting of only a few layers of cells. Figure 37.

Dioicous. *Antheridia* with hyaline necks, 125 µm long, in 1 or 2 rows along middle of branches, basally surrounded by conical cells. *Archegonia* with purple necks, in rows. *Sporangia*

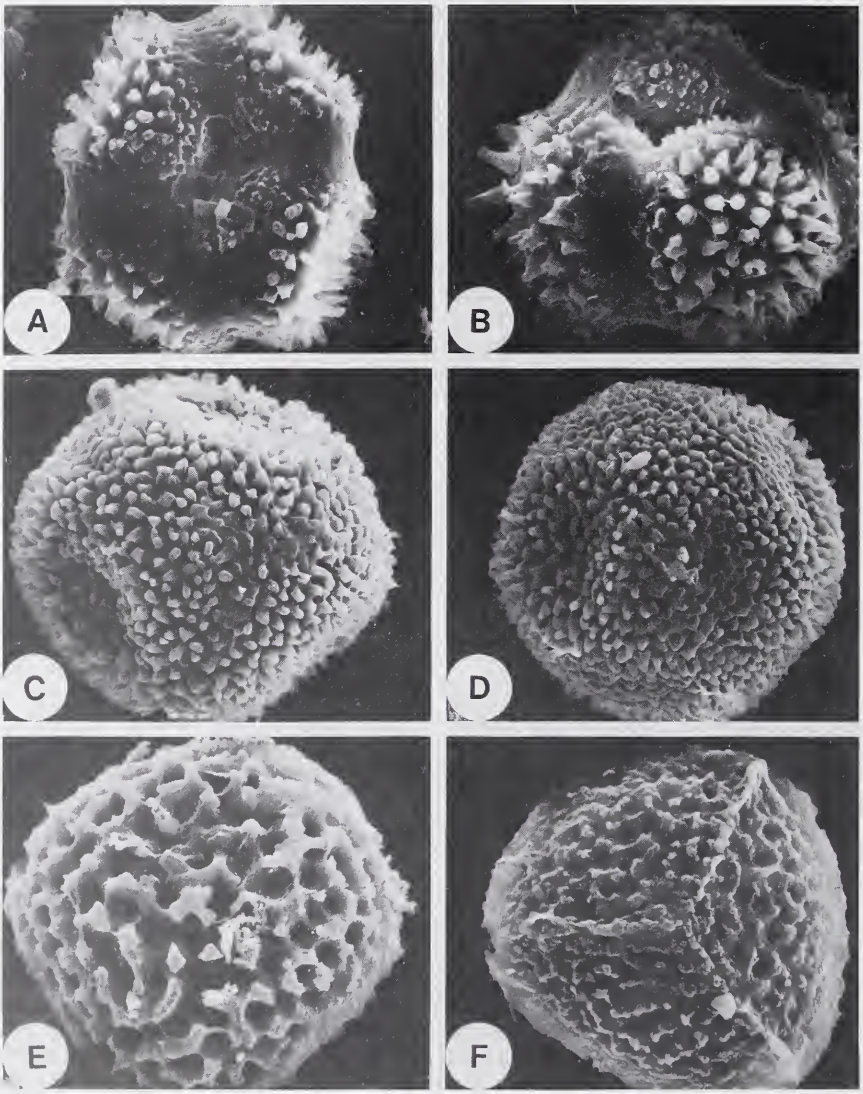


PLATE 16.—Spores. A, B, **Riccia perssonii**, spore tetrads. C, D, **R. tomentosa**, spore tetrads. E, F, **R. schelpei**: E, distal face; F, proximal face. A, B, *Volk 2059*, C, D, *S.M. Perold 1495*; E, F, *S.M. Perold 1426a*. A–D, × 600; E, F, × 700.

single, at base of branches or several crowded together in centre of thalli. *Spores* in tetrads, (90–)95–102(–110) µm diam., tan-brown, semi-transparent; wingless; all 4 spores of tetrad lying in one plane and usually visible at one time, in rhomboidal to square isobilateral tetrads, joined together by broad bands, up to 17.5 µm wide, mostly smooth or with only a few scattered granules; ornamentation with occasional small, round alveoli on convex face, obscured by tall, crowded, spinous processes, 10–15 µm high, broader at base and tapering to narrow tip, straight or bent, sometimes truncate and crowned with granules. *Chromosome number*: n = 8 (Jovet-Ast 1976). Plate 16A, B; Perold (1989e: fig. 44.1–6).

Except for Bangladesh, *R. perssonii* is also known from the north-central and northwestern African countries, Chad and Mali respectively (Jovet-Ast 1967, 1976), from Madagascar (Perold 1995b), and from southern Africa.

In the *FSA* area *R. perssonii* has only been collected twice in the far northern part of Namibia, on lime-free, damp, black, clayey soil. Map 17. It is possible that the Stephens specimen from neighbouring Botswana (Chobe), reported by Duthie & Garside (1937) under *R. curtisii* (no. 11), could be placed here, as the distribution of *R. curtisii* in southern Africa appears to be strictly confined to the winter rainfall areas of the Cape; besides, they were not familiar with it, as *R. perssonii* had not yet been described at that time. Unfortunately this specimen has not been traced.

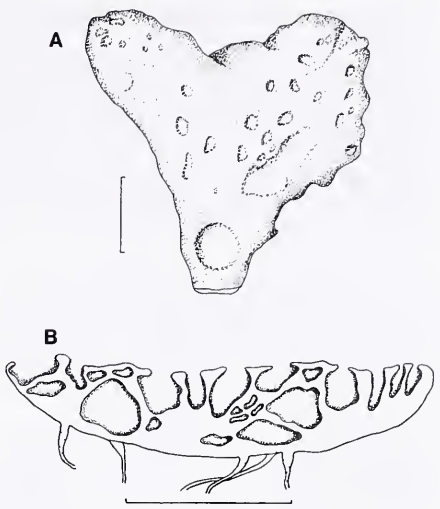


FIGURE 37.—**Riccia perssonii**. A, female thallus; B, c/s branch. A, B, *Volk 2059*. Scale bars: A, B, 1 mm.

The collections at PRE are rather fragmentary and cell dimensions could not be measured, as the fragile material failed to swell out satisfactorily on wetting. *Riccia perssonii* is distinguished from *R. curtisii* mainly by spore characters, viz. isobilateral tetrads with prominently large spines on the convex faces.

Vouchers: *Smook 7612* p.p. (PRE); *Volk 2059* (M, PRE).

C. Subgenus **Pannosae**

Pannosae *(Perold) Perold*, subgen. nov., Taxonomic revision of the Ricciaceae Rchb. (Marchantiales: Hepaticae) in southern Africa: 69 (1991c). Type: *R. tomentosa* O.H.Volk & Perold.

Pannosae Perold, pro sectione in Volk & Perold: 28 (1990).

Chaetoriccia R.M. Schust., pro sectione in R.M. Schust.: 271 (1992a).

Plants large, not heterothallic, terricolous. *Scales* large, triangular, apices filamentous.

Dorsal epidermis with numerous, long, multicellular hair-like outgrowths, slightly raised at base; air pores spaced. *Assimilation tissue* with large, elongated, polygonal air chambers.

Sporangia immersed. *Spores* in globular or tetrahedral tetrads, ornamentation papillose.

Section *Pannosae* Perold (Volk & Perold 1990), created to accommodate *R. tomentosa* on account of its tetrad spores, and placed under subgenus *Thallocarpus*, was elevated to the rank of subgenus *Pannosae* (Perold) Perold (1991c). There are several important differences which separate *R. tomentosa* from the two species in subgenus *Thallocarpus*, *R. curtisii* and *R. perssonii*: the dense hair-like cellular outgrowths from the dorsal epidermis, which does not become lacunose, the large triangular scales, apically filamentous, the absence of heterothally and the sandy, xeric habitat. These differences are regarded as radical enough to support such a decision.

13. **Riccia tomentosa** *O.H. Volk & Perold* in Bothalia 20: 25 (1990); Perold: 69 (1991c). Type: Cape, Pedroskloof, on road to Rooifontein, 2 km beyond Willem Stone Bridge, sandy soil, *S.M. Perold 1495* (PRE, holo.).

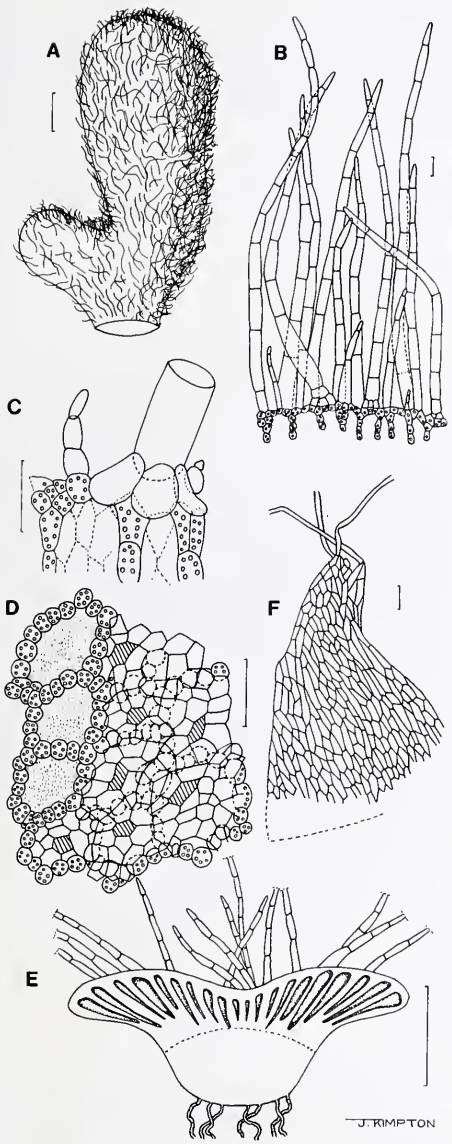
Thalli large to very large, in crowded, gregarious patches or scattered; dorsally shaggy-haired, silvery to dusty grey; when dry, deeply concave toward centre, margins erect or scarcely inflexed, hairs matted, whitish. *Branches* simple or symmetrically to asymmetrically furcate, moderately divergent, oblong to ovate-oblong, up to 18 × 2–4(–5) mm, narrower proximally, 3–4 mm thick, in section as wide as thick, apex slightly narrowed, shortly emarginate; groove short and wide, middle part concave, thallus margins raised, obtuse, shortly winged; flanks sloping steeply, green, toward lower, ventral parts occasionally reddish purple; ventral face rounded to flat, light green. *Scales* large, triangular ± 1500 µm long, base up to 1200 µm wide, imbricate, hyaline, apically divided into loose filamentous strands, one cell wide, up to 1000 µm long. Plate 13E.

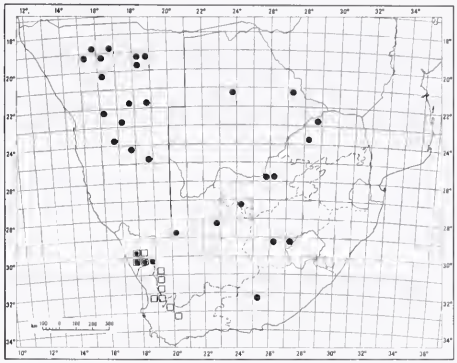
Dorsal epidermis over air chambers slightly domed, with outgrowths of free-standing, straight or bent, hair-like cell pillars, up to 2700 µm long, composed of (2–)5–14 cells, 50–270 × 50–100 µm, tapering upwards from broad base, thin-walled, hyaline; air pores spaced, surrounded by 5 or 6(7) radially arranged, wedge-shaped cells. *Assimilation tissue* ± 500 µm thick, air chambers sloping, elongated, polyhedral, bounded by unistratose, chlorophyllose walls of isodiametric cells; storage tissue in ventral part of thallus, cells angular, with small spaces between. Figure 38.

Dioicous. *Antheridia* and *archegonia* not observed, as obscured by dense dorsal hairs. *Sporangia* bulging dorsally, overlying tissue tinged with mauve. *Spores* in tetrads, 115–145 µm diam., pale yellow to rust-brown, semitransparent; wingless; in globular to tetrahedral tetrads, sometimes only 3 spores of tetrad visible, but occasionally part of 4th spore also seen, joined together by narrow bands, almost totally obscured by papillae; ornamentation densely papillate to verruculose, with papillae 3–5 µm wide and equally high, obtuse or truncate, arising from nodes of scarcely visible, to obvious reticulum. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 16C, D; Perold (1989e: fig. 48.1–6).

The species is rarely collected and is endemic to the arid shrublands of Namaqualand, Northern Cape, where it is found on reddish brown, coarse, sandy soil, overlying clay. Map 18. *Riccia tomentosa* differs from other *Riccia* species by the unique, long, vertical, hair-like, cellular outgrowths from many of the epidermal cells, often basally slightly raised in support, by the well-spaced stomata, as well as by the papillose to verruculose spores in permanent tetrads. It shares the unusual character of large triangular scales, apically split into filamentous cellular strands with *R. hirsuta* (no. 51)—see note under that species.

On account of its tetrad spores, which it shares with *R. curtisii* (no. 11) and *R. perssonii* (no. 12), *R. tomentosa*, section *Pannosae* Perold (Volk & Perold 1990), was initially also referred to subgenus *Thallocarpus*, but the marked differences in the morphology of *R. tomentosa* indicate that it is better placed in a subgenus of its own. Section *Pannosae* has





MAP 18.—■ **Riccia tomentosa**
❑ **R. schelpei**
● **R. trichocarpa**

therefore been elevated in rank to subgenus *Pannosae* (Perold) Perold.

Vouchers: *S.M. Perold 1556* (PRE); *Perold & Reid 1462* (PRE); *Perold & M.J.A.W. Crosby 2157* (PRE); *Schelpe 7784* (BOL).

FIGURE 38.—**Riccia tomentosa**. A, thallus; B, c/s dorsal hair pillars and below, top of assimilation tissue; C, cells supporting base of large hair on right and small hair on left. D, as seen from below: h/s near dorsal surface with air chambers (stippled) exposed on left, and air pores (hatched) and epidermis on right. E, c/s branch; F, scale. A, *S.M. Perold 1495*; B–D, F, *S.M. Perold & Crosby 2157*; E, *S.M. Perold 1556*. Scale bars: A, E, 1 mm; B–D, F, 100 µm. Artist: J. Kimpton.

D. Subgenus **Chartacea**

Chartacea *Perold*, in Volk & Perold in Bothalia 16: 29 (1986b). Type: *R. schelpei* Volk & Perold.

Thalli quite large, deeply grooved, acutely winged; terricolous. *Scales* extending to margins of thallus.

Dorsal epidermis with thick-walled hyaline cells, on drying becoming parchment-like; air pores surrounded by ring of smaller, superimposed thin-walled cells. *Assimilation tissue* with large, polyhedral air chambers.

Sporangia immersed. *Spores* reticulate-foveolate, alveolar walls granulate or almost smooth.

14. **Riccia schelpei** *O.H.Volk & Perold* in Bothalia 16: 29 (1986b); Perold: 70 (1991c). Type: Cape, Goegap Nature Res., Carolusberg (W), seepage area, *Schelpe 7775* (BOL, holo.!; PRE, iso.!).

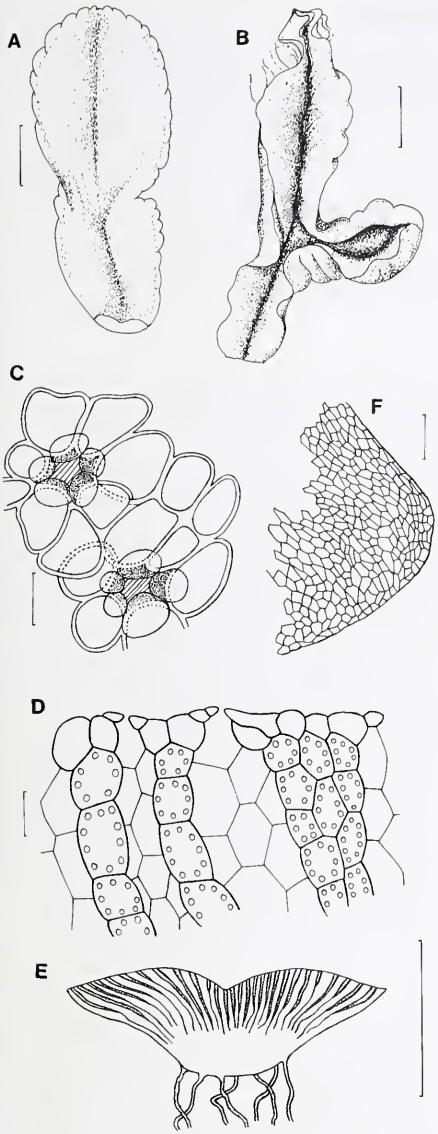
Thalli medium-sized to large, in gregarious patches or scattered; green, somewhat shiny to greasy, dorsally faintly areolate; when dry, apical sides tightly inflexed and opposing, sometimes clasped together, otherwise wings expanded, irregularly undulate, yellow and parchment-like. *Branches* simple or symmetrically or asymmetrically once or twice furcate, moderately to widely divergent, oblong-ligulate, up to 12 × 3–6 mm, 1.5–2.0 mm thick, in section 2–3 times wider than thick, apex rounded, emarginate, keeled below; groove deep distally, sides convex and steeply sloping, more proximally shallow and wide, thallus margins winged, acute, attenuate; flanks sloping steeply and abruptly into undulating wing; ventral face slightly convex, greenish. *Scales* large, up to 1500 × 300–500 µm, projecting slightly above thallus margins, imbricate, hyaline with some scattered purple cells at base, margin entire. Plate 13F.

Dorsal epidermis unistratose, cells variously shaped, polygonal, 35–70 × 30–50 µm, hyaline, thick-walled; air pores surrounded by superimposed ring of 5–8 smaller, roundish, fragile cells. *Assimilation tissue* 750–1300 µm thick, with wide polyhedral, sloping air chambers bounded by unistratose, chlorophyllose walls; storage tissue occupying ventral part of thallus, cells rounded. Figure 39.

Monoicous. *Antheridia* with short, hyaline necks. *Archegonia* with hyaline tips of necks above purple-brown bases, emerging from deep, cup-like depressions at intervals along dorsal groove, necks at their bases surrounded by numerous fragile, blunt cells. *Sporangia* crowded together or scattered along groove, bulging dorsally, enclosed in red-brown sac, later disintegrating. *Spores* 90–115 µm diam., triangular-globular, polar, reddish or yellowish brown when young, darkening to mahogany brown, opaque; wing 7.5 µm wide, with pore at marginal angles, margin crenulate and somewhat eroded; ornamentation reticulate or reticulate-foveolate, rather different on 2 spore faces; distal face with (9–)10(–12) deep, cup-like alveoli across diam., 10.0–12.5 µm wide, smaller toward margin, walls thickened, slightly raised at nodes, encrusted with granules and papillae, sometimes smoother; proximal face with triradiate mark not sharply defined, often partly obscured by dense granules, each facet with 15–20 small, shallow alveoli, ± 5 µm wide, some adjacent ones confluent, walls low, slightly raised at nodes, heavily sprinkled with granules to rather smoother. *Chromosome number*: n = 8 (Bornefeld 1984). Plate 16E, F; Perold (1989e: fig. 43.1–6).

The species is endemic to the arid shrublands of the Northern and Western Cape, where it is quite rare. It is found on decomposed granite, at seepages or at margins of flat rock outcrops. Map 18.

The unique composition of the dorsal epidermis necessitated placing this species in the



monotypic subgenus *Chartacea*. *Riccia schelpei* is characterized by the somewhat greasy appearance of the dorsal epidermis when fresh, with air pores surrounded by a ring of smaller, fragile cells superimposed over thicker-walled cells, giving it a mottled appearance; on drying out, the dorsal face turns yellowish and parchment-like, the groove is deep and the margins winged. Since the initial description (Volk & Perold 1986b), several more collections have been made and the distribution area expanded. A note by Duthie, found with a specimen of *R. schelpei*, *Giffen 3* (*PRE-CH1056*), which had previously been identified as *R. bullosa* (no. 5) (see note under that species), contained the following information: 'not correctly named, but I am not at present able to identify it; probably a new species, with shape of thallus as in *R. cilifera*, but spores different'.

Vouchers: *Oliver 8041* (PRE); *S.M. Perold 1480, 1946, 2178* (PRE); *C.M. van Wyk 2524* (PRE).

FIGURE 39.—**Riccia schelpei**. A, B, thallus: A, wet; B, dry. C, thick-walled epidermal cells seen from above, with small, thin-walled cells surrounding air pores (hatched), air chambers below partly stippled; D, c/s epidermis and assimilation tissue; E, c/s branch; F, scale. A, *S.M. Perold 1422* p.p.; B, *S.M. Perold 2052*; C–E, *Oliver 8041*; F, *C.M. van Wyk 2524*. Scale bars: A, B, E, 1 mm; C, D, 50 µm; F, 100 µm. Artist: J. Kimpton.

E. Subgenus **Riccia**

Thalli small to large; terricolous; groove deep or shallow, margins ciliate or glabrous. *Scales* lateral, rarely ventral, mostly large, extending to, or projecting above thallus margins, rounded, very occasionally triangular, variously pigmented or hyaline, scale margins entire, rarely denticulate or crenate.

Dorsal epithelium hyaline, in one or more strata; air pores as small spaces, numerous, regular. *Assimilation tissue* compact, with mostly narrow, interstitial, vertical air canals.

Spores large, (65–)80–120 µm in diam.; tetrads separating at maturity, triangular-globular or subglobose, variously ornamented.

E1. Section **Riccia**

Thalli small to large; terricolous; groove apical or along entire length of branches, margins ciliate or glabrous. *Scales* generally large, hyaline or variously pigmented, margins mostly entire, rarely crenate.

Dorsal epithelium in 1 or 2 strata, cells in close association, top cells mostly globose or pyriform along groove or apically, soon collapsing, rarely persistent.

Three informal groups are recognized within this section: Ciliatae, Mammillatae and Squamatae.

E1.1. Group **Ciliatae**

Thallus margins ciliate. *Scales* small, not, or hardly extending to thallus margins.

15. **Riccia trichocarpa** *M.Howe* in Bulletin of the Torrey Botanical Club 25: 184 (1898); M.Howe: 18 (1899); Frye & L.Clark: 27 (1937); Jovet-Ast: 39 (1983); Jovet-Ast: 332 (1986); Perold: 26 (1991c); Jovet-Ast: 227 (1991). Type: Calif., Santa Clara Co. near San Mateo Co. line [fide M.Howe: 18 (1899)], April 1892, *D.H. Campbell s.n.* [US, holo., fide Jovet-Ast: 332 (1986); NY, iso.!].

R. canescens Steph.: 320 (1898); Müll.Frib.: 445 (1951–1958); S.W.Arnell: 16 (1963a). Type: Algeria, Oran, *Balansa s.n.*, 1852.

Thalli smallish to medium-sized, in complete or incomplete rosettes, up to 20 mm across or in crowded, gregarious patches; bright green to glaucous green, margins with long cilia, flanks dark purple; when dry, margins inflexed, cilia covering dorsal face. *Branches* 2–4 times furcate, shortly to deeply divided, almost parallel to narrowly divergent, linear-ovate or ligulate, 2.5–5.5(–7) × 0.9–1.5 mm, 0.6–0.9 mm thick, in section as wide as thick to 1.5 times wider than thick, apex rounded to shortly emarginate; groove distally deep and narrow, shallow and wider proximally, lateral sides convex, gradually flattening out, thallus margins rounded; flanks somewhat bulging to steeply ascending, dark purple; ventral face slightly convex to nearly flat with narrow, transverse bands of violet or brown vestigial scales. *Cilia* in several rows at margins and flanks, along entire length of branches, crowded at apex, hyaline, smooth, rather shiny, stiff and straight to slightly flexuose, 450–750(–950) µm long, (40–)50 µm wide at base, gradually narrowing to sharply pointed apex, spirally twisted with margins alternately inflexed, appearing thick-walled. *Scales* tightly

adherent to, or fused with flanks, not detachable and not extending above margins of thallus, purple to nearly black.

Dorsal epithelium unistratose, cells globose to mammillose, 35–45 × 35–40 µm, hyaline, fragile, soon collapsing; air pores small, triangular or 4-sided. *Assimilation tissue* 300–400 µm thick, consisting of vertical columns of 7 or 8 isodiametric cells, enclosing narrow air canals; storage tissue occupying ventral part of thallus, cells closely packed, rounded, ± 45 µm wide. Figure 40.

Perennation by bulbils.

Monoicous. *Antheridia* along groove, with projecting hyaline necks up to 50 µm long. *Archegonia* scattered, necks purple. *Sporangia* bulging dorsally, with central purple spot, crowned with 2–10 cilia, in groups of 2 or 3. *Spores* 100–120 µm diam., triangular-globular, polar, very dark brown to black, opaque; wingless, marginal angles with pores, margin finely crenulate; ornamentation reticulate and similar on 2 spore faces, alveoli extending to margin; distal face convex, (10–)12–14 rounded alveoli across diam., 7.5–10.0 µm wide, alveolar walls thick, heavily encrusted with small to large wart-like papillae, and stout, blunt tubercles projecting mostly from central nodes, 5.0–7.5 µm long; proximal face with triradiate mark indistinct, ± 30 alveoli on each of 3 facets, up to 5 µm wide, walls heavily granulate. *Chromosome numbers*: n = 8; 16 (Jovet-Ast 1983; 1986); 16 (Bornefeld 1984; 1989). Plate 17A, B; Perold (1989e: fig. 3.1–6).

The species is widespread and subcosmopolitan; it is known from countries bordering the Mediterranean, Macaronesia, Kenya, Malawi, Niger, Tanzania, Uganda, Zimbabwe, Madagascar, North and South America. The Australian species, *R. crinita* Taylor, may yet prove to be conspecific (Jovet-Ast 1986).

In the *FSA* area, *R. trichocarpa* has been found throughout the semi-arid savanna/grassland biome of Namibia, but rarely in Botswana, Northern Province, North-West, Free State, Lesotho, Northern and Eastern Cape. It grows on shallow, sandy soil overlying quartzite or dolomite outcrops or on calcareous crust. Map 18.

Riccia trichocarpa is recognized by the conspicuous, long, smooth, marginal cilia, purple flanks and dark brown to black spores, with densely granulate alveolar walls.

Jovet-Ast (1986) distinguished between cilia and hairs ('poils'), the latter being thin-walled and stouter. *Riccia canescens* Steph. was placed in synonymy under *R. trichocarpa* (Jovet-Ast 1983), as the thalli are indistinguishable from each other. Volk (1984) reported the species (as *R. canescens*) to have a preference for alkaline soils, whereas Jovet-Ast (1986) gave soil pH values of 4.5–6.3 (rarely 7.0–7.5), which indicates a wide tolerance. Schuster (1992b) treats *R. trichocarpa* (and *R. canescens*) as subspecies of *R. ciliata*, but this has not been accepted here.

Vouchers: *Duthie 5494* (BOL); *S.M. Perold 748* (PRE); *Toelken 5561* (PRE); *O.H. Volk* 81/293 p.p. (M; PRE).

16. **Riccia crozalsii** *Levier* in Revue bryologique et lichénologique 29: 73 (1902); Macvicar: 16 (1926); Müll.Frib.: 447 (1951–1958); S.W.Arnell: 284 (1956a); S.W.Arnell: 17 (1963a); E.O.Campb.: 223 (1977); Na-Thalang: 80 (1980); Jovet-Ast: 337 (1986); Perold: 27 (1991c). Type: France, Hérault, prope Roquehaute (Agde), *Crozals* March 1902 (?FI); *Crozals* specimens March–May 1902 [PC, syn. fide Jovet-Ast: 337 (1986)].

R. africana Sim: 11 (1926). Type: Cape, Stellenbosch flats, *Garside* 8 (*PRE-CH1065*) [PRE, lecto.!, selected by Perold (1991c)].

R. ciliata Hoffm. var. *austroafricana* S.W. Arnell: T.XXII, fasc. 1–2 (1953a).

R. crozalsii var. *austroafricana* S.W. Arnell: 18 (1963a).

Thalli smallish to medium-sized, in scattered or incomplete rosettes 15–20 mm across; pale green or glaucous-green, sometimes with

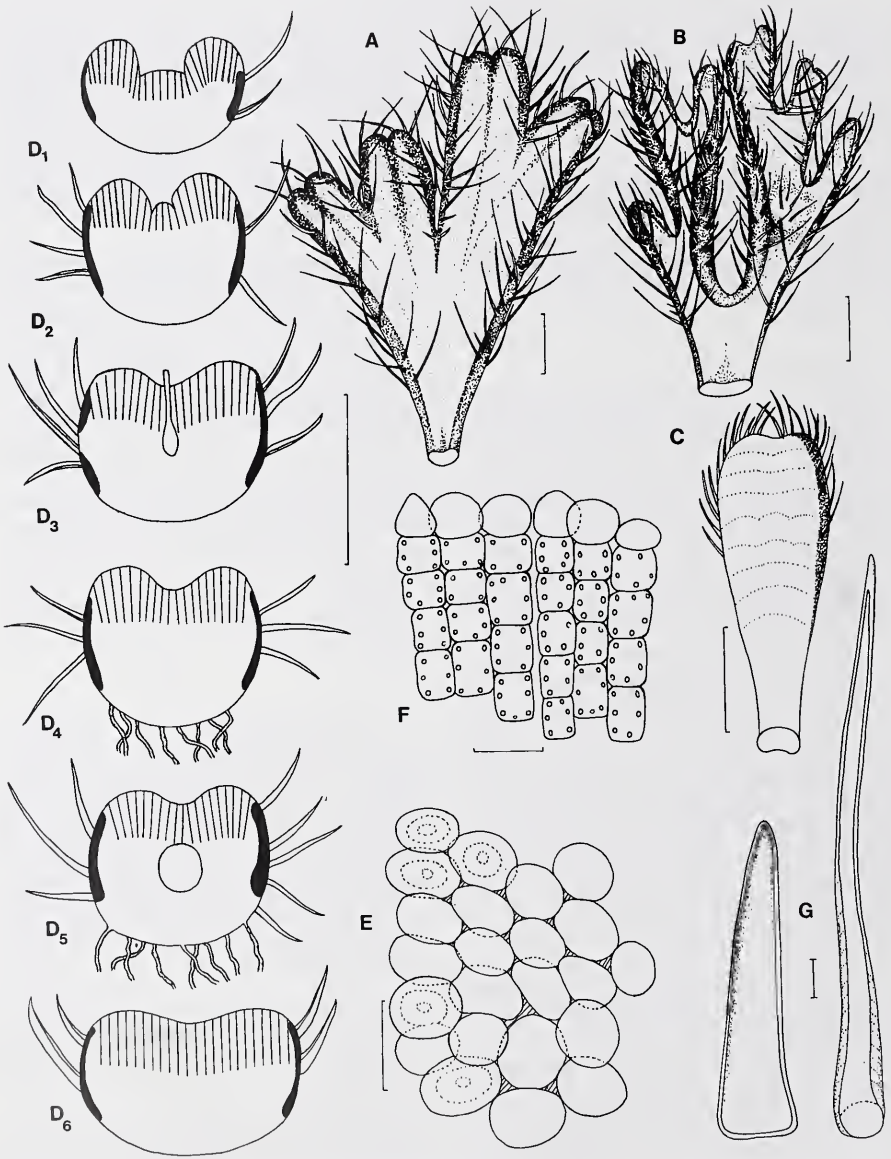


FIGURE 40.—**Riccia trichocarpa**. A, B, thallus: A, wet; B, dry. C, ventral face of branch; D, c/s branch at intervals from apex to base; E, epithelial cells and air pores (hatched), seen from above; F, c/s epithelial and assimilation tissue cells; G, cilia. A–G, *Henderson 658*. Scale bars: A–D, 1 mm; E–G, 50 µm. Artist: J. Kimpton.

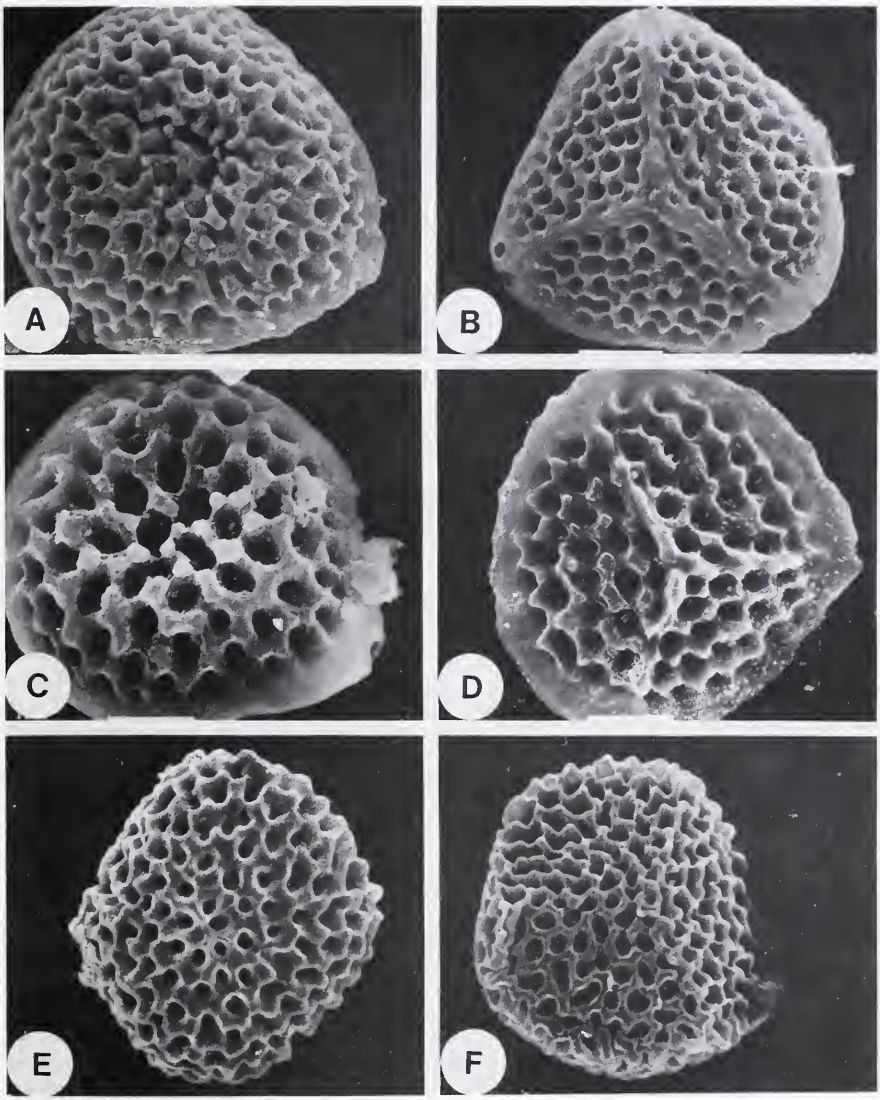


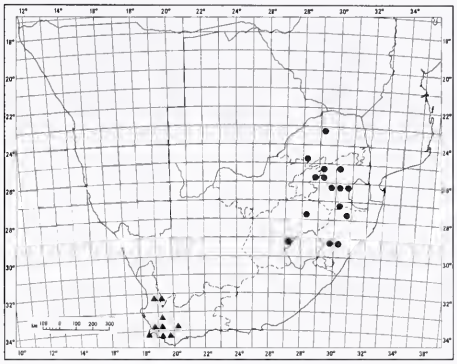
PLATE 17.—Spores. A, B, **Riccia trichocarpa**: A, distal face; B, proximal face. C, D, **R. crozalsii**: C, distal face; D, proximal face. E, F, **R. microciliata**: E, distal face; F, proximal face. A, B, *S.M. Perold 748*; C, *Morley 305*; D, *S.M. Perold 1149* p.p.; E, F, *S.M. Perold 102*. A, B, D, × 600; C, E, F, × 700.

FIGURE 41.—**Riccia crozalsii.** A–C, thallus: A, wet; B, dry; C, ventral face. D, c/s branch at intervals from apex to base; E, epithelial cells and air pores (hatched) from above; F, c/s epithelial and assimilation tissue cells; G, cilia. A–G, *S.M. Perold 473.* Scale bars: A–D, 1 mm; E–G, 50 µm. Artist: J. Kimpton.

violet blotches along ciliate margins and over sporangia; when dry, margins apically inflexed, covering dorsal face, otherwise exposed. *Branches* 1–3 times furcate, deeply divided, narrowly to moderately divergent, sometimes overlapping; linear or linear-obovate, 3–6 × 0.6–1.1 mm, 0.4–0.6 mm thick, in section 1.5 times to twice wider than thick, apex obtuse to rounded, shortly emarginate; groove narrow and deep distally, soon becoming wider and flattening out, thallus margins raised and tumid, with 1 or 2 rows of cilia; flanks steep to sloping obliquely in older parts; ventral face slightly convex, green toward apex, with two or more transverse rows of purple vestigial scales. *Cilia* hyaline, surface finely granular, straight or arched, up to 40 µm wide at base, tapering to pointed tip, 200–325(–450) µm long, margins narrowly inflexed, arising from dorsal epithelial cells along thallus margins, numerous toward apex of thallus, sparse or absent proximally. *Scales* present only toward apex, small and insignificant, barely reaching thallus margins, not imbricate, hyaline or violet.

Dorsal epithelium unistratose, cells globose, 37–45 × 30–50 µm, hyaline, fragile, soon collapsing; air pores small, triangular or 4-sided. *Assimilation tissue* ± 500 µm thick, consisting of vertical columns of 5 or 6(7) rectangular cells, enclosing narrow air canals; storage tissue occupying ventral part of thallus, cells somewhat loosely arranged, rounded, 40–50 µm wide. Figure 41.

Monoicous. *Antheridia* with hyaline necks, at intervals along distal part of groove. *Archegonia* with conspicuous purple necks, along more proximal part of branches. *Sporangia* bulging dorsally, sometimes blotched with violet, never crowned with cilia. *Spores* 85–110 µm diam., triangular-globular, polar, dark brown to black, opaque at maturity; wing prominent, ± 7.5 µm wide, margin entire, nearly smooth to granulate, wider and thicker at marginal angles, with round pore; ornamentation reticulate and similar on 2 spore faces; distal face convex, with 8–10 deep, rounded or angular alveoli across diam., up to 10 µm wide,



MAP 19.—● **Riccia natalensis**
▲ **R. crozalsii**

alveolar walls thickened, papillate with papillae sometimes spreading to inside of alveoli, raised at nodes into blunt projections; proximal face with triradiate mark distinct, its arms wider toward marginal angles near junction with wing, each of 3 facets pitted with 30–35 small, deep alveoli, 3.5 µm wide, walls raised, especially at nodes. *Chromosome number*: n = 8 (Na-Thalang 1980; Jovet-Ast 1986). Plate 17C, D; Perold (1989e: fig. 2.1–6).

Riccia crozalsii is known from England and Europe, especially the Mediterranean countries, as well as from Macaronesia, North Africa, southern India, Australia and New Zealand. In the *FSA* area, the distribution of *R. crozalzii* is confined to the fynbos biome in the winter rainfall region of the Western Cape, where it grows on sandy, damp soil overlying granitic rock outcrops or on mud at streambanks. Map 19.

Riccia crozalsii can be recognized by its long, pointed, faintly granular cilia along the thallus margins, which are absent over the sporangia; by the pale green to glaucous-green colour of the dorsal face, occasionally stained with purple blotches; and by the spores with deep, rounded or angular alveoli on the distal face and on the proximal face, the arms of the triradiate mark widening toward the marginal angles near the junction with the wing.

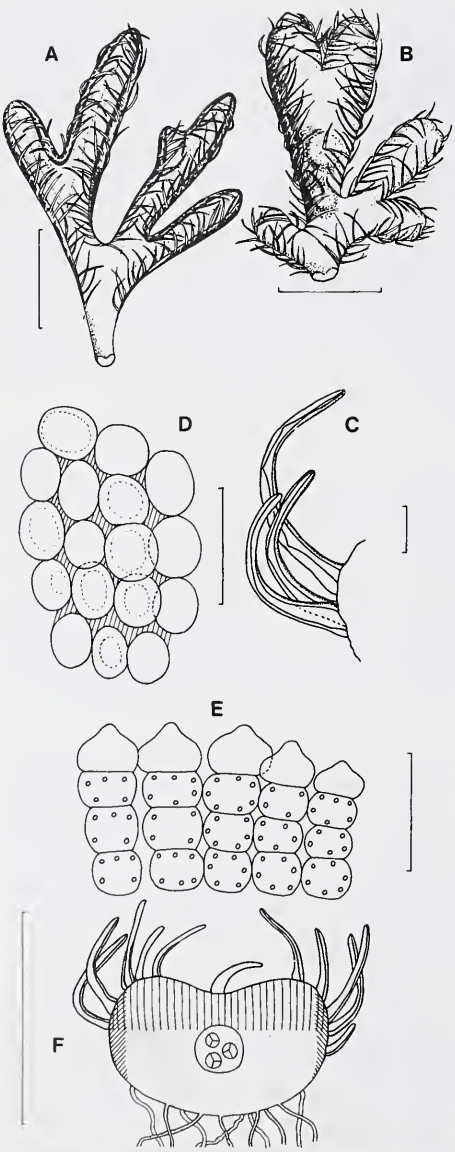


FIGURE 42.—**Riccia microciliata**. A, B, thallus: A, dry; B, wet. C, cilia at thallus margin; D, epithelial cells and air pores (hatched) from above; E, c/s epithelial and assimilation tissue cells; F, c/s branch. A–F, *S.M. Perold 1026*. Scale bars: A, B, F, 1 mm; C–E, 50 µm. Artist: J. Kimpton.

Sim (1926) described specimens of *R. crozalsii* as a new species, *R. africana*, but he regarded the cilia as 'triangular-acute scales', forming a 'marginal border, that is early caducous'. The spores he found to be adhering in tetrads, so they must have been immature; *R. africana* was subsequently placed in synonymy under *R. crozalsii* by Arnell (1963a). The type specimen of *R. crozalsii* was not available for study, but comparison of spore micrographs of all southern African specimens referred here, with micrographs published by Campbell (1977), Na-Thalang (1980) and Jovet-Ast (1986), leave no doubt that they have been correctly placed.

Vouchers: *S.W. Arnell PRE-CH4127* (PRE); *Duthie 5018* (BOL); *S.M. Perold 473* (PRE); *C.M. van Wyk 1492* (PRE).

17. **Riccia microciliata** *O.H.Volk & Perold* in Bothalia 16: 173 (1986c); Perold: 28 (1991c). Type: Transvaal, Sabie, immediately W of town, near bridge over Sabie River; on shallow soil over flat, weathered, granitic rock outcrops, *S.M. Perold 383* (PRE, holo.!).

Thalli small, in complete or incomplete rosettes, up to 10 mm across; glaucous-green, margins and dark purple flanks densely ciliate; when dry, margins inflexed, arched cilia interlocking over dorsal face. *Branches* asymmetrically bi- or trifurcate, shortly to deeply divided, narrowly to moderately divergent, linear-ovate, 1–3(–4) × 0.6–0.8 mm, 0.5 mm thick, in section as wide as thick to 1.5 times wider than thick, apex obtuse, shortly emarginate; groove distally narrow and deep, soon broader and nearly flat, thallus margins rounded, with numerous cilia; flanks steeply ascending to somewhat bulging, dark violet; ventral face rounded, green or with brown, transverse bands of vestigial scales. *Cilia* in several rows, crowded at apex and along margins, sparser toward base, occasionally a few on dorsal face of thallus, especially over sporangia, (80–) 175–300 µm long, base 35 µm wide, somewhat bulbous, narrowing to blunt tip, generally arched, channelled,

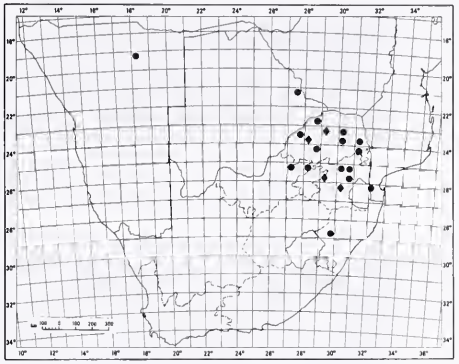
finely striate, usually one of margins more deeply inflexed, appearing thicker. *Scales* small, not quite reaching thallus margins, purple or partly hyaline. Plate 18A.

Dorsal epithelium unistratose, cells globose to nearly conical, hyaline, 30–40 × 20–30 µm, occasionally some larger; air pores small, 3- or 4-sided. *Assimilation tissue* ± 250 µm thick, in vertical columns of 6 or 7(8) isodiametric cells, enclosing narrow 3- or 4(5)-sided air canals; storage tissue occupying ventral part of thallus, cells irregularly arranged, round or angular. Figure 42.

Perennation by small bulbils formed at apices of thalli, under adverse conditions, thus enabling the plants to survive.

Dioicous. *Antheridia* with prominent hyaline necks, ± 125 µm long, spaced along groove in male thalli. *Archegonia* with purple necks. *Sporangia* up to 3 per lobe, overlying dorsal tissue bulging and turning purple, with 1 or 2 cilia, but sometimes none remaining. *Spores* 80–92 µm diam., triangular-globular, polar, chestnut-brown to almost black, becoming opaque with age; wingless, perforated at angles, margin crenate; ornamentation reticulate to vermiculate, similar on both faces; distal face with 10–12 round or oval alveoli across diam., 7.5 µm wide, some adjacent alveoli occasionally confluent, alveolar walls smooth, slightly raised at nodes, sometimes anastomosing and forming short, undulating, vermicular ridges; proximal face with triradiate mark not clearly defined, on each of 3 facets, 25–30 deep-set alveoli, 5 µm wide. *Chromosome number*: n = 8 (Bornefeld 1984; 1989). Plate 17E, F; Perold (1989e: fig. 4.1–6).

The range of the species extends northwards into Angola, Malawi, Mozambique and Tanzania. Although infrequently collected, because of its small size and therefore easily overlooked, this African endemic is widespread in locally damp to somewhat drier areas, growing on shallow soil overlying granitic rocks, in Northern Province, North-West and Mpumalanga, but is rarely found in Namibia, Botswana, Swaziland and KwaZulu-Natal. Map 20.



MAP 20.—● **Riccia microciliata**
◆ **R. mammifera**

Riccia microciliata is distinguished from the other southern African ciliate species by the small size of the thalli and by the arching, deeply channelled cilia. Its spores are wingless, the triradiate mark poorly defined and the alveolar walls smooth, never granulate.

Vouchers: *S.M. Perold 102, 1026* (PRE); *I.M. Retief 252* (PRE); *Smook 4267* (PRE); *Volk 81/130* (M; PRE).

18. **Riccia natalensis** *Sim*, The Bryophyta of South Africa: 9 (1926); S.W.Arnell: 18 (1963a); O.H.Volk & Perold: 169 (1986c); Perold: 29 (1991c). Type: Natal, Scheepers' Nek, *Sim 8228* [PRE, lecto.! selected by Perold (1991c); BOL, isolecto.!].

Thalli medium-sized to large, in more or less complete rosettes up to 25 mm across or in gregarious patches or scattered; bright green, sometimes with violet flecks or streaks, margins ciliate; when dry, apex and distal sides partly inflexed, cilia white and prominent. *Branches* bi- or trifurcate, shortly to deeply divided, moderately divergent, ligulate or obovate, 5–10 (–12) × 2–4 mm, 0.5–0.7 mm thick, in section 4–6 times wider than thick, apex rounded,

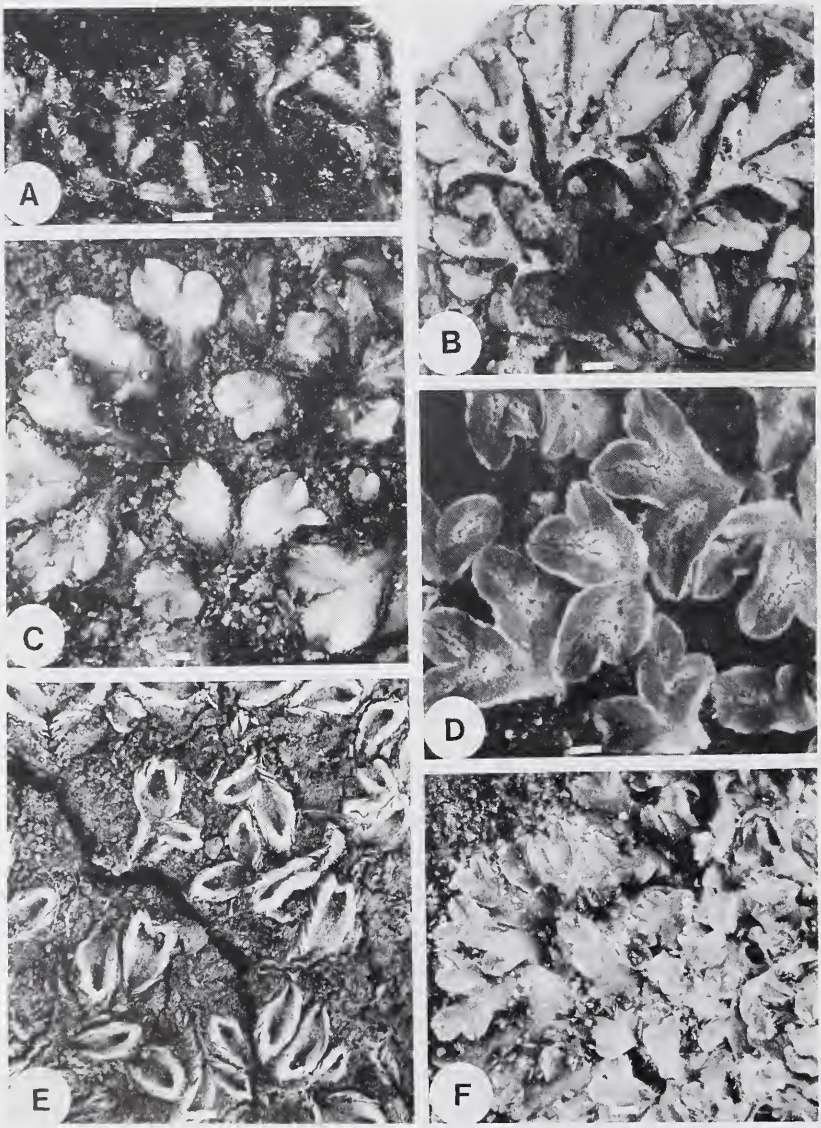


PLATE 18.—Thalli. A, **Riccia microciliata**, branches; B, **R. okahandjana**, partial rosette; C, **R. congoana**, partial rosette; D, **R. albolimbata**, scattered branches; E, **R. argenteolimbata**, scattered branches; F, **R. montana**, crowded branches. A, *S.M. Perold 383*; B, *Van Rooy s.n.*; C, *Smook 5139*, D, *Volk 86/927*; E, *Volk 84/713*; F, *Oliver 8354*. Scale bars: A–F, 1 mm.

shortly emarginate; groove deep and narrow distally, shallow and wide proximally, thallus margins raised, tumid, shortly winged in older parts; flanks obliquely sloping, pale brown to violet; ventral face slightly rounded, green. *Cilia* numerous and crowded at apical margins, proximally sparser and more distantly spaced, absent over sporangia, hyaline, surface finely granulate, long-triangular, length 160–300(–400) µm, width at base 30–50 µm, narrowing to blunt or subacute tip, straight or slightly curved to twisted, with one or both margins inflexed. *Scales* small, inconspicuous, ± 300 × 160 µm, hyaline, not persistent.

Dorsal epithelium unistratose, cells globular or mammillose, 40–50 × 50–75 µm, hyaline, soon collapsing and cup-like; air pores triangular or 4-sided. *Assimilation tissue* 250–350 µm thick, in vertical or laterally sloping columns of 6–8(–10) cells, isodiametric or short-rectangular, air canals narrow, 4-sided, toward margins wider, 6-sided; storage tissue in ventral part of thallus, cells rounded, irregularly arranged. Figure 43A–F.

Monoicous. *Antheridia* numerous in distal part of groove, hyaline necks projecting ± 100 µm. *Archegonia* scattered along median part of lobes, necks purple. *Sporangia* 2–8 per lobe, bulging dorsally, overlying epithelium sometimes blotched with purple, without cilia. *Spores* 95–125 µm diam., triangular-globular, polar, straw-coloured, semitransparent; wing undulating, width up to 10 µm, wider at marginal angles, notched or perforated; ornamentation reticulate and similar on 2 spore faces; distal face convex to slightly flattened, 8 or 9 rounded or angular alveoli across diam., 10–15 µm wide, alveolar walls low, smooth, projecting at nodes; proximal face with triradiate mark not clearly or only partly defined, 10–13 rounded alveoli on each of 3 facets, up to 10 µm wide, sometimes adjacent ones only partly separated or confluent, alveolar walls low, smooth, slightly raised at nodes. *Chromosome number*: n = 9 (Bornefeld 1984). Plate 19A, B; Perold (1989e: fig. 1.1–6).

Riccia natalensis is endemic to southern Africa and is infrequently collected on damp, loam-rich soil or black clay in the grassland biome of Northern Province, Mpumalanga, eastern Free State and KwaZulu-Natal. It has not been found in the more arid western parts of the country. Map 19.

The specimen, *Sim 8228*, was designated as lectotype [Perold (1991c), not holotype as in Volk & Perold (1986c)]; the other Sim specimens from Wellington, Rosetta, Natal, that were also cited by him (Sim 1926) have not been traced after a thorough search.

This species is easily recognized by the conspicuous marginal cilia and broad, relatively thin and somewhat lax thallus with tumid margins. The spores are also quite distinct with a wide, undulating wing, large, low-walled alveoli and pale straw colour.

In his key, Arnell (1963a) did not place *R. natalensis* with the other ciliate species (Volk & Perold 1986c), but with *R. albomarginata* Bisch. (no. 47) and *R. concava* Bisch. (No. 46), where the dorsal epithelium consists of free, multicellular pillars (section *Pilifer* Volk 1983). He appears to have misinterpreted Sim's (1926) reference to 'mamillae' (sic) and took it to apply to the epithelial cells, which he, however, reported as destroyed in the type specimen, when he examined it. Sim noted that 'all along the outer portion of the thallus surface rise pellucid, single-celled mamillae', which clearly refer to the cilia at the thallus margins, and not to multicellular epithelial hairs covering the entire dorsal face of the thallus. This confusion of cilia with dorsal cell hairs can be traced back to Bischoff's observation (in MS) that the small scales (!) in *R. concava* (no. 46) could be taken for cilia, and to Gottsche *et al.* (1844–1847), who classified *R. albomarginata* (no. 47) in their section 'Ciliatae' (See notes under those species).

Vouchers: *Braggins 338a* (PRE); *Germishuizen 2888* (PRE); *J.M. Perold 30, 38* (PRE); *S.M. Perold 103, 307* (PRE).

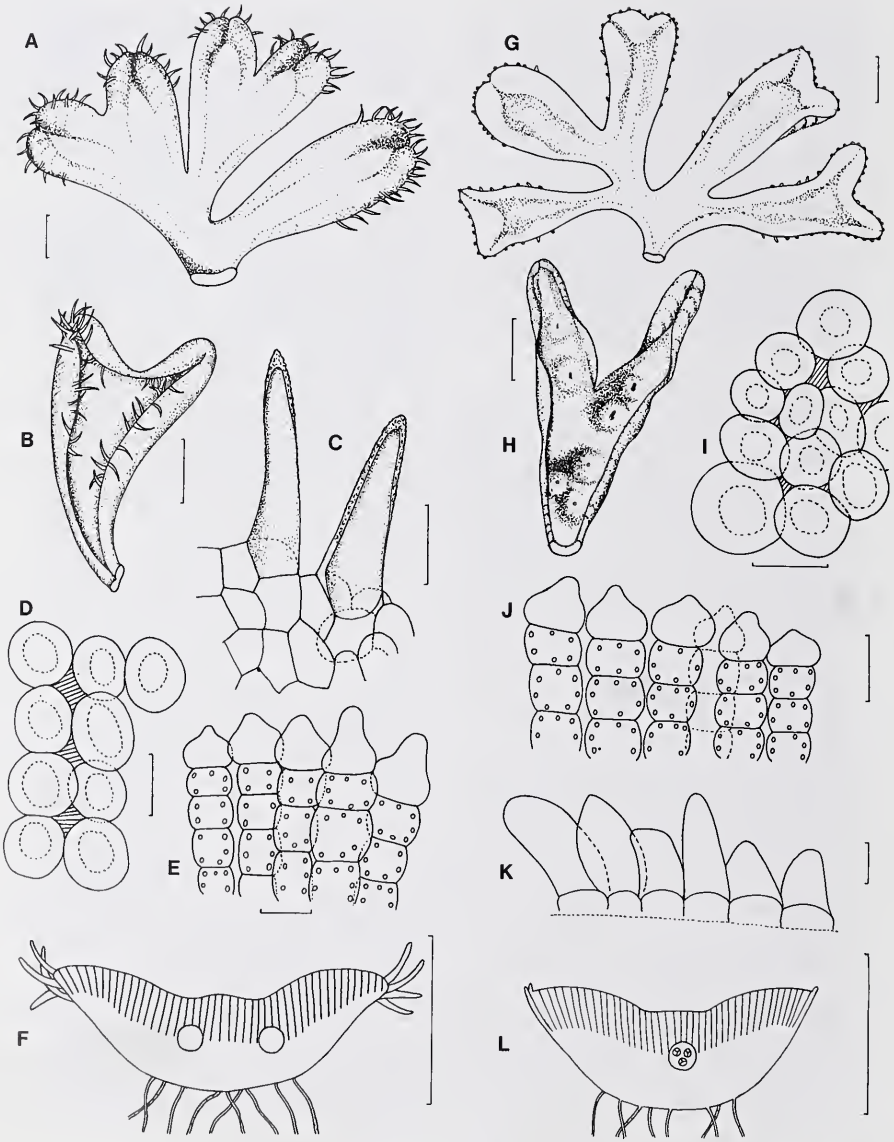


FIGURE 43.—A–F, **Riccia natalensis.** A, B, thallus: A, wet; B, dry. C, cilia at thallus margin; D, epithelial cells and air pores from above; E, c/s epithelial and assimilation tissue cells; F, c/s branch. G–L, **R. mammifera**. G, H, thallus: G, wet; H, dry. I, epithelial cells and air pores from above; J, c/s epithelial and assimilation tissue cells; K, marginal row of enlarged cells; L, c/s branch. A–F, *S.M. Perold 1048*; G–L, *S.M. Perold 447*. Scale bars: A, B, F–H, L, 1 mm; C–E, I–K, 50 µm.

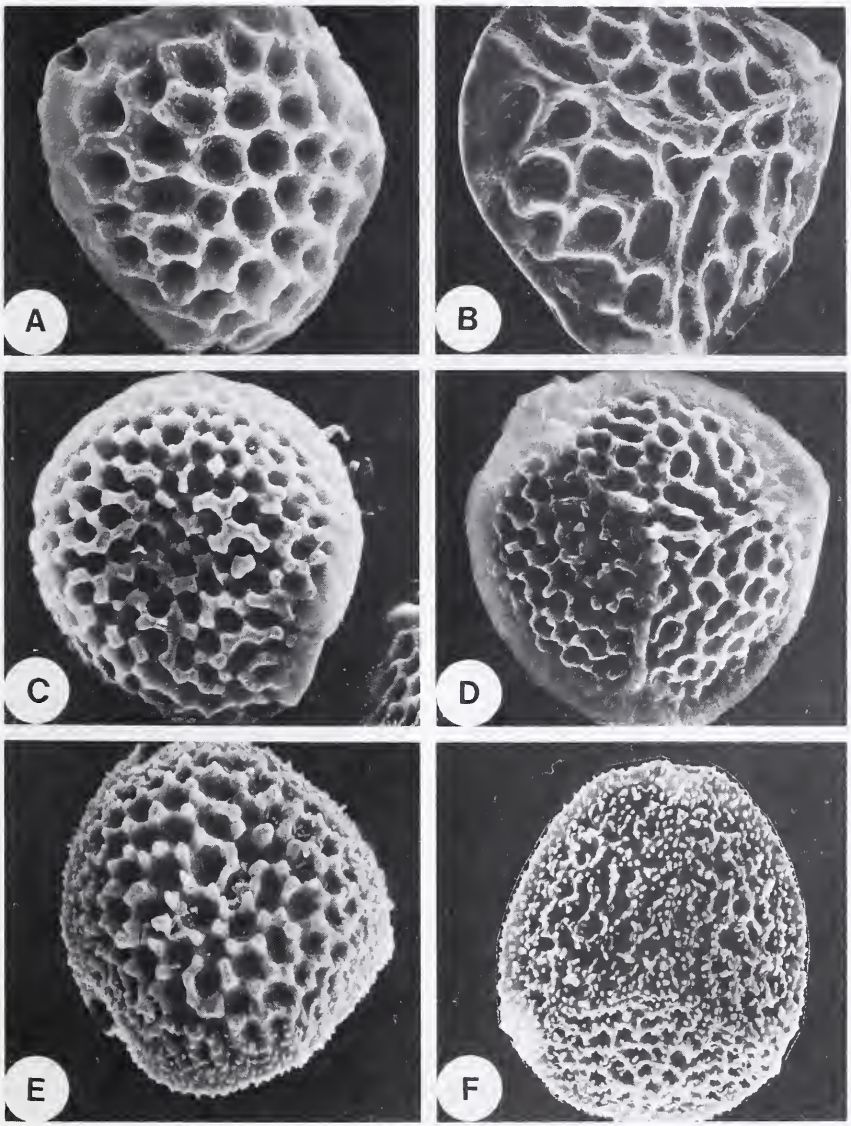


PLATE 19.—Spores. A, B, **Riccia natalensis**: A, distal face; B, proximal face. C, D, **R. mammifera**: C, distal face; D, proximal face. E, F, **R. sorocarpa**: E, distal face; F, proximal face. A, *S.M. Perold 679*; B, *S.M. Perold 430*; C, D, *S.M. Perold 447*; E, *Arnell 7*. A, C, D, × 600; B, E, F, × 700.

E1.2. Group **Mammillatae**

Thallus margins with enlarged cells. *Scales* small, not reaching thallus margins.

19. **Riccia mammifera** *O.H.Volk & Perold* in Bothalia 16: 176 (1986c); Perold: 29 (1991c). Type: Transvaal, Farm Klipfontein, Dist. Verena, 24 km E of Bronkhorstspruit/ Groblersdal road, on dirt road to Susterstroom, near small streamlet, tributary of Wilge River, *S.M. Perold 447* (PRE, holo.!); *Wagener PRE-CH4511* (PRE, para.!).

Thalli medium-sized, in complete or incomplete rosettes, up to 25 mm across; pale green to green, occasionally with violet blotches; when dry, apex and sides inflexed over dorsal face. *Branches* bi- or trifurcate, shortly to deeply divided, narrowly divergent, obcuneate or oblong, rarely linear (5–)7–10 × 1–3 mm, 0.6–1.1 mm thick, in section 2–3(–4) times wider than thick, apex mostly broad, truncate or rounded, emarginate; groove wide to nearly flat, thallus margins tumid and raised, rounded to slightly attenuate, apically with projecting cells; flanks sloping obliquely, distally violet, otherwise green; ventral face rounded to flat, green. *Mammillae* only conspicuous at apical margins, generally absent proximally, taking the form of enlarged marginal cells, vertical or slanting, thin-walled, smooth, hyaline, up to 150 µm long, 60 µm wide at base with apices rounded to pointed. *Scales* small and inconspicuous, not reaching margin of thallus, ± 315 × 225 µm, dark violet, toward apex with hyaline margins, proximally entirely hyaline.

Dorsal epithelium unistratose, cells dome-shaped or mammillose, 30–50 × 37.5–50.0 µm, hyaline, fragile and soon collapsing; air pores 3-, 4- or 5-sided. *Assimilation tissue* 300–550 µm thick, in closely packed vertical columns of 8–10 isodiametric cells, air canals narrow, 4- or 5-sided; storage tissue occupying ventral part of thallus, cells variable in size. Figure 43G–L.

Monoicous. *Antheridia* numerous, with necks projecting ± 160 µm above surface. *Archegonia* along midline, necks purple, tips hyaline. *Sporangia* crowded in groups, up to 6 per lobe, bulging dorsally, overlying tissue often purple. *Spores* 80–115 µm diam., triangular-globular, polar, straw-coloured to brown, semitransparent; wing smooth, slightly sinuate, ± 5 µm wide, broader at marginal angles, notched or with a pore; ornamentation reticulate, similar on 2 faces; distal face markedly convex, with 8–12, mostly hexagonal alveoli across diam., up to 10 µm wide, alveolar walls thin, raised into stout, truncate tubercles at nodes; proximal face with triradiate mark inconspicuous to prominent, apex sometimes nodular, up to 25 rounded alveoli on each of 3 facets, 5.0–7.5 µm wide, alveolar walls low, only slightly raised at nodes, or forming irregular, vermiculate ridges and few discrete alveoli. *Chromosome number*: n = 9 (Bornefeld 1984). Plate 19C, D; Perold (1989e: fig. 5.1–6).

To date, this endemic species, *R. mammifera*, is known from only four localities in the drier, savanna area of the Northern Province and Mpumalanga, where it grows on temporarily wet, clayey soil on the banks of small streams or at seepages. Map 20.

Riccia mammifera can be recognized by the broad thallus, small scales and enlarged cells along the thallus margins, on account of which it has been treated as a member of the Mammillatae group. Pandé & Udar (1958) reported small 'cilia', 100–150 µm long, at the margins and on the surface of the thallus in *R. melanospora*, a character not previously seen in a southern African species.

Originally it was thought (Volk & Perold 1986c) that the above collections could perhaps be specimens of *R. coronata*, of which the type and only specimen, *Sim 8730*, from Mooi River, KwaZulu-Natal, had been lost. According to Sim's diagnosis, however, *R. coronata* has 'scales fairly large, horizontal when moist', whereas the scales in *R. mammifera* are small,

inconspicuous and evanescent. Its marginal cells also appear to be much shorter, when compared with Sim's drawing. Sim (1932) and Arnell (1963a) mistakenly referred *Duthie 5004* (BOL) to *R. coronata*. It belongs in section *Pilifer*, as it has free-standing, dorsal cell pillars and has been described as a new species, *R. alatospora* (no. 41) (Volk & Perold 1985).

Vouchers: *Braggins 97/336* (PRE); *S.M. Perold 841* (PRE); *Perold & Koekemoer 2937* (PRE).

E1.3. Group **Squamatae**

Thallus margins smooth. *Scales* generally large.

20. **Riccia sorocarpa** *Bisch.* in Nova acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum 17: 1053 (1835); Steph.: 335 (1898); Frye & L.Clark: 19 (1937); Müll.Frib.: 457 (1951–1958); S.W.Arnell: 285 (1956a); S.W.Arnell: 20 (1963a); E.O.Campb.: 227 (1977); Na-Thalang: 95 (1980); Jovet-Ast: 315 (1986); Perold: 30 (1991c); Jovet-Ast: 255 (1991). Type: Schriesheim bei Heidelberg, *Bischoff* [HEID, holo., fide Jovet-Ast: 315 (1986)].

Thalli smallish to medium-sized, in gregarious patches or scattered, occasionally forming partial rosettes, 15–20 mm across; light green or glaucous-green, appearing somewhat waxy; when dry, margins recurved to distally incurved, dorsally yellowish green. *Branches* once or twice furcate, deeply divided, moderately to widely divergent, narrowly ovate to oblong, 3–6 × 1.1–1.5(–1.8) mm, 0.5–0.6 mm thick, in section 2–3 times wider than thick, apex slightly narrowed, subacute to rounded, emarginate; groove narrow and deep, continuing along most of length of thallus, becoming wider and shallower proximally, thallus margins acute, hyaline; flanks ascending obliquely distally to more steeply toward base; ventral face keeled apically, to rounded proximally. *Scales* rather small, ± 425 × 250 µm, extending to thallus margins, rounded, fragile, hyaline, hardly imbricate.

Dorsal epithelium bistratose, cells of upper layer, toward apex and groove rounded to pyriform, 37.5–45.0 × 27.5–37.5 µm, outer walls and top half of lateral walls thin, soon collapsing, leaving thick-walled bases as persistent cups above subdorsal layer of isodiametric to short-rectangular cells, also thick-walled, 30(–40) × ± 32 µm; marginal row of cells somewhat larger, hyaline, top cell rounded, intact, extending slightly above dorsal cells; air pores small, 4-sided. *Assimilation tissue* 150–200 µm thick, consisting of vertical columns of ± 5 short-rectangular cells enclosing narrow air canals; storage tissue occupying ventral part of thallus, cells closely packed, round to oval. Figure 44.

Monoicous. *Antheridia* in rows along centre of thallus, necks hyaline, not prominent. *Archegonia* with purple necks, along midline. *Sporangia* numerous, dorsal covering tissue soon disintegrating and exposing several capsules in a row along groove. *Spores* 80–100 µm diam., triangular-globular, polar, dark reddish brown, becoming almost black and opaque; wing densely granular, 5 µm wide, slightly wider at perforated marginal angles, margin crenulate or finely serrulate; ornamentation on 2 spore faces different; distal face convex, with 8–10 rounded or angular alveoli across diam., alveoli in centre of face deep-set, 10–12 µm wide with walls raised at nodes into prominent tubercles or spinous projections 5–7 µm high, toward spore margin alveoli smaller, 5 µm wide, walls low and often incomplete, nodes with low, wart-like papillae; proximal face with triradiate mark somewhat indistinct, obscured by granules, 3 flattened facets without distinct alveoli, occasionally some small, shallow depressions, densely granulose, sometimes granules joining to form short, low, irregular ridges. *Chromo-*

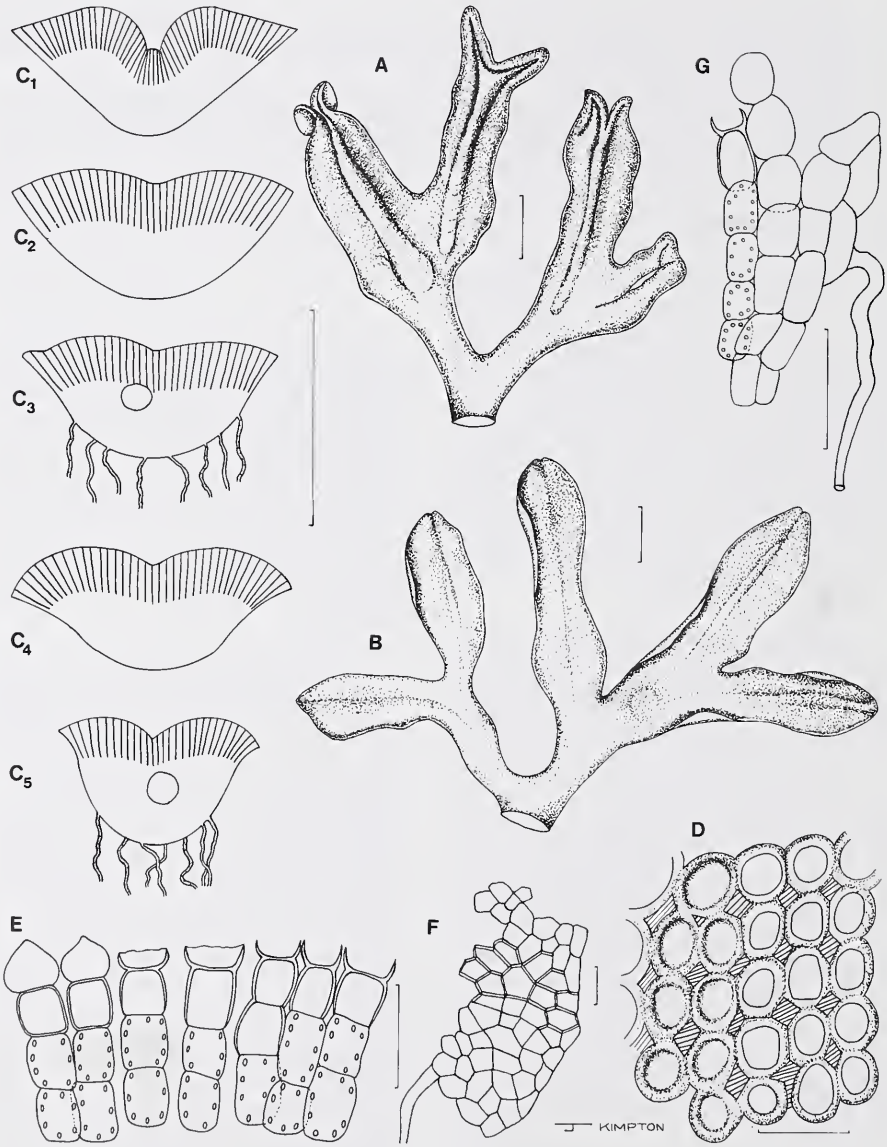


FIGURE 44.—**Riccia sorocarpa**. A, B, thallus: A, dry; B, wet. C, c/s branch at intervals from apex to base; D, epithelial cells and air pores from above; E, c/s partly thick-walled epithelial cells and thin-walled assimilation tissue cells; F, scale; G, c/s margin of thallus and scale. A, B, *Lambert 2*; C, E, *Oliver 8875*; D, *Arnell 136*; F, *S.M. Perold 1147*; G, *Arnell 7*. Scale bars: A–C, 1 mm; D, E, G, 50 μm; F, 100 μm.

some number: n = 8 (Na-Thalang 1980; Jovet-Ast 1986). Plate 19E, F; Perold (1989e: fig. 7.1–6).

Riccia sorocarpa is cosmopolitan in distribution. In southern Africa it has been infrequently collected on soil overlying weathered rock outcrops at seepages or on damp earth banks in Mpumalanga, KwaZulu-Natal, Lesotho, southwestern Northern Cape and Western Cape, sometimes at high altitudes. Map 21.

The thickened dorsal cell walls provide the most useful diagnostic character for separating this species from other southern African *Riccia* species and it can always be recognized by this. The spores, ornamented with numerous granules on the proximal face and with larger central alveoli and tall spinous processes at the nodes on the distal face, are also quite distinct.

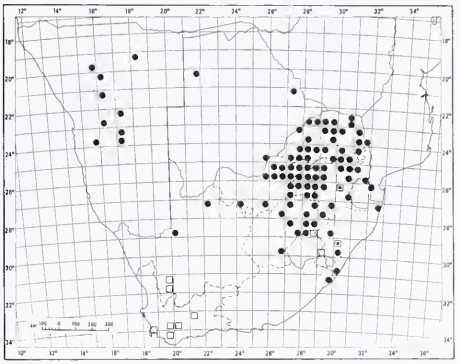
The type specimen of *R. sorocarpa* was not available for study, but there is no doubt that the South African specimens, several of which were collected and determined by Arnell, who was familiar with this species, belong here.

Schuster (1992b) recognized three subspecies of *R. sorocarpa*, namely the typical one, *R. sorocarpa* subsp. *arctica* and *R. sorocarpa* subsp. *erythrophora* in his new section *Sorocarpae*, but this is not followed here.

Vouchers: *S.W. Arnell 303* (PRE); *Lambert 2* (PRE); *Oliver 8875* (PRE); *S.M. Perold 307a, 1058a* (PRE).

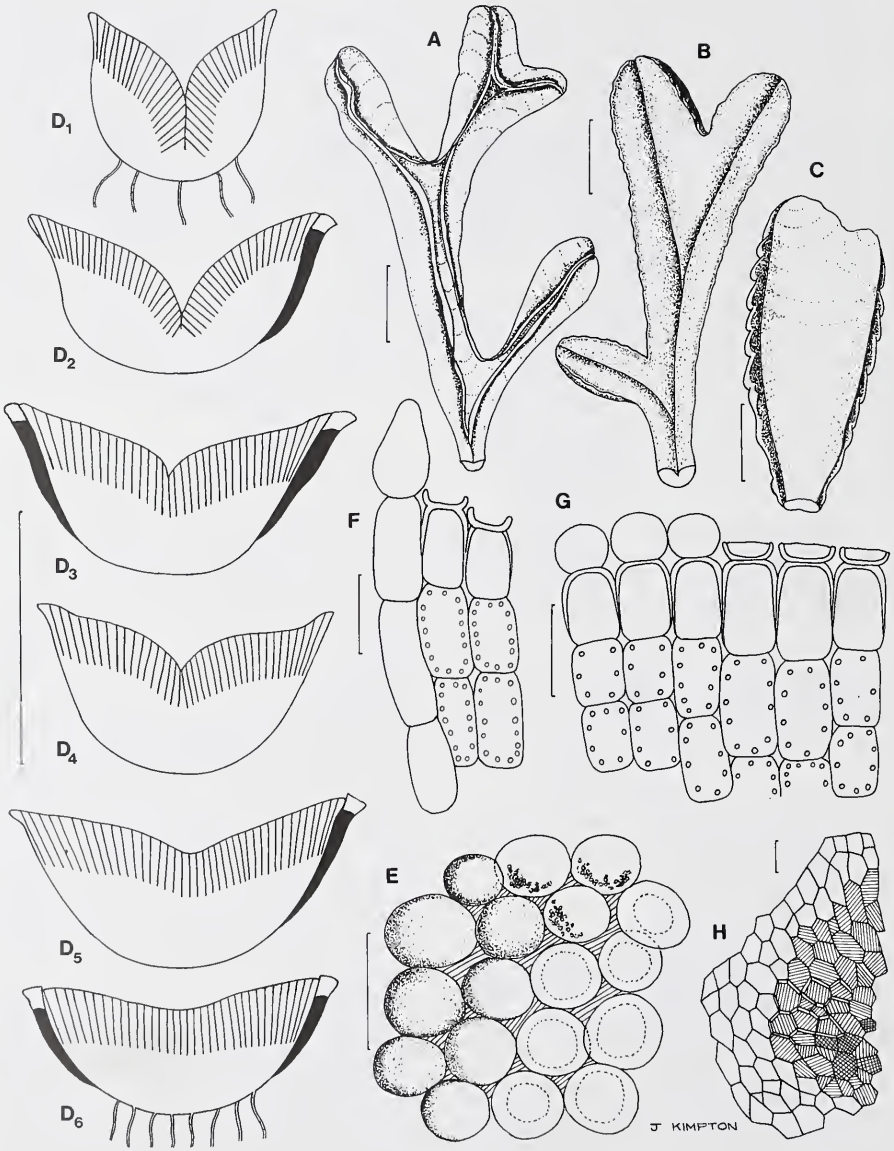
21. **Riccia atropurpurea** *Sim*, The Bryophyta of South Africa: 11 (1926); S.W.Arnell: 28 (1963a); Perold: 31 (1991c). Type: Natal, Edendale Falls, *Sim 8112* (*PRE-CH1023*) [PRE, lecto.!, selected by Perold (1991c)].

Thalli smallish to medium-sized, in irregular or incomplete rosettes up to 20 mm across, or in crowded, overlapping patches or scattered; glaucous-green to silvery grey-green, white along margins; when dry, dorsally whitish, margins inflexed and clasped together, or more usually, reflexed along edges and exposed as 2 narrow white 'lips' along length of thallus. *Branches* once to several times symmetrically or asymmetrically furcate, closely to moderately divergent, linear to narrowly ovate, 5–10 × 0.8–1.5 (–2) mm, 0.5–0.8 mm thick, in section 1.5–2.0(–2.5) times wider than thick, apex somewhat wedge-shaped to rounded, shortly emarginate; groove narrow and deep along dorsal face, persisting into proximal parts, thallus margins acute, raised, to shortly winged, hyaline, wavy; flanks vertical to sloping steeply, basally dull brown to deep violet or dark red, toward margins white to yellowish; ventral face gently rounded, entirely purple or green, with faint brown transverse bands of vestigial scales. *Scales* not conspicuous, up to 800 × 550–650 µm, projecting ± 60 µm above thallus margins, rounded, fragile, imbricate, with hyaline border of 5 or 6 cell rows above brown to deep violet-red base.



MAP 21.—● **Riccia atropurpurea**
❑ **R. sorocarpa**

Dorsal epithelium bistratose, hyaline, upper layer of cells globose, 22–25(–35) × 25–37 µm, occasionally covered with fine deposit of salts, soon collapsing and cup-shaped, second layer of cells short-rectangular, 27–35 × 25–30 µm, sometimes elongating near margins, upper and lateral walls somewhat thicker, gradually thinning toward base; air pores triangular, occasionally rectangular. *Assimilation tissue* 250–400 µm thick, consisting of vertical columns of 5–8 short-rectangular cells, enclosing narrow 4-sided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air canals; storage tissue occupying ventral part of thallus, cells rounded, irregularly arranged. Figure 45.

Asexual reproduction sometimes by forming small, round, perennating bulbils ventrally.

Monoicous. *Antheridia* with prominent hyaline necks, 200–300 µm long, in 1 or 2 rows along dorsal groove. *Archegonia* with purple-brown necks. *Sporangia* single or in groups of 2 or 3, overlying dorsal tissue becoming white and disintegrating, often exposing a row of sporangia in longitudinal hollow. *Spores* 75–105 (–120) µm diam., subglobular but generally polar, reddish when young, colour deepening to dull, dark brown, opaque; wing absent, periphery crenulate or papillate; ornamentation reticulate and the same on both faces; distal face, with 10–12(–14) alveoli across diam., 7.5–12.5 µm wide, rounded or angular, alveolar walls low, smooth, sometimes slightly sinuous, raised at nodes and projections more pronounced over centre; proximal face without triradiate mark, mostly with flattened contact marks left by sibling spores when still in tetrads, each facet with 25–30 alveoli. *Chromosome number*: n = 8 (Bornefeld 1984); 16 (Bornefeld 1989; the latter diploid karyotype is reported by Bornefeld to be eudiploid, i.e. each of the chromosomes in the basic set of 8 has doubled, which he regards as unique in *Riccia*). Plate 20A, B; Perold (1989e: fig. 8.1–6).

Riccia atropurpurea is known from collections in Angola, Ghana, Malawi, Nigeria, Rwanda, Tanzania, Uganda, Zambia and Zimbabwe. In the *FSA* area, the species is common and frequently found in Namibia, Botswana, Northern Province, North-West, Gauteng, Mpumalanga, Swaziland, KwaZulu-Natal, Free State, Northern Cape and eastern part of Eastern Cape on shallow, fine sandy or clayey soil overlying granite, quartzite or sandstone outcrops. It has not so far been collected in the Western Cape. Map 21.

The specimen, *Sim 8112 (PRE-CH1023)*, was selected as lectotype (Perold 1991c) because it was numbered (on the label) and cited by Sim (1926) and because it closely matches the protologue. The other specimens from Wellington and Rosetta, KwaZulu-Natal, that were cited by him, could not be traced.

A broad species concept is adopted here to accommodate the wide range of variation in thallus size and shape. In crowded, overgrown patches, the branches are long, narrow and linear; in damp areas with a sufficient supply of nutrients, or when scattered, the branches are more robust, wider and ovate; under xeric conditions plants are often small and stunted, with the scales nearly black at the base. It is thus a very plastic species and its identification can sometimes be problematic; the grey-green dorsal colour and hyaline, wavy margins of the thallus should, however, help to place it. *R. atropurpurea* is similar to the tropical African species, *R. lanceolata* Steph., which also has hyaline thallus margins; its spores, however, are winged and have a distinct triradiate mark on the almost plain to incompletely reticulate proximal face. Occasionally, in some specimens of *R. atropurpurea*, e.g. in *S.M. Perold 136, 396*, the pattern of spore ornamentation appears to be intermediate between the two species. Jones made the same observation in notes on *Gittins 24* (ex Herb. Jones!), except that he had referred specimens of *R. atropurpurea* to *R. rhodesiae* (see notes under *R. congoana*). *R. lanceolata* is generally a more robust plant than *R. atropurpurea.*

Arnell (1963a) remarked that the thallus of *R. atropurpurea* has the same appearance as the European *R. nigrella* DC. (no. 26), but this is hardly so, as the latter soon turns brown dorsal-

FIGURE 45.—**Riccia atropurpurea.** A, B, thallus: A, dry; B, wet. C, ventral face of branch; D, c/s branch at intervals from apex to base. E, epithelial cells as seen from above, on left intact, on right collapsed; F, c/s cells at thallus margin; G, c/s epithelial and assimilation tissue cells, top left epithelial cells intact, on right collapsed, subdorsal cells partly thicker-walled; H, scale. A, *S.M. Perold 1087*; B, F, *S.M. Perold 1241*; C, *S.M. Perold 2005*; D, *S.M. Perold 1376*; E, *S.M. Perold 397*; G, *S.M. Perold 197*; H, *S.M. Perold 124*. Scale bars: A–D, 1 mm; E–G, 50 µm; H, 100 µm. Artist: J. Kimpton.

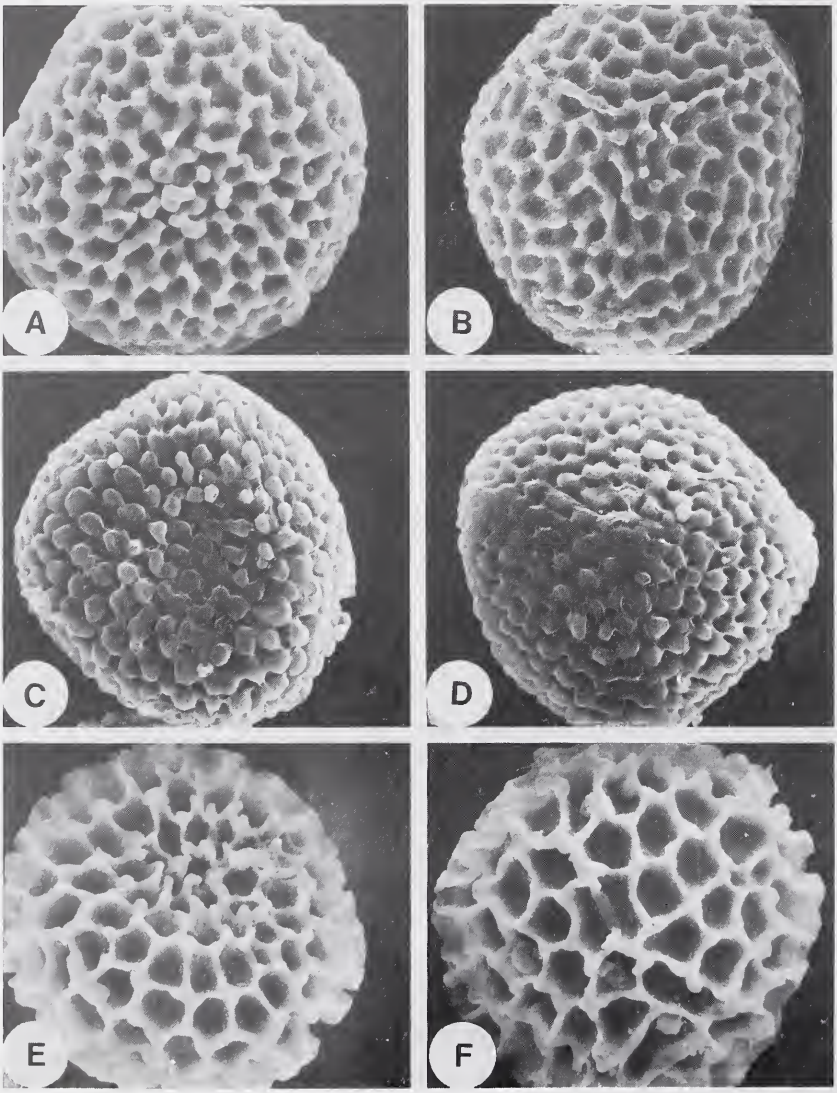


PLATE 20.—Spores. A, B, **Riccia atropurpurea**: A, distal face; B, proximal face. C, D, **R. okahandjana**: C, distal face; D, proximal face. E, F, **R. congoana**: E, distal face; F, proximal face. A, *S.M. Perold 782b*; B, *Volk 84/710*; C, D, *Volk 88/005*; E, F, *S.M. Perold 394*. A–F, × 600.

ly, is decidedly smaller and has shiny black scales; the spore ornamentation is also different.

Vouchers: *Glen 1377* (PRE); *Nicholas 2159* (PRE); *S.M. Perold 170, 206* (PRE); *Van Rooy 1831* (PRE).

22. **Riccia okahandjana** *S.W.Arnell* in Mitteilungen der Botanischen Staatssammlung, München 16: 268 (1957); S.W.Arnell: 32 (1963a); Perold: 32 (1991c); Perold: 60 (1993d). Type: Namibia: Bez. Otjiwarongo: Okosongomingo, *Volk 11944* (*PRE-CH4233*) [PRE, lecto.!, selected by Perold (1991c)].

Thalli medium-sized, in crowded gregarious patches or in rosettes, 15–30 mm across; green to glaucous-green, sometimes blotched with violet, black scales projecting vertically above margins; when dry, dorsally yellowish green, mostly hidden by tightly inflexed sides covered with shiny black scales. *Branches* simple or once or twice to several times symmetrically or asymmetrically furcate, narrowly to moderately divergent, linear to ligulate or narrowly ovate, 5–8(–10) × (1.2–)1.5–1.8 mm, 0.8–1.0 mm thick, in section 1.5 times to twice wider than thick, apex rounded, shortly emarginate; groove narrow and deep distally, shallow and wider proximally, disappearing toward base, thallus margins subacute to acute; flanks steep, covered by black scales; ventral face gently rounded to almost flat, green or with purple bands across. *Scales* conspicuous, 400–600 × 350–450 µm, projecting 100–250 µm above thallus margins, rounded to oblong, margin crenate, imbricate, shiny black, often hyaline toward base and rarely to margin, partly covering next distal scale, giving flanks a somewhat 'striped' appearance when dry. Plate 18B.

Dorsal epithelium bistratose, upper layer intact only when young, cells conical or somewhat elongated and sometimes slightly constricted in the middle, dumbbell-shaped, hyaline, 22–40 × 20–25 µm, soon collapsing, second layer of cells also without chloroplasts, 32–45 × 32–50 µm; air pores mostly triangular, small. *Assimilation tissue* ± 350 µm thick, consisting of vertical columns of 6 or 7(8) isodiametric to short-rectangular cells enclosing narrow, 4-sided air canals; storage tissue occupying ventral part of thallus with rounded cells, irregularly arranged. Figure 46.

Monoicous. *Antheridia* with hyaline necks, in 1 or 2 rows along dorsal groove. *Archegonia* with purple necks projecting 80–100 µm, scattered singly along median part of thallus. *Sporangia* single or 2(3) serially arranged, causing slight bulging of overlying dorsal tissue, which gradually disintegrates, leaving clean-edged, deep, round hollows filled with spores. *Spores* 92–110(–120) µm diam., triangular-globular, polar, straw-coloured or golden brown, semitransparent; wingless, perforated at marginal angles, margin crenulate; ornamentation densely papillate, the same on both faces, papillae blunt, smooth, rounded, up to 5 µm high and 7.5 µm wide, discrete or several joined together to form short vermiculate ridges, separated by narrow grooves or obscuring small round alveoli; distal face convex; proximal face without distinct apex or triradiate mark, but with flattening of 3 facets, caused by earlier pressure from sibling spores. *Chromosome number*: n = 8 (Bornefeld 1984; 1989). Plate 20C, D; Perold (1989e: fig. 9.1–6).

Riccia okahandjana has been found in Angola, Malawi, Mozambique, Rwanda, Tanzania, Uganda, Zaïre and Zimbabwe (Perold 1995b). It was recently also reported from the Arabian Peninsula (Frey & Kurschner 1988). In the *FSA* area the species is common and widespread, occurring in Namibia, Botswana, Northern Province, North-West, Gauteng, Mpumalanga, Swaziland, KwaZulu-Natal, Free State, Northern and Eastern Cape, on shallow soil overlying granite, quartzite, basalt or sandstone or on clayey soil. Map 22.

Arnell (1957) cited 15 specimens collected by Volk, not indicating which particular one he regarded as the type. The specimen, *Volk 11944* (*PRE-CH4233*), was selected as lectotype by Perold (1991c), because it closely matches the protologue.

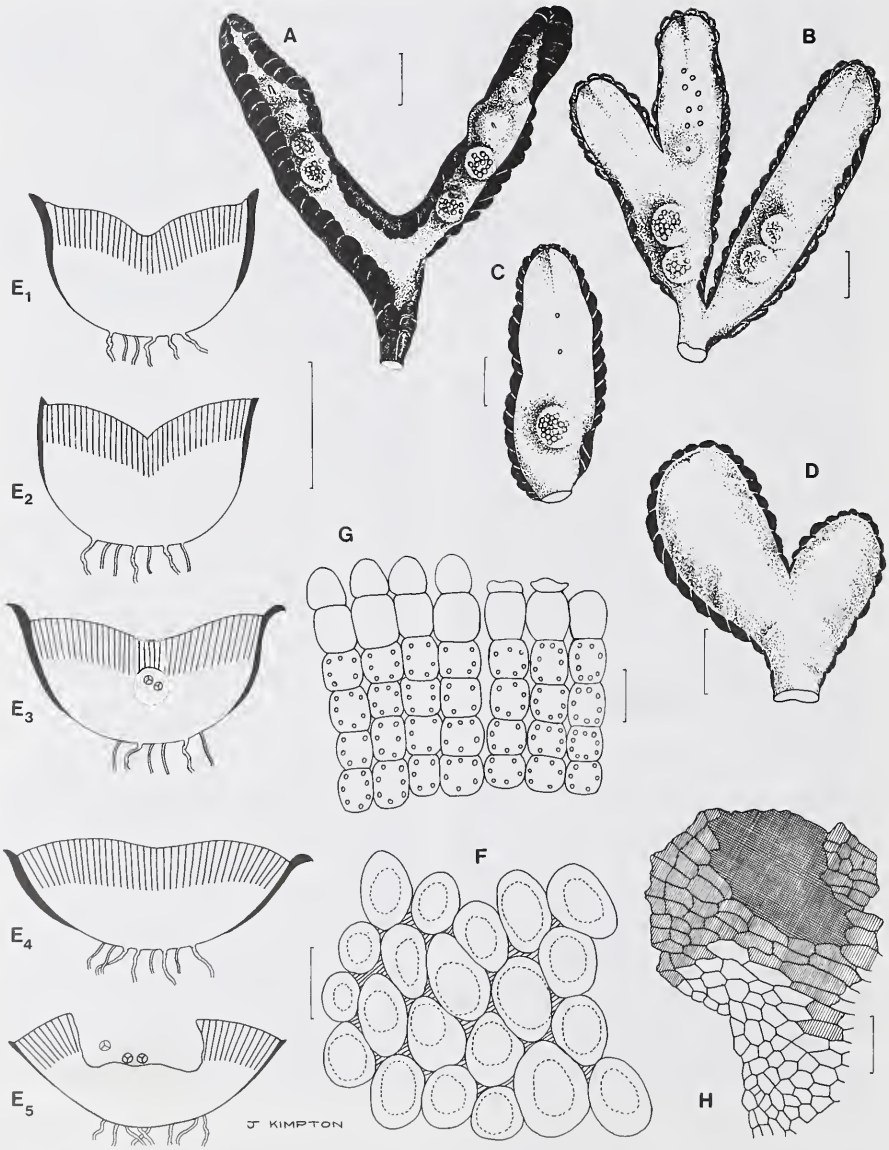
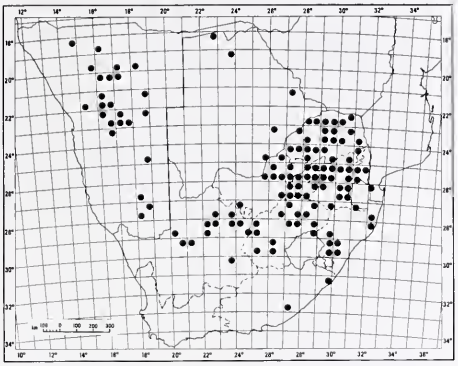


FIGURE 46.—**Riccia okahandjana**. A, B, D, thallus: A, dry; B, D, ventral face. C, wet branch; E, c/s branch at intervals from apex to base; F, epithelial cells and air pores from above; G, c/s showing epithelial cells, bistratose on left, top cells collapsing and unistratose on extreme right; H, scale. A, B, E, *S.M. Perold 1041*; C, F, G, *S.M. Perold 1365a*; D, *H. Anderson PRE-CH13443*; H, *S.M. Perold 315*. Scale bars: A–E, 1 mm; F, G, 50 µm; H, 100 µm.



MAP 22.—● **Riccia okahandjana**

Riccia okahandjana can be distinguished most readily from the other four *Riccia* species with shiny black scales, that also occur in southern Africa, by its light brown, papillate spores. Its thalli are generally smaller than those of *R. congoana* (no. 23), *R. limbata* (no. 24) and *R. angolensis* (no. 25) and larger than those of *R. nigrella* (no. 26). Although some specimens of *R. limbata* are of a similar size, its distribution is confined to the Northern and Western Cape (Map 23) and it frequently develops purple blotches dorsally, which are quite rare in *R. okahandjana*. Occasionally some specimens, notably *S.M. Perold 739*, *2594*, have scales with a wide hyaline border. In cross section, *R. okahandjana* has steep flanks and its scales are vertically arranged when the thallus is turgid. In dry plants, the inflexed margins and flanks covered by black scales, often have more soil particles clinging to the scales than in *R. angolensis* and *R. limbata*, but they are not nearly 'buried' as in *R. congoana*.

Vouchers: *Ellis PRE-CH4510* (PRE); *Leistner 3560* (PRE); *S.M. Perold* 110 (PRE); *Smook 4571* (PRE); *Volk 987* (PRE).

23. **Riccia congoana** *Steph.* in Bulletin l'Herbier Boissier 6: 328 (1898); E.W.Jones: 226 (1957); Perold: 193 (1986b); Perold: 33 (1991c). Type: Fr. Equatorial Africa (Congo), Forêt de Ceseles, *M. de F. Voz s.n.* (G, holo.!).

R. rhodesiae S.W.Arnell: 313 (1952); S.W.Arnell: 29 (1963a). Type: Zimbabwe (S. Rhod.), Victoria Falls, on soil nr Trolley Junction, *S.W. Arnell 1291* p.p. (S!; BOL!; PRE!).

R. berriei E.W.Jones: 224 (1957). Type: Nigeria, St Anne's Churchyard, Kudeti, Ibadan, *Berrie 1956* [not seen by me, but placed in synonymy under *R. nigrosquamata* by Berrie (1975)].

R. nigrosquamata E.W.Jones: 222 (1957). Type: Tanzania (Tanganyika), Lighthouse Island, Dar-es-Salaam Harbour, *Jones 699* (BM, holo.; Herb. Jones, iso.!).

R. aegyptiaca S.W.Arnell: 9 (1963b). Type: Egypt (Egyptian-Sudanese border), Gebl. Elba Dist., Wadi Aideib, *M. Kassas s.n.* (S, holo.!; CAI, iso.).

R. limbatoides, nom. prov., O.H.Volk: 58 (1984b). Namibia (South West Africa), Grootfontein, Farm Gaikos, *Volk 00747* (M, PRE!).

Thalli large to very large, scattered or in irregular, partial rosettes 25–30 mm across; bright green to bluish or greyish green, occasionally with irregular, white patches, black scales forming a narrow scalloped border; when dry, margins inflexed, with large, shiny black or deep reddish purple scales usually meeting along midline and covering all, or most of dorsal face. *Branches* once or twice symmetrically furcate, closely to widely divergent, oblong or obovate, narrowing proximally, 6–12(–15) × (2–)3–4(–5) mm, (0.65–)0.75–0.90(–1) mm thick, in section 3–5 times wider than thick, apex rounded, obtuse, slightly emarginate; groove distally narrow and deep with convex sides, proximally shallow to almost flat, thallus margins acute, attenuate, overhanging; flanks sloping obliquely; ventral face green, slightly rounded to convex. *Scales* large, 750–900 × 800 µm, projecting 200–250 µm beyond thallus margins, stiff, imbricate, crescent-shaped to rounded, margin crenate, borne mostly on ventral side of thallus wings, black or deep purple-red, shiny but sometimes duller, base often hyaline. Plate 18C.

Dorsal epithelium unistratose, cells globose or dome-shaped, 30–40 × 30–35 µm, hyaline, outer walls soon collapsing; air pores mostly 4-sided. *Assimilation tissue* 250–300 µm thick, consisting of vertical columns of 6 or 7(8) cells, enclosing narrow air canals; storage tissue occupying ventral part of thallus, cells angular to round, variable in size. Figure 47.

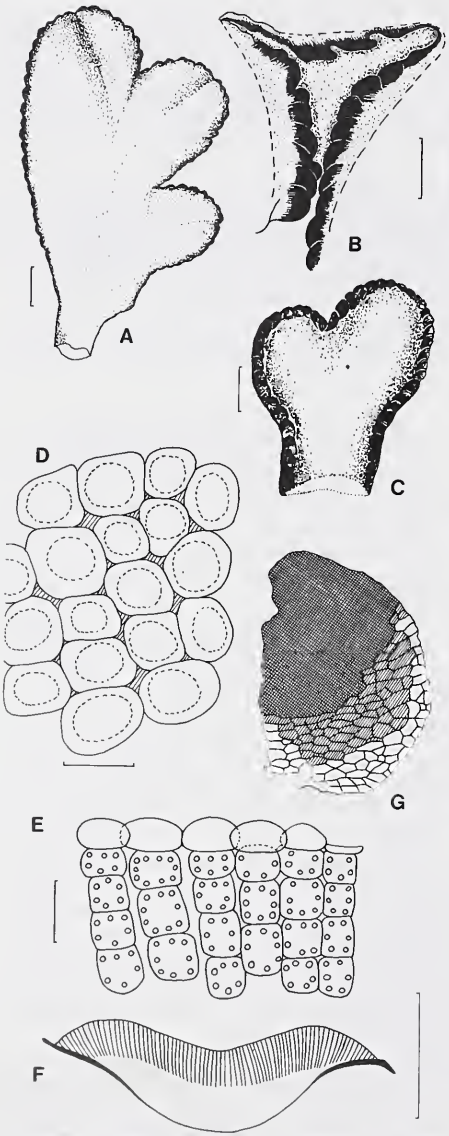
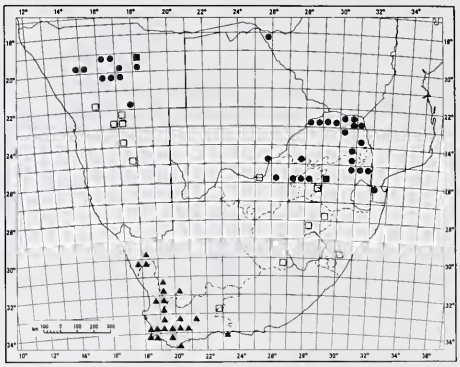


FIGURE 47.—**Riccia congoana**. A, B, thallus: A, wet; B, dry. C, ventral face of furcating branch; D, epithelial cells and air pores from above; E, c/s epithelial and assimilation tissue cells; F, c/s branch; G, scale. A, *S.M. Perold 747*; B, D, E, *S.M. Perold 763*; C, G, *Volk 00978*; F, *Arnell 1332*. Scale bars: A–C, F, 1 mm; D, E, 50 µm; G, 100 µm. Artist: J. Kimpton.



MAP 23.—● **Riccia congoana**
▲ **R. limbata**
❑ **R. angolensis**

Monoicous. *Antheridia* in 1 or 2 rows along groove, prominent necks projecting up to 250 µm, hyaline, bases sometimes tinged with reddish pink. *Archegonia* scattered along groove, necks purple. *Sporangia* single, or several along groove, bulging dorsally, overlying tissue disintegrating and spores lying free in long, broad hollows. *Spores* 80–135 µm diam., subglobular, usually apolar, yellowish brown to reddish brown, semitransparent; without wing and triradiate mark; ornamentation regularly reticulate, the same on both faces, with 6–8(–10) angular alveoli across diam., 10–15(–17.5) µm wide, alveolar walls thin and delicate, often striate, 4–6 µm high, raised at nodes into slender, blunt projections. *Chromosome number*: n = 8 (Bornefeld 1984, for *R. limbatoides* nom. prov. in Perold 1986b). Plate 20E, F; Perold (1989e: fig. 17.1–6).

In Africa, *R. congoana* is known from Angola, Chad, Egypt, Ghana, Kenya, Malawi, Nigeria, Rwanda, Sierra Leone, Sudan, Tanzania, Uganda, Zaïre, Zambia and Zimbabwe (Perold 1995). It was also recently reported from Saudi Arabia (Frey & Kurschner 1988). In the *FSA* area, *R. congoana* occurs on sandy red soil, on black clay, on dolomitic or calcareous soil in Namibia, Botswana, Northern Province, North-West, Gauteng, Mpumalanga and Swaziland. Map 23.

Riccia congoana differs from the other black-scaled *Riccia* species in southern Africa by the large size of the green to blue-green thalli, very obliquely sloping flanks covered by large, shiny black or deep purple-red, generally crescent-shaped scales and by the subglobular, apolar spores with angular, thin-walled alveoli. Few of the plants from the *FSA* area were, however, found to have sporangia.

The type specimen of *R. rhodesiae*, *S.W. Arnell 1291*, is a mixed collection, consisting mostly of *R. atropurpurea* Sim (no. 21), which caused Jones (1957) to erroneously identify and describe the *R. atropurpurea* portion of the gathering as *R. rhodesiae*. It is probable that Arnell had not seen Stephani's specimens of *R. congoana* when he described as new the two species, *R. rhodesiae* (1952, 1963a), and *R. aegyptiaca* (1963b). He made no comparisons between them, although he referred to similarities and differences between *R. aegyptiaca* and other species of *Riccia*. *R. rhodesiae* and *R. aegyptiaca* are now considered to be conspecific and both are regarded as synonyms of *R. congoana* (Perold 1986b). Bapna & Kachroo (1975) have placed *R. berriei* and *R. nigrosquamata* in synonymy under *R. billardieri*, in which case, *R. congoana* would also become a synonym of *R. billardieri*. This needs to be investigated further, but hitherto, not enough material of authentically named specimens of *R. billardieri* has been available for study.

In the key to sub-Saharan African Ricciaceae (Perold 1996), the caption to Figure 11 (concerning *R. limbata* and *R. congoana*) is incorrect; the error was corrected in *Bothalia* 27: 239 (1997).

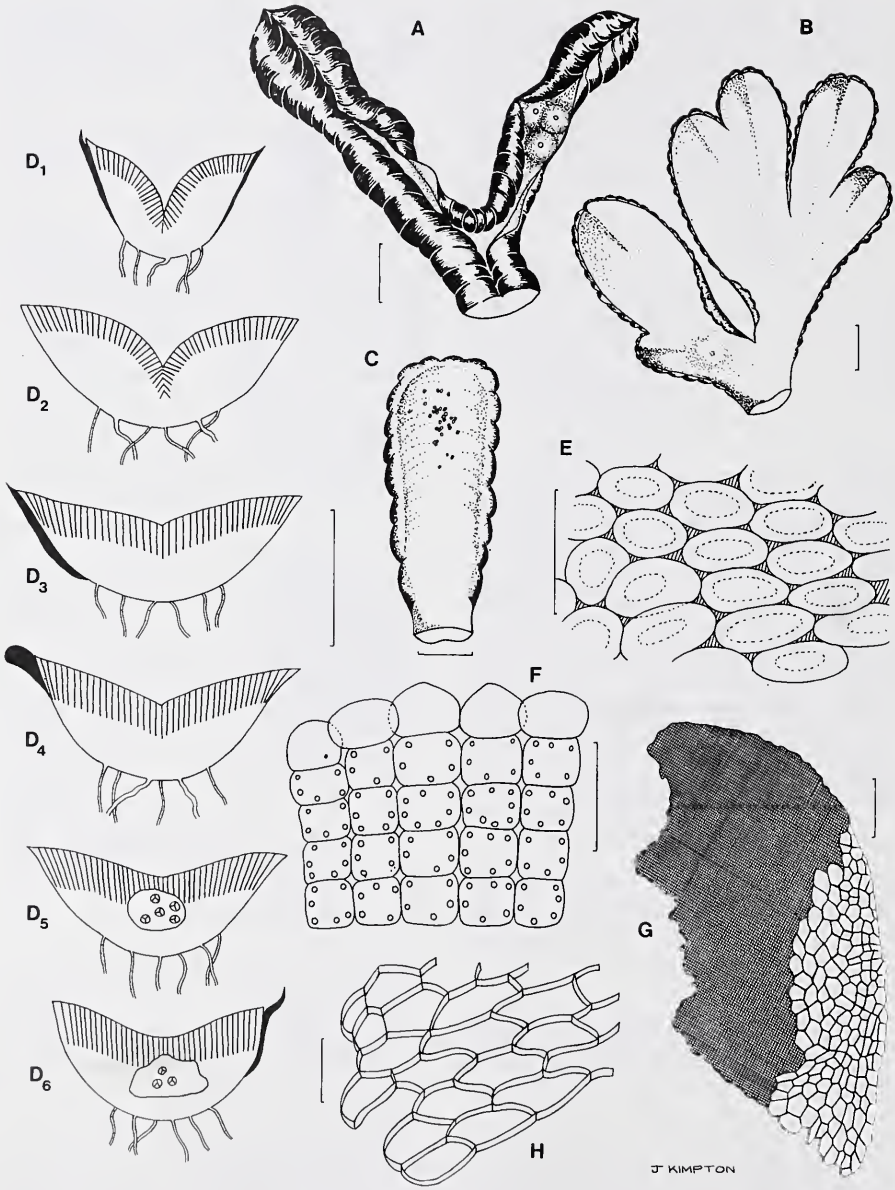
Vouchers: *Glen 1423* (PRE); *Hardy 6446* (PRE); *S.M. Perold 130, 394* (PRE); *Volk 00978* (M, PRE).

24. **Riccia limbata** *Bisch.* in Flora 29: 315 (1846); Gottsche et al.: 606 (1844–1847); Steph.: 326 (1898); Sim: 12 (1926); S.W.Arnell: 23 (1963a); Na-Thalang: 92 (1980); Perold: 34 (1991c). Type: Cape, CBS, in locis humidis ad latera Montium Tafelberg, Duyvelsberg et Leuvenberg, *Krauss s.n.*, Julio-1838 (*G13163*, holo.!).

R. capensis Steph.: 724 (1913). Type: Cape, Gnadenthal bei Caledon, *Brunnthaler s.n.*, Oct. 1909 [*G13334*, holo.! fide Grolle: 226 (1976); W (fide S.W.Arnell: 312 (1952), 'only sand in specimen packet'].

Thalli medium-sized to large, in loosely or densely crowded, gregarious patches, or scattered; bright green to light bluish green, often with purple blotches or almost entirely purple proximally and along margins, bordered by black scales; when dry, margins inflexed, with imbricate, shiny black scales meeting or tightly clasped together along midline, obscuring most of dorsal face. *Branches* simple or once or twice symmetrically or asymmetrically furcate, closely to moderately divergent, linear-ovate to obovate or obcuneate-oblong, narrower toward base, 10–12(–15) × 1.8–2.5(–3) mm, 0.6–1.0 mm thick, in section 2.5–4.0 times wider than thick, apex somewhat wider, rounded, shortly emarginate; groove narrow and deep distally, gradually flattening out over rest of thallus, disappearing altogether proximally, thallus margins acute, shortly attenuate; flanks sloping obliquely; ventral face gently rounded, green and streaked with purple or entirely purple. *Scales* large, 1000–1100 × 600–850 µm, projecting ± 200 µm above thallus margins, imbricate, oblong to rounded, appressed, stiff, shiny dark purple to black, toward basal margins hyaline to pale violet and fragile, cells in body of scale often with sinuate walls.

Dorsal epithelium bistratose apically and toward groove, hyaline, top layer of cells globose or mammillose, 35–40 × 25–30 µm, evanescent, subdorsal cells more or less barrel-shaped, 30–45 × ± 37 µm, ultimately forming uppermost layer; air pores triangular, small. *Assimilation tissue* 250–400 µm thick, consisting of vertical columns of 6 or 7(8) short-rectangular cells, enclosing narrow 4- or 5-sided air canals; storage tissue occupying remainder of thickness of thallus, cells angular, closely packed, ± 50 µm wide. Figure 48.


A
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D1
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J KIMPTON

Monoicous. *Antheridia* with prominent hyaline necks, in 1 or 2 rows along dorsal groove. *Archegonia* with purple necks, scattered along central part of thallus. *Sporangia* 3 or 4, serially arranged or crowded together in basal part of branches, dorsally bulging, covering tissue purple, gradually disintegrating. *Spores* 90–125 (–130) µm diam., triangular-globular, polar, chestnut-brown to dark brown, semitransparent; wing minutely papillate, up to 7.5 µm wide, marginal angles generally not perforated, margin entire; ornamentation partly reticulate, but different on the two faces; distal face convex, with 6–8 deep, round alveoli across central area of spore, 5 µm wide, walls thin, with slender, truncate projections at nodes, encircled by rows of papillae and short ridges spiralling outwards, with small, deep pores or fovea at their bases; proximal face with triradiate mark not sharply defined, small scattered pores or fovea on otherwise nearly smooth surface of all three facets, alveolar walls faint, visible only with light microscope and not with SEM. *Chromosome number*: n = 8 (Bornefeld 1989); n = 16 (Na-Thalang 1980). Plate 21A, B; Perold (1989e: fig. 11.1–6).

This species was also reported from Australia by Na-Thalang (1980). However, Jovet-Ast (pers. comm. 1997) is of the opinion that the Australian species is *R. inflexa* Taylor, rather than *R. limbata*, but states that they have a close affinity. In southern Africa *R. limbata* only occurs in the winter rainfall shrublands of the Northern and Western Cape on clayey or damp, sandy soil or on mud. Contrary to Arnell's (1963a) observation that *R. limbata* prefers drier areas, it has frequently been collected at seepages. Map 23.

Riccia limbata can be distinguished from other southern African *Riccia* species with shiny black scales by its generally more 'fleshy' thallus, especially toward the apex and, more reliably, by its quite large spores, up to 130 µm diam., and ornamented on the nearly smooth proximal face by fovea and on the distal face, by spiralling ridges surrounding the central alveoli. It is sometimes quite difficult to distinguish between sterile plants of *R. limbata* and *R. angolensis* (no. 25), but their geographical distribution areas do not overlap.

Sim (1926) referred to 'small' forms of *R. limbata*, which regularly grow in rosettes and are widespread in the northern provinces and in Namibia (South West Africa); he was clearly referring to *R. okahandjana* (no. 22). Best's (1990) report of *R. limbata* from Zimbabwe (*Best 2736*) obviously falls into this category.

Vouchers: *S.W. Arnell 597* (PRE); *Duthie PRE-CH1038* (PRE); *Garside 6276* (PRE); *Oliver 8858* (PRE); *S.M. Perold 1427* (PRE).

25. **Riccia angolensis** *Steph.* in Bulletin l'Herbier Boissier 6: 323 (1898); S.W.Arnell: 24 (1963a); Perold: 35 (1991c). Type: Angola, Dist. Huilla, de Serra de Oiahoia prope Humpata, *Welwitsch 255*, Mais 1860 (BM, holo.!).

R. pseudolimbata S.W.Arnell: 270 (1957). Syntypes: South West Africa/Namibia, Bez. Marienthal, Haribes, feuchte schattige Uferböschung, *Volk 12409* (M), *12412, 12413, 12462* p.p. (M, PRE).

Thalli medium-sized, in crowded, gregarious, occasionally overlying patches, or scattered; bright green to yellow-green, often with some purple coloration, black scales along margins; when dry, pale green with purple blotches, partly, or sometimes apically, completely covered by inflexed margins, exposing imbricate to more distantly spaced purple-black scales. *Branches* once or twice symmetrically or asymmetrically furcate, moderately to widely divergent, obovate to ovate, or often somewhat irreg-

FIGURE 48.—**Riccia limbata**. A, B, thallus: A, dry; B, wet. C, ventral face of branch; D, c/s branch at intervals from apex to base; E, epithelial cells and air pores from above; F, c/s epithelial and assimilation tissue cells; G, scale; H, cells in body of scale with sinuate walls. A, F, *S.M. Perold 583*; B, D, E, *E. Retief 1235*; C, G, H, *Oliver 8042*. Scale bars: A–D, 1 mm; E, F, H, 50 µm; G, 100 µm. Artist: J. Kimpton.

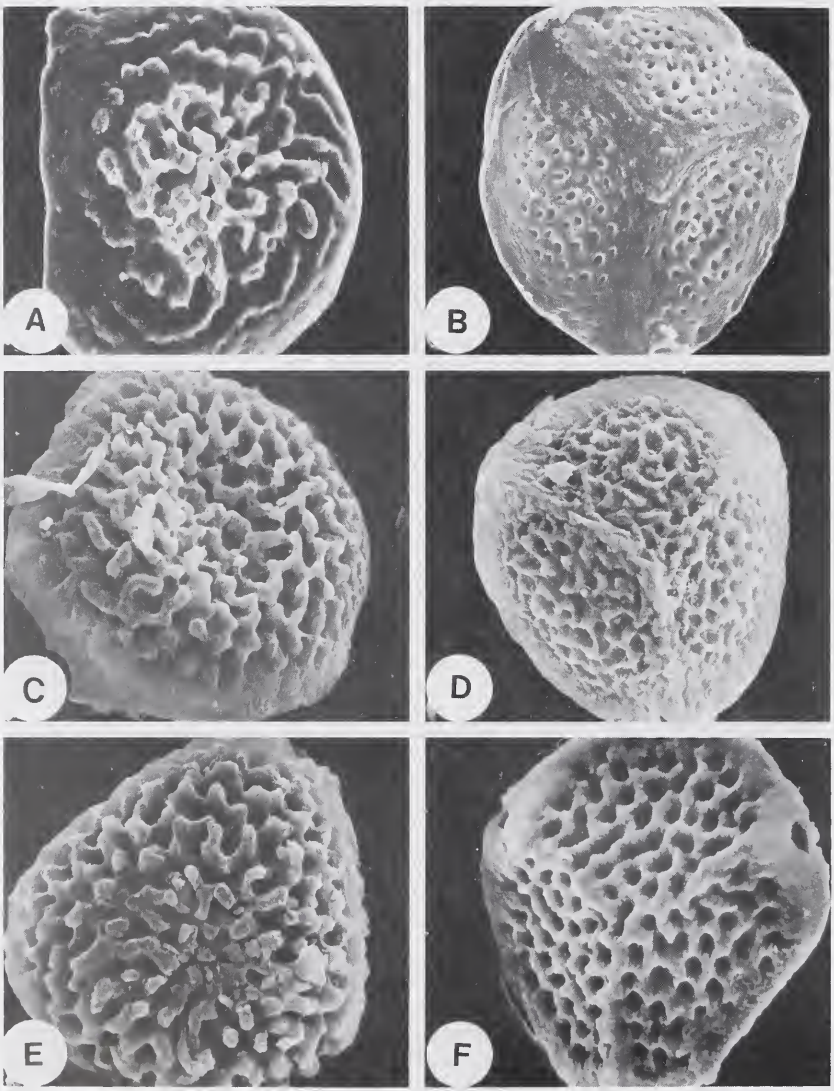


PLATE 21.—Spores. A, B, **Riccia limbata**: A, distal face; B, proximal face. C, D, **R. angolensis**: C, distal face; D, proximal face. E, F, **R. nigrella**: E, distal face; F, proximal face. A, *S. Arnell 67a*; B, *Garside 6276*; C, *E. Retief 1543a*; D, *S.M. Perold 1275*; E, *Duthie 5023a*; F, *S.M. Perold 1147*. A, D, × 700; B, × 600; C, E, F, × 800.

ularly shaped, quickly narrowing toward base, 8–10(–12) × 2–3(–4) mm, 0.5–0.75(–1) mm thick, in section 4(–5) times wider than thick, apex subacute to rounded, emarginate; groove distally narrow and deep, proximally wider and shallower, dorsal face flat to slightly concave, thallus margins acute to shortly attenuate; flanks sloping obliquely; ventrally slightly rounded to flattish, green, occasionally flecked with violet. *Scales* large, 600–850 × 375–550 µm, projecting ± 200 µm beyond thallus margins, crescent-shaped to rounded, appressed, mostly borne ventrally, imbricate apically, more distantly spaced proximally, shiny, deep purple-red to black, base often partly or mostly hyaline proximally.

Dorsal epithelium bistratose when young, upper layer of cells hyaline, dome-shaped to globose, occasionally mammillose to broadly conical, 32–42 × 45–60 µm, soon collapsing, subdorsal cells isodiametric to wider than long, 37–50 × 55–67 µm, sides slightly bulging; air pores triangular, small. *Assimilation tissue* 250–350 µm thick, consisting of vertical columns of 6 or 7(8) short-rectangular cells, enclosing narrow, 4-sided air canals; storage tissue occupying ventral part of thallus, cells irregularly arranged. Figure 49.

Monoicous. *Antheridia* with thick hyaline necks, 150 µm long, in 1 or 2 rows along dorsal groove. *Archegonia* with short purple necks, scattered along median part of thallus. *Sporangia* serially arranged along length of branches, dorsally bulging, overlying tissue gradually thinning and disintegrating, leaving spores exposed in shallow hollows. *Spores* 72–82(–95) µm diam., triangular-globular, polar, pale straw-coloured to light brown, semitransparent; wing 5 µm wide, slightly wider at perforated or notched marginal angles, smooth to sparsely papillate, margin entire or crenulate; ornamentation reticulate on both spore faces, but different; distal face convex to slightly flattened, or sometimes indented in centre, with 10–12 irregularly shaped, deep-set alveoli across diam., usually arranged in more or less concentric rings, central alveoli ± 7.5 µm wide, walls raised into tall projections at nodes, marginal alveoli smaller and with lower projections; proximal face with triradiate mark distinct, sometimes interrupted, coarsely papillate, alveoli irregular in shape and size, 2.5–7.5 µm wide, complete or incomplete, walls slightly raised at nodes, toward wing sometimes lightly sprinkled with papillae. *Chromosome number*: n = 8 (Bornefeld 1984). Plate 21C, D; Perold (1989e: fig. 10.1–6).

This species has been reported from Angola, Kenya and southern Africa. In the *FSA* area it has been relatively rarely collected in Namibia, Botswana, Gauteng, Mpumalanga and Free State, but only once in each of the following: Lesotho, KwaZulu-Natal and Western Cape. It grows on clayey or on sandy, alluvial soil, usually in damp places such as seepages and riverbanks. Map 23.

Riccia angolensis differs from the other black-scaled species of *Riccia* from southern Africa by its generally rather thin thalli and sometimes irregularly shaped branches. The spacing and pigmentation of the scales are affected by shady, wet conditions, when the scales become more distantly spaced and mostly hyaline, except for the margins which remain dark. Its spores are distinguished from those of *R. limbata* (no. 24) (with which *R. angolensis* has sometimes been confused, because it also has shiny black scales), by the more roughened ornamentation of the proximal face and the more or less concentric arrangement of the alveoli on the distal face.

Arnell (1957, 1963a) incorrectly described and illustrated the thallus margins as obtuse, whereas Stephani (1898) stated them to be 'angulis longe acuminatis, acutis'.

Vouchers: *Duckett s.n.* (PRE); *Hansen 3459* (PRE); *S.M. Perold 1275* (PRE); *E. Retief 1235* (PRE); *Smook 5897* (PRE); *Volk 5049* (M, PRE).

26. **Riccia nigrella** *DC.* in DC. & Lam. in Flore Française 6: 193 (1815); Lindenb.: 466 (1836); Nees: 390, 417 (1838); Gottsche et al.: 605 (1844–1847); F.A.Camus: 212 (1892);

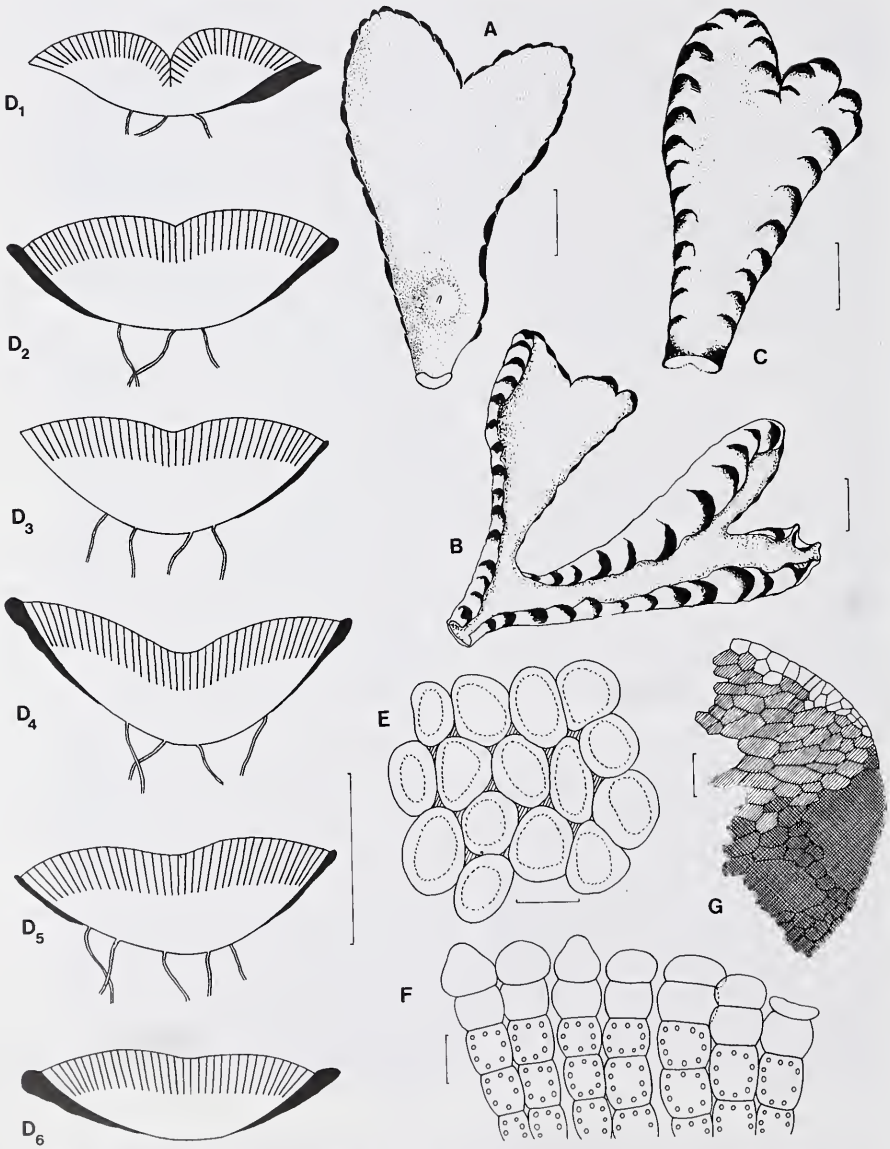


FIGURE 49.—**Riccia angolensis**. A–C, thallus: A, wet; B, dry; C, ventral face. D, c/s branch at intervals from apex to base; E, epithelial cells and air pores from above; F, c/s bistratose epithelial cells, top cells collapsing toward the right; G, scale. A, B, *Magill 6371a*; C, *Volk 01287*; D, *S.M. Perold 1354*; E, F, *S.M. Perold 1276*; G, *E. Retief 1543*. Scale bars: A–D, 1 mm; E, F, 50 µm; G, 100 µm. Artist: J. Kimpton.

Steph.: 334 (1898); M.Howe: 28 (1899); N.J.Boulay: 210 (1904); Casares-Gil: 220 (1919); Frye & L.Clark: 21 (1937); Müll.Frib.: 465 (1951–1958); Na-Thalang: 93 (1980); Jovet-Ast: 323 (1986); Perold & O.H. Volk: 43 (1988b); Perold: 36 (1991c); Jovet-Ast: 240 (1991); R.M.Schust.: 583 (1992b). Type: France, Dept. de l'Héraut, in Sylvula Grammont prope Monspessulanum, *Bouchet 1807* (PC, holo., fide Jovet-Ast: 323 (1986); *G23307*, iso.!).

R. pearsoni(i) Steph.: 335 (1898). Type: North Wales, Barmouth, *Pearson*, May-1885 (S!).

R. capensis auct. non Steph., S.W.Arnell: 312 (1952); S.W.Arnell: 28 (1963a). Types: Cape Province, Peninsula, Lion's Head above Fresnaye, *Arnell 59* (S); Wynberg, cultivated ground, Park Hotel, *Arnell 162* (BOL!).

Thalli small to medium-sized, in complete or incomplete rosettes, 8–15 mm across, or scattered; glaucous green to green, rust-brown along margins and toward base; when dry, margins tightly inflexed and clasped together, with shiny, black-scaled sides covering most of dorsal face. *Branches* simple or once or twice furcate, narrowly to moderately divergent, oblong to linear-ovate, up to 5 mm, rarely to 8.0 × 0.5–1.0 mm, 0.5–0.6 mm thick, in section as wide as thick, to twice wider than thick, apex rounded or subacute, emarginate; groove narrow and deep along length of branches, sides convex, thallus margins acute, slightly recurved, becoming somewhat obtuse toward base; flanks steep, covered by closely appressed, shiny black scales; ventral face rounded, green, often flecked with brown or purple. *Scales* ± 550 × 450 µm, not projecting above thallus margins, semilunar, appressed, imbricate, shiny violet-black, at mostly entire margin, dark-coloured and hyaline cells occasionally alternating irregularly.

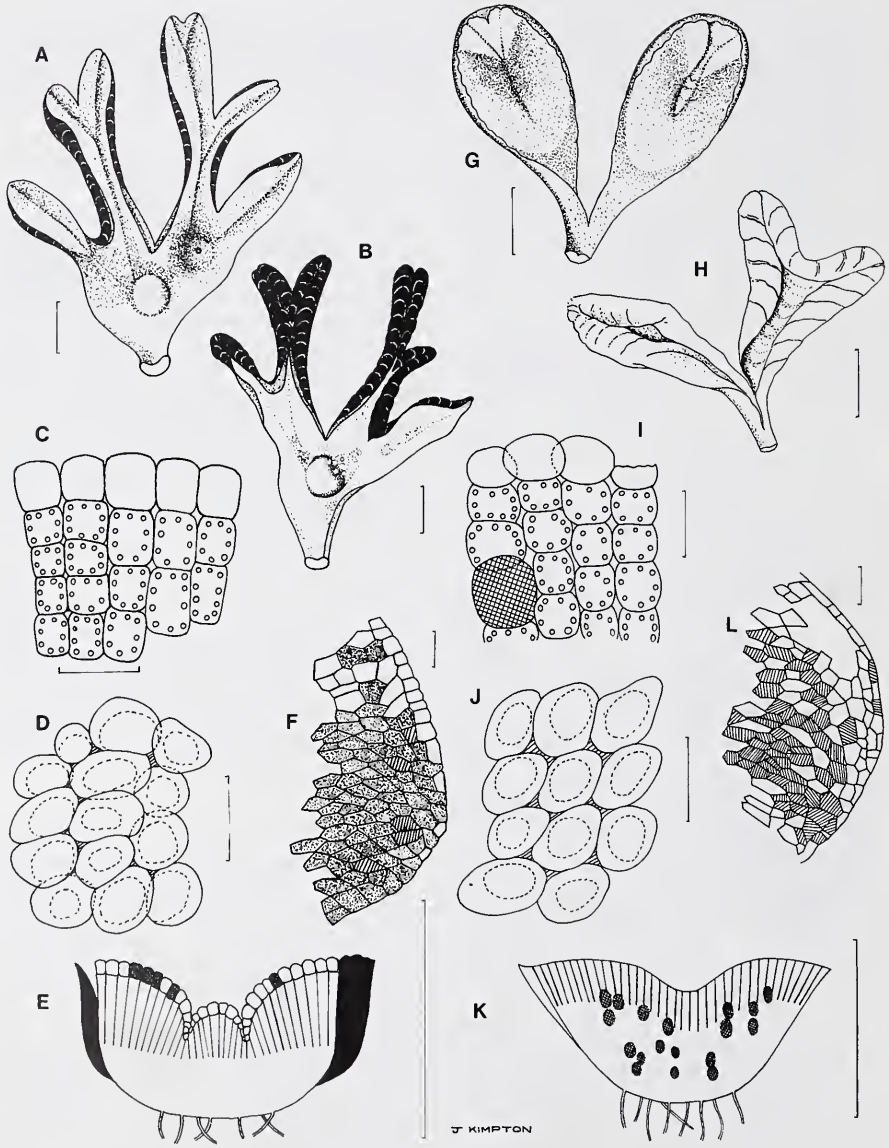
Dorsal epithelium unistratose, cells short-rectangular or subquadrate, upper surface nearly flat to slightly rounded, persistent, hyaline or often with metachromatic contents, 25–35 × 25–32 µm; air pores generally triangular, small, 7.5 µm wide. *Assimilation tissue* 250–325 µm thick, consisting of compact vertical columns of 6–10 mostly isodiametric cells [rarely a few cells enlarged, with hyaline or brownish contents (idioblasts)], enclosing narrow, 4-sided air canals; storage tissue occupying ventral part of thallus, cells closely packed, angular, ventral epidermal cells often brown or violet. Figure 50A–F.

Vegetative propagation and survival are by small, round, perennating bulbils.

Monoicous. *Antheridia* with prominent hyaline necks, along groove. *Archegonia* with purple necks. *Sporangia* bulging dorsally, covering tissue dark brown, occupying nearly the whole width of thallus, in a row or crowded together, spores extruded, forming overlying clumps when capsules disintegrate. *Spores* 62–87 µm diam., triangular-globular, polar, light brown to dark brown, semitransparent to opaque; wing narrow, 2.5–5.0 µm wide, notched or perforated at angles, margin finely crenulate; ornamentation incompletely reticulate, somewhat dissimilar on 2 faces; distal face with 10–12 incomplete, irregularly shaped alveoli across diam., or vermiculate, with thickened, short, sinuous ridges with fine granules or papillae; proximal face with triradiate mark distinct, its arms wider at juncture with wing, ± 30 small alveoli on each of 3 facets, ridges thick, slightly raised at nodes. *Chromosome number*: n = 8 (Bornefeld 1984; Jovet-Ast 1986). Plate 21E, F; Perold (1989e: fig. 12.1–6).

Riccia nigrella is nearly cosmopolitan in its distribution and is found in all Mediterranean countries as well as in Wales, Cornwall, the Channel Islands, the Macaronesian Islands, North America and in Australia. In the *FSA* area, *R. nigrella* occurs quite rarely in the summer rainfall parts of North-West, Gauteng, Mpumalanga, KwaZulu-Natal, Free State, Lesotho, the south-eastern part of Northern Cape and Eastern Cape, but it is fairly common in the winter rainfall areas of the western part of Northern Cape and Western Cape, extending to the southern part of Namibia. It grows on shallow, sandy soil, overlying rock outcrops. Map 24.

The species can be distinguished from the other southern African species with shiny black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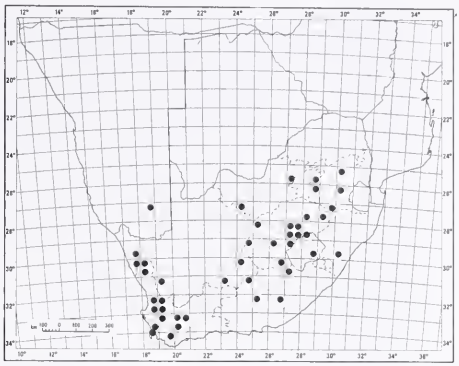
scales, by its generally smaller size, by scales that are closely appressed and do not extend above the thallus margins and by the dark brown dorsal colour of the thallus. It bears some resemblance to a small *R. macrocarpa* (no. 27) (see note under that species), which is also brown dorsally, and occasionally has a few idioblasts in the inner tissues. The dorsal and ventral epithelial cells of *R. nigrella*, however, frequently contain hyaline or brownish metachromatic substances which stain blue with dilute aqueous solutions of Toluidine blue (Perold & Volk 1988b). Several other authors have commented on the affinity that the persistent dorsal epithelial cells have for certain stains (Howe 1899; Frye & Clark 1937; Na-Thalang 1980).



MAP 24.—● **Riccia nigrella**

Arnell mistakenly referred southern African collections of *R. nigrella* to *R. capensis* Steph. (Perold & Volk 1988b). An isotype specimen of the last-named, leg. *Brunnthaler* (W), which Arnell examined, consisted only of sand (Arnell 1952), but the cross sections of the thalli of his collections from the Cape, seemed to him (incorrectly, as has lately transpired), to be similar to Stephani's figures of *R. capensis* in his *Icones hepaticarum* (microfiche 1985). Arnell thus misapplied the name *R. capensis* Steph., although his description of the margins and the dorsal face of the thallus turning yellowish brown, the deep and sharp dorsal groove with convex sides and, in cross section, the rectangular to quadrate epithelial cells, indicate clearly that he was referring to *R. nigrella*. *R. capensis* Steph. has been placed in synonymy under *R. limbata* Bisch. (Perold & Volk 1988b).

Vouchers: *Arnell 150* (PRE); *Duthie 5340* (BOL); *Garside 6650* (BOL); *Örtendahl s.n.* (UPS); *S.M. Perold 150* (PRE); *Smook 4892a* (PRE).

27. **Riccia macrocarpa** *Levier* in Goiran, Bollettino della Società Botanica Italiana 5: 114 (1894); Steph.: 343 (1898); Müll. Frib.: 442 (1951–1958); Jovet-Ast: 318 (1986); Sérgio: 263 (1991); Perold: 37 (1991c). Type: Italy, Toscane, Poggio Santo Romolo, leg. *Levier s.n.*, 30 March 1888 (PC, syn.; S, isosyn.).

R. campbelliana M.Howe: 26 (1899); Frye & L.Clark: 20 (1937); Ladyz.: 316 (1967); Perold & O.H.Volk: 37 (1988a); Jovet-Ast: 239 (1991). Type: Calif., nr Stanford Univ., on hills above Mission Dolores, *D.H. Campbell s.n.*, May 1-1896 [NY, lecto.!, fide Grolle: 225 (1976)].

Thalli medium-sized, in crowded gregarious patches or in incomplete rosettes or scattered; pale green apically, yellow to rust-brown along margins and proximally; when dry, margins inflexed, forming brown 'lips', flanks with inconspicuous, brownish scales. *Branches* simple or once or twice symmetrically furcate, narrowly to moderately divergent, oblong-linear, up to 8 × 1.0–1.5(–2) mm, 0.7–0.8 mm thick, in section nearly as wide as thick, to twice wider than thick, apex rounded and obtuse, emarginate; groove deep, sides raised and convex,

FIGURE 50.—A–F, **Riccia nigrella**. A, B, thallus: A, wet; B, dry. C, c/s epithelial and assimilation tissue cells; D, epithelial cells and air pores from above; E, c/s branch, showing persistent epithelial cells, some with finely granular contents; F, scale. G–I, **R. macrocarpa.** G, H, thallus: G, wet; H, dry; I, c/s epithelial and assimilation tissue cells with one idioblast; J, epithelial cells and air pores from above; K, c/s branch showing some idioblasts (hatched); L, scale. A, B, *S.M. Perold 520*; C, F, *Van Rooy 2414*; D, *S.M. Perold 1322*; E, *S.M. Perold* 1147; G, H, K, *S.M. Perold 888*; I, *S.M. Perold 80*; J, *Van Rooy & Perold 634*; L, *Volk 81/024*. Scale bars: A, B, E, G, H, K, 1 mm; C, D, I, J, 50 µm; F, L, 100 µm.

flatter proximally, thallus margins acute, shortly winged, slightly undulating; flanks sloping obliquely, bronze-brown; ventral face rounded, green, occasionally flecked with red and brown. *Scales* inconspicous, ± 750 × 450 µm, not projecting above thallus margins, imbricate, fragile, cells at mostly entire margin hyaline, in rest of scale, groups of cells brown and different shades of violet, interspersed between single or groups of hyaline cells.

Dorsal epithelium unistratose, cells hyaline, subglobose when young, 30–45 × 35–50 µm, becoming flatter and wider laterally, collapsed at margins and proximally, brown; air pores triangular or rectangular. *Assimilation tissue* 325–400 µm thick, consisting of vertical columns of 6–10 cells and enclosing 4- or 5-sided air canals (some cells, idioblasts, differ from the rest by their larger size and contents); storage tissue occupying ventral part of thallus, cells rounded or angular, tightly packed, usually with some interspersed idioblasts. Figure 50G–I.

Monoicous. *Antheridia* with short hyaline or white necks, along dorsal groove. *Archegonia* with purple necks scattered along median part of thalli. *Sporangia* infrequent, single or crowded, overlying, bulging tissue turning brown. *Spores* 85–110(–120) µm diam., triangular-globular, polar, pale straw-coloured to brown, semitransparent; wing 5 µm wide, notched at marginal angles, margin mostly smooth; ornamentation on both faces vermiculate to irregularly and incompletely reticulate; distal face with 10–15 incomplete alveoli across diam., 5 µm wide, ridges often sinuous and raised into blunt papillae at nodes; proximal face with triradiate mark generally clearly defined and ridges somewhat lower than those on distal face. *Chromosome number*: n = 8 (Siler 1934; Bornefeld 1989). Plate 22A, B; Perold (1989e: fig. 13.1–6).

R. macrocarpa has been reported from southern Europe, Macaronesia, North Africa, Turkey, Israel, Western Siberia, North America and Brazil in South America (Jovet-Ast 1991). There is, however, some doubt whether the specimen, *Sleumer 1755* (*LIL19853*) from Argentina, has been correctly referred here (as *R. campbelliana*) (Perold & Volk 1988a). Schuster (1992a, b) has placed it in his new subspecies, *R. campbelliana* subsp. *austrigena*. In southern Africa, *R. macrocarpa* is rare in the grasslands of North-West, Gauteng, Mpumalanga, eastern Free State and Lesotho, where it grows on soil overlying granite, quartzite or sandstone rock outcrops. Map 25.

Riccia macrocarpa can be recognized by the yellow-brown colour along the thallus margins, by the inconspicuous scales, partly hyaline, partly flecked with brown and violet, and in sections of the thallus, by the presence of idioblasts, i.e. cells larger than surrounding ones and with clear or granular contents brown, grey or hyaline. The spore ornamentation of sinuous, vermiculate ridges on both faces is also a distinguishing character.

Although small plants of *R. macrocarpa* bear a superficial resemblance to *R. nigrella* (no. 26), they can still be readily identified by the usually wider and longer branches, the thinner, slightly attenuate margins and the epithelial cells that are not persistent; sporangia are also rather rare, whereas *R. nigrella* frequently sporulates, producing masses of extruded spores.

Vouchers: *S.M. Perold 888* (PRE); *S.M. Perold & Germishuizen 1307* (PRE); *Van Rooy & S.M. Perold 634, 637* (PRE).

28. **Riccia pottsiana** *Sim*, The Bryophyta of South Africa: 10 (1926); S.W.Arnell: 30 (1963a); Perold: 38 (1991c). Type: Orange Free State, Bloemfontein, near Eagle's Nest, *G. Potts 7003*, March 1917 [BOL, lecto.!, selected by Perold (1991c)].

Thalli very small to small, in incomplete or complete rosettes up to 7 mm across, or in gregarious patches; bottle-green to dark green, tumid; when dry, margins inflexed with regular, hyaline/white-bordered, dark purple-red scales covering most of dorsal face. *Branches* simple or dichotomously furcate, moderately divergent, ovate to oblong, 1.5–2.5(–3) × (0.7–)0.9–1.1 mm, 0.5–0.6 mm thick, in section almost as wide as thick to twice wider than thick, apex rounded, shortly emarginate; groove distally narrow and

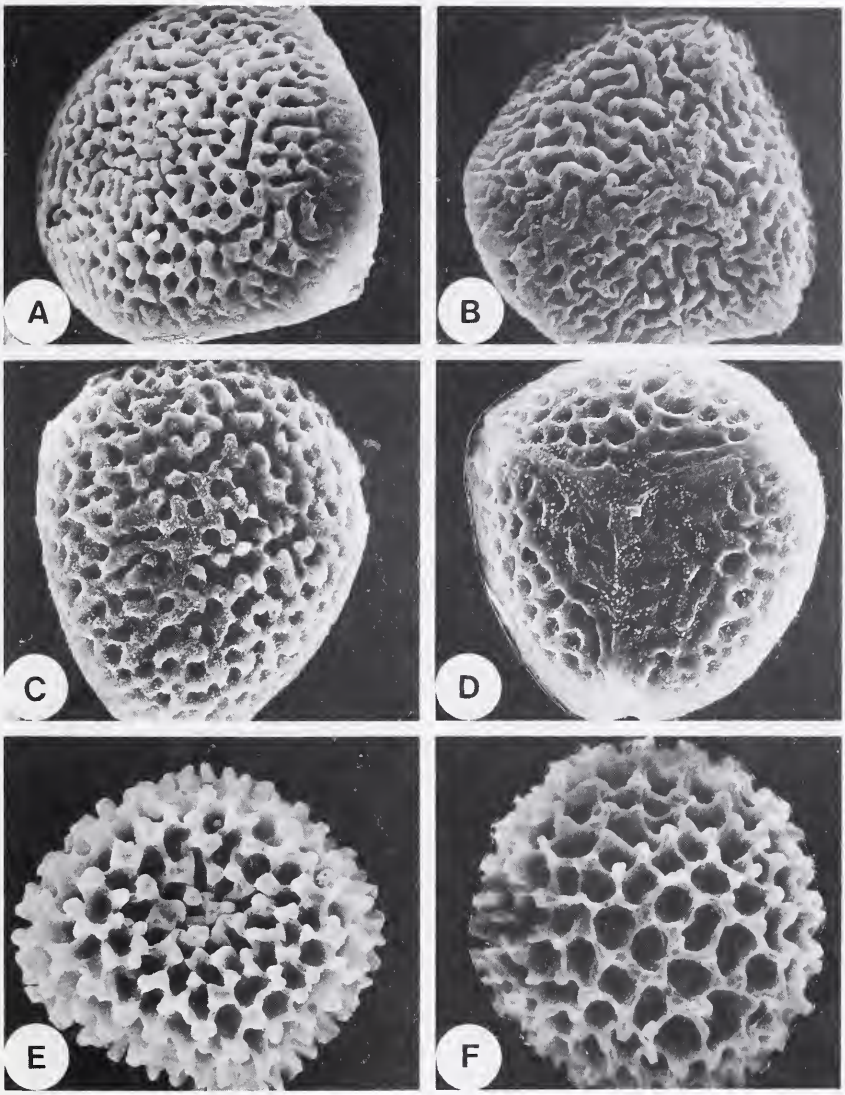


PLATE 22.—Spores. A, B, **Riccia macrocarpa**: A, distal face; B, proximal face. C, D, **R. pottsiana**: C, distal face; D, proximal face. E, F, **R. runssorensis**: E, distal face; F, proximal face. A, B, *S.M. Perold 888*; C, D, *Duthie 5463*; E, F, *Volk 81/125c*. A, B, × 700; C, D, × 1000; E, F, × 600.

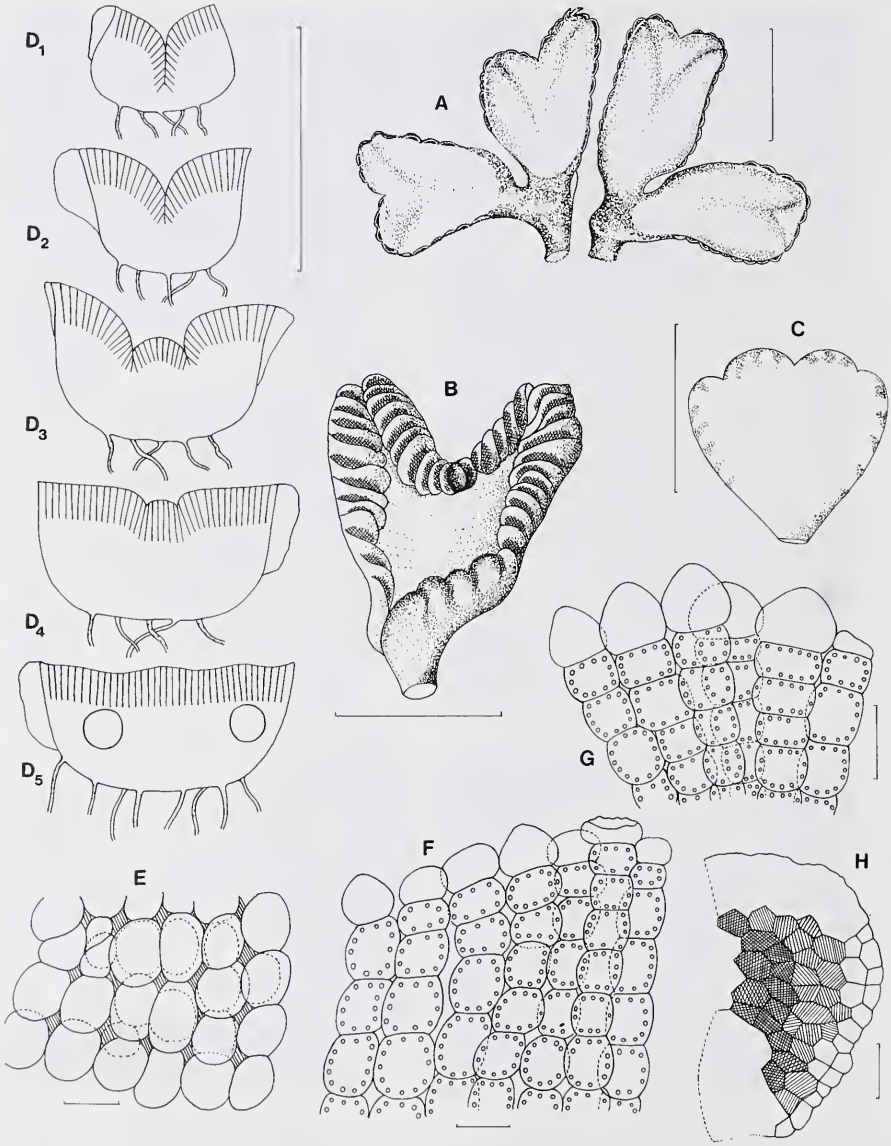


FIGURE 51.—**Riccia pottsiana**. A–C, thallus: A, wet; B, dry; C, ventral face. D, c/s branch at intervals from apex to base; E, epithelial cells and air pores from above; F, c/s epithelial and assimilation tissue cells; G, epithelial cells and assimilation tissue near apex and groove; H, scale. A, C, E–H, *S.M. Perold 1361*; B, *J.M. Perold 37*; D, *S.M. Perold 285*. Scale bars: A—D, 1 mm; E–G, 50 µm; H, 100 µm. Artist: J. Kimpton.

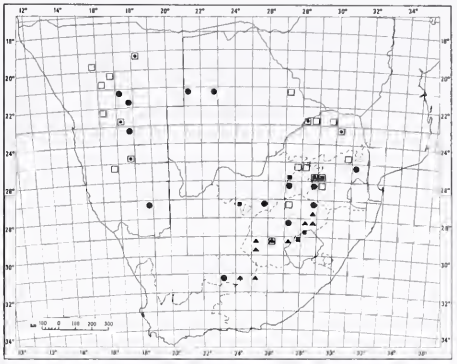
deep, its sides markedly convex, becoming shallow more proximally, thallus margins rounded; flanks ascending steeply or bulging slightly; ventral face rounded, green, sometimes with purple transverse bands of vestigial scales. *Scales* small, ± 500 × 250 µm, extending to margin of thallus or slightly above, very regular, imbricate, rounded, dark purplish red, generally with entirely or partly hyaline/white borders.

Dorsal epithelium unistratose, hyaline, cells globose or mammillose, 37–45 × 30–40 µm, intact near groove, collapsed toward margins; air pores small, mostly 4-sided, occasionally triangular. *Assimilation tissue* 300–450 µm thick, consisting of vertical columns of 8–10 short-rectangular to slightly bulging cells, enclosing narrow air canals; storage tissue generally occupying less than ventral half of thallus, cells rounded, closely packed. Figure 51.

?Monoicous. *Antheridia* not seen. *Archegonia* with purple necks, along proximal part of groove. *Sporangia* bulging dorsally. *Spores* 60–78 µm diam., triangular-globular, polar, light brown to brown, semitransparent; wing narrower than 5 µm, smooth or sparsely granulate, perforated at marginal angles, margin entire; ornamentation similar on 2 faces, reticulate; distal face convex, with 14–16 small, deep alveoli across diam., up to 5 µm wide, walls raised into papillae at nodes, sometimes adjacent ones fused to form short, irregular, convoluted ridges; proximal face with triradiate mark not prominent, each of 3 facets with 25–30 small alveoli, 2.5 µm wide, walls lower and smoother than those on distal face. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 22C, D; Perold (1989e: fig. 14.1–6).

Riccia pottsiana is a rare, endemic species and only known from a few collections in the Free State, the southeastern part of Northern Cape and the northwestern part of Eastern Cape. It grows on shallow soil overlying weathered sandstone outcrops. Map 25.

This species is characterized by its small size, in fact Sim (1926) referred to it as 'the smallest *Riccia* known to me'; by the tumid appearance



MAP 25.—■ **Riccia macrocarpa**
▲ **R. pottsiana**
● **R. runssorensis**
❑ **R. rosea**

of the bottle-green to dark green thalli and the generally bicoloured scales. The spores of *R. pottsiana* are small, with numerous, small, deep alveoli, the walls papillose at the nodes; it rarely sporulates, however. Sim's description of the spores is very brief, only stating that they are round and indistinctly reticulate. He named this species in honour of Prof. George Potts, for many years Professor of Botany at the University College of OFS, Bloemfontein.

The holotype specimen, *Potts 5* (PRE), as well as the isotype (BOL), were mixed collections and no material matching the protologue of *R. pottsiana* is left. A lectotype was selected from other original material in Sim's herbarium (Perold 1991c).

A rather puzzling observation by Sim, that this species is related to *R. concava*, concludes his description. *Riccia concava* (no. 46) belongs to section *Pilifer*, as it has free-standing dorsal cell pillars (see note under that species), and is thus distinctly different from *R. pottsiana*, besides which, it is a much larger plant. Sim must have mistaken another species for *R. concava* (Perold 1989d).

Vouchers: *Duthie 5450, 5452, 5463a* (BOL); *S.M. Perold 285* (PRE); *Smook 6962b* (PRE).

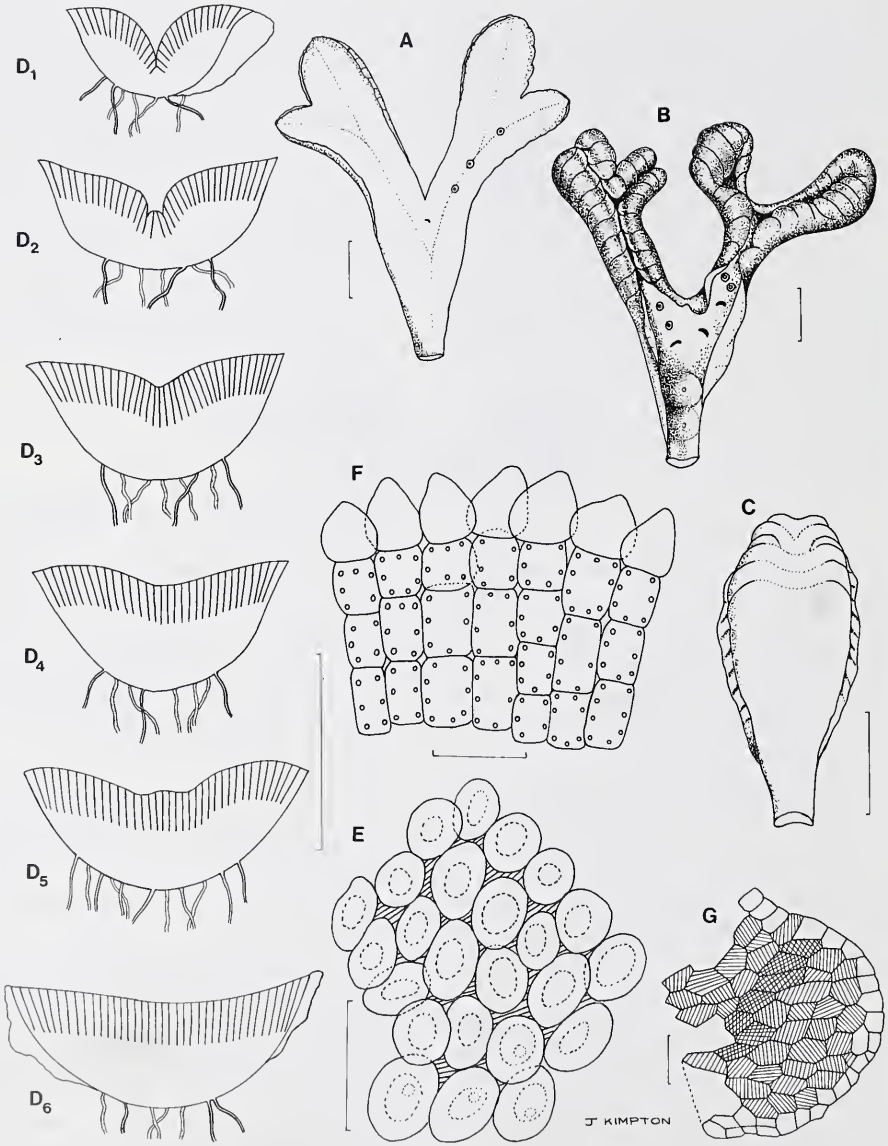


FIGURE 52.—**Riccia runssorensis**. A,B, thallus: A, wet; B, dry. C, ventral face of branch. D, c/s branch at intervals from apex to base; E, epithelial cells and air pores from above; F, c/s epithelial and assimilation tissue cells; G, scale. A, C, *S.M. Perold 2004*; B, *S.M. Perold 219*; D, *S.M. Perold 785*; E, G, *S.M. Perold 1208a*; F, *S.M. Perold 782*. Scale bars: A–D, 1 mm; E, F, 50 µm; G, 100 µm. Artist: J. Kimpton.

29. **Riccia runssorensis** *Steph.* in Bulletin l'Herbier Boissier 6: 330 (1898); S.W.Arnell: 271 (1957); S.W.Arnell: 32 (1963a); Perold: 39 (1991c). Type: Uganda, Mt Ruwenzori, Kivani, leg. *Scott Elliott 5, 20* [*G13176* holo., fide Na-Thalang: 86 (1980); BM!].

Thalli smallish to medium-sized, in incomplete rosettes or in crowded gregarious patches; bright green to yellowish green, occasionally streaked with red dorsally, dark red scales along margins; when dry, margins tightly inflexed, meeting along midline, edged with white, flanks covered with shiny, very dark red to purple scales. *Branches* twice to several times ± symmetrically furcate, closely to moderately divergent, ovate to oblong, narrow toward base, 7–9 mm long, segments 3–4 × 1.2–1.6 mm, 0.7–0.9 mm thick, in section 1.5 times to nearly twice wider than thick, apex rounded, shortly emarginate; groove narrow and deep distally, gradually becoming shallower and disappearing toward base, thallus margins acute; flanks sloping steeply; ventral face rounded, green, often with faint, violet-red, transverse bands of vestigial scales. *Scales* 500–800 × 350–550 µm, projecting less than 100 µm above thallus margins, rounded, imbricate, shiny, very dark red to almost purple, at margin 1 or 2 cell rows hyaline.

Dorsal epithelium unistratose, hyaline, cells mammillose to pyriform, 25–40 × 30.0–37.5 µm, soon collapsing toward margins and proximally; air pores generally triangular, occasionally 4-sided. *Assimilation tissue* 250–430 µm thick, consisting of vertical columns of 5–8 rectangular cells, enclosing narrow, mostly 4-sided air canals; storage tissue occupying ventral part of thallus. Figure 52.

Monoicous. *Antheridia* with hyaline necks, at intervals along groove. *Archegonia* numerous, in 1 or 2 rows, necks purple. *Sporangia* serially arranged along proximal part of thallus, bulging dorsally. *Spores* 80–105 µm diam., subglobular to globular, apolar, ruby-red, colour deepening to almost black, opaque; wing and triradiate mark absent, periphery with prominent truncate projections, characteristically cog-wheel-like in profile; ornamentation regularly reticulate, (6–)8–10 rounded or angular alveoli across diam. of spore, 10–12 µm wide, alveolar walls thin and low, raised at nodes into very prominent, truncate projections up to 7.5 µm high, occasionally some projections confluent and forming a short ridge. *Chromosome number*: n = 8 (Bornefeld 1984). Plate 22E, F; Perold (1989e: fig. 15.1–6).

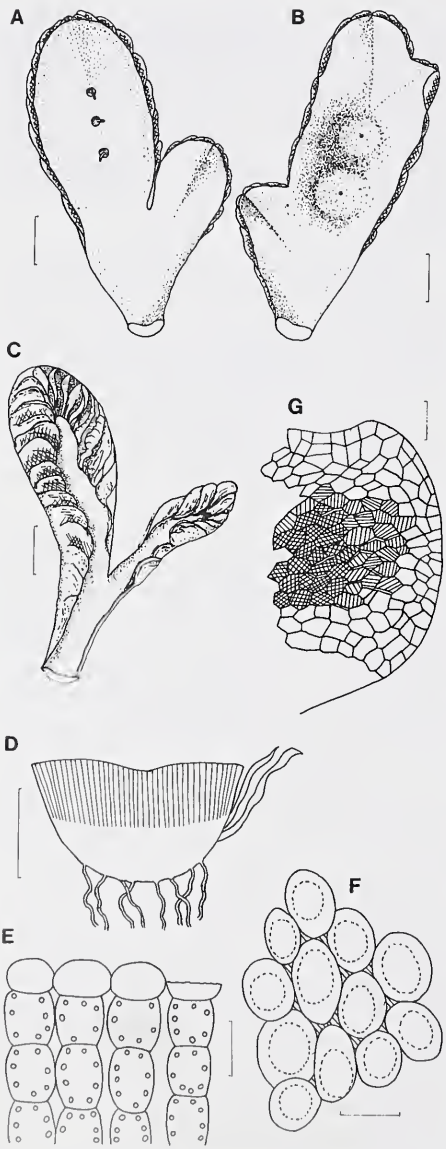
The type specimen of *R. runssorensis* is from the Ruwenzori Mountains in southwestern Uganda. The species is also known from Angola and Tanzania. In southern Africa, it is fairly rare but widespread and has been collected on damp, clayey soil at the edge of vleis, or on shallow soil overlying dolerite outcrops in Namibia, Botswana, Northern Province, North-West, Gauteng, Mpumalanga, Free State and Northern Cape. Map 25.

Riccia runssorensis may be confused with *R. atropurpurea* (no. 21), which is similar in size, and is sometimes mixed with it. On growing actively, *R. runssorensis* is, however, a bright, clear green, not silvery to glaucous-green like *R. atropurpurea*. It also lacks the hyaline thallus margins of the latter, and its spores have far more prominent projections at the alveolar nodes than any of the other local species with apolar spores (see note under *R. rosea*, no. 30). *Riccia rosea* is a more robust plant, and its reddish pink scales are larger and have a wider hyaline edge, projecting above the thallus margin; it also is dioicous.

Na-Thalang (1980) placed *R. runssorensis* in synonymy under *R. macrospora* Steph., an Australian species, but this is not accepted here. *Riccia macrospora* is a larger plant, 7–12 × 3–4 mm, with attenuate thallus margins and the spores are 120(–150) µm diam.; moreover, its chromosome number is reported to be: n = 48.

Vouchers: *Glen 1403* (PRE); *S.M. Perold 219, 782* p.p., *785* (PRE); *Volk 5374* (BOL).

30. **Riccia rosea** *O.H.Volk & Perold* in Bothalia 16: 181 (1986d); Perold: 39 (1991c). Type: Transvaal, Farm Valschspruit, 19 km N of



Bronkhorstspruit, on hilltop, *S.M. Perold 324* (PRE, holo.!); *Volk 81/023* (M, PRE, para.!).

Thalli medium-sized, in crowded gregarious patches or scattered; light green, white along margins and proximally; when dry, dorsally greenish white to white, apex and sides inflexed, mostly covered by prominent pink scales. *Branches* simple or once or twice symmetrically or asymmetrically furcate, moderately divergent, ligulate, narrow proximally, up to 12 × 1.0–2.5 mm, 0.8–1.0 mm thick, in section as wide as thick, to 2.5 times wider than thick, apex rounded, shortly emarginate; groove narrow and deep distally, becoming shallow proximally, thallus margins acute; flanks steep to oblique, reddish pink; ventrally rounded, green, often with narrow, violet transverse bands. *Scales* 800–900 × 500–750 µm, projecting ± 175 µm above thallus margins, wavy, closely imbricate, rounded, reddish or rose-pink, with hyaline margins one to several cell rows wide.

Dorsal epithelium in one or two layers, top cells 35 × 35–55 µm, soon collapsing, subdorsal cells becoming echlorophyllose; air pores mostly triangular. *Assimilation tissue* 375–450 µm thick, consisting of vertical columns of 7 or 8 short-rectangular cells, enclosing narrow, 3- or 4-sided air canals; storage tissue occupying ventral part of thallus, cells rounded, irregularly arranged. Figure 53.

Dioicous. *Antheridia* with prominent hyaline necks, up to 370 µm long, along groove in 1 or 2 rows, dorsal epithelium pitted at their bases. *Archegonia* scattered along median part of female plants, necks purple. *Sporangia* rare, but if present, spaced along length of lobe, overlying dorsal surface bulging, soon disintegrating, seldom developing purple blotches. *Spores* 92–105 µm diam., subglobular to globular, apolar, light brown to brown, semitransparent; without wing and triradiate mark; ornamentation regularly reticulate with 9–11 well-defined,

FIGURE 53.—**Riccia rosea**. A–C, thallus: A, wet male; B, wet female; C, dry; D, c/s branch; E, c/s epithelial and assimilation tissue cells; F, epithelial cells and air pores from above; G, scale. A, B, *S.M. Perold 2018a*; C, D, G, *S.M. Perold 346*; E, F, *H. Anderson PRE-CH13445*. Scale bars: A–D, 1 mm; E, F, 50 µm; G, 100 µm. Artist: J. Kimpton.

rounded or angular alveoli across diam., up to 10 μm wide, alveolar walls up to 5 μm high, raised at nodes. *Chromosome number*: n = 8 (Bornefeld 1984). Plate 23A, B; Perold (1989e: fig. 16.1–6).

The range of *R. rosea* extends northward into central Africa and it is known from Angola, Kenya, Tanzania, Uganda, Zaïre and Zambia. In the *FSA* area *R. rosea* is found in Namibia, Botswana, Northern Province, North-West, Gauteng, Mpumalanga and northern and central Free State, on shallow, sandy soil overlying granite, quartzite or sandstone outcrops or between rotting roots of grasses. Map 25.

This species can be recognized by the near-white to pale green dorsal surface of the entire dry and basal parts of the wet thallus, which seldom develops any purple coloration, by the large, wavy scales, hyaline at the margin, but soon developing pink to reddish bases, as well as by the prominent antheridial necks in male plants. In the specimens, *D. Fourie 23c*, *24c*, the scale colour darkens progressively toward the base, eventually becoming dark, bluish red.

A few other species with red or purple scales also have subglobular spores, but the papillae at the alveolar nodes of *R. rosea* spores are intermediate in length between the very prominent, truncate projections of *R. runssorensis* (no. 29) and the low tubercles of *R. atropurpurea* (no. 21). Furthermore, *R. rosea* has light brown spores, whereas *R. runssorensis* and *R. atropurpurea* have much darker, red to black spores. It is also the only dioicous species of the three mentioned here.

Vouchers: *Glen 1403b* (PRE); *S.M. Perold 344, 408, 785* p.p. (PRE); *Volk 81/111* (M, PRE).

31. **Riccia albolimbata** *S.W.Arnell* in Mitteilungen der Botanischen Staatssammlung, München 16: 264 (1957); S.W.Arnell: 25 (1963a); Perold: 17 (1989b); Perold: 40 (1991c); R.M.Schust.: 545 (1992b). Type: South West Africa/Namibia, Farm Voigtland, bei Windhoek, gegen Ondekaremba, *Volk 11419* (M, holo.; PRE, iso.!).

R. albosquamata S.W.Arnell: 266 (1957); S.W.Arnell: 25 (1963a). Type: South West Africa/Namibia, Damaraland: Neitsas, Grootfontein, am Rande einer Kalkpfanne, *Volk 452* p.p. (M!).

Thalli medium-sized, in rosettes 15–20 mm across, or in crowded, gregarious patches; green to bluish green, shiny, turning chalk-white and spongy over sporangia, hyaline to white scales along margins; when dry, margins inflexed, with wavy, white scales covering most of dorsal face. *Branches* furcate or bifurcate, shortly to deeply divided, diversely divergent, ovate to oblong, up to 8 × 1.5–2.2(–3) mm, 0.8–1.1 mm thick, in section 2.0–2.5 times wider than thick, apex rounded, emarginate; groove narrow and deep distally, soon disappearing, proximally flat to somewhat concave, thallus margins acute to subacute; flanks generally sloping obliquely, green or brownish to dark red; ventrally flat to slightly rounded, green. *Scales* large, 800–900 (–1200) × 600 μm, projecting ± 150 μm above thallus margins, undulating, imbricate, hyaline to white, base occasionally flecked with brown or dark red, surface often encrusted with calcium carbonate deposits. Plate 18D.

Dorsal epithelium unistratose, cells dome-shaped or globose, hyaline, mostly covered with a film of fine calcium carbonate granules, 42–48 × 45–50 μm, fragile and soon collapsing, each cell generally with a single corresponding column of assimilation cells beneath; air pores 4- or 5-sided, toward margins and proximally conspicuously wider, 6-sided. *Assimilation tissue* 400–500 μm thick, consisting of vertical columns of 6–10 short-rectangular cells, enclosing 4, 5(6)-sided air canals; storage tissue occupying ventral part of thallus, cells angular. Figure 54.

Monoicous. *Antheridia* with hyaline necks, in 1 or 2 rows along middle of branch. *Archegonia* with purple necks, at intervals along centre. *Sporangia* with bulging, overlying tissue turning white and spongy, soon disintegrating and leaving several capsules exposed. *Spores* 82–105 μm diam., triangular-globular, polar, yellow-brown to dark brown, semitransparent to opaque; wing narrow, 3–5 μm wide, with pore at marginal

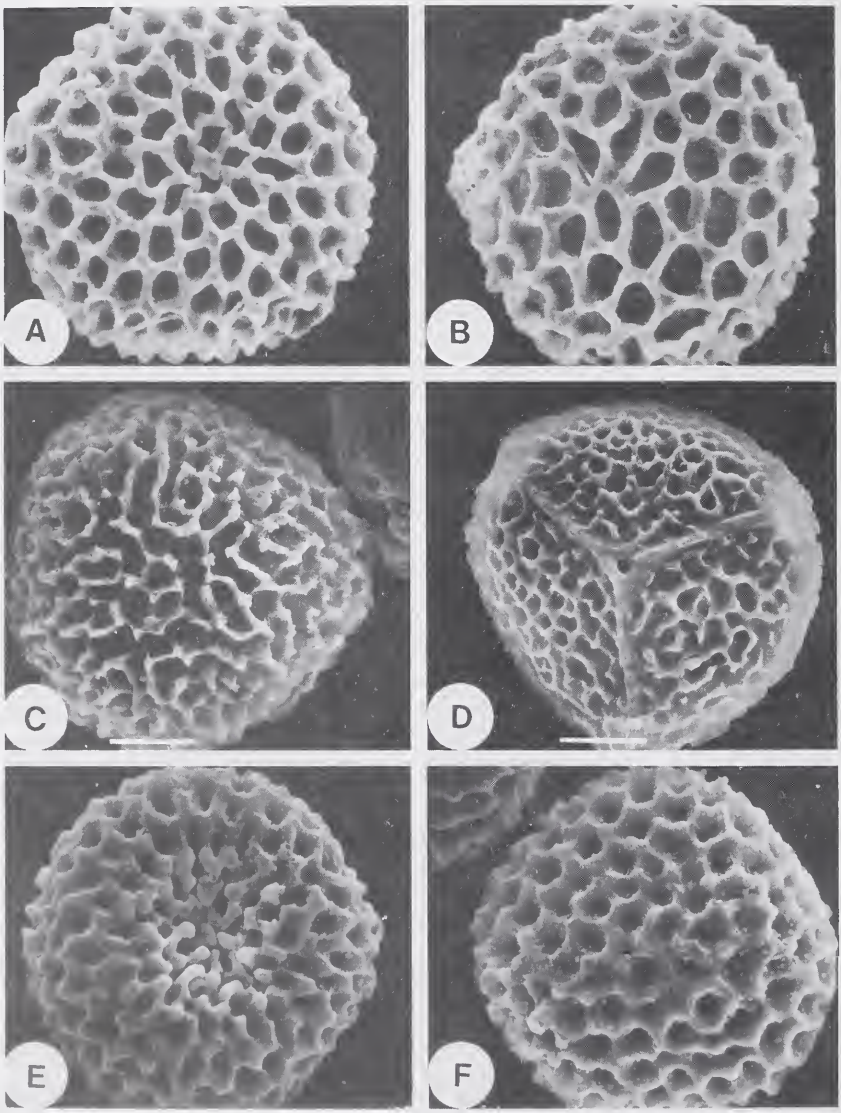


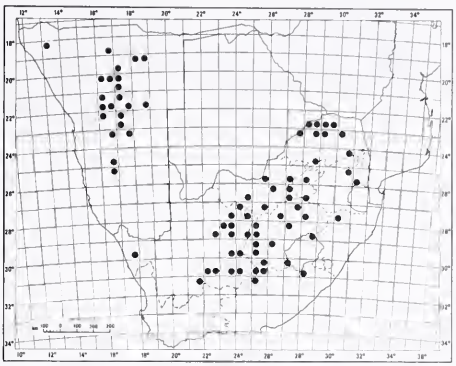
PLATE 23.—Spores. A, B, **Riccia rosea**: A, distal face, B, proximal face. C, D, **R. albolimbata**: C, distal face, D, proximal face. E, F, **R. argentcolimbata**: E, distal face; F, proximal face. A, B, *S.M. Perold 135a*; C, *Volk 81/921*; D, *Stephansen 5393*; E, F, *Volk 86/930a*. A–F, × 700.

angles, margin crenulate or finely eroded; ornamentation generally incompletely reticulate but rather different on 2 faces; distal face convex, ornamentation quite variable, (7–)10–12 angular to round alveoli across diam., 5.0–7.5(–10) μm wide, alveolar walls thick or thin, raised at nodes, often only central alveoli complete, surrounded by short, irregular, radiating ridges extending onto wing; proximal face with triradiate mark distinct, mostly incompletely reticulate, walls thinning out or anastomosing to form irregularly branching ridges. *Chromosome numbers*: n = 12, 16, 24 (Bornefeld 1984; 1989). Plate 23C, D; Perold (1989e: fig. 18.1–6).

Schuster (1992b) has recently reported *R. albolimbata* from North America. Its range in Africa extends to Kenya and Tanzania. The species is widely distributed in the *FSA* area: Namibia, Northern Province, North-West, Gauteng, Mpumalanga, Free State, Northern and Eastern Cape, but it is seemingly quite rare in KwaZulu-Natal. It grows on calcrete, loam or shallow soil overlying rock outcrops. Map 26.

Riccia albolimbata is characterized by its large, frilly, hyaline or white ventral scales, frequently encrusted with deposits of calcium carbonate, by the dorsal covering of the sporangia turning chalk-white and spongy and by the spores which are generally incompletely reticulate on the distal face with the outer ridges radially elongated.

Arnell (1957, 1963a) recognised two white-scaled species, *R. albolimbata* and *R. albosquamata*, but failed to distinguish clearly between them. He based his description of the latter on *R. albolimbata* and the recently named *R. argenteolimbata* (no. 32), using characters from both in mixed, sterile collections, e.g. *Volk 881, 883*. The type specimen of *R. albosquamata*, *Volk 452* p.p., however, consists only of sporulating material of *R. albolimbata* and no *R. argenteolimbata* is present. *R. albosquamata* is therefore regarded as a taxonomic synonym of *R. albolimbata* and the other white-scaled species in the above mixed collections, has been described as a new species, *R. argenteolimbata* (Volk *et al.* 1988, see note under



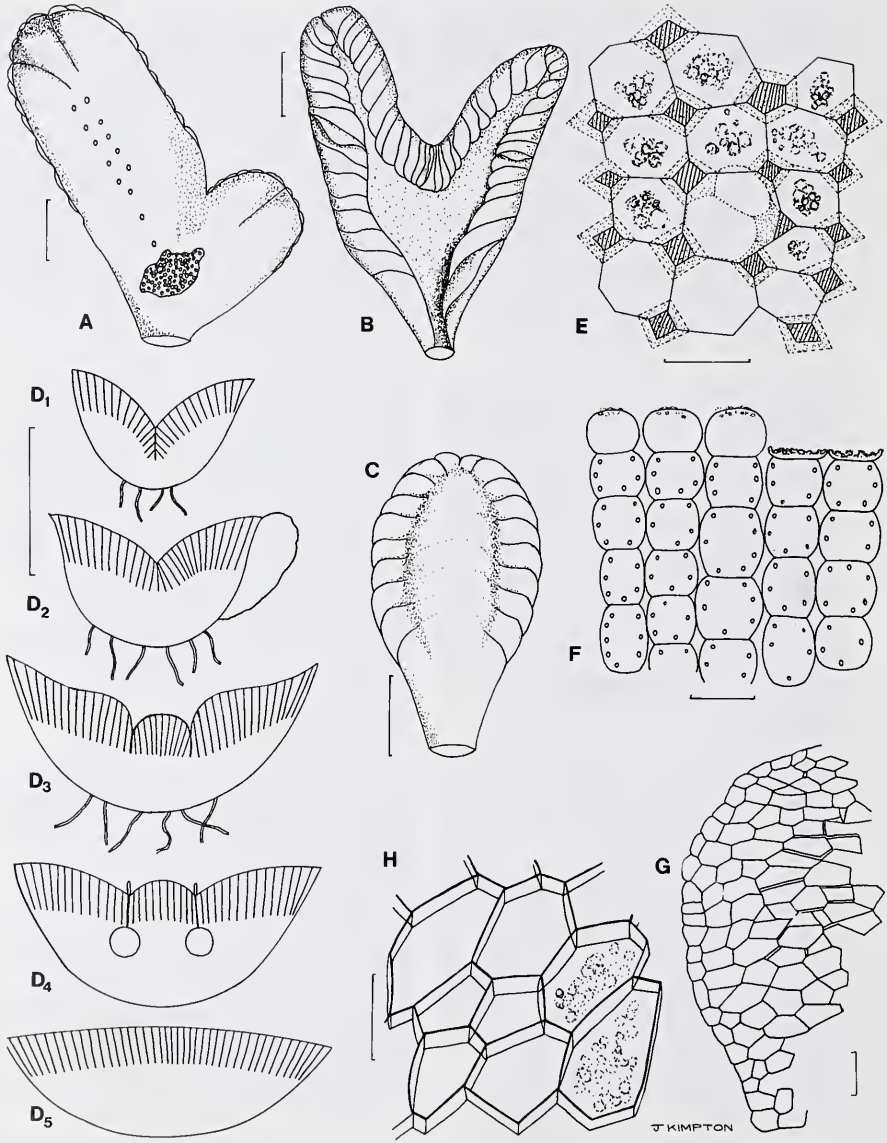
MAP 26.—● **Riccia albolimbata**

that species, no. 32). In Arnell's (1963a) key to the *Riccia* species, *R. albomarginata* (no. 47) has been listed twice on p. 14, at nos 7 and 11, whereas *R. albolimbata* has been left out. At his no. 11, *R. albomarginata* must therefore be replaced by *R. albolimbata* (and also on p. 25), as he is comparing *R. albosquamata* with *R. albolimbata*.

Vouchers: *Duthie 5110* (BOL); *S.M. Perold 1380* (PRE); *E. Retief 1459* (PRE); *Toelken 5558* (PRE); *Volk 84/703* (M, PRE).

32. **Riccia argenteolimbata** *O.H.Volk & Perold* in Volk et al. in Bothalia 18: 155 (1988); Perold: 41 (1991c). Type: South West Africa/ Namibia, Marienhof (Dunroamin), *Volk 00910* (M, holo.!); Hatsamas, *Volk 00762* (M, para.).

Thalli small to medium-sized, in gregarious patches or scattered, rarely in rosettes; greenish grey, mat, occasionally brownish along margins; when dry, margins tightly inflexed, with flanks covered by regular, appressed, stiff, white to silvery mauve scales. *Branches* asymmetrically bi- or trifurcate, segments short, moderately to widely divergent, obovate-ligulate, 2–7 × 0.7–1.2(–2) mm, 0.6–0.9 mm thick, in section as wide as thick to twice wider than thick, apex wedge-shaped; groove narrow and deep along length of branches, sides convex, becoming flatter proximally, thallus margins acute; flanks steep, dark grey or brown; ventral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face rounded, green, apically with arched, narrow brown bands across. *Scales* 600–800 × 500 µm, projecting ± 100 µm above thallus margins, stiff, closely imbricate, entirely white or only marginally, base mostly silvery mauve, proximally dark grey-brown. Plate 18E.

Dorsal epithelium in regular, honeycomb pattern, bistratose, cells in upper layer intact only when young, globose, hyaline, 20–35 × 30–40 µm, capped with calcium deposits, soon collapsing, cells in second layer without chloroplasts, short-rectangular, 25–37 × 22–32 µm, upper transverse and upper lateral walls thicker, the latter thinning out below; air pores mostly triangular, some quadrate, small. *Assimilation tissue* 300–450 µm thick, in compact vertical columns of 8–10 rectangular cells, enclosing very narrow, 4-sided air canals; storage tissue occupying ventral part of thallus, cells angular. Figure 55A–F.

During the dry season, from April onwards, *R. argenteolimbata* tends to form bulbils which enable it to survive and propagate, as it rarely forms sporangia.

Dioicous. *Antheridia* in male thalli with short hyaline necks. *Archegonia* in female thalli with dark purple necks. *Sporangia* rarely formed, usually single, bulging slightly dorsally. *Spores* 80–120(–130) µm diam., globular to subglobular, apolar, reddish brown to almost black, semi-opaque to opaque; wing and triradiate mark absent, periphery tuberculate; ornamentation reticulate with 12–15(–16) round to angular alveoli across diam., 3–7 µm wide, ridges thick, raised at nodes into conical or truncate processes. *Chromosome numbers*: n = 8, 9, 20, 24 (Bornefeld in Volk *et al.* 1988). Plate 23E, F; Perold (1989e: fig. 19.1–6).

In Africa *R. argenteolimbata* is also known from Kenya and Tanzania (Perold 1995). In the *FSA* area, the species is found on fine, greyish soil overlying calcrete, crystalline limestone or dolomite in Namibia, Botswana, Northern Province, North-West, Free State and Northern Cape. Map 27.

The species can be recognized by its generally smaller-sized, compact, dioicous thalli, its mat and glaucous or grey dorsal surface, and its stiff, regular, white to silvery mauve scales and apolar spores.

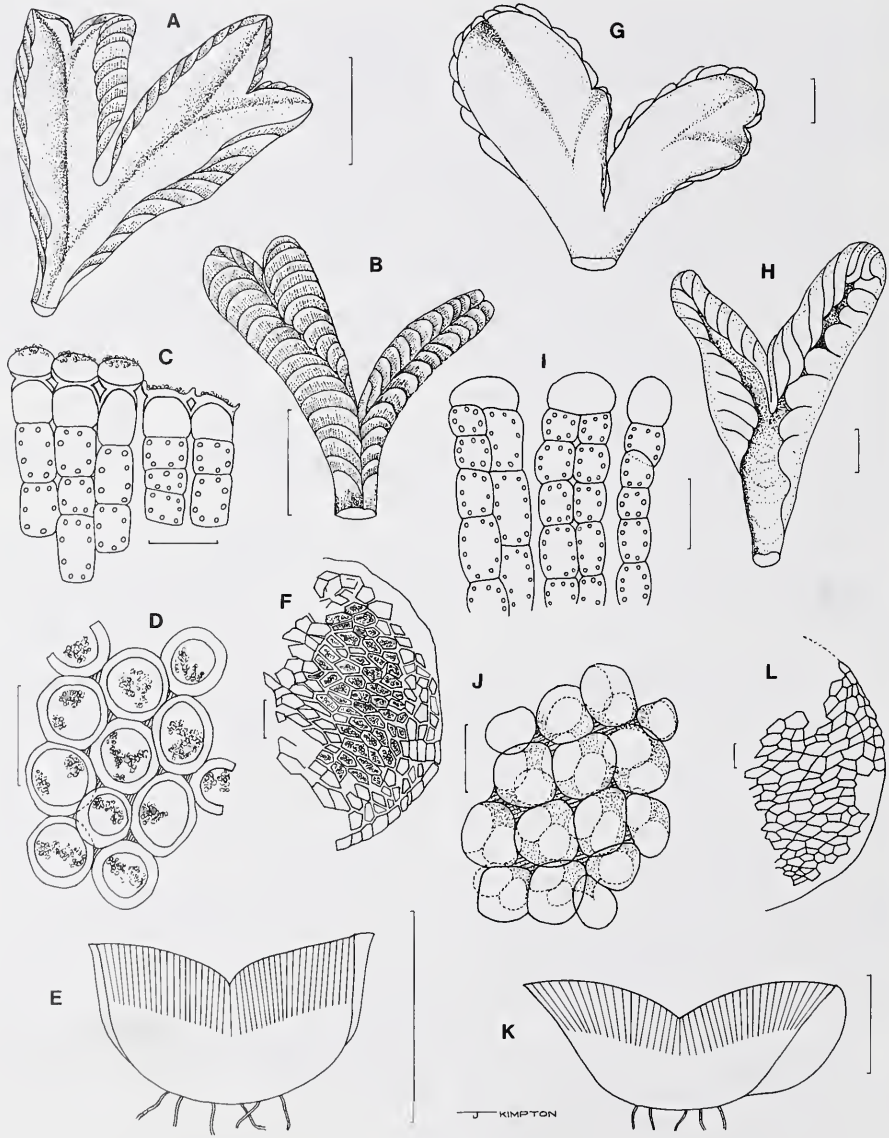
Volk *et al.* (1988) reported very small plants of this species, mixed with plants of normal size (*Volk 85/775*, *86/930*). These may represent a different subspecies.

Vouchers: *Henderson 659* (PRE); *S.M. Perold 737* (PRE); *E. Retief 1493a* (PRE); *Smook 4487* (PRE); *Volk 81/164* (M, PRE).

33. **Riccia albornata** *O.H.Volk & Perold* in Volk et al. in Bothalia 18: 160 (1988); Perold: 42 (1991c). Type: Cape, ca. 10 km westl. Kenhardt, an der Strasse nach Kakamas, *Volk 81/081* (M, holo.!).

Thalli medium-sized to large, in crowded gregarious patches, not in rosettes; green, shiny toward margins and proximally whitish green or yellowish, hyaline scales along margins; when dry, margins inflexed with large, frilly, hyaline or white, lime-encrusted scales covering most of dorsal face. *Branches* simple or symmetrically or asymmetrically bi- or trifurcate, generally widely divergent, oblong, 5–9(–12) × 1.5–2.0 (–4) mm, 1.0–1.5 mm thick, in section 1.5–2.5 or more times wider than thick, apex rounded, obtuse, emarginate; groove deep distally, gradually wider and shallow, flat proximally, thallus margins acute, slightly attenuate; flanks sloping obliquely outward and upward, violet or green; ventral face flat to rounded, green. *Scales* large, ± 1250 × 750 µm, projecting up to 100 µm

FIGURE 54.—**Riccia albolimbata**. A, B, thallus: A, wet; B, dry. C, ventral face of branch; D, c/s branch at intervals from apex to base; E, epithelial cells, some with overlying calcium crystals, and air pores (hatched) seen from above, air canals stippled; F, c/s assimilation tissue with row of epithelial cells, intact on left, collapsed on right; G, scale; H, scale cells enlarged, on right with overlying calcium crystals. A–D, *S.M. Perold 1380*; E, F, *S.M. Perold 398*; G, H, *S.M. Perold 803*. Scale bars: A–D, 1 mm; E, F, H, 50 µm; G, 100 µm. Artist: J. Kimpton.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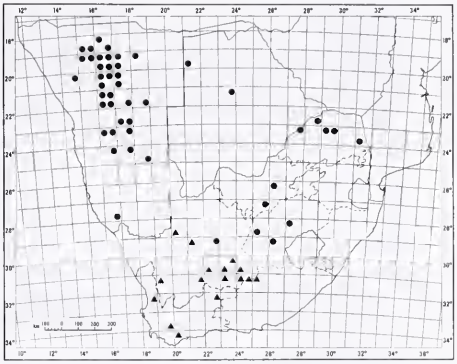
above thallus margins, frilly, imbricate, apically hyaline, proximally white, lime-encrusted, sometimes bases reddish purple.

Dorsal epithelium unistratose, cells hyaline, globose or mammillose, surface occasionally dusted with fine calcium carbonate deposits, 30–40(–50) × 40–60 µm, hyaline, soon collapsing, a single cell often spanning two columns of assimilation tissue cells beneath; air pores rectangular, toward margins wider and 5- or 6-sided. *Assimilation tissue* 500–750 µm thick, in vertical columns of 6–8(–10) short-rectangular cells, enclosing mostly 6-sided air canals; storage tissue occupying ventral part of thallus. Figure 55G–L.

Monoicous. *Antheridia* with prominent hyaline necks along midline. *Archegonia* with purple necks scattered singly along groove. *Sporangia* bulging dorsally, covering tissue with enlarged air pores, disintegrating later and leaving capsules exposed in hollow. *Spores* 85–115 µm diam., triangular-globular, polar, straw-coloured or yellow to brown, semitransparent to opaque; wing up to 5 µm wide, notched or perforated at marginal angles, margin crenulate; ornamentation finely and generally incompletely reticulate, similar on both faces; distal face with 14–16(–20) small, deep, irregular alveoli across diam., 2.5 µm wide, alveolar walls thick, raised into processes at nodes and frequently anastomosing to form short, convoluted ridges; proximal face with triradiate mark distinct, 30–40 small alveoli on each of 3 facets. *Chromosome number*: n = 15 (Bornefeld in Volk *et al.* 1988). Plate 24A, B; Perold (1989e: fig. 20.1–6).

Riccia albornata is a rare endemic species and infrequently collected on coarse gravelly soil overlying granite or quartzite rock outcrops in the shrublands of Northern, Western and the northern part of Eastern Cape. Map 27.



MAP 27.—● **Riccia argenteolimbata**
Δ **R. albornata**

Vegetatively *R. albornata* is not easily distinguished from *R. albolimbata* (no. 31), but it never grows in rosettes; the scales are generally larger and frillier; the dorsal epithelial cells are somewhat larger and the air canals are wider, enclosed by six columns of cells; the spore ornamentation is also markedly different with numerous small, irregular alveoli and convoluted ridges on both faces. With the collection of more specimens, it has become evident that there is some overlap in the distribution of the two species in the Northern Cape.

Vouchers: *Duthie 5149* (BOL); *Oliver 1463* (PRE); *S.M. Perold 1800* (PRE); *Smook 6961* (PRE); *Volk 84/667* (M, PRE).

34. **Riccia montana** *Perold* in Bothalia 19: 9 (1989a); Perold: 43 (1991c). Type: Cape, Witteberg Mountains, basalt cliffs at top of Joubert's Pass, 10 km E of Lady Grey, *Van Rooy 2712* (PRE, holo.!).

Thalli medium-sized, gregarious, not in rosettes; light green to green, finely spongy and

FIGURE 55.—A–F, **Riccia argenteolimbata.** A, B, thallus: A, wet; B, dry. C, c/s assimilation tissue with epithelial cells, partly thicker-walled, on left intact, on right collapsed; D, collapsed, thicker-walled epithelial cells with overlying calcium crystals, air pores mostly three-sided, from above; E, c/s branch; F, scale. G–L, **R. albornata**. G, H, thallus: G, wet; H, dry. I, c/s epithelial and assimilation tissue cells; J, epithelial (solid lines) and subdorsal (broken lines) cells, air pores (hatched) overlying air canals (dotted), from above; K, c/s branch; L, scale. A, B, *Volk 84/692*; C, D, *S.M. Perold 772*; E, F, *Volk 881*; G, H, J, *Smook 6961*; I, *Oliver 8854a*; K, L, *Volk 81/081*. Scale bars: A, B, E, G, H, K, 1 mm; C, D, I, J, 50 µm; F, L, 100 µm.

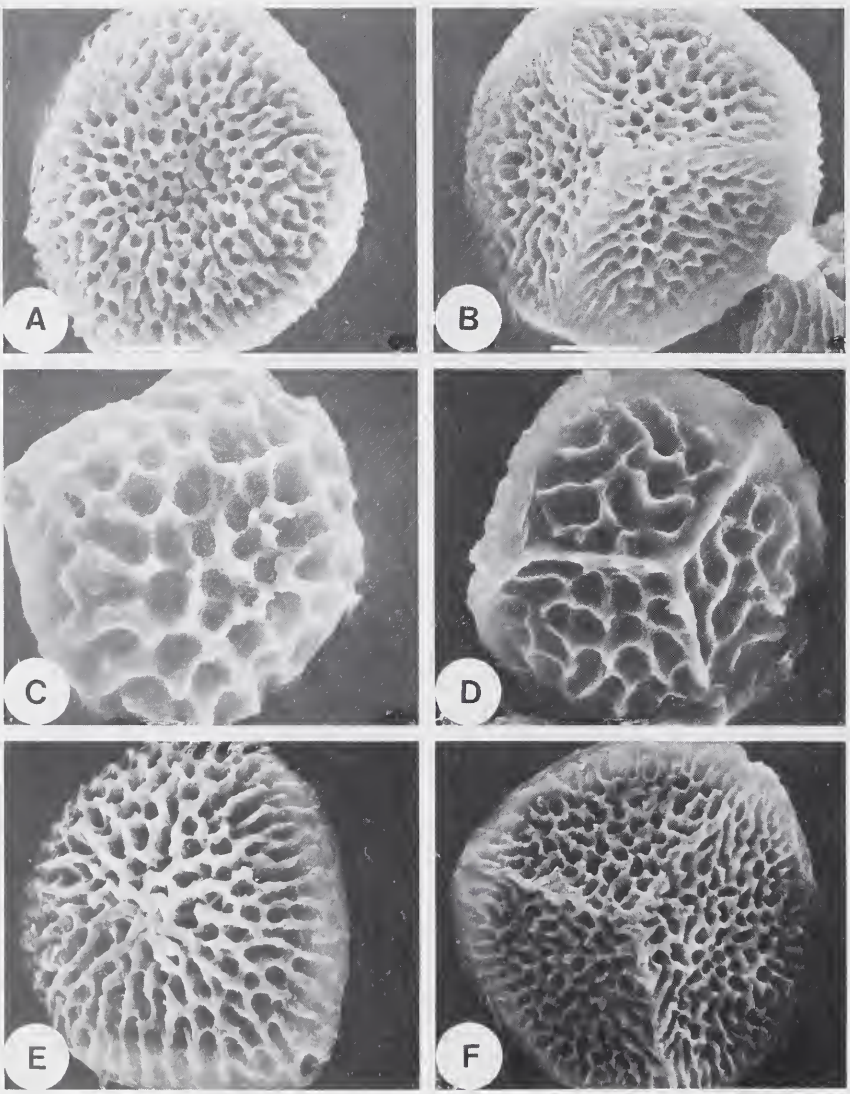


PLATE 24.—Spores. A, B, **Riccia albornata**: A, distal face; B, proximal face. C, D, **R. montana**: C, distal face; D, proximal face. E, F, **R. alboporosa**: E, distal face; F, proximal face. A, B, *Smook 6862a*; C, D, *Van Rooy 3549a*; E, F, *Oliver 8849*. A, B, E, F, × 700; C, D, × 800.

glistening; when dry, dorsally white to yellowish, margins inflexed, or more usually, reflexed along edges forming 2 'lips' proximally, flanks covered with white scales. *Branches* symmetrically or asymmetrically furcate, often with short lateral branching more proximally, moderately to widely divergent, ligulate, up to 8 × 1.7–2.0 (–2.5) mm, 0.6–0.75 mm thick, in section 2.5 to 3 times wider than thick, apex rounded to somewhat keeled, emarginate; groove narrow and deep along most of dorsal face, proximally flat to slightly concave, thallus margins acute; flanks almost vertical distally to sloping obliquely proximally, green; ventrally rounded, green. *Scales* ± 850 × 500 µm, hardly projecting above thallus margins, wavy at apex, soon appressed to flanks, imbricate, hyaline or whitened with calcium deposits, sometimes flecked with red toward base. Plate 18F.

Dorsal epithelium unistratose, cells hyaline, globose, covered with fine film of calcium deposits, 20–30 × 35–50 µm, cell width rather irregular, sometimes single cell spanning 1 $^1/_2$–2(–3) subdorsal cells, fragile, soon collapsing; air pores (3–)4–5(–6)-sided, becoming wider toward thallus margins, often only partly aligned with air canals below. *Assimilation tissue* 300–350 µm thick, consisting of vertical columns of 6–10 isodiametric or short-rectangular cells, enclosing 5- or 6-sided air canals; storage tissue occupying ventral part of thallus, cells angular, tightly packed. Figure 56.

Dioicous. *Antheridia* with hyaline or white necks ± 160 µm long, projecting from small, shallow pits on either side of dorsal groove. *Archegonia* purple-necked, scattered along groove in female thalli. *Sporangia* single or adjacent in pairs, bulging conspicuously dorsally, overlying tissue not turning white, but shrinking and disintegrating. *Spores* 70–85 µm diam., triangular-globular, polar, brown, semitransparent; wing up to 5 µm wide, wider at perforated marginal angles, margin somewhat wavy, finely eroded, crenulate; ornamentation on both faces completely or incompletely coarsely reticulate; distal face with 7 or 8 rounded to angular alveoli across diam., ± 7.5 µm wide, alveolar walls thick, 5 µm high, extending partly onto wing, with raised papillae at nodes; proximal face with triradiate mark distinct, to less clearly defined, alveoli often incomplete, irregularly ridged, or with complete, angular alveoli, walls raised at nodes. *Chromosome number*: n = 9 (Bornefeld pers. comm). Plate 24C, D; Perold (1989e: fig. 21.1–6).

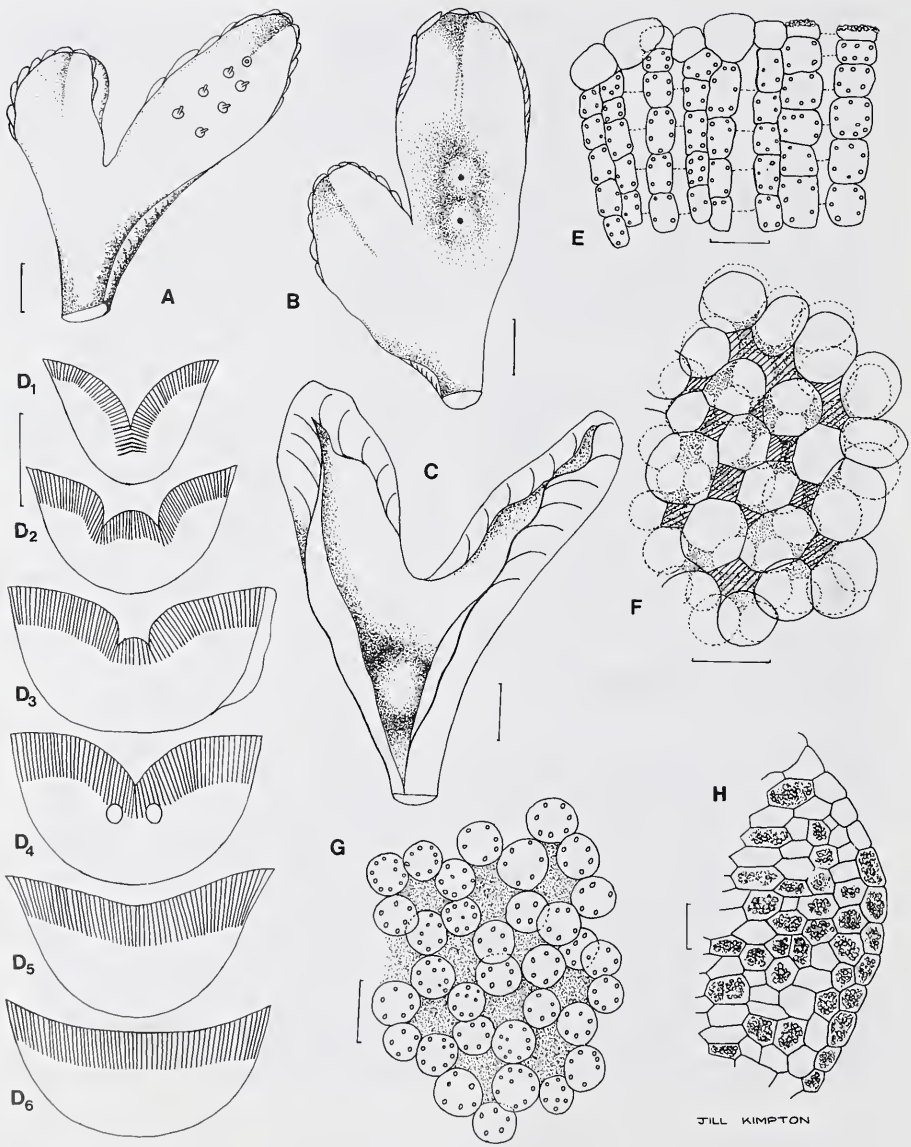
Riccia montana is endemic to southern Africa and is so far only known from high altitudes in the Witteberg Mountains of the Eastern Cape and the Drakensberg in Lesotho and KwaZulu-Natal, where it is found on black, humus-rich soil, overlying basalt outcrops. Map 28.

The species can be recognized by the fine, spongy texture of the dorsal face of the thallus, by the grooved, ligulate branches with lip-like, reflexed margins along the proximal parts when dry, and by the coarsely reticulate, polar spores. In the white-scaled group of species, *R. montana* (no. 34) and *R. argenteolimbata* (no. 32) are the only two dioicous species. *R. argenteolimbata*, however, has a more compact thallus, stiff, regular scales, apolar spores and its distribution is restricted to the drier, western parts of the country.

Vouchers: *Glen 1728* (PRE); *J.M. Perold 31* (PRE); *Schelpe s.n.* (BOL); *Van Rooy 2718, 3045* (PRE).

35. **Riccia alboporosa** *Perold* in Bothalia 19: 12 (1989a); Perold: 43 (1991c). Type: Cape, NE of Nieuwoudtville, Groothoek, at Soetlandsfontein River, on sandy/clay flats alongside river, in rock crevices and on ledges, *Oliver 8854* (PRE, holo.!).

Thalli medium-sized, gregarious or scattered, not in rosettes; bright yellowish green, with conspicuous air pores; when dry, greenish white to white, puffy, slightly concave, margins erect to inflexed or apically clasped together, revealing regular white, appressed ventral scales. *Branches* once or twice symmetrically or occasionally asymmetrically furcate, moderately to widely divergent, bluntly wedge-shaped to broadly ovate, up to 7 × 1.8–3.5(–4) mm,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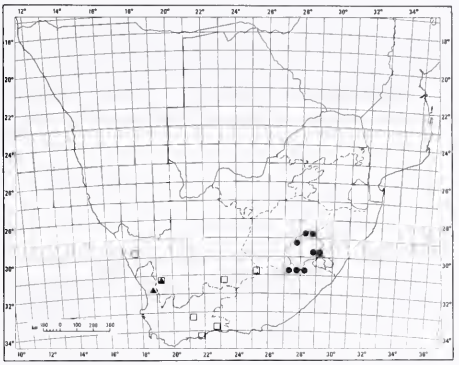
0.8–1.2 mm thick, in section 2–3 times wider than thick, apex rounded, emarginate; groove distally deep and wide, flattening out proximally, thallus margins raised and blunt; flanks sloping obliquely, green; ventral face gently rounded, green. *Scales* mostly inconspicuous, ± 550 × 350 µm, hardly extending to thallus margins, appressed to flanks, imbricate, heavily encrusted with calcium salts.

Dorsal epithelium unistratose, cells hyaline, dome-shaped in and near dorsal groove, but soon collapsing and becoming heavily encrusted with thick calcium carbonate deposits, obscuring cells; air pores wide, regularly spaced, generally surrounded by 5 or 6(7) wedge-shaped, radially arranged cells, 60–75 µm long, ± 50 µm wide at broadest part, partly roofing wide air canals below. *Assimilation tissue* ± 400 µm thick, topmost cells generally somewhat thicker-walled, often 2 under each dorsal cell, soon becoming echlorophyllose as overlying dorsal cells collapse, otherwise consisting of vertical columns of 6–8 rectangular cells enclosing air canals; storage tissue occupying ventral part of thallus. Figure 57.

Monoicous. *Antheridia* with hyaline necks, spaced at intervals along groove. *Archegonia* with purple necks, scattered. *Sporangia* single near base, or crowded in groups along middle of branch, bulging dorsally. *Spores* 75–88 µm diam., triangular-globular, polar, yellow-brown, semitransparent; wing 5 µm wide, slightly wider at perforated marginal angles, margin mostly entire; ornamentation reticulate, but dissimilar on 2 faces; distal face with 11–13 alveoli across diam., 5 µm wide, toward centre somewhat larger and with thicker, higher walls, radial ridges generally more pronounced than those across, slightly raised at nodes, extending onto wing; proximal face with triradiate mark distinct, each facet with up to 50 small, round alveoli, ± 3 µm wide, sometimes adjacent ones confluent, ridges low. *Chromosome number*: n = 10 (Bornefeld 1989). Plate 24E, F; Perold (1989e: fig. 22.1–6).



MAP 28.—● **Riccia montana**
▲ **R. alboporosa**
❑ **R. bicolorata**

This species is endemic to, and only known from three localities in the arid shrublands of the western parts of Northern Cape and the northern parts of Western Cape, where it grows on fine, sandy or brackish soil overlying tillite rocks. Map 28.

Riccia alboporosa is easily recognized by its widely, but regularly spaced air pores, encircled by dorsal epithelial cells, the inner parts of which rapidly become white on drying. The species differs from the other white-scaled species by its inconspicuous scales, heavily encrusted with calcium salts, by the puffy appearance of the dorsal surface in the dry plant and by the finely reticulate spores.

Vouchers: *Oliver 8849* (PRE); *S.M. Perold 1772, 1775* (PRE); *Magill 3905* (F; PRE).

FIGURE 56.—**Riccia montana**. A–C, thallus: A, wet male; B, wet female; C, dry female. D, c/s branch at intervals from apex to base; E, c/s epithelial and assimilation tissue cells; F, epithelial (solid lines) and subdorsal (broken lines) cells, air pores (hatched) overlying air canals (stippled), seen from above; G, h/s through assimilation tissue, air canals stippled; H, scale. A–C, *Van Rooy 3046*; D, *Van Rooy 2712*; E, *Oliver 8354*; F, G, *J.M. Perold 31*; H, *Van Rooy 2718*. Scale bars: A–D, 1 mm; E–G, 50 µm; H, 100 µm. Artist: J. Kimpton.

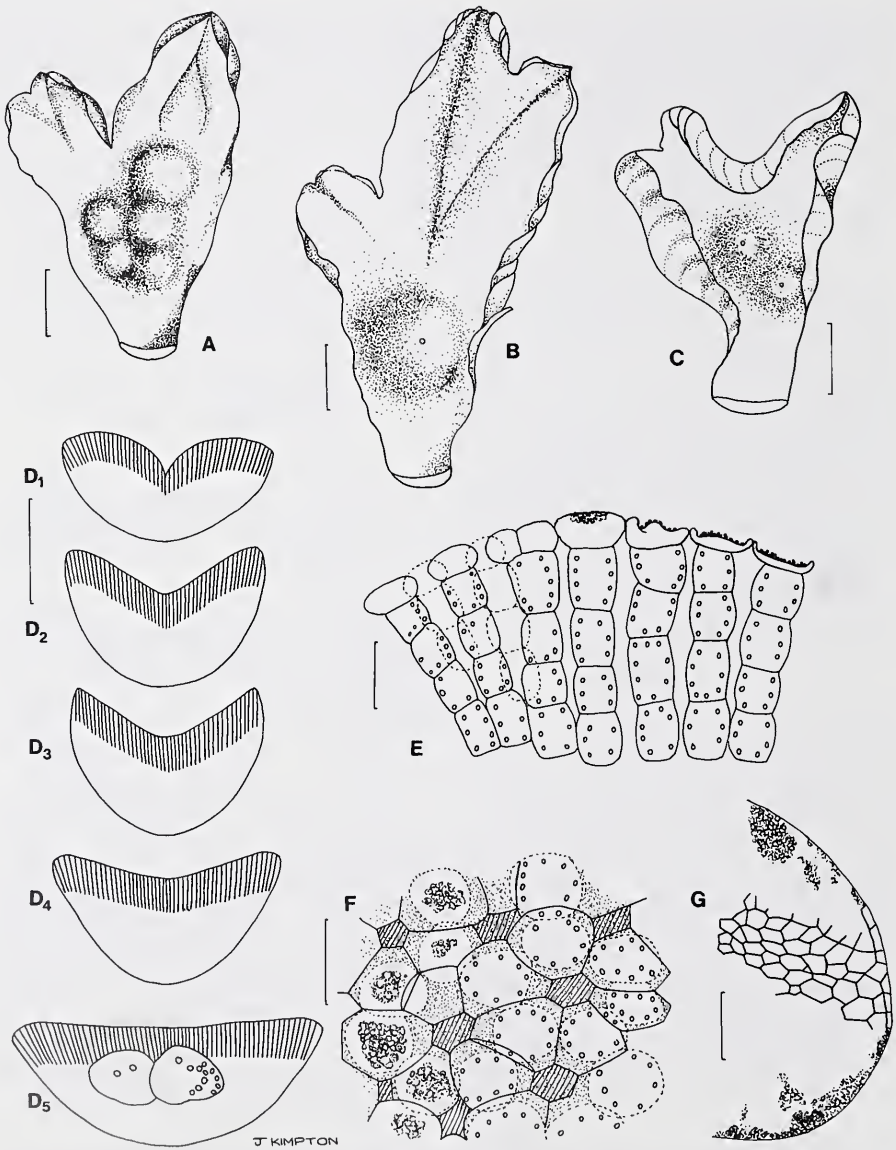
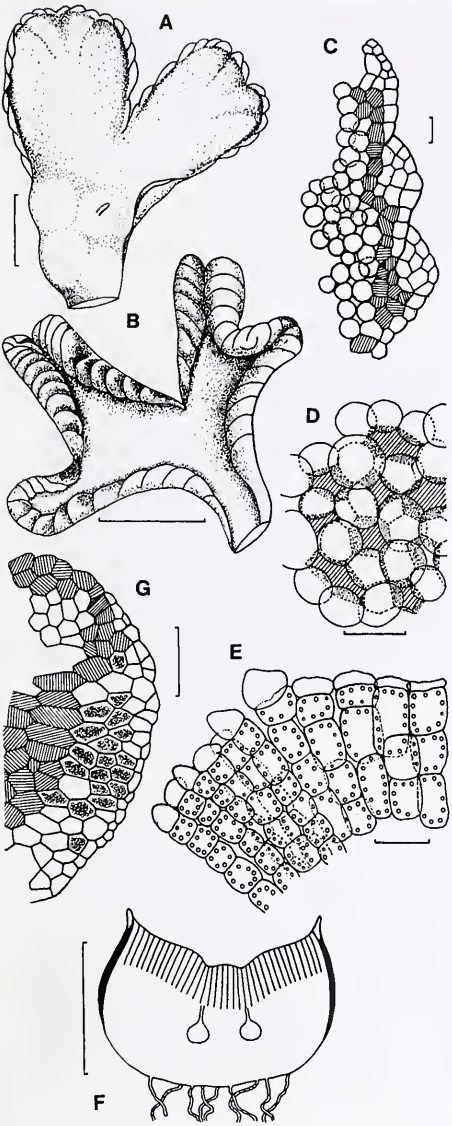


FIGURE 57.—**Riccia alboporosa**. A–C, thallus: A, B, wet; C, dry. D, c/s branch at intervals from apex to base; E, c/s assimilation tissue with row of epithelial cells, intact on left, collapsed on right and covered with calcium deposits; F, epithelial (solid lines) and subdorsal (broken lines) cells, air pores (hatched) overlying air canals (stippled), seen from above; G, scale. A, B, F, *S.M. Perold 1775*; C–E, G, *Oliver 8854*. Scale bars: A–D, 1 mm; E, F, 50 µm; G, 100 µm.



36. **Riccia bicolorata** *Perold* in Bothalia 20: 188 (1990b); Perold: 44 (1991c). Type: Cape, Victoria West, 48.6 km NE of Farm Kalkfontein, common in damp areas around bushes, *Smook 6990a* (PRE, holo.!).

Thalli rather small, in gregarious patches or in partial rosettes 8–10 mm across; green to yellowish green or whitish green and encrusted with calcium deposits; when dry, dorsally concave, margins raised or incurved to inflexed, flanks covered with imbricate, bicoloured scales. *Branches* once or twice symmetrically or asymmetrically furcate, moderately divergent, obovate to ovate, up to 4.5(–5) × 1.0–1.3 (–1.5) mm, 0.6–0.8 mm thick, in section 1.5 times to nearly twice wider than thick, apex rounded, emarginate; groove sharp and deep distally, soon becoming wide and shallow, thallus margins subacute; flanks steep to sloping slightly obliquely, green; ventral face rounded, green. *Scales* up to 500 × 300 µm, projecting ± 100 µm above thallus margins, rounded, appressed to slightly wavy, imbricate, base deep purple and shiny, margins dull white, encrusted with calcium deposits.

Dorsal epithelium unistratose, hyaline, cells globose to conical or mammillose, 25–55 × 30–42 µm in and near groove, soon collapsing and often becoming covered with fine deposits of calcium salts; air pores 4- or 5-sided, small medianly, enlarging rapidly to 60 µm wide toward margins. *Assimilation tissue* 280–350 µm thick, consisting of vertical columns of 6–8(–10) isodiametric cells, enclosing air canals which widen laterally; storage tissue occupying ventral part of thallus. Figure 58.

Monoicous. *Antheridia* in a row along midline, hyaline necks arising from small pits. *Archegonia* with purple necks, scattered. *Sporangia* toward base, single or in pairs, adjacent or

FIGURE 58.—**Riccia bicolorata**. A, B, thallus: A, wet; B, dry. C, dark thallus margin (hatched) and projecting scales from above; D, epithelial (solid lines) and subdorsal (broken lines) cells, air pores (hatched) overlying air canals (stippled), from above; E, c/s epithelial cells, intact at groove on left, collapsing to the right, assimilation tissue below; F, c/s branch; G, scale. A–G, *Smook 6990a*. Scale bars: A, B, F, 1 mm; D, E, 50 µm; C, G, 100 µm. Artist: J. Kimpton.

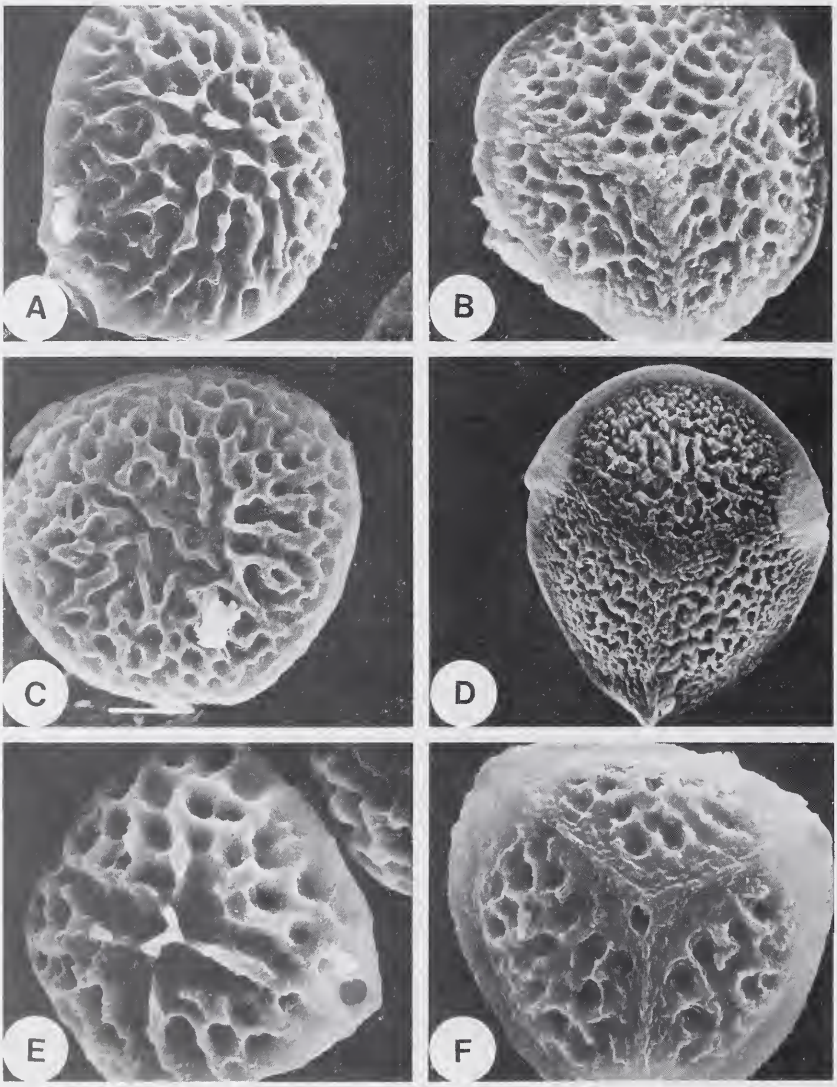


PLATE 25.—Spores. A, B, **Riccia bicolorata**: A, distal face; B, proximal face. C, D, **R. pulveracea**: C, distal face; D, proximal face. E, F, **R. furfuracea**: E, distal face; F, proximal face. A, B, *Smook 6990a*; C, Duthie *5484*; D, *Duthie 5455*; E, *Oliver 8957a*; F, *Oliver* 8910a. A–F, × 700.

serially arranged, bulging dorsally. *Spores* 77–93 µm diam., triangular-globular, polar, light brown to brown, semitransparent; wing ± 5 µm wide, thin, slightly undulating, notched or perforated at angles, margin entire; ornamentation reticulate, rather different on the 2 spore faces; distal face with mostly 10 incomplete alveoli across diam., 5.0–7.5 µm wide, cross walls often undeveloped and radial walls thickened, fading out toward margin, papillae projecting from nodes, especially over spore centre; proximal face with triradiate mark rather poorly defined, dotted with granules, facets with incomplete alveoli, walls sprinkled with granules and raised into papillae at nodes. *Chromosome number*: n = 16 (T. Bornefeld pers. comm.). Plate 25A, B.

Endemic to southern Africa, the species is so far only known from a few collections in the shrublands of the Northern and Western Cape, where it is found on alkaline soil, sometimes in association with other *Riccia* species, such as *R. alboporosa* (no. 35), *R. albornata* (no. 33) and *R. pulveracea* (no. 37). Map 28.

Riccia bicolorata is most easily identified by the appressed bicoloured scales, often appearing 'striped', when the flanks are inflexed in the dry state. When wet, the adherent purple bases of the scales are visible through the tissues above and form an interrupted dark line along the inside of the thallus margins. In young plants the primal branches are closely associated and butterfly-shaped, often tearing apart along the middle, as growth continues. *R. bicolorata* is somewhat similar to *R. argenteolimbata* (no. 32), but the latter has a more compact thallus, triangular air pores and apolar spores. *R. pottsiana* (no. 28) also bears some similarity to *R. bicolorata*, but it is smaller and its dark red scales are more regularly arranged.

Vouchers: *Koekemoer 300* (PRE); *Oliver 8849* p.p. (PRE); *S.M. Perold 1772a*, *2318* (PRE); *Smook 3215a* (F; PRE).

E2. Section **Pilifer**

Pilifer *O.H.Volk* in Mitteilungen der Botanischen Staatssammlung, München 19: 455 (1983). Type: *R. albomarginata* Bisch.

Pteroriccia R.M.Schust. pro gen.: 72 (1984a). Type: *R. villosa* Steph.

Pteroriccia (R.M.Schust.) R.M.Schust. pro subgen.: 412 (1985). Type: *R. villosa* Steph.

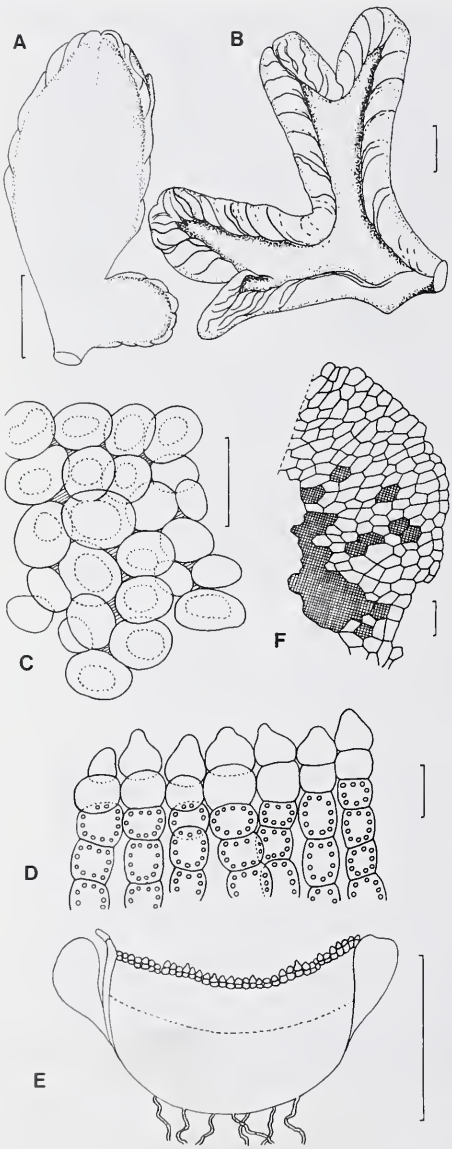
Micantes O.H.Volk & Perold pro sectione: 187 (1986)e. Type: *R. hirsuta* O.H.Volk & Perold.

Thalli medium-sized to quite large; terricolous. *Scales* lateral, very rarely ventral, generally large, hyaline, sometimes base partly red or violet, margins entire, very rarely denticulate or apically filamentous.

Dorsal epithelium in bi- to multicellular pillars, free-standing, uniseriate, cells longer than wide or wider than long.

37. **Riccia pulveracea** *Perold* in Bothalia 21: 185 (1990d); Perold: 57 (1991c). Type: Cape, 18 km from Noupoort, on road to Hanover, at bottom of slope, on ground between bushes; false upper Karoo, *Smook 3339* (PRE, holo.!; F, iso.).

Thalli smallish to medium-sized, in gregarious patches; green to pale yellowish green; when dry, dorsally powdery, rather concave, margins erect, sometimes inflexed and meeting in middle, revealing hyaline scales. *Branches* simple or once, occasionally twice, symmetrically or asymmetrically furcate, moderately to widely divergent, ovate to lingulate, up to 6 × 1.1–1.3(–1.5) mm, 0.9 mm thick, in section slightly wider to 1.5 times wider than thick, apex rounded, slightly emarginate; groove dis-



tally deep and sharp, soon shallow and wide, thallus margins subacute; flanks steep, green; ventral face rounded, green. *Scales* conspicuous toward apex, 750–925 × 400–600 µm, projecting 100–200 µm above thallus margins, almost semilunar, wavy, imbricate, hyaline, sometimes basal and scattered cells higher up reddish purple, margin mostly entire. Plate 26A.

Dorsal epithelium generally two-celled, low, free-standing, hyaline pillars 70–105 µm long, top cell globose to markedly mammillose, small, 35–55 × 37–42 µm, basal cell 35–47 × 37–52 µm, soon collapsing, appearing powdery; air pores mostly 4-sided, small. *Assimilation tissue* 300–400 µm thick, consisting of vertical columns of 8–10 cells, (25–)32–46 × 30–37 µm, enclosing narrow, 4-sided air canals; storage tissue occupying ventral part of thallus, cells angular, 45–55 µm wide. Figure 59.

?Dioicous. *Antheridia* in one or two rows along middle of thallus, necks yellowish brown at base, 110–200 µm long. *Archegonia* with purple necks, scattered. *Sporangia* 3 or 4 in a row, bulging dorsally, overlying tissue gradually disintegrating to liberate spores. *Spores* 75–92 µm diam., triangular-globular, polar, light brown to greyish brown, semitransparent to nearly opaque; wing thin, rather undulate, width somewhat variable, 5.0–7.5 µm wide, broader at perforated marginal angles, margin mostly entire; ornamentation different on the 2 faces; distal face with 12–14 rather irregularly shaped alveoli across diam., 2.5–5.0(–7.5) µm wide, cross walls often incomplete and adjacent alveoli confluent, sometimes with thick, knotted loops, or with sinuate to shortly radiating ridges; proximal face with triradiate mark distinct to indistinct, quite heavily sprinkled with granules, each facet with numerous small, incomplete and rather poorly defined alveoli forming an open network, the walls low, granular to verruculose. *Chromosome number*: not known. Plate 25C, D.

FIGURE 59.—**Riccia pulveraceae**. A, B, thallus: A, wet; B, dry. C, epithelial cells and air pores (hatched) from above; D, c/s low epithelial cell pillars with assimilation tissue below; E, c/s branch; F, scale. A–F, *Smook 6962c*. Scale bars: A, B, E, 1 mm; C, D, 50 µm; F, 100 µm. Artist: J. Kimpton.

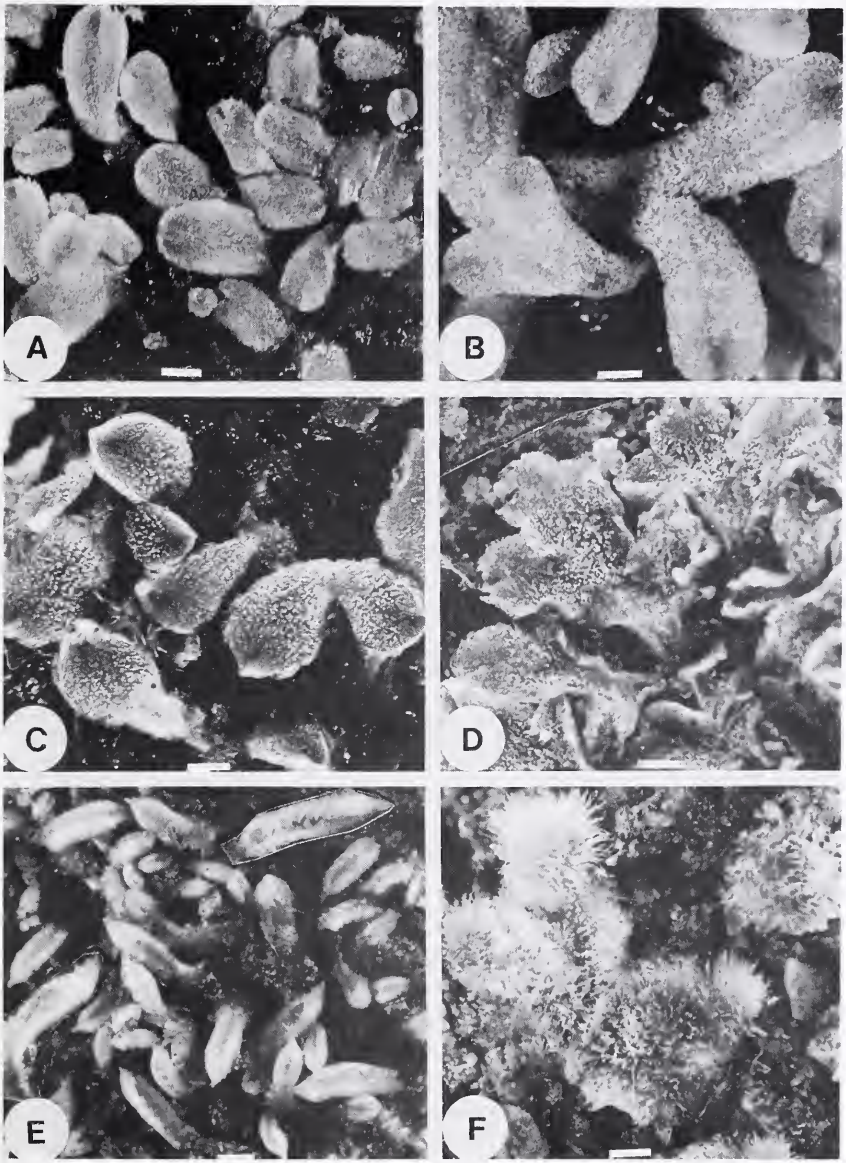
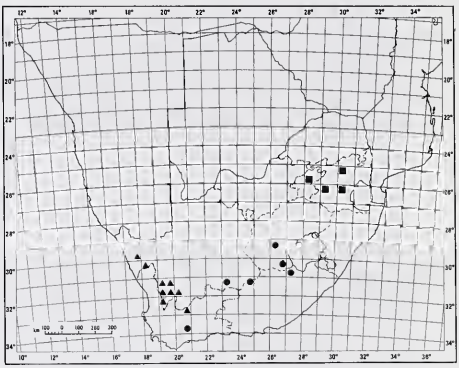


PLATE 26.—Thalli. A, **Riccia pulveracea**, crowded branches; B, **R. hantamensis**, overlapping branches; C, **R. parvo-areolata**, scattered branches; D, **R. namaquensis**, crowded thalli; E, **R. villosa**, crowded thalli; F, **R. hirsuta**, scattered branches. A, *Smook 6990*; B, *S.M. Perold 1830*; C, *S.M. Perold 1726*; D, *S.M. Perold 2136*; E, *Oliver s.n.*; F, *S.M. Perold 2101*. Scale bars: A–F, 1 mm.

Riccia pulveracea is endemic to southern Africa and is so far only known from the Free State, the southeastern part of Northern Cape and the northern part of Eastern Cape, where it grows on alkaline soil between karroid bushes. Map 29.



MAP 29.—● **Riccia pulveracea**
▲ **R. furfuracea**
■ **R. elongata**
○ **R. trachyglossum**

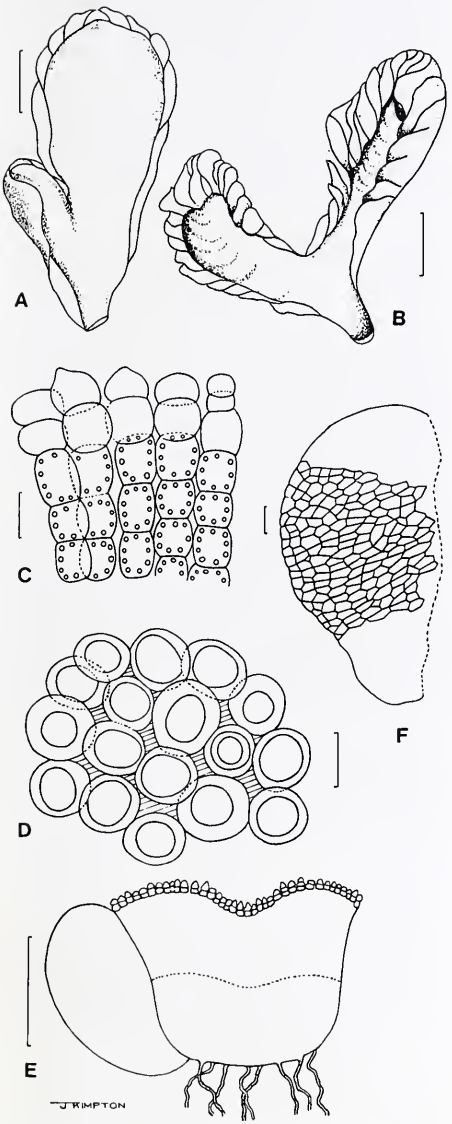
The species can be recognized by low, generally two-celled, fragile dorsal pillars, with the top cell often markedly mammillose when fresh and turgid; when dry, these cells collapse and form a fine, somewhat powdery covering on the dorsal face of the thallus and may even be overlooked. The specimens, *Duthie 5455*, *5461a*, *5484*, *5485* and *5498*, had been incorrectly referred to *R. concava* (no. 46) by Duthie. *R. pulveracea*, however, is a smaller plant with shorter, more delicate dorsal pillars. The spore ornamentation is rather different as the proximal face has fewer alveoli with thicker walls and it is quite coarsely granular; the distal face occasionally also has 3–5 short radiating ridges, but the alveoli lack a central nodule, as is sometimes found in *R. concava* (no. 46).

Riccia furfuracea (no. 38), *R. elongata* (no. 39) and *R. trachyglossum* (no. 40) are another three species that have rather low dorsal pillars. Only in *R. trachyglossum* are the thalli also quite small, but it has differently ornamented spores and is so far only known from the highlands of Lesotho.

Vouchers: *Duthie 5455*, *5484* (BOL); *Smook 6962c* (PRE); *Van Rooy 2451*, *2598* (PRE).

38. **Riccia furfuracea** *Perold* in Bothalia 21: 176 (1990c); Perold: 56 (1991c). Type: Cape, Klein Roggeveld, SW of De Kom, damp east slope with dense, short scrub, *Oliver 8957a* (PRE, holo.!).

Thalli medium-sized, in crowded gregarious patches, shiny, almost papillose to scurfy proximally; glaucous-green to green, often purple along margins; when dry, margins inflexed, apically meeting along midline above dorsal face, flanks covered by large, conspicuous, hyaline scales. *Branches* once to several times symmetrically or asymmetrically furcate, moderately to widely divergent, ovate to broadly ovate, up to 8 × (1.1–)1.5–1.8(–2.0) mm, 0.9–1.2 mm thick, in section 1.5 times to twice wider than thick, apex bluntly wedge-shaped; groove deep distally, sides convex, flattening out at ± midway along length of branches, thallus margins subacute, somewhat raised distally, becoming shortly winged; flanks erect to sloping steeply or more obliquely proximally, green to purple; ventral face rounded, green. *Scales* large and conspicuous, 750–1200 × 500–625 µm, projecting up to 125 µm above thallus margins, mostly semicircular, imbricate, hyaline, base often partly purple-red, margin more or less entire. *Dorsal epithelium* free-standing, thin-walled, hyaline, 2- or 3-celled pillars, 75–150(–180) µm long, not tapering, cells generally shorter than wide, top cell mammillose or round, rarely conical, 32–47 × 40–52 µm, basal cells 37–40(–50) × 50–62(–75) µm, frequently collapsed toward margins and proximally; air pores small, 3- or 4(occasionally 5)-sided. *Assimilation tissue* 350–450 µm thick, consisting of vertical columns of 6–8 cells, enclosing narrow, mostly 4-sided air canals; storage tissue occupying ventral part of thallus, cells angular to rounded, with numerous starch granules. Figure 60.

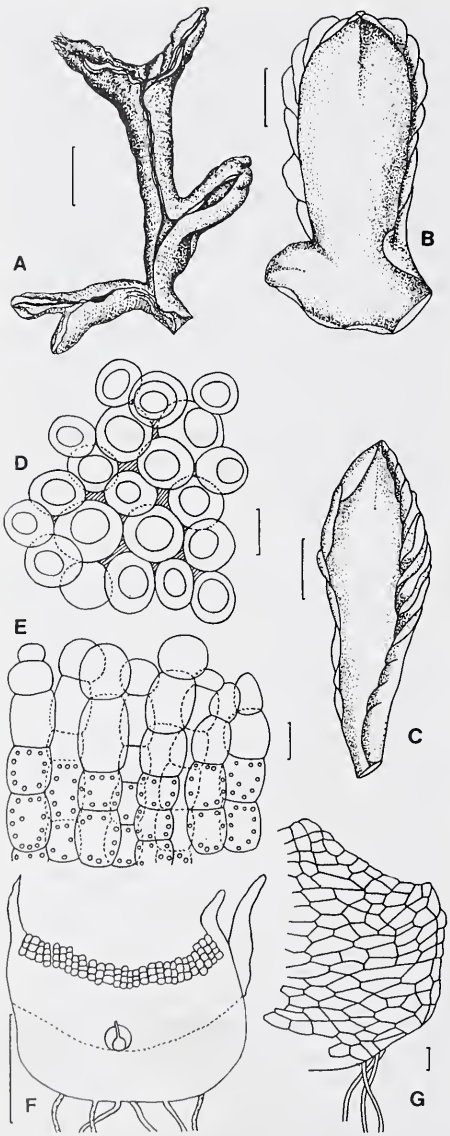


?Monoicous. *Antheridia* with hyaline necks in a row along groove. *Archegonia* scattered, with purple-brown necks. *Sporangia* bulging dorsally, solitary along middle of proximal part. *Spores* 70–78(–88) µm diam., triangular-globular, polar, light brown to brown, semitransparent; wing 5 µm wide, notched or perforated at marginal angles, margin finely crenulate; ornamentation reticulate, rather similar to dissimilar on 2 spore faces; distal face with (6–)7–9(–10) alveoli across diam., 7–8 µm wide, alveolar walls thick, rounded, often dotted with granules, slightly raised at nodes, toward centre some cross walls absent or poorly developed, others linked up, generally forming an irregular, complete or incomplete cross; proximal face with triradiate mark narrow, distinct, granulate, alveoli generally poorly defined, incomplete, walls indistinct, low. *Chromosome number*: not known. Plate 25E, F.

Riccia furfuracea is an endemic species. It is known from the shrublands of the western part of Northern Cape and north-central Western Cape and grows on shallow soil overlying granitic rock outcrops, at seepage areas or on stream banks. Map 29.

The species can be distinguished from others in section *Pilifer* by its very low dorsal cell pillars, composed of only two (or three) cells, mostly wider than long, the top cell often being mammillose. From above, it is not very obvious that the cells are in free-standing pillars, the cells are closely packed, not in rows, nor uniform in size, as smaller cells are wedged in between larger ones. The dorsal surface is scurfy when dry and plants from drier areas in Namaqualand are bluish or purplish green. In cross section the flanks are generally steep, not sloping. The spores are usually easily recognized by a central cross on the distal face and low-walled, generally poorly demarcated alveoli on the proximal face.

FIGURE 60.—**Riccia furfuracea**. A, B, thallus: A, wet; B, dry. C, c/s epithelial cell pillars and assimilation tissue below; D, epithelial cells and air pores (hatched) from above; E, c/s branch; F, scale. A, *S.M. Perold 2180*; B, *Oliver 8910*; C, D, *S.M. Perold 1476*; E, *S.M. Perold 1398a*; F, *S.M. Perold 1475*. Scale bars: A, B, E, 1 mm; C, D, 50 µm; F, 100 µm. Artist: J. Kimpton.



Vouchers: *Oliver 8910*, *8921* (PRE); *S.M. Perold 1476*, *1515*, *1854* (PRE).

39. **Riccia elongata** *Perold* in Bothalia 21: 167 (1990b); Perold: 55 (1991c). Type: Transvaal, 5 km NE of Kriel on road to Vandijksdrift, near disused bridge, on dry slope, *S.M. Perold 2018* (PRE, holo.!).

Thalli medium-sized, in gregarious patches, branches sometimes overlying each other; bluish green to green, crystalline, shiny; when dry, margins tightly inflexed, white wavy scales meeting along midline, covering greyish white dorsal face. *Branches* simple or once to several times symmetrically or asymmetrically furcate, moderately to widely divergent, ligulate to oblong, up to 8 mm long, segments 1–4 × 1.1–2.0 mm, 0.8–1.1(–1.2) mm thick, in section as wide as thick to twice wider than thick, apex acute; groove narrow and deep distally, soon becoming wide and shallow, thallus margins subacute; flanks steep to somewhat obliquely sloping, green; ventral face rounded, green. *Scales* large, 500–850 × 600–800 µm, projecting ± 200 µm above thallus margin, imbricate, rounded, hyaline, base occasionally with some purple-red cells, margins mostly entire.

Dorsal epithelium free-standing, 3- or 4-celled, fragile, hyaline pillars, up to 200 µm long, top cell smallest, globose, occasionally conical or mammillose, (35–)40–50(–60) × 45–65 µm, lower cells larger, with bulging lateral walls, 58–80 (–100) × 40–75 µm; air pores small, generally 4-sided, occasionally triangular. *Assimilation tissue* ± 350 µm thick, mostly consisting of vertical columns of ± 6 cells, enclosing narrow, 4- or 6(7)-sided air canals; storage tissue occupying ventral part of thallus, cells tightly packed, angular, containing starch granules. Figure 61.

?Monoicous. *Antheridia* not seen. *Archegonia* only seen in sections, immature. *Sporangia* bulg-

FIGURE 61.—**Riccia elongata**. A–C, thallus: A, dry; B, wet and fully expanded; C, with partly inflexed sides. D, epithelial cells and air pores (hatched) from above; E, c/s epithelial cell pillars and assimilation tissue below; F, c/s branch, scales projecting beyond margins; G, scale. A, D–G, *S.M. Perold 2476*; B, C, *S.M. Perold 2018*. Scale bars: A–C, F, 1 mm; D, E, 50 µm; G, 100 µm. Artist: J. Kimpton.

ing dorsally, singly along middle of proximal part of thallus. *Spores* 70–85(–90) µm diam., triangular-globular, polar, light brown, semi-transparent; wing 3–5 µm wide, wider at perforated marginal angles, margin smooth to finely crenulate; ornamentation irregularly and incompletely reticulate, similar on two spore faces; distal face with 5–7 incomplete alveoli across diam., irregularly shaped and variable in size, 10–25 µm wide, often with central boss, free-standing or attached, walls thick and prominent, sparsely granular, occasionally raised at nodes, extending onto wing; proximal face with triradiate mark clearly defined, joined by some alveolar walls, alveoli incomplete, 7 µm wide, occasionally with central boss, walls nearly smooth, slightly raised at nodes. *Chromosome number*: n = 16 (Bornefeld 1989, as *R. furfuracea*, *S.M. Perold 424*). Plate 27A, B.

Riccia elongata is a rare, endemic species and has so far been found at only a few localities in Gauteng and Mpumalanga where it grows on soil on gentle slopes or at rock outcrops near seepages. Map 29.

The species can be distinguished from other members in section *Pilifer* by the rather long, narrow, frequently simple branches, with the sides tightly inflexed when dry, and by large, imbricate, wavy, white scales. It is somewhat like *R. simii* (no. 52) in habit, but with the scales less prominent and not so closely imbricate. The dorsal cell pillars, spore ornamentation and distribution are also different.

The shiny, round, bulging cells in the dorsal cell pillars are a character shared by a few members in section *Pilifer*, e.g. *R. concava* (no. 46), *R. furfuracea* (no. 38) and *R. trachyglossum* (no. 40), but these species frequently develop purple coloration on exposure to the sun and differ from *R. elongata* in habit, spore ornamentation and distribution.

Vouchers: *S.M. Perold 1058, 2476* (PRE); *Smook 4912* (PRE).

40. **Riccia trachyglossum** *Perold* in Bothalia 21: 172 (1990e); Perold: 56 (1991c). Type: Lesotho, Sani Top, mountain slopes west of Border Post, on soil bank of small pond in bog, *Van Rooy 3539* (PRE, holo.!).

Thalli smallish, in crowded, gregarious patches or in partial rosettes or scattered; blue-green, glistening, proximally roughened; when dry, margins apically inflexed, meeting along midline, otherwise raised or incurved, dorsal face white to faintly purplish, roughened, scales only apically visible, flanks occasionally yellowish to reddish brown. *Branches* once or twice symmetrically or asymmetrically furcate, narrowly to moderately divergent, obcuneate to ovate, up to 5 × 1–2 mm, 0.7–0.9 mm thick, in section 1.5 times to twice wider than thick, apex wedge-shaped; groove distally present, its sides raised, tumid, thallus margins subacute; flanks rather steep to sloping obliquely, green; ventral face gently rounded to almost flat, green. *Scales* 750 × 500–550 µm, projecting slightly above thallus margins, rounded, imbricate, hyaline, margin mostly entire.

Dorsal epithelium in free-standing, 2- or 3(4)-celled, fragile, hyaline pillars, ± 180 µm long, top cell globose, rarely conical, 32–45 × 47–55 µm, lower cells with sides bulging, 55–75(–100) × 47–65 µm; air pores 4-sided. *Assimilation tissue* 350 µm thick, consisting of vertical columns of 6 or 7 cells, enclosing narrow, (3–)4(–5)-sided air canals; storage tissue occupying ventral part of thallus, cells angular, closely packed. Figure 62.

Monoicous. *Antheridia* with hyaline necks up to 125 µm long, in one or two rows along middle of thallus. *Archegonia* with thin purple necks. *Sporangia* bulging dorsally along midline, numerous. *Spores* 70–87(–92) µm diam., triangular-globular, polar, light brown, semi-transparent; wing 5 µm wide, rather wider at perforated angles, margin finely crenulate; ornamentation reticulate, dissimilar on 2 faces: distal face with 8 angular or irregular alveoli across diam., 5–8 µm wide, central ones often incomplete, walls sprinkled with granules, raised at nodes; proximal face with triradiate mark distinct, facets with mostly incomplete alveoli, 3–5 µm wide, walls thin, irregular.

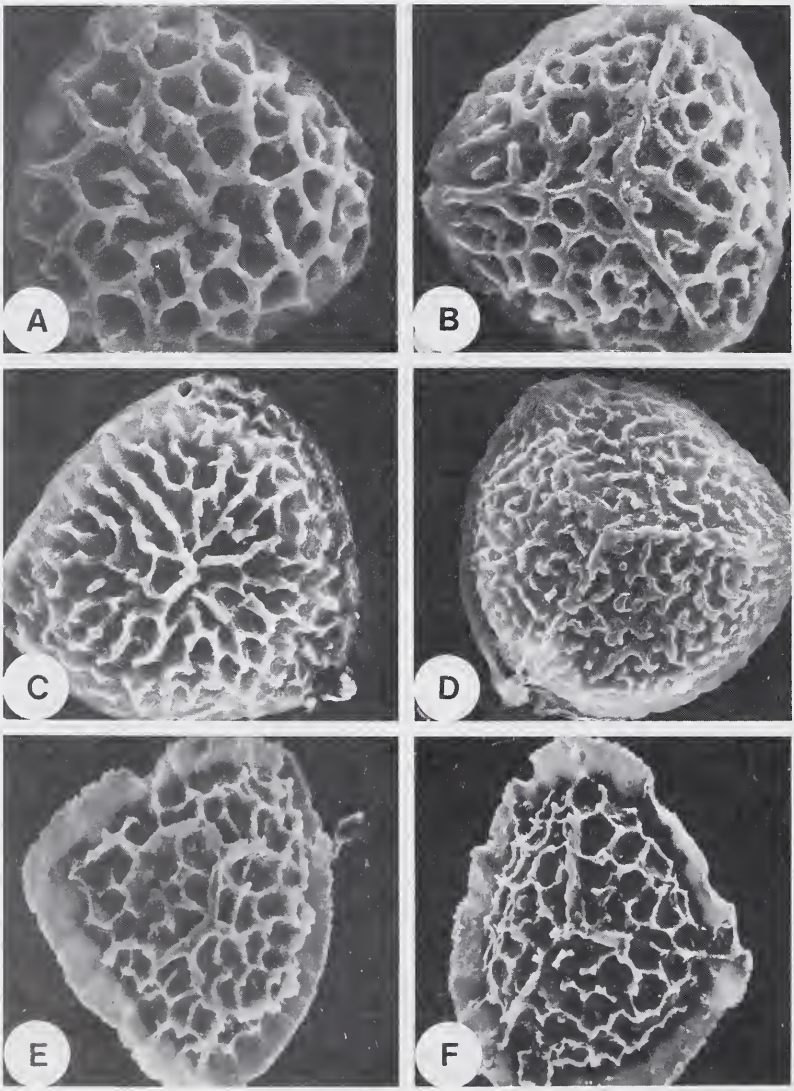
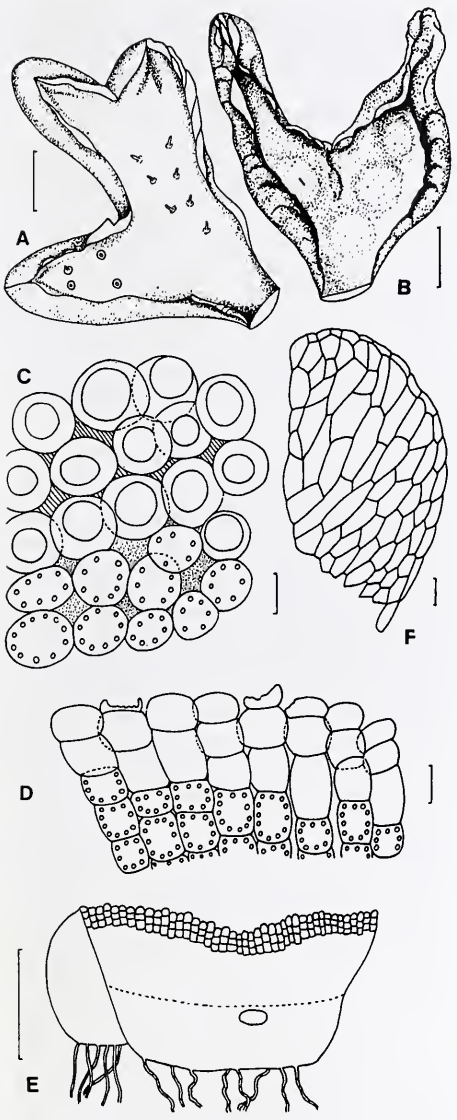


PLATE 27.—Spores. A, B, **Riccia elongata**: A, distal face; B, proximal face. C, D, **R. trachyglossum**: C, distal face; D, proximal face. E, F, **R. alatospora**: E, distal face; F, proximal face. A, B, *S.M. Perold 2018*; C, D, *J.M. Perold 34*; E,F, *Duthie 5004b*. A, B, × 600; C, D, × 700; E, F, × 500.



Chromosome numbers: n = 16, 17 (T. Bornefeld pers. comm.). Plate 27C, D.

Riccia trachyglossum is so far only known from the alpine heath-grassland in Lesotho, at altitudes of ± 2 500–3 000 m above sea level; it grows on soil banks in bogs. Map 29.

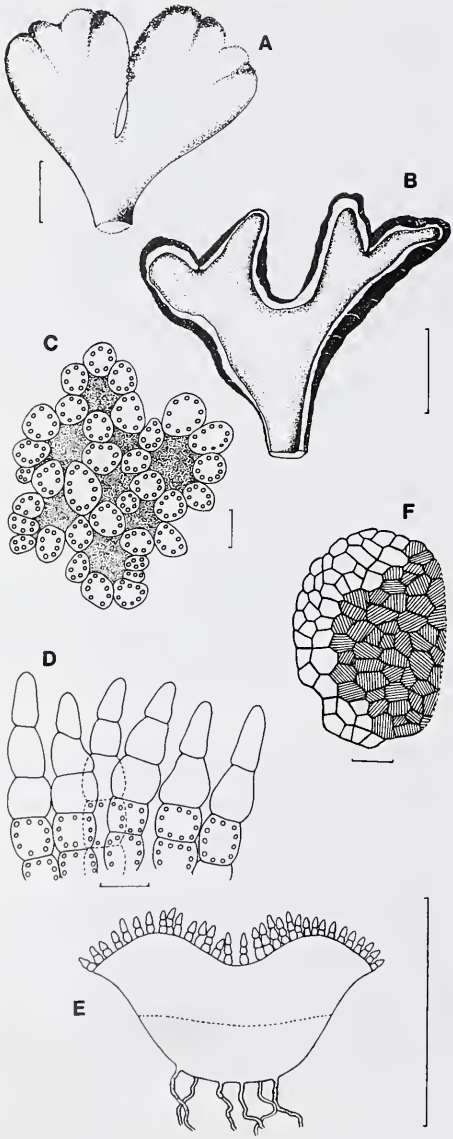
The species is distinguished from others in section *Pilifer*, which also have globose to bulging dorsal cells [e.g. *R. concava* (no. 46), *R. elongata* (no. 39) and *R. furfuracea* (no. 38)], by its somewhat smaller size, rather low, hyaline scales, raised, tumid thallus margins toward the apex, and faintly bluish to purplish, roughened dorsal face. It also differs in spore ornamentation and in distribution.

Vouchers: *J.M. Perold 33, 34* (PRE); *S.M. Perold 2530, 2531* (PRE).

41. **Riccia alatospora** *O.H.Volk & Perold* in Bothalia 15: 534 (1985); Perold: 52 (1991c). Type: Cape, Stellenbosch, Platklip, on moist sand in hollows on granite outcrop, June-1929, *Duthie 5004* (BOL, holo.!); *PRE-CH1007* (PRE, iso.!).

Thalli small, in crowded gregarious patches or scattered; green to bright green, in older plants glistening to almost crystalline; when dry, dorsally somewhat concave, greenish white, felt-like, margins incurved to apically inflexed, exposing rather small, pinkish red scales. *Branches* once or twice symmetrically furcate, terminal segments short, variously divergent, obcuneate to obovate, base narrow, 3.5(–5.0) × 0.9–1.5(–2.0) mm, 0.6–1.2 mm thick, in section 1.5 times to twice wider than thick, apex obtuse, shortly emarginate; groove narrow and deep distally, soon shallow and wide, dorsal face becoming flat to slightly convex, thallus margins subacute; flanks sloping obliquely, proximally steeper, green; ventral face gently round-

FIGURE 62.—**Riccia trachyglossum**. A, B, thallus: A, wet; B, dry. C, h/s epithelial cell pillars and air pores (hatched) from above, assimilation tissue with air canals (stippled); D, c/s epithelial cell pillars and assimilation tissue; E, c/s branch; F, scale. A, C, D, F, *S.M. Perold 2530*; B, *Van Rooy 3539*; E, *J.M. Perold 33*. Scale bars: A, B, E, 1 mm; C, D, 50 µm; F, 100 µm. Artist: J. Kimpton.



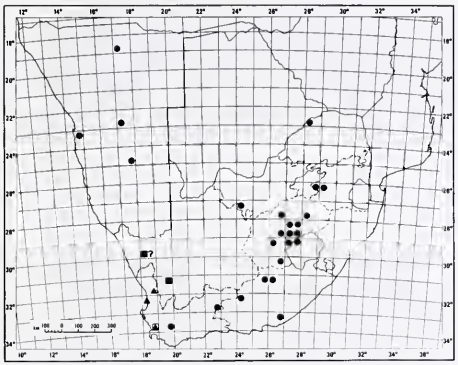
ed to almost flat, green. *Scales* present at apex and distal flanks, ± 550 × 450 µm, hardly extending to thallus margins, absent proximally, mostly rounded, imbricate, pinkish red with hyaline, more or less entire margins.

Dorsal epithelium in free-standing cell pillars, tapering, 120–160 µm long, consisting of 2 or 3 fragile, hyaline cells, longer than wide, 35–75 × 30–40 µm, top cell conical, occasionally mammillose; air pores 4–6-sided, enlarging proximally. *Assimilation tissue* 300– 600 µm thick, consisting of vertical columns of 7 or 8 cells, enclosing 4–6 or 8-sided air canals, up to 80 µm wide; storage tissue in ventral part of thallus with rounded, irregularly arranged, thin-walled cells. Figure 63.

Dioicous. *Antheridia* scattered, necks colourless, up to 150 µm long. *Archegonia* along centre of female thallus, necks purple. *Sporangia* dorsally bulging. *Spores* 90–110(–125) µm diam., triangular-globular, polar, straw-coloured to brownish yellow, semitransparent; wing slightly and irregularly undulate, 12.5–15.0 µm wide, margin finely crenulate, sometimes partly eroded, occasionally with round perforations; ornamentation reticulate, dissimilar on the two faces; distal face with 4 or 5 large central alveoli up to 40 µm across, with thick crenulate walls 12 µm high, partially or completely subdivided into smaller alveoli by low ridges, all surrounded by an outer row of smaller alveoli, walls raised at nodes; proximal face with pronounced triradiate mark, its arms thin and high, each facet with ± 30 smallish complete or incomplete alveoli, up to 12.5 µm wide, walls raised into spinous thickenings at nodes. *Chromosome number*: n = 8 (Bornefeld 1984). Plate 27E, F; Perold (1989e: fig. 31.1–6).

This endemic species is very rare and only known from one locality in the southwestern part of Western Cape, where it grows on damp sand or soil overlying granite. Map 30. It is now thought that the specimen, *S.M. Perold 1426*

FIGURE 63.—**Riccia alatospora**. A, B, thallus: A, wet; B, dry. C, h/s assimilation tissue, air canals stippled; D, c/s epithelial cell pillars, assimilation tissue below; E, c/s branch; F, scale. A, C–E, *Oliver 9025*; B, F, *S.M. Perold 468*. Scale bars: A, B, E, 1 mm; C, D, 50 µm; F, 100 µm. Artist: J. Kimpton.



MAP 30.—❑ **Riccia alatospora**
■ **R. hantamensis**
● **R. albovestita**
▲ **R. parvo-areolata**

p.p. from Carolusberg, Northern Cape, previously referred here (Perold 1989c), is actually a depauperate form of *R. hantamensis* (no. 42).

Riccia alatospora is the smallest species in section *Pilifer*. Its size, reddish pink scales and wide-winged, highly ornamented, large spores, distinguish it from other species in this section. It is closely related to *R. hantamensis* (no. 42), which is, however, a much larger plant, but with similarly ornamented, though smaller spores.

In a pencilled note found with Duthie's collections of this species, she named it '*R. alatospora*' (Volk & Perold 1985), but she did not publish a description of it, as she and Sim (1932) later came to believe it to be a specimen of *R. coronata* Sim. Sim's (1926) description of the latter, however, refers to one upper epidermal layer of hyaline cells, and not to 3-celled pillars as depicted by Duthie in her notes on *R. alatospora* (Volk & Perold 1985). The type (and only) specimen of *R. coronata*, *Sim 8730*, has been lost and Sim's description and illustrations of it are not exact enough for a definite identification. Apparently, Arnell (1963a) did not investigate these plants independently and merely copied Duthie's drawings and notes, thus failing to classify this species with *R. albomarginata* (no. 47), *R. concava* (no. 46) and *R. villosa* (no. 50), the other, then known species with free-standing dorsal cell pillars, which he referred to as 'velvety'.

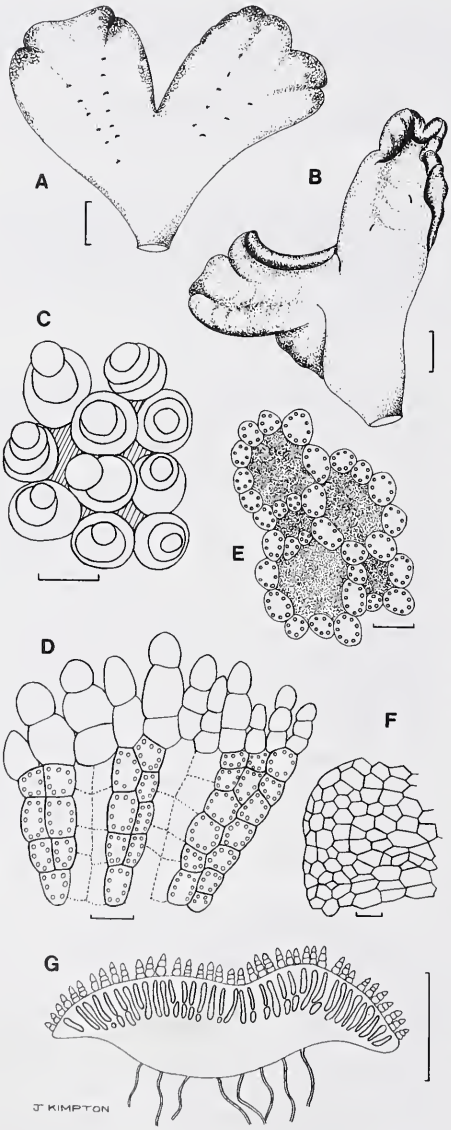
Vouchers: *Duthie 5324* (BOL); *Oliver 8058, 9025* (PRE); *Pretorius s.n.* (BOL).

42. **Riccia hantamensis** *Perold* in Bothalia 19: 157 (1989c); Perold: 53 (1991c). Type: Cape, Hantams Mountain, Van Rhynshoek Farm, 8 km to FM tower, on soil at streamlet next to road, Sept. 1987, *S.M. Perold 1830* (PRE, holo.!).

Thalli medium-sized to rather large, in crowded gregarious patches or scattered; bright green, almost crystalline; when dry, margins raised and incurved, dorsally flat to slightly concave, yellowish green, felt-like. *Branches* once or twice symmetrically furcate, closely to moderately divergent, oblong to obovate, up to 10 mm long, terminal segments generally short, 1.5–3.0 × 2.5–3.8 mm, 0.7–1.2 mm thick, in section 3.0–3.5 times wider than thick, apex rounded to truncate, emarginate; groove distally deep, soon flattening out and disappearing at ± midway along length of thallus, thallus margins rounded, obtuse, overhanging; flanks sloping very obliquely upward and outward, green; ventral face gently rounded to flat, green. *Scales* ventrally situated, small and inconspicuous, up to 800 × 250 µm, only present toward apex, fragile, hyaline, partly overlapping to somewhat spaced, margin more or less entire. Plate 26B.

Dorsal epithelium in free-standing cell pillars, tapering, 135–160 µm long, consisting of 3 or 4 fragile, thin-walled, hyaline cells, mostly shorter than wide, 40–58 × 48–80 µm, top cell small, rounded to conical, basal cells wide and bulging at sides; air pores 3- or 4(5)-sided, wider proximally. *Assimilation tissue* ± 350 µm thick, consisting of vertical columns of ± 8 cells, enclosing 4–6- or 8-sided, obliquely sloping air canals; storage tissue in ventral part of thallus, cells rounded. Figure 64.

Dioicous. *Antheridia* along groove, numerous, with conspicuous hyaline necks up to 500



µm long. *Archegonia* with purple necks, scattered along length of lobes in female plants. *Sporangia* bulging slightly dorsally. *Spores* 60–80(–85) µm diam., triangular-globular, polar, pale yellow-brown, semitransparent; wing up to 10 µm wide, perforated at marginal angles and occasionally also elsewhere, margin finely crenulate; ornamentation reticulate, dissimilar on 2 faces; distal face mostly with 4 large, central alveoli, 15–20 µm wide, some with central boss and often partly subdivided, outer row(s) of alveoli smaller, 5–12 µm wide, walls granulate and raised at nodes, extending across wing; proximal face with triradiate mark distinct, the arms 5 µm high and extending onto wing, alveoli on each of 3 facets angular, 5–10 µm wide, walls raised at nodes, often irregular and incompletely separating alveoli. *Chromosome number*: n = 9 (Bornefeld 1989, as *R. alatospora* var. *hantamensis*). Plate 28A, B; Perold (1989e: fig. 32.1–6).

This extremely rare and endemic species in section *Pilifer*, is so far only known from one locality [perhaps 2; see note under *R. alatospora* (no. 41)] in the southwestern part of Northern Cape which has succulent Karoo vegetation. It was found on clayey soil on the bank of a small stream. Map 30.

Riccia hantamensis is closely related to, but distinguished from *R. alatospora* (no. 41) (see note under that species), on account of its much more robust thalli, the inconspicuous, hyaline scales on the ventral face, the rounded apical cells in the loose dorsal cell pillars, and the much smaller, but similarly ornamented, and far more numerous spores. Spores collected from the same population during a dry season, appear to be more highly ornamented and rather smaller than those collected in a wet season. The air canals in the thalli of *R. hantamensis* (and *R. alatospora*), are generally wider than is usual for species in section *Pilifer*. Specimens of *R.*

FIGURE 64.—**Riccia hantamensis**. A, B, thallus: A, wet male; B, dry female. C, short, tapering epithelial cell pillars and air pores (hatched) from above; D, c/s epithelial cell pillars, assimilation tissue below, with wider air canals; E, h/s assimilation tissue, air canals stippled; F, scale; G, c/s branch. A, C–E, G, *Germishuizen 4034*; B, F, *S.M. Perold 1830*. Scale bars: A, B, G, 1 mm; C–E, 50 µm; F, 100 µm. Artist: J. Kimpton.

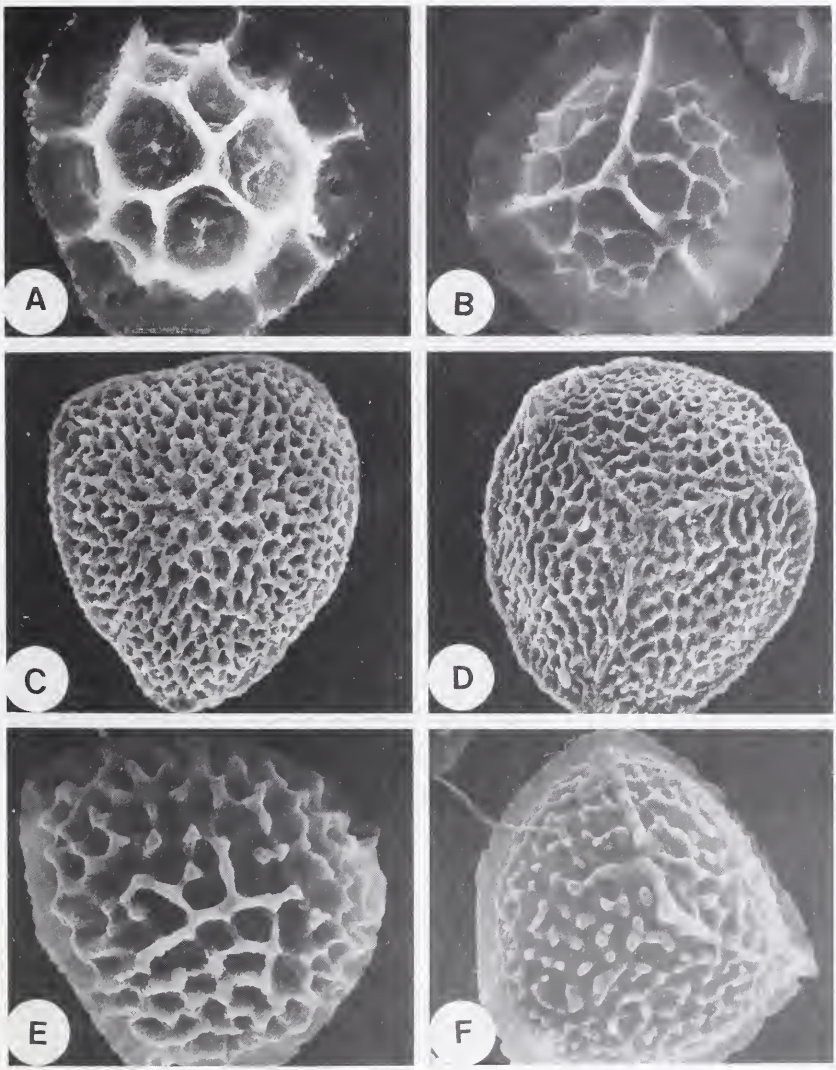
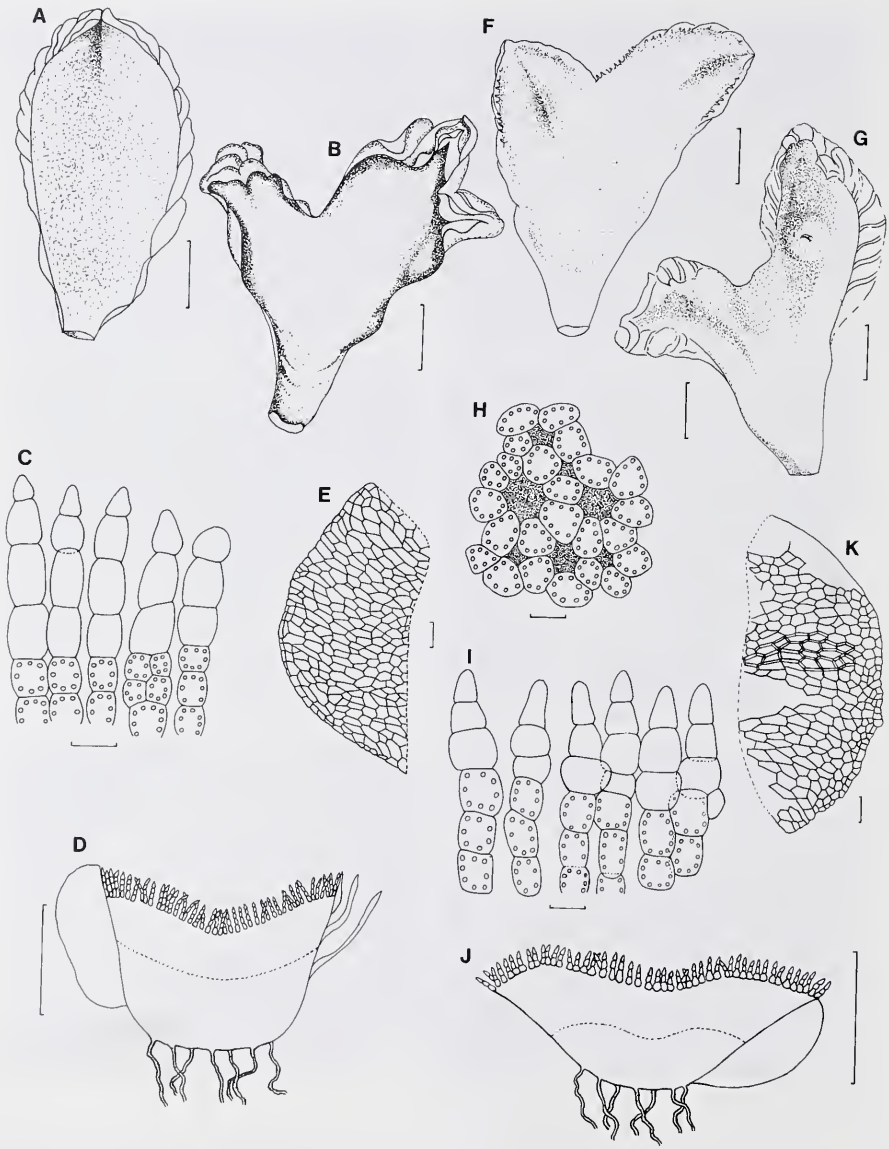


PLATE 28.—Spores. A, B, **Riccia hantamensis**. A, distal face; B, proximal face. C, D, **R. parvo-areolata**: C, distal face; D, proximal face. E, F, **R. albovestita**: E, distal face; F, proximal face. A, B, *S.M. Perold 1830*; C, D, *J.M. Perold 24*, E,F, *J.M. Perold 39*. A, B, × 800; C–F, × 700.


A
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hantamensis cultivated in seed trays and in Petri dishes, together with *R. alatospora*, throughout maintained the above differences in thallus size, ventral scales and shape of the cells in the dorsal epithelial pillars.

Vouchers: *Germishuizen 4034* (PRE); *S.M. Perold 2338* (PRE).

43. **Riccia parvo-areolata** *O.H.Volk & Perold* in Bothalia 15: 117 (1984); Perold: 51 (1991c). Type: Cape, near Doringbaai, W of Vredendal, Kliphoek Farm, gravel on sandstone, *J.M. Perold 23* (PRE, holo.!).

Thalli medium-sized, scattered or in loose patches, never in rosettes; light green to glaucous-green, not quite velvety, but ± furry, proximally tangled or matted, slightly glistening; when dry, margins toward apex inflexed, covering groove and exposing flanks with white scales, otherwise erect to incurved, sometimes partly recurved, dorsally broadly concave, greenish white, scurfy. *Branches* simple or asymmetrically once to several times furcate, segments generally short, moderately divergent, broadly oblong-obovate, up to 10 × 2.5–4.0 (–5.0) mm, 1.2 mm thick, in section 2–4 times wider than thick, apex slightly keeled to roundly truncate and shortly emarginate; groove only distally present, soon flattening out, even becoming somewhat convex dorsally, thallus margins subacute; flanks sloping obliquely distally, steeper proximally, green; ventral face slightly rounded, green, sometimes flecked with violet. *Scales* apically prominent, up to 1200 × 600 µm, projecting slightly above thallus margins, semicircular, imbricate, hyaline, base flecked with mauve, margins mostly entire. Plate 26C.

Dorsal epithelium free-standing, uniseriate hairs, not tapering, ± 200 µm long, consisting of 3 or 4 fragile, inflated, hyaline cells, slightly longer than wide, size variable, 25–75 × 25–65 µm, top cell bluntly conical or mammillose to rounded; air pores obscured by cell pillars, apically small, generally 4-sided, soon enlarging laterally and proximally, becoming 5- or 6-sided. *Assimilation tissue* up to 600 µm thick, consisting of vertical columns of 8–12 cells, enclosing air canals, centrally narrow, 4-sided, laterally widening and 5- or 6-sided; storage tissue occupying ventral part of thallus, cells often with oil droplets. Figure 65A–E.

?Dioicous. *Antheridia* with necks not seen, obscured by dorsal cell pillars. *Archegonia* with purple necks, scattered along central part of thallus. *Sporangia* bulging dorsally, when ripe, spores lying free in decaying thallus. *Spores* 70–80(–90) µm diam., triangular-globular, polar, brown, semitransparent; wing finely granular, narrow, width less than 5 µm, inconspicuous pores at marginal angles, margin crenulate; ornamentation finely reticulate, the same on both faces; distal face convex, with 18–22 small round or oval alveoli across diam. of spore, ± 2.5 µm wide, sometimes larger toward centre, walls densely covered with fine granules and raised at nodes; proximal face with triradiate mark somewhat obscured by granules, each of 3 facets with 45–50 small, round alveoli with granulate walls. *Chromosome number*: n = 8 (Bornefeld 1984; 1989). Plate 28C, D; Perold (1989e: fig. 27.1–6).

Riccia parvo-areolata is endemic to, and known from only a few collections in the Western Cape where it grows on damp, shallow, sandy loam. Map 30.

The species can be distinguished from others in section *Pilifer* mainly by the finely alveolate and granular ornamentation of its spores and by the variously shaped, but generally conical or

FIGURE 65.—A–E, **Riccia parvo-areolata.** A, B, thallus: A, wet; B, dry. C, c/s epithelial cell pillars, assimilation tissue below; D, c/s branch; E, scale. F–K, **R. albovestita.** F, G, thallus: F, wet; G, dry. H, h/s assimilation tissue, air canals stippled; I, c/s short tapering epithelial cell pillars, assimilation tissue below; J, c/s branch; K, scale. A, *S.M. Perold 1727*; B–D, *S.M. Perold 1726*; E, *J.M. Perold 26*; F, G, *Smook 6583*; H, I, *Volk 81–274b*; J, *Volk 84–646b*; K, *Volk 81–292*b. Scale bars: A, B, D, F, G, J, 1 mm; C, H, I, 50 µm; E, K, 100 µm. Artist: J. Kimpton.

mammillose apical cells of the four-celled, dorsal epithelial pillars. The rounded scales are apically prominent, but less so proximally. In the dry state the thallus is markedly concave, when it can easily be confused with *R. concava* (no. 46). *R. concava* is, however, rather glaucous-green dorsally, the apical cells of the dorsal pillars are small, globose and often collapsed, with the lower cells conspicuously larger and inflated; the spores frequently have radially arranged ridges on the distal face.

Several species in section *Pilifer* are extraordinarily difficult to distinguish; living material is mostly required for identification, as the dorsal cell pillars, a critical character, cannot be reconstituted in dried herbarium specimens. It is now thought that *Schelpe 7759*, *7776* and *Duthie 5407*, previously placed here (Volk & Perold 1984), probably belong to a different, as yet undescribed species, as the spores have wings nearly 10 µm wide, not narrower than 5 µm as in *R. parvo-areolata.*

Vouchers: *Duthie 5141* (BOL); *J.M. Perold 15, 19, 22* (PRE); *S.M. Perold 1727* (PRE).

44. **Riccia albovestita** *O.H.Volk* in Mitteilungen der Botanischen Staatssammlung, München 17: 245 (1981); Perold: 51 (1991c). Type: SWA/Namibia, Bezirk Windhoek Nr. 85 (Rietfontein), zeitweise wenig durchrieselter, flachgrundiger Granitzersatz, fast eben, voll exponiert; pH 7.2–7.8; mit *Anthoceros* sp., *Riccia volkii*, *Exormotheca holstii*, *Archidium microthecium*, *Bruchia* sp., *Lobelia depressa* u.a., *Volk 01164/b* (M, holo.!).

R. duthieae O.H.Volk & Perold in Bothalia 15: 531 (1985); Perold (1989e: fig. 29.1–6). Type: Cape, Aberdeen, next to road R57, 2 km north-east of junction with R61, at shallow edges of vleis temporarily damp or occasionally inundated, 1981.04.11, *Volk 81/273* (M, holo.!; PRE, iso.!).

R. sarcosa O.H.Volk & Perold in Bothalia 16: 23 (1986b); Perold (1989e: fig. 30.1–6). Type: Cape, Aberdeen, next to road R57, 2 km north-east of junction with R61, at shallow edges of vleis temporarily damp or occasionally inundated, 1981.04.11, *Volk 81–274b* (M, holo.!; PRE, iso.!).

Thalli medium-sized, scattered, in incomplete rosettes ± 20 mm across, or in gregarious patches; pale green to bright green, dorsally glistening, almost papillose, white in older parts and along thinnish, slightly irregular margins, hyaline scales projecting apically only; when dry, thallus margins incurved, apical scales prominent, dorsal face plane to concave, creamy green to greenish white, felt-like. *Branches* occasionally simple, usually once or twice furcate, variously divergent, obovate to oblong-obcordate, up to 10 × 1.5–2.3(–3.0) mm, 0.8–1.0 mm thick, in section twice wider than thick, apex slightly narrowed, subacute to rounded, emarginate; groove deep and narrow distally with steep, convex sides, but soon shallow and wide, disappearing proximally, thallus margins acute to subacute, shortly winged; flanks steep near apex, otherwise sloping obliquely, green, toward base occasionally flecked with dark red; ventral face almost flat to gently rounded, green. *Scales* large, 1000–1350 (–1500) × 500–750 µm, conspicuous at apex, more proximally appressed to flanks and hardly reaching thallus margins, imbricate, semi-circular, hyaline, base often wine-red to reddish purple, occasionally a few conical cells projecting from margin of apical scales.

Dorsal epithelium in free-standing, short, tapering pillars, 120–220 µm long, composed of 3 or 4 fragile, hyaline cells, top cell smallest, mostly longer than wide, ± 45 × 35 µm, conical, mammillose or occasionally globose, central and basal cells shorter than wide, 45–75 × 45–95 µm, lateral walls bulging; air pores 4-sided to polygonal, partly obscured by dorsal cells and by occasional unicellular, globose outgrowths at bases of pillars. *Assimilation tissue* 400–500 µm thick, consisting of vertical columns of 8–10 cells, enclosing 4–8-sided air canals which widen upwardly; storage tissue occupying ventral part of thallus, cells closely packed. Figure 65F–K.

Dioicous. *Antheridia* along groove, necks colourless, ± 500 µm long. *Archegonia* scattered along centre, necks purple-brown. *Sporangia* bulging dorsally. *Spores* 60–80(–90) µm diam., triangular-globular, polar, yellow-brown to light brown to brown, semitransparent, becoming opaque with age; wing narrow, up to

5 µm, notched or perforated at marginal angles, margin finely crenulate; ornamentation reticulate, dissimilar on 2 faces; distal face with 4–6(–7) large, complete or incomplete central alveoli, 12.5–25.0 µm wide, usually partly subdivided by low walls radiating from papilla in middle, outer 1 or 2 rows of smaller, mostly complete alveoli, 5.0–7.5 µm wide, surrounding central ones, walls granulate and raised at nodes; proximal face with triradiate mark well-defined, sprinkled with granules, each of 3 facets covered with fine network of low, toothed ridges, often only partly complete or reduced to simple projections and stipplings. *Chromosome number*: n = 8 (Bornefeld 1984). Plate 28E, F; Perold (1989e: fig. 28.1–6).

Riccia albovestita is endemic to southern Africa and grows on clayey soil at streambanks, at the margins of vleis or dams or on damp, shallow soil overlying granite. It has been collected in Namibia, Northern Province, North-West, Gauteng, Mpumalanga, Free State, Lesotho, Western and Eastern Cape. It is therefore far more widespread than Volk (1981) originally thought, and not confined to Namibia. Map 30.

The species is recognized by the creamy green colour of the thallus, often turning white along the margins and by the hyaline scales, conspicuous only toward the apex, but sometimes with the bases a deep wine-red. The short, free-standing dorsal pillars are generally three- or four-celled and markedly tapering, with the basal cell widest. The spores are mostly rather smallish, light brown and usually incompletely reticulate with larger, partly subdivided alveoli over the centre of the distal face.

When Volk (1981) originally described this species, it was from one of his earlier collections from Namibia, which Arnell (1957) had incorrectly referred to *R. albomarginata* (no. 47), presumably because of the loose dorsal cell pillars and the large hyaline scales. Arnell's (1963a) illustrations of his concept of the spores of *R. albomarginata* were drawn from one of these specimens (Volk 1981).

Two species subsequently described as new, *R. duthieae* O.H. Volk & Perold (1985) and *R. sarcosa* O.H. Volk & Perold (1986b), are now regarded as synonyms of *R. albovestita* (Perold 1990c).

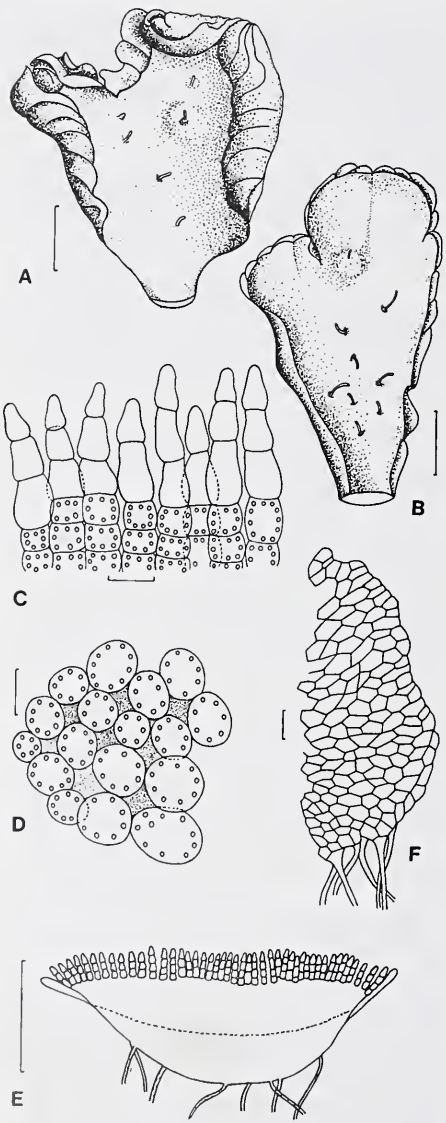
Vouchers: *M.J.A.W.Crosby 520* (PRE); *Duthie 5182* (BOL); *S.M. Perold 1319* (PRE); *Smook 4036* (PRE); *Van Rooy 2419* (PRE).

45. **Riccia ampullacea** *Perold* in Bothalia 20: 168 (1990b); Perold: 50 (1991c). Type: Lesotho, Sani Pass, mountain slopes W of Border Post, on soil in small cave, *Van Rooy 3573* (PRE, holo.!).

Thalli medium-sized, in crowded gregarious patches; bright green to bluish green, glistening, shaggy-haired proximally; when dry, dorsally concave, whitish green, felt-like, margins incurved, occasionally inflexed, rarely meeting along midline, revealing flanks covered with imbricate, slightly wavy, hyaline scales. *Branches* simple or once or twice furcate, variously divergent, broadly oblong, up to 8 × 1.5–2.5 mm, 0.6–0.9(–1.1) mm thick, in section 2.0–2.5 times wider than thick, apex rounded, shortly emarginate; groove only present distally, otherwise dorsal face concave, thallus margins acute; flanks sloping obliquely, green; ventral face slightly rounded to flat, green. *Scales* large, 1000–1100 × 500 µm, projecting above thallus margins, rounded, imbricate, hyaline, occasionally dark red toward base, margins mostly entire.

Dorsal epithelium in free-standing, 3- or 4-celled, fragile, hyaline pillars, 200–250 µm long, cells longer than wide, top cell conical, 45–67(–80) × 30–37 µm, lower cells often somewhat constricted in middle, 50–80(–110) × 35–52 µm; air pores small, ± 25 µm wide, 4- or 5-sided. *Assimilation tissue* 300–400 µm thick, consisting of vertical columns of 7 or 8 cells, enclosing 4–6(–8)-sided air canals; storage tissue occupying ventral part of thallus, cells round or angular. Figure 66.

Monoicous. *Antheridia* numerous, with conspicuous hyaline necks, up to 180 µm long, at



intervals along middle of thallus, often in close proximity to archegonial necks. *Archegonia* with long, thread-like, purple necks. *Sporangia* bulging dorsally, overlying tissue disintegrating and exposing spore sac. *Spores* 90–95(–105) µm diam., triangular-globular, polar, chestnut-brown, semitransparent to nearly opaque; wing 5 µm wide, margin crenulate, marginal angles perforated; ornamentation finely reticulate and radiately ridged, rather dissimilar on two faces; distal face with alveoli 3–5 µm wide, rarely complete, mostly confluent and walls anastomosing into thick, high ridges, radiating from centre to margin; proximal face with triradiate mark distinct or indistinct, on each facet, numerous small, mostly incomplete alveoli less than 5 µm wide, walls granulate, raised at nodes, sometimes anastomosing into short, semiradiating ridges. *Chromosome number*: n = 16 (Bornefeld 1989). Plate 29A, B.

Riccia ampullacea appears to be restricted to alpine heath-grassland localities in the Drakensberg of the Free State, Lesotho and KwaZulu-Natal as well as the Witteberg of the Eastern Cape Province, all in the summer rainfall region, where it is infrequently collected in damp places on humus-rich soil overlying basalt outcrops. Map 31.

The species is rather similar to *R. parvo-areolata* (no. 43) as both have wide, concave thalli when dry, with large, hyaline scales and dorsal cell pillars consisting of three or four elongated cells. In *R. ampullacea*, however, the dorsal cells are frequently somewhat constricted toward the middle, and more or less ampulla-shaped. The antheridial necks are also more conspicuous and numerous, and often in close association with the archegonial necks; the spores differ from the finely reticulate ornamentation in *R. parvo-areolata* by generally having thick radiating ridges on the distal face; its distribution is also different.

FIGURE 66.—**Riccia ampullacea**. A, B, thallus: A, dry; B, wet. C, c/s epithelial cell pillars and assimilation tissue below; D, h/s assimilation tissue, air canals stippled; E, c/s branch; F, scale. A–F, *Van Rooy 3573*. Scale bars: A, B, E, 1 mm; C, D, 50 µm; F, 100 µm. Artist: J. Kimpton.

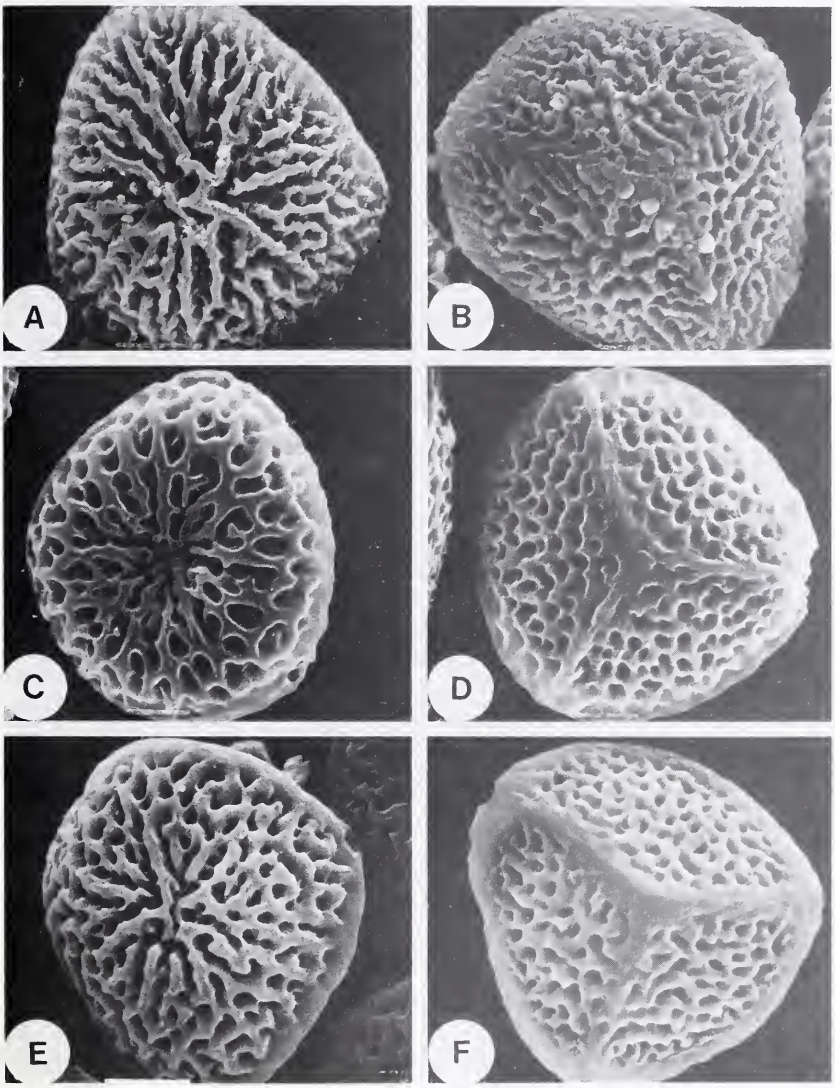
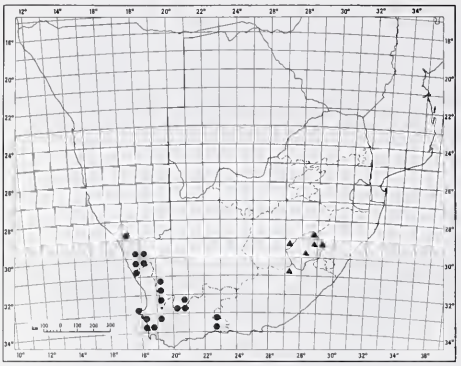


PLATE 29.—Spores. A, B, **Riccia ampullacea**: A, distal face; B, proximal face. C, D, **R. concava**. C, distal face; D, proximal face. E, F, **R. albomarginata**: E, distal face; F, proximal face. A, B, *Van Rooy 3164a*; C, D, *S.W. Arnell 30*; E, F, *S.M. Perold 2383*. A–D, × 700; E, F, × 600.



MAP 31.—● **Riccia concava**
▲ **R. ampullacea**

Vouchers: *Van Rooy 2724*, *2971*, *3045*, *3240* (PRE).

46. **Riccia concava** *Bisch.*, in Flora 29: 135 (March 1846); Gottsche et al.: 604 (Oct. 1846); Steph.: 325, 378 (1898); Sim: 12 (1926); S.W. Arnell: 22 (1963a); Perold: 161 (1989d); Perold: 54 (1991c). Type: Cape, in locis humidis in kloof inter M. Tafelberg et Leuwenberg, *Krauss s.n.*, Julio-1838, [(*G8979* holo.!), ex Herb. Musci. Palat. Vindob.; (S, iso.!) fide Grolle: 226 (1976)].

Thalli medium-sized to large, in crowded gregarious patches; bright green to bottle-green, rather shiny, becoming basally dull, scurfy and bluish green, hyaline scales projecting at apical margins only; when dry, margins raised to incurved, flanks covered with wrinkled, dull, creamy white scales, toward base with faintly mauve sheen, dorsal face broadly concave, glaucous, flaky. *Branches* once or twice furcate, rarely simple, moderately to widely divergent, broadly ovate to obovate, 6–10 × 3–4 mm, 0.9–1.2 mm thick, in section 3–4 times wider than thick, apex rounded, emarginate; groove narrow and deep distally, its sides convex, soon wide and shallow, somewhat concave proximally, thallus margins acute to subacute, shortly winged, slightly recurved; flanks sloping obliquely, green to mauve; ventral face rounded, green to purple laterally. *Scales* 900–1200 × 600 µm, not or hardly projecting beyond thallus margins except at apex where they do, semicircular, imbricate, hyaline, margins entire.

Dorsal epithelium free-standing, 3- or 4-celled, fragile, hyaline pillars, 180–260 µm long, cells generally shorter than wide, not tapered but top cell smallest, globose or conical, frequently collapsed, 34–42 × 45–60 µm, lower cells 50–75 × 68–85 µm, lateral walls bulging; air pores small, 4- or 5-sided, obscured by bulging dorsal cells. *Assimilation tissue* ± 450 µm thick, consisting of vertical columns of 6–8 short-rectangular cells, enclosing narrow, 4- or 5-sided air canals; storage tissue occupying ventral part of thallus, cells round or angular. Figure 67.

Monoicous. *Antheridia* with hyaline necks ± 250 µm long, in 2 rows along middle of lobes. *Archegonia* with purple necks. *Sporangia* single or in pairs, toward base bulging dorsally. *Spores* 75–100 µm diam., triangular-globular, polar, dark brown, nearly opaque; wing narrow, up to 5 µm wide, marginal angles notched or perforated, margin finely crenulate; ornamentation somewhat variable, reticulate, often with radiating ridges; distal face with 10–14 deep-set alveoli across diam. of spore, up to 7.5 µm wide, radial walls thick, often granular, raised at nodes, occasionally forming short, irregular ridges radiating outwards from centre; proximal face with triradiate mark not prominent, sparsely granular, 30–40 small round alveoli on each facet, walls raised at nodes. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 29C, D; Perold (1989e: fig. 26.1–6).

R. concava is restricted to the shrublands of the Northern and Western Cape and southwestern part of Eastern Cape. It grows on sandy, well-drained soil overlying granite. Map 31.

Arnell (1961, 1963a) reported *R. concava* from the Canary Islands; although his collections from there (*Arnell UPS20635–20637*) belong to section *Pilifer*, they are not *R. concava*, nor is it as widespread as he and Sim (1926) believed it to be. Best's (1990) checklist record

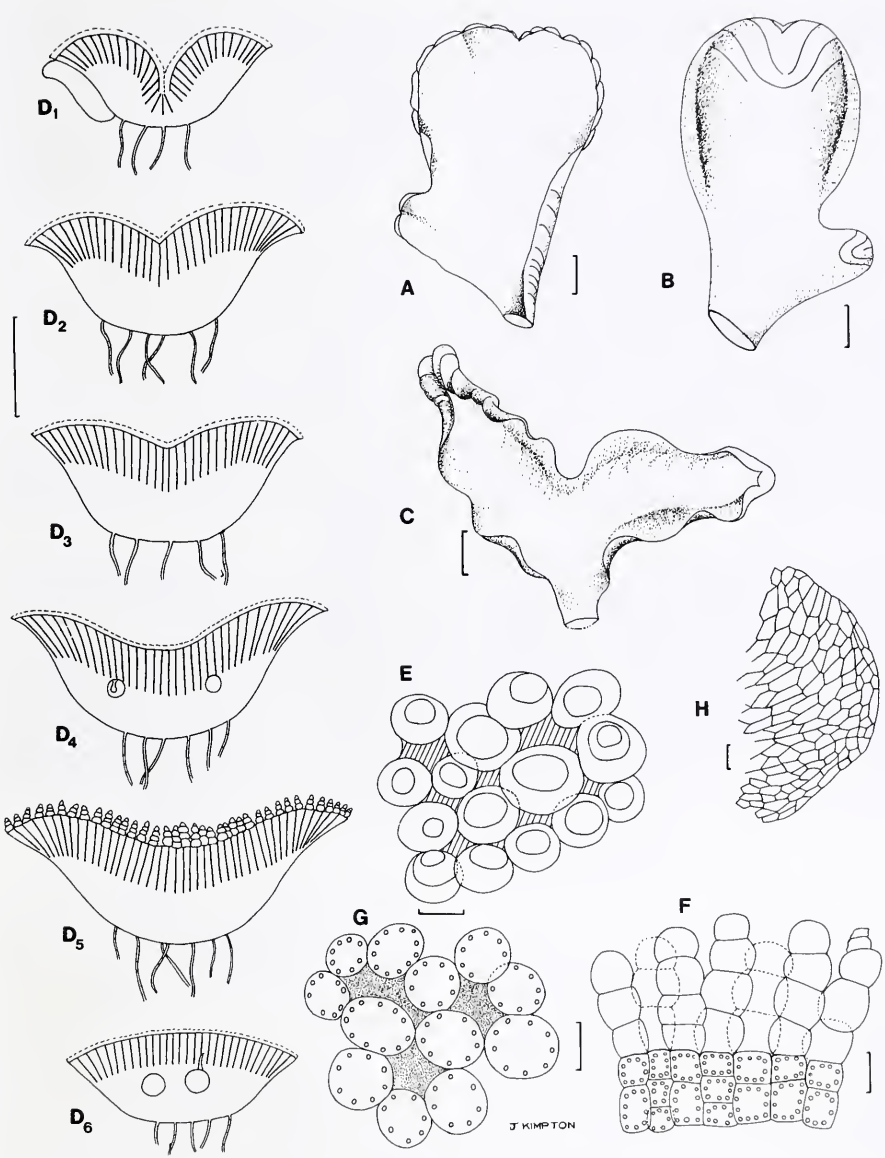


FIGURE 67.—**Riccia concava**. A–C, thallus: A, wet; B, ventral face; C, dry. D, c/s branch at intervals from apex to base; E, epithelial cells and air pores (hatched) from above; F, c/s epithelial cell pillars and assimilation tissue below; G, h/s assimilation tissue, air canals stippled; H, scale. A, B, D, *S.M. Perold 1431*; C, *S.M. Perold 1899*; E, H, *Morley 214*; F, *S.M. Perold 1447*; G, *Moll 6015*. Scale bars: A–D, 1 mm; E–G, 50 μm; H, 100 μm. Artist: J. Kimpton.

from Zimbabwe (as in Sim 1932), is obviously incorrect.

Riccia concava can be distinguished from other species in section *Pilifer*, by its broad thallus, up to 4 mm wide when fully expanded, concave when dry, its glaucous-green or scurfy blue-green colour, rounded apex, and overhanging margins mostly obscuring the scales, except those at the apex. The cells in the free dorsal pillars are generally wider than long and fragile, with the top cell small, globose and often collapsed. From above, toward the apex, the dorsal cells are closely packed in quite regular rows, inflated and shiny, like small round glass beads, but proximally collapsed and less orderly arranged. *Riccia concava* can be confused with *R. parvo-areolata* (no. 43), which also becomes concave when dry, but the dorsal cells and spores are different (see note under that species).

It is questionable whether Sim, in his description of *R. concava*, referred to the correct species, as he made no mention of any free dorsal cell pillars, but then, neither did Stephani in any of his publications cited, nor Bischoff (1846) or Gottsche *et al.* (1844–1847). Bischoff, who named the plant, observed (in litt.) that the small scales of the dry plant, when superficially observed, could be taken for cilia. He possibly mistook the collapsed dorsal cell pillars toward the margins for cilia!

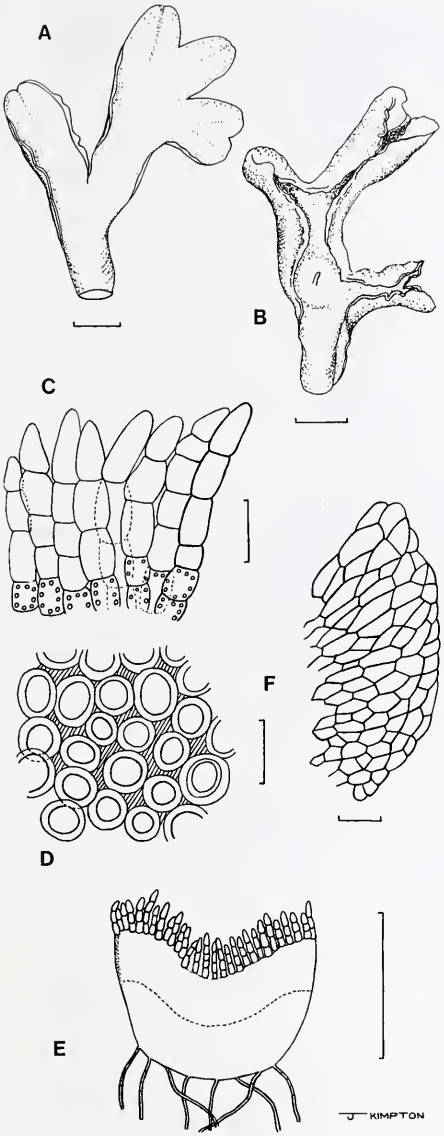
Vouchers: *Duthie 5005* (BOL; S); *Garside 6108, 6128* (BOL); *Oliver 8949* (PRE); *S.M. Perold 1414* (PRE).

47. **Riccia albomarginata** *Bisch.* in Flora 29: 135 (March 1846); Gottsche et al.: 604 (Oct. 1846); Steph.: 329 (1898) based on Zeyher's specimen only; Perold: 31 (1990a); Perold: 49 (1991c). Type: In locis humidis circa urbem Capstad, *Krauss s.n.* p.p., 1838 (specimen in middle of herbarium sheet BM, lecto.!; W, isolecto.!).

Thalli rather small, in crowded gregarious patches, or in partial rosettes, or scattered; olivaceous green to green, velvety; when dry, dorsally concave, often slightly brownish, scurfy or streaked with thin white threads of collapsed epithelial cell pillars, margins distally inflexed, proximally incurved, scales crisp, white or hyaline above brown flanks. *Branches* once or several times symmetrically or asymmetrically furcate, moderately divergent, lingulate to oblong, or linear, 5–7 mm long, terminal segments 1–3 × 0.7–1.8 mm, 0.6–1.1 mm thick, in section as wide as thick to twice wider than thick, apex rounded, emarginate; groove deep distally, soon shallow and wide, dorsal face concave, thallus margins subacute; flanks steep, purple or brown, distally covered by fragile, hyaline scales, proximally often denuded of scales, ventral face gently rounded, green to brown. *Scales* 700–800 × ± 400 µm, projecting up to 150 µm above thallus margins, rounded, imbricate, fragile, hyaline, some basal cells occasionally with purple colouring, cell walls sometimes stained faintly yellow.

Dorsal epithelium in free-standing, 3- or 4(5)-celled, fragile, hyaline pillars, 130–200(–230) µm long, cells longer than wide, top cell conical, or uniformly wide, sometimes bent, 45–65 × 20–30 µm, lower cells 42–60 × 32–37 µm, basal cells 25–37 × 30–40 µm; air pores small, 4- or 5-sided, obscured. *Assimilation tissue* 250–350 µm thick, consisting of vertical columns of 7 or 8 cells, enclosing narrow air canals; storage tissue occupying ventral part of thallus, cells rounded. Figure 68.

Monoicous. *Antheridia* numerous, with hyaline necks, along median part of thallus. *Archegonia* with purple necks. *Sporangia* along length of branches, single or in pairs, bulging dorsally. *Spores* 75–95(–105) µm diam., triangular-globular, polar, brown to dark brown, semitransparent to opaque; wing 5–7 µm wide, wider at perforated marginal angles, margin more or less entire to faintly crenulate; ornamentation reticulate, somewhat similar to dissimilar on the 2 faces; distal face with ± 14 irregular alveoli across diam., complete or incomplete, up to 7 µm wide, walls thick, slightly raised at nodes, otherwise smooth, convoluted or anastomosing to form thick ridges



that radiate outwards from centre; proximal face with triradiate mark poorly to well defined, 30–35 small, completely or incompletely separated alveoli on each facet, walls thick, convoluted, raised at nodes, otherwise mostly smooth. *Chromosome number*: not known. Plate 29E, F; Perold (1989e: fig. 25.1–6).

The distribution of *R. albomarginata* appears to be confined to a few areas in the western part of Northern Cape and Western Cape where it grows on coarse, gravelly soil, overlying granitic or sandstone outcrops. Map 32. In Best's (1990) checklist of bryophytes from Zimbabwe, a Sim specimen is cited under the above name. This specimen has been misidentified and actually is *R. moenkemeyeri* Steph. (no. 3). It is clearly a duplicate of one of the following collections held at PRE: *Sim 9068*, *9069*, *9070*, *9072*, all of which have been re-assigned to *R. moenkemeyeri*.

Riccia albomarginata is generally smaller than most of the other species in section *Pilifer*. Although it has no other outstanding vegetative characters by which it can readily be recognized, in the dry state it is often light brown dorsally, with white streaks of collapsed, dried dorsal cell pillars; the somewhat undulating, incurved flanks are purple to brown, and distally fringed with crisp, hyaline or white scales; proximally, the flanks are frequently denuded of scales. The distal face of the spores often has thick radiating ridges.

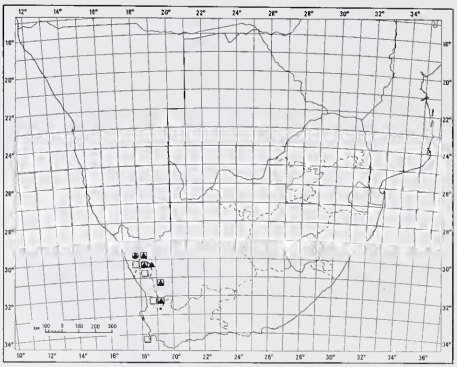
The label of the type specimen held at BM bears Bischoff's signature and the letters 'α et β', but no collector's name; the specimen held at W identifies Krauss as the collector, but only one of his specimens was described, although two different taxa are clearly present in his gathering. Gottsche *et al.* (Oct. 1846) reported the presence of two varieties in the Zeyher collection of this species from the Cape, but Stephani treated it as one species only, so did Sim (1926) and Volk

FIGURE 68.—**Riccia albomarginata**. A, B, thallus: A, wet; B, dry. C, c/s epithelial cell pillars toward margin and scale; D, epithelial cell pillars and air pores from above; E, c/s branch; F, scale. A, C, E, *S.M. Perold 1979*; B, *S.M. Perold 2118*; D, *S.M. Perold 538*; F, *S.M. Perold 2031* p.p. Scale bars: A, B, E, 1 mm; C, D, 50 µm; F, 100 µm. Artist: J. Kimpton.

(1983), who both applied the name, *R. albomarginata*, to a different taxon. Arnell (1963a) applied the name to yet another taxon, recently described by Volk (1981) as *R. albovestita* (no. 44). The specimens previously assigned to *R. albomarginata* have now been referred to *R. simii* (no. 52) (Perold 1990a). *R. simii* is characterized by large, wavy, hyaline scales.

Vouchers: *S.M. Perold 1930, 1979, 2118, 2382* (PRE).

48. **Riccia namaquensis** *Perold* in Bothalia 20: 180 (1990f); Perold: 48 (1991c). Type: Cape, Goegap Nature Res., Carolusberg, near old mine, flat granitic outcrop, at seepage, (–CA), *S.M. Perold 1420* (PRE, holo.!).

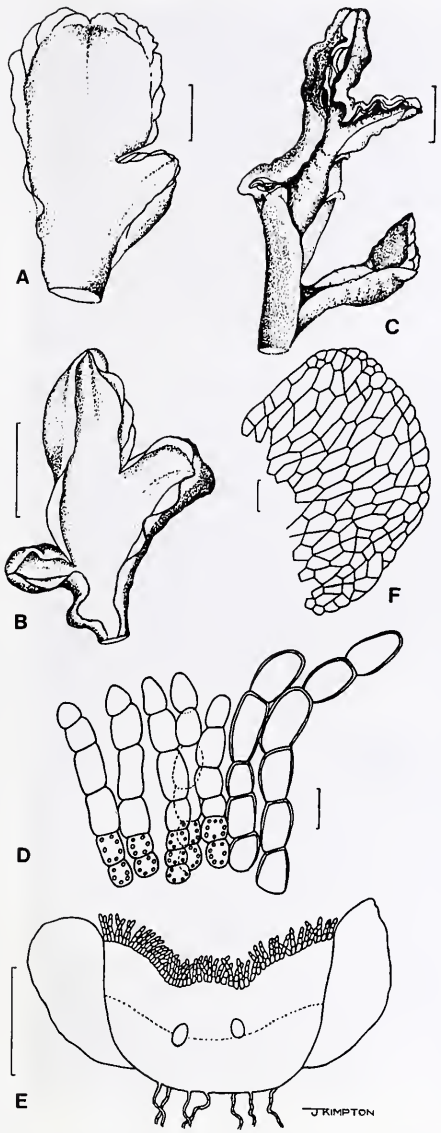


MAP 32.—❑ **Riccia albomarginata**
▲ **R. namaquensis**
❍ **R. vitrea**

Thalli medium-sized, in crowded gregarious patches, occasionally in partial rosettes 25 mm across; purplish green to bright green, shiny to rather dull toward base; when dry, margins tightly inflexed, white scales often clasped together along midline and covering dorsal face. *Branches* once or twice furcate, occasionally simple, variously divergent, oblong to obovate, somewhat keeled below, up to 8 × 1.8–2.3(–2.5) mm, 1.2–1.4(–1.6) mm thick, in section generally 1.5 times to twice wider than thick, apex rounded, emarginate; groove distally present, but soon becoming flat to slightly concave dorsally, thallus margins rather obtuse to subacute; flanks distally nearly erect or slightly bulging, steeply sloping to more oblique toward base, often turning deep purple below; ventral face rounded to nearly flat, green. *Scales* large, 1100–1350 × 650 µm, projecting 150–250 µm above thallus margins, closely imbricate, wavy, hyaline, but appearing white, base sometimes with purple blotches, margins entire. Plate 26D.

Dorsal epithelium in free-standing, 3- or 4(5)-celled pillars, densely crowded, hyaline, 200–350(–400) µm long, cells longer than wide but top cell variable, often conical, ± 65 × 50–60 µm, rarely small and rounded, ± 30 × 25 µm, second cell 50–67 × 40–52(–60) µm, very occasionally also small and rounded, like some top cells, third and fourth (i.e. basal) cells up to 100 × 37–52(–62) µm, soon collapsing toward margins and proximally; air pores obscured by dense dorsal pillars, generally 4-sided, small. *Assimilation tissue* 300–450 µm thick, consisting of vertical columns of 6–8(–10) cells, enclosing narrow air canals; storage tissue occupying ventral part of thallus, consisting of angular, closely packed cells. Figure 69.

?Monoicous. *Antheridia* in one or two rows along midline of thallus, necks hyaline. *Archegonia* scattered, necks purple. *Sporangia* mostly present toward base, dorsally bulging. *Spores* 65–78(–85) µm diam., triangular-globular, polar, light brown to deep brown, semitransparent to opaque; wing ± 5 µm wide, perforated at marginal angles, stippled with granules, margin crenulate; ornamentation reticulate, rather dissimilar on the 2 faces; distal face with (12–) 14–16 crowded alveoli across diam., up to 5 µm wide, some adjacent alveoli toward centre incompletely separated, walls irregular, raised papillae at nodes; proximal face with triradiate mark distinct, sprinkled with fine granules, each facet with ± 50 small alveoli, sometimes incomplete, walls low, often granulate. *Chromosome number*: n = 9 (Bornefeld pers. comm.). Plate 30A, B.



The species is known only from the dry shrublands of the western part of Northern Cape, where it grows on shallow, coarse-grained to clayey soil, overlying granitic outcrops, and occasionally also at seepages. Map 32.

Riccia namaquensis has large, closely imbricate, hyaline scales, which appear white, as several layers are superimposed; the dorsal cell pillars are 250–400 µm long, and intermediate in length between the lower, bulging cells of both *R. furfuracea* (no. 38) and *R. concava* (no. 46) and the taller cells of *R. vitrea* (no. 49), all of which grow in the same region of the Cape. Other species from this area, which have cell pillars of 'intermediate' length, are *R. albomarginata*, not *sensu* Sim (no. 47) and *R. parvoareolata* (no. 43). *R. namaquensis* can usually be distinguished from both by not becoming pronouncedly concave on drying, its margins being mostly tightly inflexed and meeting along the midline, and by its spore ornamentation.

Vouchers: *S.M. Perold 1421, 1557, 1756, 2372* (PRE).

49. **Riccia vitrea** *Perold* in Bothalia 20: 178 (1990c); Perold: 47 (1991c). Type: Cape, 19 km NE of Kamieskroon, 5 km after turnoff on road to Rooifontein, at large flat rocks, seepage area, *S.M. Perold 1475* (PRE, holo.!).

Thalli medium-sized to rather large, in crowded gregarious patches; steel-grey to silvery green, shiny, proximally shaggy-haired, matted; when dry, margins distally inflexed, meeting along midline, flanks covered with large, wavy or billowing, hyaline scales. *Branches* once to several times furcate, narrowly to moderately divergent, obovate, up to 9 mm long, segments ± 4 × 1.2–1.8(–2.3) mm, (0.9–)1.2–1.5 mm thick, in section as wide as thick, to 1.5 times wider than thick, apex acute, thick and fleshy; groove from apex to ± midway

FIGURE 69.—**Riccia namaquensis**. A–C, thallus: A, wet, from seepage area; B, wet, from drier habitat; C, dry. D, c/s epithelial cell pillars toward margin and scales; E, c/s branch; F, scale. A, *S.M. Perold 2136*; B, *S.M. Perold 2036*; C, *S.M. Perold 1420*; D, E, *S.M. Perold 565*; F, *S.M. Perold 1832*. Scale bars: A–C, E, 1 mm; D, 50 µm; F, 100 µm.

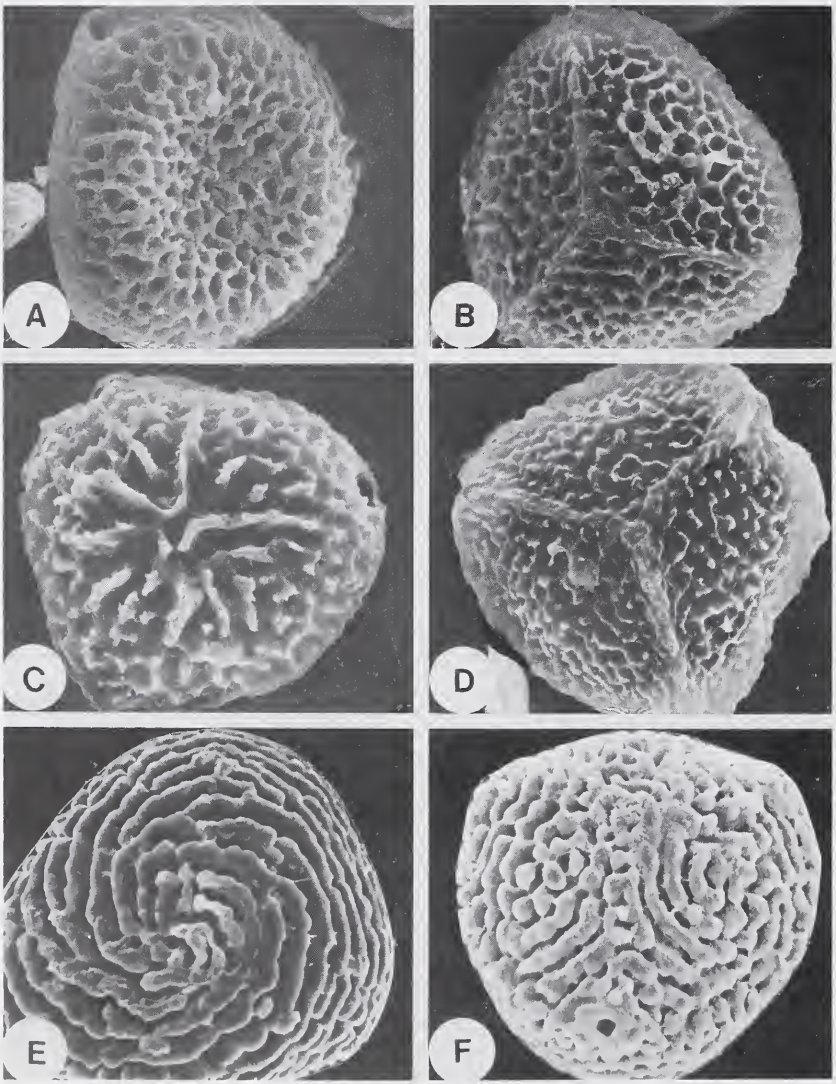
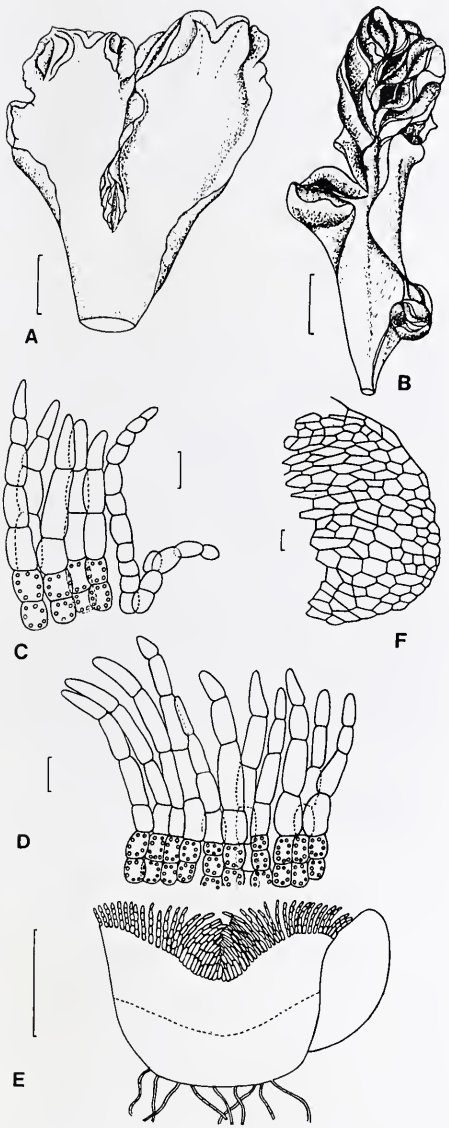


PLATE 30.—Spores. A, B, **Riccia namaquensis**: A, distal face; B, proximal face. C, D, **R. vitrea**: C, distal face; D, proximal face. E, F, **R. villosa**: E, distal face, F, proximal face. A, B, *S.M. Perold 1420*; C, D, *S.M. Perold 1425*; E, F, *Oliver 8039*. A, B, × 800, C–F, × 700.



along dorsal face, but mostly obscured by tall dorsal cell pillars which arch and interlock over it, thallus margins acute, raised; flanks steep toward apex, becoming somewhat obliquely sloping proximally, purplish; ventral face rounded to almost flat, green. *Scales* large, 1250–1750 × 600–850 µm, projecting ± 200 µm above thallus margins, rounded, imbricate, hyaline to pale cream, base sometimes reddish purple, margins mostly entire.

Dorsal epithelium consisting of free-standing, 4- or 5(6)-celled, fragile, hyaline pillars, uniformly wide to somewhat wider toward base, 320–450(–500) µm long, cells 2(–3) times longer than wide, top cell long-conical to bent, (60–)75–92 × 25–37 µm, lower cells 62–125 (–150) × 25–55 µm; air pores 4- or 5(6)-sided, obscured. *Assimilation tissue* (350–)400–500 µm thick, consisting of vertical columns of up to 10 cells, enclosing narrow air canals; storage tissue occupying ventral part of thallus, cells closely packed. Figure 70.

?Monoicous. *Antheridia* with long hyaline necks, obscured by tall dorsal cell pillars. *Archegonia* with purple necks, scattered along groove. *Sporangia* obscured, or bulging dorsally toward base. *Spores* 72–100(–110) µm diam., triangular-globular, polar, brown to dark brown, opaque; wing 5.0–7.5 µm wide, sprinkled with granules, perforated at wider marginal angles, margin crenulate; ornamentation completely or incompletely reticulate to radiately ridged, dissimilar on the 2 spore faces; distal face with up to 16, rather irregular alveoli across diam., 5 µm wide, walls thin, granular, raised at nodes, but frequently thickened and linked up to form short radiating ridges, with alveoli confluent, especially toward centre; proximal face with triradiate mark well to poorly defined, alveoli small, generally very incomplete, often only coarse granules or low papillae at nodes, intervening walls absent or very low. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 30C, D.

FIGURE 70.—**Riccia vitrea**. A, B, thallus: A, wet; B, dry. C, c/s erect epithelial cell pillars toward margin and scales; D, c/s arched and erect epithelial cell pillars, assimilation tissue below; E, c/s branch; F, scale. A, D, F, *S.M. Perold 2149*, B, *S.M. Perold 1475*; C, E, *S.M. Perold 1419*. Scale bars: A, B, E, 1 mm; C, D, 50 µm; F, 100 µm. Artist: J. Kimpton.

This species is so far only known from a few localities in the dry shrublands of Namaqualand, Northern Cape, where it grows on coarse-grained soil overlying granite rock outcrops. Map 32.

Riccia vitrea can be recognized by the large, billowing, hyaline to pale cream-coloured scales and by the tall dorsal cell pillars of the epithelium, similar to those in *R. villosa* (no. 50) and *R. simii* (no. 52) (= *R. albomarginata* auct. non Bisch.), but not so 'fine', not really tapering and often interlocking.

Vouchers: *S.M. Perold 1398* p.p., *1419*, *2046* (PRE).

50. **Riccia villosa** *Steph.*, in Brunnth. in Denkschriften der Kaiserlichen Akademie der Wissenschaften 88: 724 (1913); S.W.Arnell 19: (1963a); O.H.Volk & Perold: 120 (1984); Perold: 45 (1991c). Type: Kapland, Karoo bei Matjiesfontein, auf sandigem Boden, *Brunnthaler s.n.*, XI-1909 (*G13342*, holo.!).

Thalli smallish to medium-sized, in crowded gregarious patches or scattered, not in rosettes; velvety green; when dry, margins inflexed, large, white to silvery grey, triangular scales clasped together above and covering dorsal surface. *Branches* simple or once or twice symmetrically or asymmetrically furcate, narrowly to moderately divergent, narrowly oblong-ovate, up to 8 × 1.8–2.5 mm, 1.5 mm thick, in section ± 1.6 times wider than thick, apex slightly narrowed, rounded; groove narrow distally, soon widening and shallow, obscured by dorsal cell pillars, thallus margins somewhat obtuse; flanks steep to slightly bulging, deep purple to nearly black; ventral face flat to slightly rounded, with brown or purple, transverse, arched bands of vestigial scales. *Scales* very conspicuous, up to 1800 µm from base to apex and 1000 µm across base, projecting ± 500 µm above thallus margins, imbricate, triangular-acuminate, hyaline, with deep purple base, margins denticulate apically, sometimes ending with a narrow caducous terminal cell. Plate 26E.

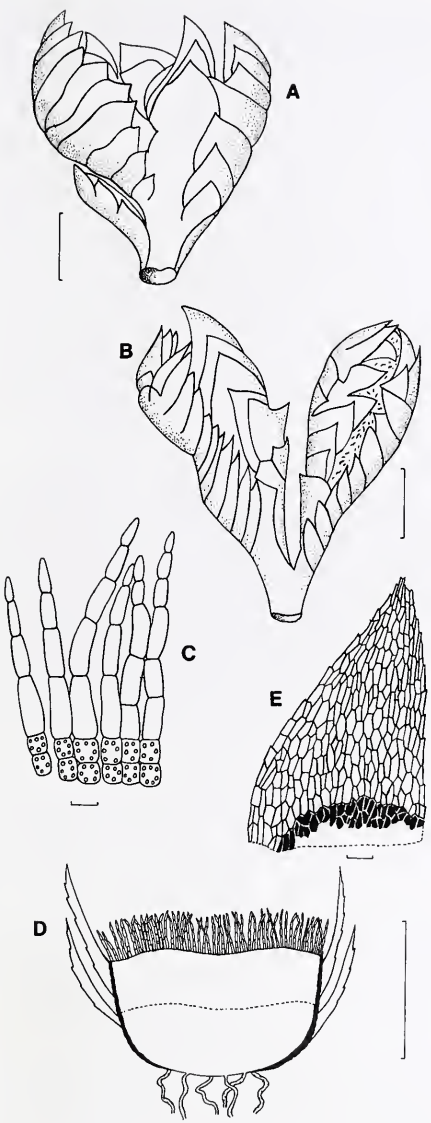
Dorsal epithelium consisting of free-standing, tapering pillars, ± 450 µm long, composed of 4 or 5(6) fragile, hyaline cells, 2–3 times longer than wide, 45–130 × 25–50 µm; air pores obscured by cell pillars, small, generally 4-sided. *Assimilation tissue* 250–400 µm thick, consisting of vertical columns of 6 or 7(8) cells enclosing narrow air canals; storage tissue occupying ventral part of thallus, consisting of polygonous cells, sometimes with numerous oil droplets. Figure 71.

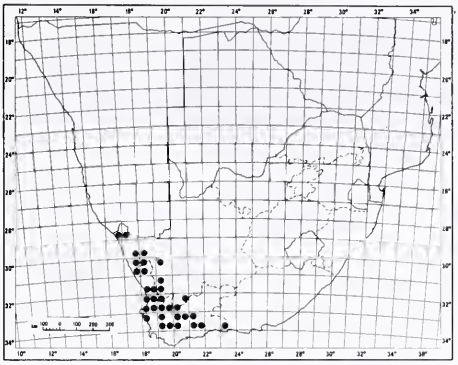
Asexual propagation by bulbils.

?Dioicous. *Antheridial* necks not seen, hidden between dense dorsal cell pillars. *Archegonia* with purple necks, ± 60 µm long. *Sporangia* single or 2 or 3 close together along median part of thallus, dorsally bulging, overlying tissue blotched with purple. *Spores* 85–110 (–115) µm diam., triangular-globular, polar, brown to very dark brown or black and opaque, wingless; ornamentation papillate or vermiculate, similar on 2 faces; distal face generally with papillae in a whorl, spiralling outward from centre to margin in 10–15 thick or sometimes rather flattened ridges; proximal face with papillae not in obvious spirals, triradiate mark not prominent, each of its 3 arms terminating at a marginal pore. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 30E, F; Perold (1989e: fig. 23.1–6).

The species is endemic to southern Africa and grows on sandy to fine, gravelly, non-calcareous soils. Its distribution is restricted to the shrublands of the western part of Northern Cape, and Western and Eastern Cape. Map 33.

Riccia villosa is easily distinguished from other species in section *Pilifer* by its large, triangular scales with apically, denticulate margins. *Riccia hirsuta* (no. 51) also has triangular scales, but the apices are filiform, the spores reticulate and it is very rare. The spores of *R. villosa* are generally dark brown to black and the ornamentation papillate to vermiculate. The only other species of *Riccia* with somewhat similar spores is *R. okahandjana* (no. 22) (see note under that species), but the latter's spores are light brown, its scales semilunar and black,





MAP 33.—● **Riccia villosa**

and its dorsal epithelium not multicellular. Most plants of *R. villosa* are sterile; only four of the many specimens examined had sporangia.

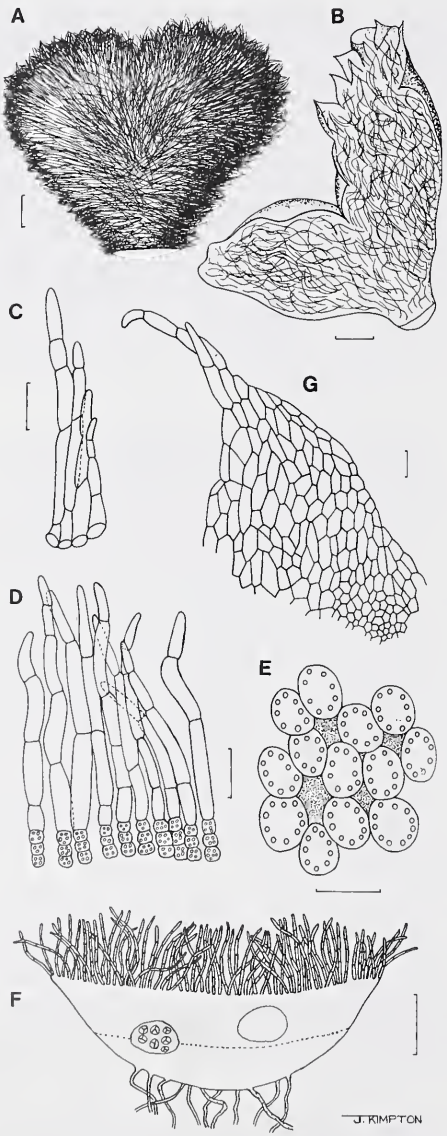
Schuster (1984a) initially placed *R. villosa* in a new monotypic genus, *Pteroriccia*, but later (Schuster 1985) changed its rank to subgenus to include all those species, with the dorsal cells in free-standing, multicellular uniseriate pillars and compact assimilation tissue, pillars lacking large polyhedral air chambers. In this revision, Schuster's genus or subgenus *Pteroriccia*, has not been accepted (Perold 1986a).

Vouchers: *Brusse 5217* (PRE); *Compton 5428* (BOL); *Germishuizen 4783* (PRE); *Oliver 8039* (PRE); *S.M. Perold 504* (PRE).

51. **Riccia hirsuta** *O.H.Volk & Perold* in Bothalia 16: 187 (1986e); O.H.Volk & Perold: 23 (1990); Perold: 46 (1991c). Type: Cape, Kamiesberg plateau, north of Leliefontein, towards Draaiklip, on sandy, periodically moist soil, *Oliver 8040* (PRE, holo.!).

Thalli medium-sized to large, scattered, not in rosettes; green to greyish green over centre,

FIGURE 71.—**Riccia villosa**. A, B, thallus: A, wet; B, dry. C, c/s long tapering epithelial cell pillars and assimilation tissue below; D, c/s branch; E, scale. A, C, D, *C.M. van Wyk 2522*; B, E, *S.M. Perold 504*. Scale bars: A, B, D, 1 mm; C, 50 µm; E, 200 µm. Artist: J. Kimpton.

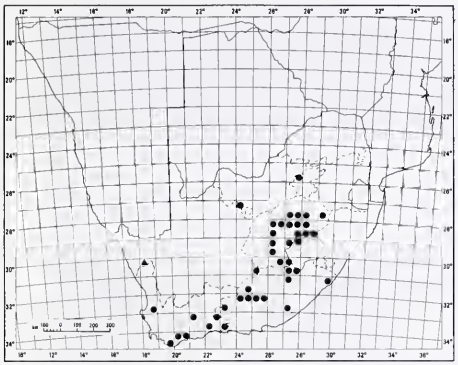


whitish along margins, dorsally furry and shiny; when dry, margins partly inflexed, dorsally concave, grey, matted. *Branches* simple or once or twice symmetrically furcate, moderately divergent, oblong to obovate, up to 10 × 2–4 mm, 1.5–2.0 mm thick, in section as wide as thick to twice wider than thick, apex truncate; groove short, wide and shallow, obscured by thick pelt of cell pillars, thallus margins subacute, short-winged to overhanging; flanks steep to sloping obliquely, green, occasionally flecked with reddish purple; ventral face slightly rounded to flat, pale green. *Scales* large, up to 1500 µm high, 650–1200 µm wide at base, projecting above thallus margins, triangular, overlapping, hyaline, occasionally with reddish purple cells at base, apices split into several loose cellular strands, variously bending and twisting. Plate 26F.

Dorsal epithelium consisting of free-standing, very tall, tapering cell pillars, ± 1000 µm long, composed of (2–)4–7 thin-walled, hyaline cells, 4–5 times longer than wide, 150–375 × 42–70 µm; air pores 4-sided, closely spaced, obscured by tall, dense dorsal cell pillars. *Assimilation tissue* 300–400 µm thick, consisting of vertical columns of 5 or 6(7) cells, enclosing 4–8-sided air canals, widening proximally; storage tissue occupying ventral part of thallus, cells 50–55 µm wide, angular. Figure 72.

?Monoicous. *Antheridia* with tall hyaline necks, hidden by dorsal cell pillars. *Archegonia* with purple necks, scattered along centre of thallus. *Sporangia* often side by side, up to 700 µm wide, overlying epithelium tinged with purple. *Spores* 95–125(–130) µm diam., triangular-globular, polar, deep, dull brown to nearly black, semitransparent to opaque; wing ± 10 µm wide, slightly undulating, notched or perforated at marginal angles, margin crenulate to somewhat eroded; ornamentation completely or incompletely reticulate, dissimilar on 2 faces; distal face with 3–5(6) large, central alveoli across, 25–38 µm wide, mostly partly subdivid-

FIGURE 72.—**Riccia hirsuta**. A, B, thallus: A, wet; B, dry. C, filiform apex of scale; D, c/s very long, slightly tapering epithelial cell pillars and assimilation tissue below; E, h/s assimilation tissue, air canals stippled; F, c/s branch; G, scale. A, B, D, F, *S.M. Perold 2182*; C, E, G, *Oliver 8040*. Scale bars: A, B, F, 1 mm; C, D, G, 100 µm; E, 50 µm. Artist: J. Kimpton.



MAP 34.—▲ **Riccia hirsuta**
● **R. simii**

ed into smaller alveoli, 12 µm wide, often with a papilla in the middle, occasionally alveoli equal in size and then 8–10 µm wide, central walls more prominent; proximal face with triradiate mark distinct, but sometimes poorly delineated, each facet generally incompletely reticulate, walls low, thickened and slightly raised at nodes. *Chromosome number*: n = 8 (Bornefeld in O.H. Volk & Perold 1986e). Plate 31A, B; Perold (1989e: fig. 33.1–6).

Riccia hirsuta is endemic to southern Africa and has to date only been found in a very restricted area in Namaqualand, Northern Cape, north of Leliefontein. It grows on moist, sandy or clayey soil, overlying the edges of granitic rock outcrops near seepages. Map 34.

The very tall, shiny dorsal cell pillars, triangular scales, apically split into loose, filamentous strands which mingle with the epithelial hairs at the margins and the quite large, dull brown, incompletely reticulate spores, distinguish this species from other members of section *Pilifer*. An earlier description of *R. hirsuta* (Volk & Perold 1986e) was based on two distinct, but superficially rather similar species, the other taxon being *R. tomentosa* (no. 13). It, however, has well-spaced, circumscribed air pores, tall, polygonal air chambers and papillose spores in permanent tetrads, and is also equipped with very tall, shiny, dorsal cell pillars and triangular scales apically split into loose filamentous strands. Collection of more and fruiting material of both species clearly demonstrated the differences between them, and *R. hirsuta* has been redescribed and re-assigned to section *Pilifer* O.H.Volk, with section *Micantes* O.H.Volk & Perold (where it had previously been classified), sunk under section *Pilifer*. *R. tomentosa* is placed in subgenus *Pannosae*. Schuster's (1992a, b) subgenus *Micantes* is thus not recognized here.

Vouchers: *S.M. Perold 2099–2101, 2182* (PRE).

52. **Riccia simii** *Perold* in Bothalia 20: 36 (1990a): Perold: 47 (1991c). Type: Cape, Pirie Mission Station, Kaffraria, *T.R. Sim 338* (*PRE-CH1035*) (PRE, holo.!).

Riccia albomarginata auct. non Bisch. emend. Sim, The Bryophyta of South Africa: 9 (1926); O.H.Volk: 453 (1983). Type: not designated.

Thalli medium-sized to large, in crowded gregarious patches or scattered; bright green to emerald green, velvety, large hyaline scales projecting above and beyond thallus margins; when dry, margins tightly inflexed, meeting along midline over white, finely granular dorsal face, flanks covered with large, imbricate, wavy, white scales. *Branches* simple or once or twice symmetrically or asymmetrically furcate, moderately to widely divergent, oblong to obovate, up to 12 mm long, segments 4–5 × 1.8–2.5 mm, 0.9–1.3(–1.5) mm thick, in section twice wider than thick, apex acute; groove narrow and deep distally only, soon disappearing and dorsally flat, thallus margins subacute; flanks steep to proximally sloping obliquely, green, sometimes flecked with violet; ventral face gently rounded to flat, green. *Scales* large, ± 1500 × 600–900 µm, projecting 200–500 µm above thallus margins, nearly semicircular, closely imbricate, wavy, hyaline, margins entire.

Dorsal epithelium consisting of free-standing, 4- or 5-celled, gradually tapering, fine pil-

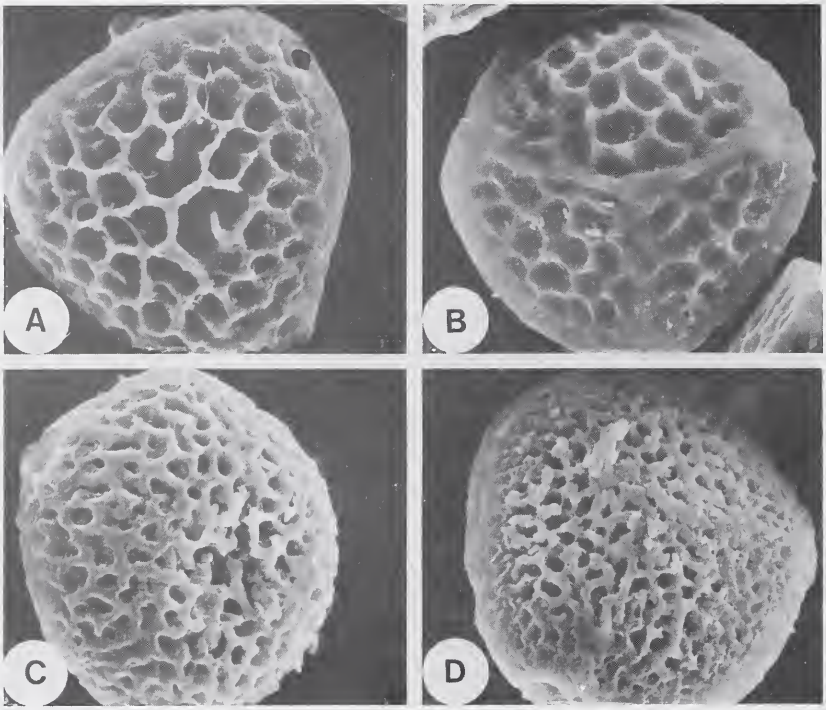
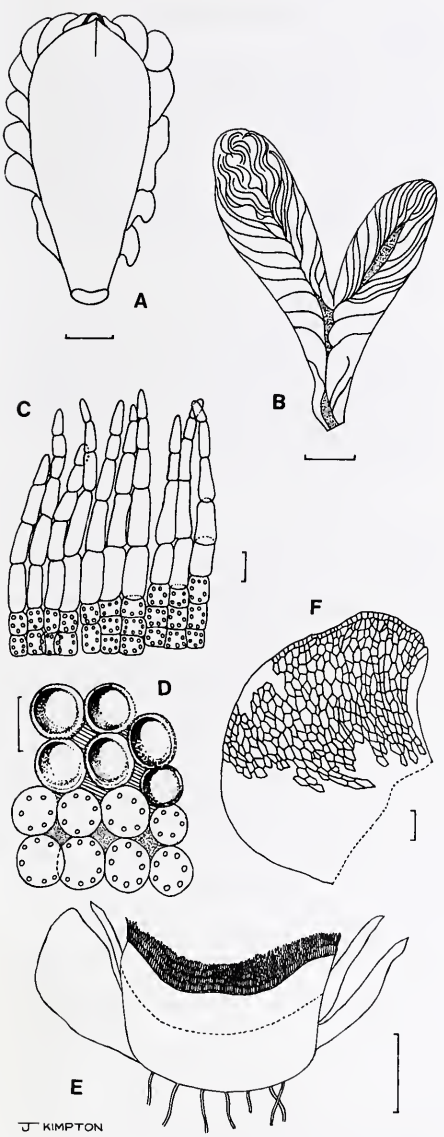


PLATE 31.—Spores. A, B, **Riccia hirsuta**: A, distal face; B, proximal face. C, D, **R. simii**: C, distal face; D, proximal face. A, *Oliver 8040;* B, *S.M. Perold 2100*; C, D, *J.M. Perold 39a*. A, B, × 500; C, D, × 700.

lars, basally somewhat thicker-walled, hyaline, up to 250(–350) µm long, top cells 25–50 × 18–20(–25) µm, often slightly bent, tips rounded, intermediate cells 45–75(–80) × 25–35 µm, basal cells 62–80 × 30–38 µm, mostly equally long; air pores small, 4(–8)-sided, obscured by tall cell pillars. *Assimilation tissue* ± 350 µm thick, consisting of vertical columns of up to 8 cells, enclosing narrow 4- or 5-sided air canals; storage tissue occupying ventral part of thallus, cells rounded to angular, closely packed. Figure 73.

Monoicous. *Antheridia* with hyaline necks, nearly 500 µm long. *Archegonia* with purple necks, scattered along median part of thallus. *Sporangia* rare, mostly single, very occasionally up to 3 crowded together in narrow proximal part of thallus, dorsally bulging. *Spores* 70–105 (–120) µm diam., triangular-globular, polar, yellow or light brown, colour deepening to mahogany brown or turning black on ageing, semitransparent to opaque; wing narrow, ± 5 µm wide, marginal angles perforated, margin finely crenulate; ornamentation reticulate or partly reticulate, similar or dissimilar on 2 spore faces; distal face with only outer rows of alveoli usually complete, occasionally all complete, variable in size, 5–10 µm wide, irregularly shaped, rounded or elongate, adjacent alveoli frequently confluent, walls raised at nodes, sometimes anastomosing to form ridges, irregularly branching and twisting or radiating outwards from centre; proximal face with triradiate mark clearly defined, sometimes papillate, on each of 3 facets 25–30 complete or incomplete



alveoli, up to 5 µm wide, walls thin, raised at nodes, sometimes sprinkled with papillae toward wing. *Chromosome numbers*: n = 8 (Bornefeld 1984); 8, 10 (Bornefeld 1989), as *R. albomarginata* Bisch. *sensu* Sim. Plate 31C, D; Perold (1989e: fig. 24.1–6).

The distribution of this endemic species, *R. simii*, ranges from Gauteng to the North-West, Free State, Lesotho, the southeastern part of Northern Cape, Western and Eastern Cape. It grows on shallow soil overlying dolerite or sandstone outcrops. Map 34.

Sim (1926) reported this species, as *R. albomarginata* (no. 47), from Transvaal and Natal. Plants from Namibia that Arnell (1957, 1963a) identified as *R. albomarginata*, have been reassigned to another species, *R. albovestita* (no. 44) (see note under that species).

Riccia simii can be distinguished from other species in section *Pilifer* by the large, rounded, hyaline, wavy, closely imbricate scales, up to 1500 µm long and projecting as much as 500 µm above the thallus margins. The dorsal face is velvety and covered with fine cell pillars, which are usually relatively thick-walled at the base and less fragile than is usual in this section; the basal cells are ± equally long with the upper cross walls forming an interrupted horizontal line running across the width of the thallus. The spore ornamentation is variable and not really useful as a diagnostic character.

Sim (1926) and Volk (1981, 1983) applied the name *R. albomarginata* to this species, but close examination of the type specimen collected by Krauss (and of Zeyher's collection), showed them to be mixed collections of different species, see note under *R. albomarginata* (no. 47).

Vouchers: *Duthie 5115* (BOL); *S.M. Perold 1304* (PRE); *Smook 3908* (PRE); *Van Rooy 1823* (PRE); *Volk 81/289a* (M, PRE).

FIGURE 73.—**Riccia simii**. A, B, thallus: A, wet; B, dry. C, c/s long tapering epithelial cell pillars and assimilation tissue below; D, h/s basal cells of dorsal pillars with air pores hatched, and below, through assimilation tissue with air canals stippled; E, c/s branch; F, scale. A, E, *S.M. Perold 1318*; B, *S.M. Perold 1346*; C, *S.M. Perold 505*; D, *Smook 6631*; F, *C.M. van Wyk 1781*. Scale bars: A, B, E, 1 mm; C, D, 50 µm; F, 100 µm.

Insufficiently known species

Riccia coronata Sim, The Bryophyta of South Africa: 9 (1926). Type: Natal, Mooi River, *Sim 8730*. This is the only specimen cited by Sim and it could not be traced. The description is very brief and it is suspected that it refers to smaller plants of *R. natalensis*. *Duthie 5004* (BOL; PRE), which had been identified as near *R. coronata*, has been described as *R. alatospora* (Volk & Perold 1985).

Riccia dinteri Steph. ined. According to Evans (1922) this appears to be a manuscript name. Dinter (1926–1927) reported it from Okozongomuinja and Arnell (1956) from Mt Kenia. The type specimen has not been seen, and a single, sterile specimen held at Compton Herbarium, could not be distinguished from *R. stricta*.

Riccia gemmifera O.H.Volk, Nova Hedwigia 39: 117 (1984a). Type: 30 km nördlich von Tsumeb an der Hauptstrasse nach Angola, *Volk 81/153a* p.p. (M). Only sterile, cultured specimens have been examined, and it is suspected that this species is close to *R. atropurpurea* Sim, which occasionally also forms numerous brood bodies.

Riccia warnstorfii Limpr. ex Warnst. Only twice collected by Garside in Pillans's garden in 1954. This species has not been collected again in southern Africa and is thought to have been a short-lived introduction. It is therefore excluded from the *FSA*.

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INDEX TO HEPATOPHYTA PART 1 FASCICLE 1

APPENDIX

PLAN OF *FLORA OF SOUTHERN AFRICA*

Cryptogam volumes will in future not be numbered, but will be known by the name of the group they cover. The number assigned to the volume on Charophyta therefore becomes redundant. Occasional contributions to the *Flora* are published in *Bothalia* under the title *FSA contributions*.

Exotic families are marked with an asterisk.

Published volumes and parts are shown in bold.

INTRODUCTORY VOLUMES

The genera of southern African flowering plants
Vol. 1: Dicotyledons (1975)
Vol. 2: Monocotyledons (1976)

Botanical exploration of southern Africa (1981)

CRYPTOGAM VOLUMES

Charophyta (as Vol. 9 in 1978)

Bryophyta: Part 1: Musci: **Fascicle 1: Sphagnaceae, Andreaeaceae, Fissidentaceae, Nanobryaceae, Archidiaceae, Ditrichaccae, Seligeriaceae, Dicranaceae, Calymperaceae, Encalyptaceae, Pottiaceae, Bryobartramiaceae, Grimmiaceae (1981)**
Fascicle 2: Gigaspermaceae, Ephemeraceae, Funariaccae, Splachnaceae, Bryaceae, Mniaceae, Eustichiaceae, Rhizogoniaceae, Aulacomniaceae, Bartramiaceae (1987)
Fascicle 3: Erpodiaceae, Rhachithcciaceae, Ptychomitriaceae, Orthotrichaceae, Rhabdoweisiaceae, Racopilaceae, Fontinalaceae, Wardiaceae, Hedwigiaceae, Cryphaeaceae, Leucodontaceae, Prionodontaceae, Trachypodaceae, Pterobryaceae, Meteoriaceae, Leptodontaceae, Neckeraceae, Thamnobryaccae, Hookeriaceae (1998)
Fascicle 4: Fabroniaceae, Leskeaceae, Thuidiaceae, Rigodiaceae, Amblystegiaceae, Brachytheciaceae, Entodontaceae, Plagiotheciaceae, Catagoniaceae, Sematophyllaceae, Hypnaceae, Hylocomiaceae, Polytrichaceae

Hepatophyta: Part 1: Marchantiopsida: **Fascicle 1: Targioniaccae, Lunulariaceae, Aytoniaceae, Cleveaccae, Exormothecaceae, Marchantiaceae, Oxymitraceae, Ricciaceae (1999)**

Anthocerotophyta

Pteridophyta (1986)

FLOWERING PLANTS VOLUMES

Vol. 1: Stangeriaceae, Zamiaceae, Podocarpaccae, Pinaceae*, Cupressaccae, Welwitschiaccae, Typhaceae, Zosteraceae, Potamogetonaceae, Ruppiaceae, Zannichelliaceae, Najadaceae, Aponogetonaceae, Juncaginaceae, Alismataccae, Hydrocharitaceae (1966)

Vol. 2: Poaceae

Vol. 3: Cyperaceae, Arecaceae, Araceae, Lemnaccae, Flagellariaceae

Vol. 4: Part 1: Restionaceae
Part 2: Xyridaceae, Eriocaulaceae, Commelinaceae, Pontederiaceae, Juncaceae (1985)

Vol. 5: Part 1: Colchicaceae, Eriospermaceae, Asphodelaceae (*Chortolirion*, 1995 in *Bothalia* 25: 31–33; *Poellnitzia*, 1995 in *Bothalia* 25: 35, 36)

Part 2: Alliaceae, Liliaceae*, Hyacinthaceae, **Agavaceae (1996 in *Bothalia* 26: 31–35)**
Part 3: Dracaenaceae, Asparagaceae, Luzuriagaceae, Smilacaceae (1992)

Vol. 6: Haemodoraceae, Amaryllidaceae, Hypoxidaceae, Tecophilaeaceae, Velloziaceae, Dioscoreaceae

Vol. 7: Iridaceae: Part 1: Nivenioideae, Iridoideae
Part 2: Ixioideae: Fascicle 1: **Ixieae (First part): Ixiinae, Tritoniinae (1999)**
Fascicle 2: *Syringodea, Romulea* (1983)

Vol. 8: Musaceae, Strelitziaceae, **Zingiberaceae (1998 in *Bothalia* 28: 35–39)**, Cannaceae*, Burmanniaceae, Orchidaceae (***Holothrix*, 1996 in *Bothalia* 26: 125–140)**

Vol. 9: Casuarinaceae*, Piperaceae, Salicaceae, Myricaceae, Fagaceae*, Ulmaceae, Moraceae, Cannabaceae*, Urticaceae, Proteaceae

Vol. 10: Part 1: **Loranthaceae, Viscaceae (1979)**, Santalaceae, Grubbiaceae, Opiliaceae, Olacaceae, Balanophoraceae, Aristolochiaceae, Rafflesiaceae, Hydnoraceae, Polygonaceae, Chenopodiaceae, Amaranthaceae, Nyctaginaceae

Vol. 11: Phytolaccaceae, Aizoaceae, Mesembryanthemaceae

Vol. 12: Portulacaceae, Basellaceae, Caryophyllaceae, Illecebraceae, Cabombaceae, Nymphaeaceae, **Ceratophyllaceae (1997 in *Bothalia* 27: 125–128)**, Ranunculaceae, Menispermaceae, Annonaceae, Trimeniaceae, Lauraceae, Hernandiaceae, Papaveraceae, Fumariaceae

Vol. 13: Brassicaceae, Capparaceae, Resedaceae, Moringaceae, Droseraceae, Roridulaceae, Podostemaceae, Hydrostachyaceae (1970)

Vol. 14: Crassulaceae (1985)

Vol. 15: Vahliaceae, Montiniaceae, Escalloniaceae, Pittosporaceae, Cunoniaceae, Myrothamnaceae, Bruniaceae, Hamamelidaceae, Rosaceae, Connaraceae

Vol. 16: Fabaceae: **Part 1: Mimosoideae (1975)**
Part 2: Caesalpinioideae (1977)
Part 3: Papilionoideae: Fascicle 1: Swartzieae–Robinieae
Fascicle 2: Indigofereae
Fascicle 3: Desmodieae, Phaseoleae
Fascicle 4: Psoraleeae–Galegeae
Fascicle 5: Loteae–Liparieae
Fascicle 6: Crotalarieae (*Aspalathus*) (1988)
Fascicle 7: Crotalarieae (*Bolusia–Lebeckia*)
Fascicle 8: Crotalarieae (*Lotononis–Wiborgia*)
Fascicle 9: Crotalarieae (*Pearsonia–Argyrolobium*), Genisteae (*Cytisus–Ulex*)

Vol. 17: Geraniaceae, Oxalidaceae

Vol. 18: Part 1: Linaceae, Erythroxylaceae, Zygophyllaceae, Balanitaceae
Part 2: Rutaceae
Part 3: Simaroubaceae, Burseraceae, Ptaeroxylaceae, Meliaceae (Aitoniaceae), Malpighiaceae (1986)

Vol. 19: Part 1: Polygalaceae, Dichapetalaceae
Part 2: Euphorbiaceae, Callitrichaceae, **Buxaceae (1996 in *Bothalia* 26: 37–40)**
Part 3: Anacardiaceae: **Fascicle 1: *Rhus* (1993)**
Fascicle 2: remaining genera
Aquifoliaceae (1994 in *Bothalia* 24: 163–166)

Vol. 20: Celastraceae, Icacinaceae, Sapindaceae, Melianthaceae, Greyiaceae, Balsaminaceae, Rhamnaceae, Vitaceae

Vol. 21: **Part 1: Tiliaceae (1984)**
Malvaceae, Bombacaceae, Sterculiaceae

Vol. 22: Ochnaceae, Clusiaceae, Elatinaceae, Frankeniaceae, Tamaricaceae, Canellaceae, Violaceae, Flacourtiaceae, Turneraceae, Passifloraceae, Achariaceae, Loasaceae, Begoniaceae, Cactaceae (1976)

Vol. 23: Geissolomataceae, Penaeaceae, Oliniaceae, Thymelaeaceae, Lythraceae, Lecythidaceae

Vol. 24: Rhizophoraceae, Combretaceae, Myrtaceae, Melastomataceae, **Onagraceae (1997 in *Bothalia* 27: 149–165)**, **Trapaceae (1998 in *Bothalia* 28: 11–14)**, Haloragaceae, Gunneraceae, Araliaceae, Apiaceae, Cornaceae

Vol. 25: Ericaceae

Vol. 26: Myrsinaceae, Primulaceae, Plumbaginaceae, Sapotaceae, Ebenaceae, Oleaceae, Salvadoraceae, Loganiaceae, Gentianaceae, Apocynaceae (1963)

Vol. 27: Part 1: Periplocaceae, Asclepiadaceae (*Microloma–Xysmalobium*)
Part 2: Asclepiadaceae (*Schizoglossum–Woodia*)
Part 3: Asclepiadaceae (*Asclepias–Anisotoma*)
Part 4: Asclepiadaceae (*Brachystelma, Ceropegia, Riocreuxia*) (1980)
Asclepiadaceae (remaining genera)

Vol. 28: Part 1: Cuscutaceae, Convolvulaceae
Part 2: Hydrophyllaceae, Boraginaceae
Part 3: Stilbaceae, Verbenaceae (*Vitex*, **1996 in *Bothalia* 26: 141–151)**
Part 4: Lamiaceae (1985)
Part 5: Solanaceae, Retziaceae

Vol. 29: Scrophulariaceae

Vol. 30: Part 1: Bignoniaceae, Pedaliaceae, Martyniaceae, Orobanchaceae
Part 2: Gesneriaceae, Lentibulariaceae
Part 3: Acanthaceae: Fascicle 1: Justiciinae (1995)
Acanthaceae (remaining genera), Myoporaceae

Vol. 31: Part 1: Fascicle 1: **Plantaginaceae (1998 in *Bothalia* 28: 151–157)**, Rubiaceae (Rubioidcae—First part)
Fascicle 2: Rubiaceae (Rubioideae—Second part): Paederieae, Anthospermeae, Rubieae (1986)
Fascicle 3: Ixoroideae, Chinchonoideae
Part 2: Valerianaceae, Dipsacaceae, Cucurbitaceae

Vol. 32: Campanulaceae, Sphenocleaceae, Lobeliaceae, Goodeniaceae

Vol. 33: Asteraceae: Part 1: Lactuceae, Mutisieae, 'Tarchonantheae'
Part 2: Vernonieae, Cardueae
Part 3: Arctotideae
Part 4: Anthemideae
Part 5: Astereae
Part 6: Calenduleae
Part 7: Inuleae: Fascicle 1: Inulinae
Fascicle 2: **Gnaphaliinae (First part) (1983)**
Part 8: Heliantheae, Eupatorieae
Part 9: Senecioneae

FSA CONTRIBUTIONS IN *BOTHALIA*

FSA contributions 1: Aquifoliaceae. S. ANDREWS. 1994. *Bothalia* 24: 163–166.

FSA contributions 2: Asphodelaceae/Aloaceae, 1029010 *Chortolirion*. G.F. SMITH. 1995. *Bothalia* 25: 31–33.

FSA contributions 3: Asphodelaceae/Aloaceae, 1028010 *Poellnitzia*. G.F. SMITH. 1995. *Bothalia* 25: 35, 36.

FSA contributions 4: Agavaceae. G.F. SMITH & M. MÖSSMER. 1996. *Bothalia* 26: 31–35.

FSA contributions 5: Buxaceae. H.F. GLEN. 1996. *Bothalia* 26: 37–40.

FSA contributions 6: Orchidaceae: *Holothrix*. K.L. IMMELMAN. 1996. *Bothalia* 26: 125–140.

FSA contributions 7: Verbenaceae: *Vitex*. C.L. BREDENKAMP & D.J. BOTHA. 1996. *Bothalia* 26: 141–151.

FSA contributions 8: Ceratophyllaceae. C.M. WILMOT-DEAR. 1997. *Bothalia* 27: 125–128.

FSA contributions 9: Onagraceae. P. GOLDBLATT & P.H. RAVEN. 1997. *Bothalia* 27: 149–165.

FSA contributions 10: Trapaceae. B. VERDCOURT. 1998. *Bothalia* 28: 11–14.

FSA contributions 11: Zingiberaceae. R.M. SMITH. 1998. *Bothalia* 28: 35–39.

FSA contributions 12: Plantaginaceae. H.F. GLEN. 1998. *Bothalia* 28: 151–157.

FLORA OF SOUTHERN AFRICA
ALPHABETICAL LIST OF PUBLISHED TAXA

* exotic families

Acanthaceae: Justiciinae, Vol. 30, Part 3, Fasc.1 (1995)
Achariaceae, Vol. 22 (1976)
Agavaceae (*Bothalia* 26, 1996)
Alismataceae, Vol. 1 (1966)
Anacardiaceae: *Rhus*, Vol. 19, Part 3, Fasc. 1 (1993)
Andreaeaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Anthospermeae, Rubiaceae: Rubioideae (second part), Vol. 31, Part 1, Fasc. 2 (1986)
Apocynaceae, Vol. 26 (1963)
Aponogetonaceae, Vol. 1 (1966)
Aquifoliaceae (*Bothalia* 24, 1994)
Archidiaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Asclepiadaceae: *Brachystelma–Riocreuxia*, Vol. 27, Part 4 (1980)
Aspalathus, Fabaceae: Papilionoideae, Vol. 16, Part 3, Fasc. 6 (1988)
Asparagaceae, Vol. 5 (1992)
Asphodelaceae: *Chortolirion, Poellnitzia* (*Bothalia* 25, 1995)
Asteraceae: Inuleae: Gnaphaliinae (first part), Vol. 33, Part 7, Fasc. 2 (1983)
Aulacomniaceae, Bryophyta, Part 1, Fasc. 2 (1987)
Aytoniaceae, Hepatophyta, Part 1, Fasc. 1 (1999)
Bartramiaceae, Bryophyta, Part 1, Fasc. 2 (1987)
Begoniaceae, Vol. 22 (1976)
Brachystelma, Asclepiadaceae, Vol. 27, Part 4 (1980)
Brassicaceae, Vol. 13 (1970)
Bryaceae, Bryophyta, Part 1, Fasc. 2 (1987)
Bryobartramiaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Bryophyta (three fascicles published 1981, 1987, 1998: see plan of *FSA*)
Burseraceae, Vol. 18 (1986)
Buxaceae (*Bothalia* 26, 1996)
Cactaceae, Vol. 22 (1976)
Caesalpinioideae, Fabaceae, Vol. 16, Part 2 (1977)
Calymperaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Canellaceae, Vol. 22 (1976)
Capparaceae, Vol. 13 (1970)
Ceratophyllaceae (*Bothalia* 27, 1997)
Ceropegia, Asclepiadaceae, Vol. 27, Part 4 (1980)
Charophyta, Cryptogams 'Vol. 9' (1978)
Chortolirion, Asphodelaceae (*Bothalia* 25, 1995)
Cleveaceae, Hepatophyta, Part 1, Fasc. 1 (1999)
Clusiaceae, Vol. 22 (1976)
Commelinaceae, Vol. 4 (1985)
Crassulaceae, Vol. 14 (1985)
Crotalarieae, *Aspalathus*, Fabaceae: Papilionoideae, Vol. 16, Part 3, Fasc.6 (1988)
Cryphaeaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Cupressaceae, Vol. 1 (1966)
Dicranaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Ditrichaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Dracaenaceae, Vol. 5 (1992)
Droseraceae, Vol. 13 (1970)
Ebenaceae, Vol. 26 (1963)
Elatinaceae, Vol. 22 (1976)
Encalyptaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Ephemeraceae, Bryophyta, Part 1, Fasc. 2 (1987)
Eriocaulaceae, Vol. 4 (1985)
Erpodiaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Eustichiaceae, Bryophyta, Part 1, Fasc. 2 (1987)
Exormothecaceae, Hepatophyta, Part 1, Fasc. 1 (1999)
Fabaceae: Caesalpinioideae, Vol. 16, Part 2 (1977)
Fabaceae: Mimosoideae, Vol. 16, Part 1 (1975)
Fabaceae: Papilionoideae, Crotalarieae, *Aspalathus*, Vol. 16, Part 3, Fasc. 6 (1988)
Fissidentaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Flacourtiaceae, Vol. 22 (1976)
Fontinalaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Frankeniaceae, Vol. 22 (1976)
Funariaceae, Bryophyta, Part 1, Fasc. 2 (1987)
Gentianaceae, Vol. 26 (1963)
Gigaspermaceae, Bryophyta, Part 1, Fasc. 2 (1987)
Gnaphaliinae (first part), Asteraceae: Inuleae, Vol. 33, Part 7, Fasc. 2 (1983)
Grimmiaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Hedwigiaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Hepatophyta, Part 1, Fasc. 1 (1999)
Holothrix, Orchidaceae (*Bothalia* 26, 1996)
Hookeriaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Hydrocharitaceae, Vol. 1 (1966)
Hydrostachyaceae, Vol. 13 (1970)
Inuleae, Asteraceae: Gnaphaliinae (first part), Vol. 33, Part 7, Fasc. 2 (1983)
Iridaceae: *Syringodea, Romulea*, Vol. 7, Part 2, Fasc. 2 (1983)
Juncaceae, Vol. 4 (1985)
Juncaginaceae, Vol. 1 (1966)
Justiciinae, Acanthaceae, Vol. 30, Part 3, Fasc. 1 (1995)
Lamiaceae, Vol. 28 (1985)
Leptodontaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Leucodontaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Loasaceae, Vol. 22 (1976)
Loganiaceae, Vol. 26 (1963)
Loranthaceae, Vol. 10 (1979)
Lunulariaceae, Hepatophyta, Part 1, Fasc. 1 (1999)

Luzuriagaceae, Vol. 5 (1992)
Malpighiaceae, Vol. 18 (1986)
Marchantiaceae, Hepatophyta, Part 1, Fasc. 1 (1999)
Marchantiales, Hepatophyta, Part 1, Fasc. 1 (1999)
Marchantiidae, Hepatophyta, Part 1, Fasc. 1 (1999)
Marchantiopsida, Hepatophyta, Part 1 (1999)
Meliaceae, Vol. 18 (1986)
Meteoriaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Mimosoideae, Fabaceae, Vol. 16, Part 1 (1975)
Mniaceae, Bryophyta, Part 1, Fasc. 2 (1987)
Moringaceae, Vol. 13 (1970)
Myrsinaceae, Vol. 26 (1963)
Nanobryaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Najadaceae, Vol. 1 (1966)
Neckeraceae, Bryophyta, Part 1, Fasc. 3 (1998)
Ochnaceae, Vol. 22 (1976)
Oleaceae, Vol. 26 (1963)
Onagraceae (*Bothalia* 27, 1997)
Orchidaceae: *Holothrix* (*Bothalia* 26, 1996)
Orthotrichaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Oxymitraceae, Hepatophyta, Part 1, Fasc. 1 (1999)
Paederieae, Rubiaceae: Rubioideae (second part), Vol. 31, Part 1, Fasc. 2 (1986)
Passifloraceae, Vol. 22 (1976)
Pinaceae*, Vol. 1 (1966)
Plantaginaceae *(Bothalia* 28, 1998)
Plumbaginaceae, Vol. 26 (1963)
Podocarpaceae, Vol. 1 (1966)
Podostemaceae, Vol. 13 (1970)
Poellnitzia, Asphodelaceae (*Bothalia* 25, 1995)
Pontederiaceae, Vol. 4 (1985)
Potamogetonaceae, Vol. 1 (1966)
Pottiaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Primulaceae, Vol. 26 (1963)
Prionodontaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Ptaeroxylaceae, Vol. 18 (1986)
Pteridophyta (1986) (for list of families, see p. v of Pteridophyta volume)
Pterobryaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Ptychomitriaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Racopilaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Resedaceae, Vol. 13 (1970)
Rhabdoweisiaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Rhachitheciaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Rhizogoniaceae, Bryophyta, Part 1, Fasc. 2 (1987)
Rhus, Anacardiaceae, Vol. 19, Part 3, Fasc. 1 (1993)
Ricciaceae, Hepatophyta, Part 1, Fasc. 1 (1999)
Riocreuxia, Asclepiadaceae, Vol. 27, Part 4 (1980)
Romulea, Iridaceae, Vol. 7, Part 2, Fasc. 2 (1983)
Roridulaceae, Vol. 13 (1970)
Rubiaceae: Rubioideae (second part): Paederieae, Anthospermeae, Rubieae, Vol. 31, Part 1, Fasc. 2 (1986)
Rubieae, Rubiaceae: Rubioideae (second part), Vol. 31, Part 1, Fasc. 2 (1986)
Rubioideae (second part), Rubiaceae, Vol. 31, Part 1, Fasc. 2 (1986)
Ruppiaceae, Vol. 1 (1966)
Salvadoraceae, Vol. 26 (1963)
Sapotaceae, Vol. 26 (1963)
Seligeriaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Simaroubaceae, Vol. 18 (1986)
Smilacaceae, Vol. 5 (1992)
Sphagnaceae, Bryophyta, Part 1, Fasc. 1 (1981)
Splachnaceae, Bryophyta, Part 1, Fasc. 2 (1987)
Stangeriaceae, Vol. 1 (1966)
Syringodea, Iridaceae, Vol. 7, Part 2, Fasc. 2 (1983)
Tamaricaceae, Vol. 22 (1976)
Targioniaceae, Hepatophyta, Part 1, Fasc. 1 (1999)
Thamnobryaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Tiliaceae, Vol. 21 (1984)
Trachypodaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Trapaceae *(Bothalia* 28, 1998)
Turneraceae, Vol. 22 (1976)
Typhaceae, Vol. 1 (1966)
Verbenaceae: *Vitex* (*Bothalia* 26, 1996)
Violaceae, Vol. 22 (1976)
Viscaceae, Vol. 10 (1979)
Vitex, Verbenaceae (*Bothalia* 26, 1996)
Wardiaceae, Bryophyta, Part 1, Fasc. 3 (1998)
Welwitschiaceae, Vol. 1 (1966)
Xyridaceae, Vol. 4 (1985)
Zamiaceae, Vol. 1 (1966)
Zannichelliaceae, Vol. 1 (1966)
Zosteraceae, Vol. 1 (1966)