A TAXONOMIC REVISION OF THE RICCIACEAE REICHENB. (MARCHANTIALES : HEPATICAE) IN SOUTHERN AFRICA

by

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Submitted in partial fulfilment of the requirements

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Promoter: Prof. Dr. A.E. van Wyk

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Dedicated to my mentor

Prof. (emer.) Dr. O.H. Volk
(Würzburg University, Germany)

in recognition of many years of guidance, help and encouragement.

ABSTRACT

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A taxonomic revision of 51 species of *Riccia*, nearly three quarters of which are probably endemic to southern Africa, as well as the cosmopolitan, monotypic species, *Ricciocarpos natans*, is presented. The systematic treatment includes keys to the genera, subgenera, sections, groups and species. Each species is described in detail, accompanied by its nomenclature, as well as information on its geographical distribution and ecology. Several thousand specimens have been collected by the author and by others, notably O.H. Volk, over the last 10 years or more, and are listed, together with older collections by Arnell, Duthie and Garside and by Sim, to name but a few. Illustrations include line drawings of the thalli of every species, plus photographs of the thalli of some and spore micrographs of all. The phylogeny is briefly considered with reference to the following criteria: palaeobotanical, phytogeographical, morphological, cytological and biochemical. A hypothetical ancestor is postulated and primitive character states as opposed to advanced ones are examined. An extensive bibliography is provided.

TABLE OF CONTENTS

PART 1
FORMAL TAXONOMIC TREATMENT

* * *

PART 2
FIGURES, PHOTOGRAPHIC & SEM MICROGRAPHIC PLATES & DISTRIBUTION MAPS

PART 1

FORMAL TAXONOMIC TREATMENT

INDEX TO SCIENTIFIC NAMES

Accepted names of taxa occurring in southern Africa plus their page numbers are in roman type; all other names are in italics.

CHAPTER 1

INTRODUCTION

The Ricciaceae is the most widespread family of all the liverworts and is known from every continent except Antarctica. During the 1830's the first specimens of *Riccia* were collected at the Cape by Krauss, Ecklon and Zeyher. Some of this material found its way to G.W. Bischoff at Heidelberg, Germany. He was probably the foremost authority on the family at that time. Although he made manuscript notes on *R. albomarginata*, *R. concava* and *R. limbata* from the Cape and is cited as the author of these species, he actually failed to publish descriptions, and it was left to Krauss (March 1846) and Gottsche, Lindenberg and Nees (Oct. 1846) to do so. These early descriptions were, however, incomplete and mostly lacked illustrations, as did Stephani's (1898), except for those in the latter's Icones Hepaticarum which were available for a fee, but were not always very enlightening.

In his paper on South African Hepatics or Liverworts, Sim (1915) made only brief reference to *Riccia* with nine species listed, one merely as *R.* sp. Later, in his Bryophyta of South Africa, he (Sim 1926) described 14 species, five as new, but not all have been retained. Duthie & Garside (1937, 1939) published an authoritative history of the taxonomy of the family, as well as very detailed descriptions of five species. They built up an extensive collection (held at BOL), some of which has only recently become available to me for study. Unfortunately, Duthie retired in 1940 and their excellent work was discontinued. Arnell (1963a) treated 36 species of the family in his work on South African hepatics, seven of which were newly described by him. Magill & Schelpe (1979) included 34 species of *Riccia* as well as *Ricciocarpos natans* in their checklist of southern African Bryophyta.

In recent years, Volk (emeritus professor at Würzburg University), myself and others have made many fresh collections of *Riccia* in southern Africa. Between Volk and me more than 30 papers have been published, some under joint authorship. A scanning electron microscope study of the spore-wall ornamentation as an aid to identifying the southern African species of *Riccia* was recently published (Perold 1989e) and was also included in a thesis submitted in the Department of Botany, University of Pretoria, for the MSc degree (1990), which was titled 'Taxonomic relevance of the spore-wall ornamentation in the southern African species of *Riccia* L. (Hepaticae: Ricciaceae)'. These two contributions should be treated as companions to this volume, as they each contain six spore micrographs of every species, whereas only two per species appear in the present work.

Jovet-Ast's (1986) authoritative text on the life cycle, morphology, anatomy, biology and ecology of Mediterranean *Riccia* should also be consulted.

The principal objective of this study is to provide a taxonomic account of the Ricciaceae for the Flora of Southern Africa (FSA) project and, with the exception of Chapter 3 (Material and methods) and Chapter 8 (Discussion and notes on phylogenetic criteria), it conforms to that format, as the main section is intended to form part of the first fascicle of part 2 of the volume **'Bryophyta in the FSA Cryptogam series'**. The FSA area covers the following independent states: Bophuthatswana, Botswana, Ciskei, Lesotho, Namibia, Republic of South Africa, Swaziland, Transkei and Venda.

The phylogenetic criteria referred to in Chapter 8, are examined with a view to possibly constructing an acceptable phylogeny at some future date, but this is not, however, within the scope of the present study. For convenience, this dissertation is presented in two parts: Part 1 comprises the text of the formal taxonomic treatment, whereas Part 2 contains all the illustrations, photographs, micrographs and distribution maps.

CHAPTER 2

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY

Seven major vegetation biomes are encountered in the Flora area (Rutherford & Westfall 1986), namely fynbos, Nama-Karoo, succulent Karoo, grassland, savanna, forest and desert biomes. Members of the Ricciaceae are found in practically all these areas, but are limited to only *Riccia rubricollis* and *R. stricta* as well as *Ricciocarpos natans* in the forest areas, as most of them clearly prefer 'open' spaces. Certainly, they are entirely absent from habitats covered with leaf litter and are terricolous, whether riparian mesophytes on alluvial soil or xerophytes on shallow soil on intermittently wet edges of flat granitic, basaltic or sandstone rock outcrops in arid or semi-arid areas. They prefer finely textured substrates, although the rather more coarsely granular soil derived from decomposing granite in the northwestern Cape, supports a unique *Riccia* flora.

Riccia are pioneer plants, but mostly avoid disturbed areas and are poor competitors. Some species such as *R. okahandjana*, *R. atropurpurea* and *R. runssorensis* appear to show a preference for acid soil; others such as *R. trichocarpa*, *R. albolimbata*, *R. argenteolimbata* and *R. congoana* grow on alkaline soil, whereas some are indifferent (Volk 1984). *Riccia stricta* and *Ricciocarpos natans* can be either aquatic or grow on damp soil.

Perhaps even more critical for the distribution of the different species than soil conditions, appears to be the climate. Some species are strictly confined to the winter rainfall areas of the northwestern, southwestern and southern Cape. Among these are the following endemics: *Riccia villosa*, *R. concava*, *R. furfuracea*, *R. schelpei*, *R. purpurascens*, *R. garsidei* and *R. cupulifera*. The latter has also been reported from the central Orange Free State and eastern Transvaal, but these two localities may have been temporary ones. The almost cosmopolitan species, *R. crozalsii*, is in southern Africa confined to the southwestern Cape; *R. curtisii*, otherwise fairly widespread, but with a disjunct distribution, is here only known from the northwestern, southwestern and southern Cape.

Most of the rest of southern Africa gets summer rain, from less than 200 mm annually in the far northwestern parts to more than 1 000 mm along the eastern coastal belt. The majority of species which prefer summer rain, share a rather similar distribution pattern, ranging from Namibia to the northern and eastern Cape, Natal, Orange Free State and Transvaal. Botswana is clearly under-collected, but is also sandy in large parts and much of it cannot support bryophyte populations. Some species, such as *R. bullosa* and *R. sorocarpa*, have disjunct distributions, growing in the western Cape, frequently in mountainous regions, as well as in the alpine heath-grassland of the Drakensberg. A number of species are only known from these eastern mountains, namely *R. montana*, *R. ampullacea* and *R. trachyglossum*; others are widespread in both winter and summer rainfall areas, e.g. *R. cavernosa*, *R. crystallina* and *R. nigrella*. Some species are extremely rare and only known from one or two localities, e.g. *R. alatospora*, *R. hirsuta*, *R. hantamensis*, *R. alboporosa*, *R. tomentosa*, *R. rubricollis*, and *R. mammifera*.

CHAPTER 3

MATERIAL AND METHODS

It is best to collect specimens of *Riccia* after rain has fallen 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 species roll their margins inwards, and so cover the dorsal face for protection against evaporation and heat. In this 'folded' state, *Riccia* plants, which are in any case difficult to find because of their small size, become virtually hidden and are hardly distinguishable from the substrate. Some species are perennial and have ripe spores during most of the year; others are annual and sporulate on reaching maturity, which can be in a matter of a few weeks only. As the spore ornamentation is such an important taxonomic character, collecting specimens with mature spores is advisable.

The procedure for collecting *Riccia* material is the same as that for moss specimens, except that the samples, once they have been 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 standard packets, folded from A4 paper. No other treatment is necessary and washing and pressing, or the use of glue to mount specimens on cardboard or preservation in spirit, should be avoided (Jovet-Ast 1985).

A dissecting and a compound microscope, as well as the standard materials for preparing microscope slides, are needed for the identification of *Riccia* species. Two pairs of fine-tipped forceps and two fine needle probes are used for the dissection of specimens; a conventional, thin, double-sided razor blade is required to make transverse and horizontal sections of the thallus branches.

Prior to dissection, the dry specimen is examined and the habit, colour and consistency of the thallus, as well as the presence or absence of scales and their colour are noted. Some of the material is then removed to a microscope slide and moistened with a few drops of water (at room temperature), delivered by squirting from a Pasteur pipette to wash away dust particles. When it has revived and regained its normal appearance, it is again examined and observations concerning the colour, shape, groove and position of the scales are made. Some 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 or bulbils should be noted. Transverse sections of the cleaned branch are cut serially by hand at intervals from the apex to the base. Horizontal sections are also 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 scales (in those species that have them) are carefully detached and they and the sections are transferred to a drop of water on a clean slide and a coverslip is applied. As the water evaporates during examination under the compound microscope, more can be added. For taking measurements and for photography, water-mounted material is routinely used. A calibrated ocular micrometer is used to measure the structures under the compound microscope. To make more durable preparations, the sections and scales can be mounted in Hoyer's medium (Anderson 1954); it does, however, cause shrinkage and bleaching of the delicate tissues.

For the identification of most species in section *Pilifer*, it is necessary to examine reasonably fresh and living material, as the cells in the loose dorsal pillars, a very important taxonomic character, collapse when dry and cannot be reconstituted, even if the rest of the thallus revives.

As mentioned in the introductory chapter, this dissertation is presented in two parts. Part 1 comprises the formal taxonomic treatment and Part 2 the illustrations, photographs, micrographs and distribution maps.

A traditional morphologic-taxonomic approach or taxonomic species concept was employed for the present revision of the Ricciaceae. Taxonomic decisions and descriptions of taxa were based on observations of field and cultured plants as well as on microscopic studies of the latter plus those of more than three thousand dried herbarium specimens. Spores from all sporulating specimens were also examined and a great many were photographed. The majority of Ricciaceae specimens collected in southern Africa are held at PRE. The PRE collection includes duplicates received from BOL and Herb. Volk. Type and other specimens not represented in southern African herbaria, have been obtained on loan from BM, BR, E, EGR, G, L, M, MO, NY, S, STR, as well as the private herbaria Jones, Townsend and Volk (herbaria acronyms are after Vitt *et al.* 1985).

All specimens studied are listed for each species (Chapter 10) and are located at PRE unless otherwise indicated. They are arranged alphabetically by the collector's name and then numerically for each collector. Quarter-degree grid references (Edwards & Leistner 1971) are given for each specimen. This is followed by the country of origin (in brackets) for specimens from the rest of Africa, north of the FSA region. For the following reasons a list of specimens examined is considered to be worthwhile : (a) to draw up distribution maps and to check distributions; (b) to give an indication of the specimens examined for each taxon; (c) cited specimens can be requested on loan; (d) names of duplicate specimens in other herbaria can be updated.

Except for *Riccia perssonii*, *R. rubricollis* and *Ricciocarpos natans*, live material of all the other species have been collected by the author during numerous field excursions between 1980 and 1990. The geographical distributions of southern African taxa were obtained from my own findings and from locality information recorded on herbarium labels. Grid references for collecting localities are based on a list of southern African Place Names (Leistner & Morris 1976). Where a grid is doubtful, this is indicated by a question mark preceding the grid reference; where only part of a grid reference is known the characters which are not known are replaced with x's. Notes on the ecology of the taxa are based on field observations and information recorded on herbarium labels.

In the formal taxonomic treatment only validly published names (see Greuter *et al.* 1988), followed by the author citations are dealt with. The citations of sources of original descriptions are followed by references to other important taxonomic works in which that particular taxon was also described. The citations of taxon type specimens are quoted from the original labels and material that has been seen is denoted by (!).

Descriptions of 51 species of *Riccia*, 24 of them recently described, are given. Only 13 of the species also occur outside the FSA region. The majority are endemics, with southern Africa clearly a main centre of diversity/evolution. The cosmopolitan, monotypic species, *Ricciocarpos natans*, is also described. Chromosome counts are mostly by Bornefeld (1984, 1989).

The illustrations (Figs 1-47), presented in Part 2 of the dissertation, were prepared by Ms Jill Kimpton. The habit drawings were done by direct observation of selected wet and dry plants, using a dissecting microscope. All other parts were drawn from photographs taken by the author, using photographic equipment attached to a compound microscope. Photographs (Plates 1-3) of the thalli of 18 species (many in cultivation), as well as two SEM micrographs (Plates 4-21) of the spores of all the species are included. The thalli were photographed by Mrs A. Romanowski, except for Plate 1D and 1E which were by Prof. Volk and permission for their use is gratefully acknowledged. All SEM micrographs of the spores are by the author. The distribution maps (Maps 1-63) indicate the geographical distribution of the Ricciaceae in southern Africa, Africa and world-wide, depending on whether the species are endemic, African or cosmopolitan. A black dot, triangle or occasionally a square on the southern African maps represent one or more collecting localities in a quarter-degree square. In the African and world maps exact localities are not shown, but ranges are indicated by dotted areas.

CHAPTER 4

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 stance of the margins and scales are sometimes important in identification and should be observed in both the wet and dry state. 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 apt to occur. The lengths of the branches are 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) mm long x 0,6—1,5(—2,0) mm wide
- smallish to medium-sized: 5,0—10,0 mm long x (0,6—)0,8—2,0 mm wide
- medium-sized: 5,0—10,0(—12,0) mm long x (1,0—)3,0—4,0 mm wide
- large: up to 15,0 mm long x 2,0—5,5 mm wide
- very large: up to 18,0 mm long x 4,0—6,0(—8,0) mm wide

The thickness of the branches is measured on cross sections, as is also the determination of the ratio of the width to thickness. The slope of the flanks can also be observed on cross sections.

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

Scales. The presence or absence, colour, size, shape, stance, position and margins of the scales are very important taxonomic characters and are frequently used in the key to identify species of *Riccia*.

Dorsal covering. Whether the dorsal cells form an even, more or less homogeneous upper surface of echlorophyllose cells in one or two strata, or form free-standing, multicellular pillars or whether the cells are chlorophyllose and interrupted by defined pores which soon enlarge, should be observable when examining the thalli under the dissecting microscope, but subdorsal horizontal and transverse sections are always taken to measure the cells and to note their shape. In 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.

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

Sporangia. It should be noted whether the sporangia bulge dorsally or ventrally or whether they are deeply imbedded.

Spores. Mature, well-formed spores are mounted on microscope slides in Hoyer's medium to measure their diameter, as well as the width of the areolae and the wing, if present. 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 are gold-coated. Spore characters are very important in distinguishing between species and many can easily be recognized solely by their ornamentation.

CHAPTER 5

EXPLANATION OF TERMS

For reasons of clarity and unambiguity it is deemed necessary to add a glossary and so to also convey the author's concept of the terms used. Magill (1990) was freely consulted.

acropetal sexual organs developing from the base toward the apex.

air pores minute, regular spaces or simple, 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, chlorophyllose cell plates in the assimilation tissue.

anastomose interconnecting, applied to ornamentation in some spores.

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).

areola (pl. **areolae**) small angular or polygonal areas bordered by ridges and forming a pattern or network; applied to ornamentation in many spores (some authors prefer the term 'alveola' (pl. 'alveolae'))

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.

cavernous with numerous cavities in the tissue.

chlorophyllose containing chlorophyll; green as opposed to hyaline.

cilia (sing. **cilium**) hair-like appendages along thallus margins of some species.

crenate with rounded teeth; applied to scale margins.

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

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

dichotomous an equal division which yields two equal branches.

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

emarginate marginal indentation or notch at the thallus apex.

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

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

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

filiform filamentous, thread-like.

flanks sides of thallus.

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

globose spherical.

granular roughened with minute, blunt projections.

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

groove furrow along centre of dorsal face of thallus, narrow and deep to wide and shallow.

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 an 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.

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.
papillate loosely applied to minutely rough surface; applied to spore ornamentation.
polar spore spore with a discernable to conspicuous triradiate mark on the proximal face.
proximal the internal face of a spore (opposed to distal).
reticulate netted, the network pattern produced by areolae on spore faces.
rhizoid roothair-like structures that theoretically function in absorption and anchorage, one-celled and usually hyaline, smooth or tuberculate.
rosette growth habit with thalli radiating from a central point.
scales thin, membranous structures, in two or more rows, on the undersides of thallus.
sporangium spore-producing structure, usually embedded in thallus tissue, occasionally bulging ventrally.
stolon slender, more or less vertical underground stem.
storage tissue the ventral 1/3 of thallus, composed of cells often containing starch or oil.
succulent thick and fleshy.
tetrad a group of 4 developing or rarely mature spores.
tetrahedral four-sided.
thallus a more or less flattened vegetative body, without differentiation into a stem and leaves.
triangular-globular inner spore face with 3 facets separated by arms of triradiate mark; outer face rounded.
triradiate mark y-shaped, prominent ridge on the proximal face of spore.
tumid swollen.
undulate wavy.
ventral the lower surface, next to the substrate (opposed to dorsal).
vermiculate long, narrow, somewhat wavy, usually with rounded ends; applied to ornamentation of some spores.
verruculate irregularly roughened; applied to ornamentation of some spores.
wing the thin, flat expansion at the margin of the spore.

CHAPTER 6

CLASSIFICATION AT SECTIONAL LEVEL AND ABOVE

Classification is partly after Grolle (1983), with the recognition of the two subgenera *Riccia* and *Ricciella*, and also partly after Jovet-Ast (1975) with the elevation of *Thallocarpus* (Lindb.) Jovet-Ast to the status of subgenus. Two other subgenera, unique to southern Africa, have been instituted: *Chartacea* Perold and *Pannosae* (Perold) Perold. Another two recently recognized subgenera, *Viridisquamata* Jovet-Ast and *Leptoriccia* Schust., do not occur in southern Africa. Volk's section *Pilifer* is treated as a subdivision of subgenus *Riccia*, and not as the subgenus *Pteroriccia* (Schuster 1985). Na-Thalang (1980) was followed in dividing section *Riccia* into the two informal groups: 'Ciliatae' and 'Squamatae'; section *Spongodes* was divided into the groups: 'Crystallina' and 'Vesiculosa').

Conspectus of the classification is as follows:

CLASS **HEPATICOPSIDA** *Rothm.*

SUBCLASS **MARCHANTIIDAE** *Schust.*
ORDER **MARCHANTIALES** *Limpr.*
SUBORDER **RICCIINEAE** *Buch*
Family Ricciaceae *Reichenb.*
The family Ricciaceae comprises 2 genera:
Riccia L.
Ricciocarpos Corda
In southern Africa, the genus *Riccia* consists of 5 subgenera:
subgenus **Riccia:**
  section *Riccia*
  section *Pilifer* Volk
subgenus **Ricciella** (A. Braun) Reichenb.:
  section *Spongodes* Nees
  section *Ricciella*
subgenus **Thallocarpus** (Lindb.) Jovet-Ast
subgenus **Chartacea** Perold
subgenus **Pannosae** (Perold) Perold
The genus *Ricciocarpos* has only one representative, the species *R. natans*.

CHAPTER 7

SYSTEMATIC TREATMENT OF THE SOUTHERN AFRICAN RICCIACEAE

RICCIACEAE

Plants thalloid, small to large, scattered or in gregarious patches or in rosettes, green; terricolous, rarely aquatic. Branches 2 or 3 times dichotomously furcate, linear to obovate; apex truncate to rounded, emarginate. Groove median along dorsal face. Thallus margins acute to obtuse, glabrous or occasionally ciliated. Flanks sloping obliquely or steep; ventral face rounded to flat. *Scales* small to large, rarely absent, generally imbricate, lateral or ventral, hyaline or variously coloured, purple, red or black.

Dorsal covering either an *epithelium*, hyaline, echlorophyllose cells in 1 or 2 strata, or in free uniseriate, multicellular pillars; air pores numerous, small, regular spaces; or else, dorsal covering an *epidermis*, chlorophyllose, generally unistratose; air pores simple, delimited stomata, scattered, often becoming cavernous. *Assimilation tissue* compact, cell columns enclosing narrow vertical air canals; or spongy, with mostly unistratose cell plates enclosing wide polyhedral air chambers; storage tissue occupying ventral 1/2 or less of thallus; rhizoids long, unicellular, smooth or tuberculate, arising from ventral epidermis.

Monoicous or dioicous. Gametangia acropetally arranged, embedded, only necks projecting, single, median along groove or scattered. *Sporangia* without stalk or foot, enclosed by venter wall, soon disintegrating to liberate spores, elaters absent. *Spores* generally large, separating at maturity, rarely remaining coherent in tetrads, triangular-globular or subglobular, ornamentation mostly reticulate, often specific.

The family comprises two genera: firstly, the species-rich genus *Riccia* with up to about 200 species world-wide, and particularly well represented in southern Africa; and secondly, the monotypic, cosmopolitan genus *Ricciocarpos*.

Key to the two genera of the Ricciaceae

Thalli mostly terricolous; assimilation tissue compact, with cell columns enclosing narrow vertical air canals, or else spongy, with air chambers; scales small to large, imbricate, mostly rounded, margins smooth, rarely denticulate; oil cells absent; gametangia along groove or scattered.....1. **Riccia**

Thalli floating or terricolous; assimilation tissue with large air chambers in several tiers; scales long, pendant, purple ribbons, but small in land form, margins dentate; oil cells present; gametangia only along deep central groove.....2. **Ricciocarpos**

1. RICCIA

Riccia *L.*, Species Plantarum: 1138 (1753); Steph.: 314 (1898); Sim: 8 (1926); Müller: 416 (1952); S. Arnell: 13 (1963a); Hässel: 208 (1962); Na-Thalang: 71 (1980); Jovet-Ast: 291 (1986). Lectotype species: *R. glauca* L., fide Hässel in Opera Lilloana 7: 208 (1962).

Euriccia Lindb. ex Lacouture : 23 (1905).
Ricciella A. Braun : 756 (1821).

Lichenoides (Bisch.) Lindley : 57 (1853).
Thallocarpus Lindb. : 377 (1874).
Cryptocarpus Aust. : 231 (1870). nom. illeg.
Angiocarpus Trev. : 444 (1877).
Riccinia Trab. in Douin & Trab. : 326 (1919).
Fysonia Kashyap : 203 (1923). Type species: *F. tenera* S.R. Kashyap
Pteroriccia Schust.: 72 (1984). Type species: *R. villosa* Steph.

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* vestigial to conspicuous, hyaline or variously coloured, lateral or ventral, usually imbricate, rounded, very rarely triangular.

Dorsal epithelium hyaline, echlorophyllose, cells in 1 or 2 strata or in free uniseriate, multicellular pillars; air pores small spaces, regular; or *dorsal epidermis* chlorophyllose, unistratose (rarely otherwise), air pores simple, delimited stomata, scattered, becoming cavernous. *Assimilation tissue* generally 1/2 the thickness of thallus, compact, in vertical cell columns, enclosing narrow air canals; or spongy, with wide polyhedral air chambers; storage tissue occupying ventral 1/2 or less of thallus, cells rounded, often containing starch granules; rhizoids arising from ventral epidermis and sometimes from base of scales, some smooth, others tuberculate, 15—25 μm wide. Oil cells absent.

Monoicous or dioicous. Antheridia with hyaline necks, along groove. Archegonia with purple necks. *Sporangia* bulging dorsally or not, rarely conspicuously bulging ventrally, containing several hundred spores, released by decay of surrounding tissue. *Spores* with tetrads separating at maturity, rarely remaining coherent, mostly 80—110 μm in diameter, triangular-globular or subglobose; ornamentation generally reticulate, areolae small to large, otherwise papillate, verruculate 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 about 200 species currently recognized and has a world-wide distribution. It is primarily distributed in the temperate zones and the 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 Cape has yielded several new, unusual species. *Riccia* frequently grow on soil at the margin of flat rock outcrops or at streambanks.

ARTIFICIAL KEY TO THE SUBGENERA, SECTIONS, GROUPS AND SPECIES OF *RICCIA*.

(A diagrammatic representation of the principal characters in a somewhat condensed and abbreviated form has been tabulated; it appears in the text after the key).

1a Thallus covered by a dorsal 'epithelium' of echlorophyllose cells in one or several strata; air pores numerous, small and regular intercellular spaces; assimilation tissue compact, in vertical rows of chlorophyllose cells separated by mostly very narrow interstitial air canals; scales small to large; habitat often xeric, sometimes mesic; spores separating at maturity (Subgenus *Riccia*):

2a Epithelial cells closely associated, in one or two layers, top cells globose, mammillose or pyriform, outer walls (or cells) often collapsing; generally orientated regularly and in parallel rows running from central groove to margin; scales small to large, rounded (Section *Riccia*):

3a Thallus with cilia along margins, occasionally also present over sporangia; ventral scales not conspicuous, sometimes flanks dark purple:

4a Thallus medium-sized to large, up to 12,0 mm long x 4,0 mm wide; cilia white when dry, 300(—400) μm long, finely granular (Figure 4C), absent over sporangia; spores straw-coloured, with wing 10 μm wide, slightly undulating..... ..... 4. *R.natalensis*

4b Thallus smaller, less than 8,0 mm long x 1,5 mm wide; cilia hyaline, dry or wet, long or short; spores brown to black, with or without wing:

5a Distribution in Flora area restricted to winter rainfall region of southwest Cape; cilia generally quite sparse, 250(—400) μm long, finely granular, absent over sporangia; scales small, purple; flanks green; spores with wing about 7,5 μm wide.....2. *R. crozalsii*

5b Widespread in summer rainfall areas; cilia crowded, dense, variously long, not granular, present over sporangia; flanks dark purple; spores mostly wingless:

6a Thallus 5,0—6,0 mm long x 0,9—1,5 mm wide, cilia straight to slightly flexuose, up to 950 μm long, smooth; spores 100—120 μm in diameter, ornamentation reticulate, areolar walls heavily encrusted with papillae (Plate 4A & B).....1. *R. trichocarpa*

6b Thallus small, 1,0—4,0 mm long x 0,6—0,8 mm wide; cilia arched (Figure 3C), up to 300 μm long, channelled and finely striate; spores 80—90 μm in diameter, ornamentation reticulate, areolar walls mostly smooth.....3. *microciliata*

3b Thallus margins not ciliate, marginal cells enlarged or not; ventral scales, small to large:

7a Thallus margins apically with row of mammillate cells (Figure 4K) up to 150 μm long; scales small, not extending to thallus margins, violet to hyaline.....5. *R. mammifera*

7b Thallus margins glabrous; scales larger, extending to margins or projecting above, hyaline or variously pigmented:

8a 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:

9a Dorsal epithelial cells always with markedly thicker walls (Figure 5E) ; thallus light green, appearing almost waxy; flanks green; spores polar, dark reddish brown to black, proximal face densely granulate (Plate 5F); widespread (nearly cosmopolitan) but rare in Flora area.....6. *R. sorocarpa*

9b Dorsal epithelial cells with walls sometimes thicker; thallus glaucous green to silvery grey-green; flanks dark red-brown; spores almost apolar, dull dark brown to nearly black, reticulate; endemic and common in summer rainfall areas.....7. *R. atropurpurea*

8b Scales large and conspicuous, pigmented, with or without hyaline border or entirely hyaline to white; groove various; dorsal epithelial cell walls not thickened:

10a Scales dark, black or reddish black to deep violet, shiny; thallus size variable; dorsally glaucous green to green or purplish, rarely brown:

11a Thallus medium-sized to large; in section 2,5—5 times wider than thick; flanks sloping obliquely:

12a Thallus large, up to 15,0 mm long x 5,0 mm wide; margins winged, overhanging; spores subglobular, apolar, ornamentation reticulate with thin, high areolar walls.....9. *R. congoana*

12b Thallus medium-sized to large, up to 15,0 mm long x 3,0(—4,0) mm wide; margins attenuate, not overhanging; spores triangular-globular, polar, areolar walls thick, low:

13a Distribution in Flora area restricted to winter rainfall regions of Cape; thallus quite fleshy; scales imbricate, clasped together along midline when dry (Figure 9A); spores 90—125 μm in diameter, distal face with short spiralling ridges, proximal face almost smooth, with scattered pores.....10. *R. limbata*

13b Widespread in summer rainfall regions, but not common; thallus mostly thinner; scales imbricate to proximally wider spaced; when dry, opposite scales meet or do not, never clasped together; spores 72—82 μm in diameter; distal face with areolae in more or less concentric rings; proximal face completely or incompletely reticulate.....11. *R. angolensis*

11b Thallus smallish to medium-sized; in section once to twice wider than thick; flanks steeply rising:

14a Thallus medium-sized; bluish green; scales projecting above thallus margins, edge crenate (Figure 7H), rather dull black, dry; spores golden brown, wingless, densely papillate.....8. *R. okahandjana*

14b Thallus smallish; glaucous green, rust-brown along margins and proximally; scales appressed, not projecting above thallus margins, edge smooth, shiny dry or wet; spores light brown to dark brown, winged, incompletely reticulate.....12. *R. nigrella*

10b Scales other than black, variously coloured or white; thallus small to medium-sized; dorsally green to yellow-green, white or brownish:

15a Scales brown or various shades of pink to red:

16a Thallus margins and scales brownish yellow; idioblasts (enlarged cells with brown contents) present throughout thallus (Figure 11K); spores vermiculate; species very rare.....13. *R. macrocarpa*

16b Thallus margins not brown; scales pink to red, idioblasts absent; spores reticulate:

17a Thallus very small, 1,5—2,5(—3,0) mm long x 0,7—1,0 mm wide; bottle green, tumid; scales regular, appressed, dark red, white-bordered; distribution restricted; spores 60—78 μm in diameter, triangular-globular, polar.....14. *R. pottsiana*

17b Thallus medium-sized; bright green or light green to whitish; scales wine-red or rose-pink; widespread; spores 80—105 μm in diameter, globular to subglobular, apolar:

18a Thallus 7,0—9,0 mm long x 1,2—1,6 mm wide; bright green, turning grey-green; scales dark red, shiny, with narrow hyaline border; monoicous; spores red to black, periphery with prominent projections, cogwheel-like.....15. *R. runssorensis*

18b Thallus up to 12,0 mm long x 1,0—2,5 mm wide; pale green but white along margins; scales wavy, rose-pink with wide hyaline border; dioicous; spores rare, light brown, periphery with low projections.....16. *R. rosea*

15b Scales predominantly white or hyaline, often encrusted with calcium deposits, wavy or appressed:

19a Scales large, up to 1 250 x 750 μm, irregularly wavy to frilly, closely imbricate; thallus mostly 8,0—9,0 (rarely up to 12,0) mm long x 1,5—2,0(—4,0) mm wide; apically grooved; dorsally green, turning white and spongy over sporangia:

20a Thalli in rosettes or gregarious; widespread and quite common; spores with 10—12 round to angular areolae across diameter of distal face.....17. *R. albolimbata*

20b Thalli not in rosettes; quite rare, distribution apparently restricted to Cape Province; spores with 14—20 small deep areolae across diameter of distal face.....19. *R. albornata*

19b Scales smaller, up to 850 x 500 μm, mostly appressed and regular, imbricate; thallus generally rather smaller, 7,0—8,0 mm long x 0,7—2,0(—4,0) mm wide; apically grooved or along almost the entire length; dorsally mat or shiny:

21a Thallus deeply grooved along most of its length; dioicous; spores apolar or polar:

22a Dorsally mat, grey-green; compact; dorsal epithelial cells thick-walled, collapsed, in regular honeycomb pattern; scales tightly appressed (Figure 16B), base silvery purple-grey; fairly widespread; spores apolar.....18. *R. argenteolimbata*

22b Dorsally glistening, light green to green; finely spongy; dorsal epithelial cells thin-walled, not in regular pattern; scales apically wavy, soon appressed; distribution restricted to eastern mountainous regions; spores polar.....20. *R. montana*

21b Thallus only apically grooved; monoicous; spores polar:

23a Thallus with wide, shallow groove; 8,0 mm long x 4,0 mm wide; dorsally very heavily encrusted with calcium deposits; air pores large, regular; scales white; spores finely reticulate.....21. *R. alboporosa*

23b Thallus narrowly grooved; up to 5,0 mm long x 1,0—2,0 mm wide; dorsally with fine calcium deposits; air pores small to large, irregular; scales bicoloured, with deep purple base; spores more coarsely reticulate.....22. *R. bicolorata*

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

24a Dorsal pillars tall, more than 200 μm and up to about 450 μm (rarely 1 000 μm) long, consisting of (3—)4—6 narrow, elongated cells (1 1/2—)2—3 (or more) times longer than wide:

25a Dorsal surface of thallus generally somewhat velvety or furry when fresh; emerald green to lighter green; pillars gradually tapering to narrower apical cell:

26a Scales rounded, wavy, large, 1 500 x 600—900 μm; margin smooth; thallus emerald green; basal cells of pillars almost equally long, walls somewhat thickened; spores polar, ornamentation finely or coarsely reticulate.....25. *R. simii*

26b Scales triangular, very large, up to 1 800 μm long; basal cells of pillars variably long, walls not thickened; spores variously ornamented:

27a Triangular scales with dentate margins (Figure 20E); dorsal pillars up to 450 μm long; spores papillose; not rare, but distribution restricted to the western and southern Cape.....23. *R. villosa*

27b Triangular scales with filamentous apices (Figure 21G); dorsal pillars up to 1 000 μm long; spore ornamentation incompletely reticulate; very rare.....24. *R. hirsuta*

25b Dorsal surface of thallus rarely velvety or furry; steel-grey to bright green or olivaceous green; cell pillars not, or hardly tapering:

28a Dorsally steel-grey; tall pillars (up to 450 μm long) like slivers of glass, often interlocking over groove; thalli larger, up to 9,0 mm long; scales large and billowing, basal cell walls appearing 'stretched'; proximal spore face incompletely reticulate and granulate; distal face with a few short, well-spaced, radiating, central ridges.....26. *R. vitrea*

28b Dorsally olivaceous green or crystalline; pillars shorter (mostly less than 350 μm long), not interlocking, or if so, only temporarily toward the apex; thalli mostly less than 8,0 mm long; scales smaller and not billowing; spore ornamentation completely reticulate on proximal face, not granulate; distal face reticulate or with several, long, thick, radiating ridges:

29a Dried thalli with brown, parchment-like flanks, proximally almost denuded of scales; wet thalli velvety, olivaceous green; distal spore face with thick radiating ridges.....28. *R. albomarginata*

29b Dried thalli frequently with somewhat purple flanks; wet thalli rather crystalline, bright green or purplish green:

30a In section, thalli 1,5 times to nearly twice wider than thick; sides tightly inflexed when dry.....
.....27. *R. namaquensis*

30b In section, thalli 2—4 times wider than thick; sides incurved when dry:

31a Cells in dorsal pillars mostly somewhat constricted in the middle, ampulla-shaped; spores 90—95(—105) μm in diameter; distal face with several radiating ridges; distribution restricted to eastern mountains.....29. *R. ampullacea*

31b Cells in dorsal pillars not constricted; spores 70—80(—90) μm in diameter; ornamentation with numerous small areolae; distribution restricted to southwestern Cape.....30. *R. parvo-areolata*

24b Dorsal pillars short, often less than 200 μm long, consisting of 2 or 3(4) cells, mostly wider than long, tapering or not tapering:

32a Dorsal pillars tapering; air canals rather wide, width up to 100 μm:

33a Spores wide-winged, wing width up to 10 μm; elaborately ornamented; very rarely found:

34a Thalli large, up to 10,0 mm long x 2,5—3,8 mm wide; scales hyaline.....33. *R. hantamensis*

34b Thalli small, up to 5,0 mm long x 0,9—1,5(—2,0) mm wide; scales red.....32. *R. alatospora*

33b Spores narrow-winged, wing width up to 5 μm; ornamentation less elaborate, especially on proximal face where often reduced to simple projections and stipplings; widespread.....31. *R. albovestita*

32b Dorsal pillars not tapering; air canals narrow:

35a Thalli quite large, up to 10,0 mm long x 3,0—4,0 mm wide; broadly ovate to obovate; in section 3—4 times wider than thick; flanks sloping obliquely; distal spore face with 10—14 areolae across diameter, sometimes with central papilla or short radiating ridges.....34. *R. concava*

35b Thalli smaller, up to 8,0 mm long x 1,0—2,0 mm wide; ligulate to ovate; in section as wide as, to twice wider than thick; flanks steep; spores variously ornamented:

36a Branches frequently simple, long and narrow; spore distal face with 5—7 large, incomplete areolae across diameter, often with central boss.....35. *R. elongata*

36b Branches mostly several times furcate; spore distal face with more than 7 smaller areolae across diameter, lacking central boss:

37a Branches apically keeled to wedge-shaped; margins somewhat tumid; dorsal cell pillars up to 180 μm long; proximal spore face reticulate:

38a Dorsal pillars with top cell mammillose; distal spore face with ridges generally forming a central cross (Plate 16A); distribution restricted to western Cape.....37. *R. furfuracea*

38b Dorsal pillars with top cell globose; distal spore face with about 8 angular, irregular areolae across diameter; distribution apparently restricted to Lesotho.....36. *R. trachyglossum*

37b Branches apically rounded; margins not tumid; dorsal cell pillars only 70—105 μm long; proximal spore face granulate.....38. *R. pulveracea*

1b Thallus covered by a dorsal epidermis of mostly thin-walled, generally chlorophyllose cells, very rarely bearing dorsal cellular outgrowths; air pores mostly delimited, often ringed by smaller cells, well-spaced, fewer, frequently becoming cavernous; assimilation tissue loosely arranged, spongy, unistratose cell plates enclosing large polyhedral air chambers; scales small and evanescent to occasionally large and persistent; habitat mostly mesic, rarely xeric or aquatic; spores separating at maturity or remaining in tetrads:

39a Dorsal epidermis a single layer of thin-walled, closely joined, flattened cells (rarely globose, and then somewhat loosely connected), interrupted by air pores; becoming cavernous over air chambers or not; scales ventral, mostly hyaline and inconspicuous, evanescent:

40a Thalli annual or perennial; sometimes in rosettes; branches not strap-shaped (1,0—)3,0—6,0(—8,0 mm) wide; mostly cavernous to markedly cavernous; monoicous or dioicous; sporangia deeply imbedded or bulging somewhat above or below:

41a Spores separating at maturity (Subgenus *Ricciella*):

42a Thalli finely to coarsely spongiose; dorsally not deeply grooved; often in rosettes; glaucous green to yellow green, sometimes tinged with red (Section *Spongodes*, group 'Crystallina'):

43a Thalli monoicous; from above air chambers visible or not; spores completely or incompletely reticulate:

44a Thalli blue-green, crystalline; dorsally with rounded cells, in loosely connected double tiers; from above air chamber walls not visible; spores 65—85 μm in diameter; light brown; areolae regular, walls thin..... 39. *R. crystallina*

44b Thalli yellow-green, faintly red at margins; from above air chamber walls visible or air chambers cavernous; spores 85—115 μm in diameter; red-brown to black; with thicker, irregularly bi- or trichotomously branching ridges (Plate 17B).....40. *R. cavernosa*

43b Thalli dioicous; markedly heterothallic with small male gametophyte (Figure 36B); bright green to yellowish green; from above air chamber walls visible or cavernous; spores foveolate, triradiate mark pronounced (Plate 17D).....41. *R. cupulifera*

42b Thalli swollen to rather flat; usually markedly cavernous; dorsally deeply grooved along entire length or only apically; rarely in rosettes; green to straw-coloured or whitish, very rarely tinged with purple (Section *Spongodes*, group 'Vesiculosa'):

45a Thalli large and very wide, 5,0—15,0 mm long x 3,5—5,5(—8,0) mm wide; when dry, yellowish to straw-coloured or white; spores 100—150(—160) μm in diameter, with 8—12 areolae across distal face; wing thin, 10 μm wide:

46a Thalli straw-coloured dry; deeply grooved along entire length; cavernous in older parts only; spores with areolae on distal face 10—15 μm wide.....42. *R. bullosa*

46b Thalli white when dry; mostly only apically grooved; honeycomb-pitted dorsally; spores with areolae on both faces larger, up to 20 μm wide.....43. *R. garsidei*

45b Thalli narrower, up to 12 mm long x 2,5—3,0 mm wide; when dry, greyish white to yellowish; spores 88—112 μm in diameter, with 5—8 areolae across distal face; wing narrow, width 3—5 μm:

47a Rarely in rosettes; widespread in summer rainfall areas; antheridial necks inconspicuous, hyaline.....
.....44. *R. volkii*

47b Not in rosettes, somewhat linear; very rare, only known from Knysna dist.; antheridia with conspicuous purple necks (Figure 40B).....45. *R. rubricollis*

40b Thalli generally annual; not in rosettes; branches linear, strap-shaped or 'ribbon-like', 15,0—20,0 mm long and up to 2,0 mm wide; not cavernous; sporangia bulging markedly ventrally (Section *Ricciella*):

48a Thalli monoicous; sometimes aquatic; widespread in mostly summer rainfall areas; sporangia oblique (Figure 41D); distal spore face with areolar walls thick and prominent.....46. *R. stricta*

48b Thalli dioicous; thin and lax; strictly terrestrial; distribution restricted to winter rainfall areas of the western and southern Cape; sporangia vertical; distal spore face with areolar walls thin.....47. *R. purpurascens*

41b Spores remaining in tetrads (Subgenus *Thallocarpus*):

49a 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 19E, F).....48. *R. curtisii*

49b Thalli reportedly in rosettes up to 11 mm across; male gametophytes small; spores joined together by wide band into rhomboidal tetrads; ornamentation with stout spines 10—15 μm long (Plate 20A, B).....49. *R. perssonii*

39b Dorsal epidermis other than thin-walled, single-layered flat cells interrupted by air pores:

50a 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 (Subgenus *Chartacea*).....51. *R. schelpei*

50b 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 20C, D)(Subgenus *Pannosae*).....50. *R. tomentosa*

TABLE 1.—Diagrammatic representation of principal characters employed in the key

Family	Ricciaceae				
Genera	Riccia: mostly terricolous; scales small to large, imbricate; oil cells absent; polytypic (species nos. 1–51)				Ricciocarpos: mostly aquatic and floating; scales generally long, pendant, purple ribbons; oil cells present; monotypic (species no. 52)
Subgenera	1a dorsal epithelium thin-walled cells, echlorophyllose, uni- or multistratose; air pores numerous, small, regular, intercellular spaces; thalli compact; thallus margins ciliated or scaled; spores single (species nos. 1–38)				
	Riccia	Sections	2a Riccia	Groups	3a 'Ciliatae': epithelium unistratose; thallus margins ciliated (species nos. 1–5)
					3b 'Sqaumatae': epithelium unistratose; thallus margins scaled (species nos. 6–22)
			2b Pilifer		epithelium bi- to multistratose, in loose cell pillars (species nos. 23–38)
	1b dorsal epidermis mostly thin-walled cells, chlorophyllose, unistratose, very rarely with cellular outgrowths; air pores fewer, larger, spaced and well-defined, often ringed by smaller cells; thalli spongy spores single or in tetrads (species nos. 39–51)				
	41a Ricciella	Sections	Spongodes	Groups	42a 'Crystallina': thalli not strap-shaped; not deeply grooved; often in rosettes; sporangia mostly deeply imbedded; spores single (species nos. 39–41)
					42b 'Vesiculosa': thalli not strap-shaped; deeply grooved; rarely in rosettes; sporangia mostly deeply imbedded; spores single (species nos. 42–45)
			40b Ricciella		thalli strap-shaped; sporangia bulging ventrally; spores single (species nos. 46, 47)
	41b Thallocarpus	spores remaining in tetrads (species nos. 48, 49)			
	50a Chartacea	dorsal epidermis with thick-walled cells; air pores ringed by smaller, thin-walled, superimposed cells; spores single (species no. 51)			
	50b Pannosae	dorsal epidermis with cellular outgrowths of hair-like pillars; air pores ringed by wedge-shaped cells; spores in tetrads (species no. 50)			

Couplet numbers appear in the top left corners of the blocks.

1. Subgenus **Riccia**

Thalli small to large; terricolous. Groove deep or shallow, margins ciliated or glabrous. *Scales* mostly large, lateral, rarely ventral, rounded, very occasionally triangular, variously pigmented or hyaline, extending to, or projecting above thallus margins, scale margins entire, rarely denticulate or crenate.

Dorsal epithelium hyaline, in one or more strata, air pores small spaces, numerous, regular. *Assimilation tissue* compact, with mostly narrow interstitial vertical air canals.

Spores large, (65—)80—120 μm in diameter; tetrads separating at maturity, triangular-globular or subglobose, variously ornamented.

1. Section **Riccia**

Thalli small to large; terricolous. Groove apical or along entire length of branches, margins ciliated or glabrous. *Scales* mostly large, hyaline or variously pigmented, margins mostly smooth, 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.

Two informal groups are recognized within this section: group 'Ciliatae' and group 'Squamatae'.

Group 'Ciliatae'

Thallus margins ciliated. *Scales* small, not, or hardly extending to thallus margins.

1. **Riccia trichocarpa** *Howe* in Bulletin of the Torrey Botanical Club 25: 184 (1898); Howe: 18 (1899); Frye & Clark: 27 (1937); Jovet-Ast: 315 (1983); Jovet-Ast: 332 (1986). Type: Calif., Santa Clara Co. near San Mateo Co. line (fide Howe: 18 (1899)), April 1892, *D.H. Campbell* (US, holo., fide Jovet-Ast: 332 (1986); NY, iso.!).

R. canescens Steph. in Bulletin l'Herbier Boissier 6: 320 (1898); Müller: 445 (1952); S. Arnell: 16 (1963a). Type: Algeria, Oran, *Balansa* s.n., 1852.

R. tumida Lindenb., Monographie der Riccieen, Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum 18: 459 (1836). Type: California, on rocky ground, *Bolander* (NY!).

Thallus smallish to medium-sized, in complete or incomplete rosettes, up to 20 mm across or in crowded, gregarious patches; bright green to glaucous green, with long cilia at margins and dark purple flanks; 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) mm long, 0,9—1,5 mm wide, 0,6—0,9 mm thick and in section as wide as thick to 1,5 times wider than thick; apex rounded to shortly emarginate. Groove apically deep and narrow, becoming shallow and wider proximally, lateral sides convex, gradually flattening out. Thallus margins rounded. Flanks somewhat bulging to steeply rising, 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, somewhat 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 x 35—40 μm, hyaline, fragile, soon collapsing; air pores triangular or 4-sided, small. *Assimilation tissue* 300—400 μm thick, almost 1/2 the thickness of thallus, consisting of vertical rows of 7 or 8 isodiametric cells, mostly 30 x 25 μm, enclosing narrow air canals; storage tissue occupying ventral 1/2 of thallus, cells closely packed, rounded, about 45 μm wide. Fig. 1A—G.

Monoicous. Antheridia in row along groove, hyaline necks projecting up to 50 μm. Archegonia scattered, necks purple. *Sporangia* bulging dorsally,

with a purple spot over centre and crowned with 2—10 cilia, in groups of 2 or 3, each containing 190—230 spores. *Spores* 100—120 μm in diameter, triangular-globular, polar, very dark brown to black, opaque; wingless, pores at marginal angles, margin finely crenulate; ornamentation reticulate and similar on 2 spore faces, areolae extending to margin: distal face convex, (10—) 12—14 rounded areolae across diameter, 7,5—10,0 μm wide, areolar 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, about 30 areolae 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 4A, B.

In the FSA area, *R. trichocarpa* has been found throughout the semi-arid savanna/grassland biome of Namibia, but rarely in Botswana, northern and western Transvaal, Orange Free State, Lesotho, northern and eastern Cape. It grows on shallow, sandy soil overlying quartzite or dolomite outcrops or on calcareous crust. Map 1.

The species is widespread and subcosmopolitan; it is also known from countries bordering the Mediterranean, Macaronesia, North and East Africa, Madagascar and North America. The Australian species, *R. crinita* Tayl., may yet prove to be conspecific (Jovet-Ast 1986). Map 44.

Riccia trichocarpa is recognized by the conspicuous, long, smooth marginal cilia, purple flanks and dark brown to black spores, with densely granulate areolar walls.

Jovet-Ast (1986) distinguishes between cilia and hairs ('poils'), the latter being thin-walled and stouter. *R. canescens* Steph. was placed in synonymy under *R. trichocarpa* (Jovet-Ast 1983), as the thalli are indistinguishable from each other, yet there appear to be other small differences. The spores of some specimens from Namibia (e.g. *Toelken* 5561), have a definite wing, up to 5 μm wide, and the triradiate mark is more distinct and usually free of papillae. At 82—95 μm, the spore diameter is also slightly smaller. In specimens from Uganda and Kenya, *Jones* (1957) reported a well-defined triradiate mark, but he found the areolae on the inner faces to be indistinct. Volk (1984) reported *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 indicate a wide tolerance.

Riccia trichocarpa occasionally forms bulbils, which enable the plants to survive adverse conditions.

Vouchers: *Duthie* 5494 (BOL); *S.M. Perold* 748 (PRE); *Toelken* 5561 (PRE); *Volk* 81/293 p.p. (M; PRE).

2. **Riccia crozalsii** *Levier* in Revue Bryologique & Lichénologique 29: 73 (1902); Macvicar: 16 (1926); Müller: 447 (1952); S. Arnell: 284 (1956); S. Arnell: 17 (1963a); Campbell: 223 (1977); Na-Thalang: 80 (1980); Jovet-Ast: 337 (1986). 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, The Bryophyta of South Africa: 11 (1926). Type: Cape, Stellenbosch flats, *Garside* 8 (PRE-CH 1065) (PRE, lecto.!, selected here).

Thallus smallish to medium-sized, in incomplete rosettes 15—20 mm across, or scattered; pale green or glaucous green, sometimes with violet blotches along ciliated margins and over sporangia; when dry, margins apically inflexed, covering dorsal face, which is otherwise exposed. *Branches* 1—3 times furcate, deeply divided, narrowly to moderately divergent, sometimes overlapping; linear or linear-obovate, 3,0—6,0 mm long, 0,6—1,1 mm wide, 0,4—0,6 mm thick and in section 1,5 times to twice wider than thick; apex obtuse to rounded, shortly emarginate. Groove narrow and deep apically, soon becoming wider and flattening out. Thallus margins raised and tumid, with 1 or 2 rows of cilia. Flanks steep to sloping obliquely outwards 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 margins of thallus, numerous toward apex of thallus, sparse or absent proximally. *Scales* small and insignificant, barely reaching thallus margins, present only toward apex, hyaline or violet, not imbricate, cells oblong-hexagonal.

Dorsal epithelium unistratose, cells globose, 37—45 x 30—50 μm, hyaline, fragile, soon collapsing; air pores small, triangular or 4-sided. *Assimilation tissue* 500 μm thick, 1/2 the thickness of thallus, consisting of vertical columns of 5 or 6(7) rectangular cells, 32—50 x 30—37 μm, enclosing narrow air canals; storage tissue occupying ventral 1/2 of thallus, cells somewhat loosely arranged, rounded, 40—50 μm wide. Fig. 2A—G.

Monoicous. Antheridia with hyaline necks, at intervals along distal part of groove. Archegonia with conspicuous purple necks, along more proximal part of branches. *Sporangia* single or several in a row, bulging dorsally, sometimes blotched with violet, never crowned with cilia, each containing 150—210 spores. *Spores* 85—110 μm in diameter, triangular-globular, polar, dark brown to black, opaque at maturity; wing prominent, about 7,5 μm wide, margin entire, nearly smooth to granulate, wider and thicker at marginal angles, with round pore; ornamentation reticulate and similar on both spore faces: distal face convex, with 8—10 deep,

rounded or angular areolae across diameter, up to 10 μm wide, areolar walls thickened, papillate with papillae sometimes spreading to inside of areolae, 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 areolae, 3,5 μm wide, walls raised, especially at nodes. *Chromosome number*: n = 8 (Na-Thalang 1980; Jovet-Ast 1986). Plate 4C, D.

In the Flora area, the distribution of *R. crozalzii* is confined to the winter rainfall, fynbos biome of the southwestern Cape, where it grows on sandy, damp soil overlying granitic rock outcrops or on mud at streambanks. Map 2. *Riccia crozalsii* is also known from England and Europe, especially those countries surrounding the Mediterranean, as well as from Macaronesia, North Africa, at high altitude in Tanzania, southern India, Australia and New Zealand. Map 45.

Riccia crozalsii can be recognized by its long, pointed, faintly granular cilia along the thallus margins, absent, however, 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 areolae 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.

Arnell (1963a) referred to *R. crozalsii* var. *austroafricana* mihi as probably only a local modification without taxonomic value, but he did not elaborate, apart from stating that sometimes the cilia were few or lacking. Previously, he (Arnell 1953) had, however, identified these specimens as *R. ciliata* Hoffm. var. *austroafricana* mihi, stating that they differed but little from the European species, although the branches of the thalli were mostly longer.

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. Arnell* PRE-CH 4127 (PRE); *Duthie* 5018 (BOL); *S.M. Perold* 473 (PRE); *C.M. van Wyk* 1492 (PRE).

3. **Riccia microciliata** *Volk & Perold* in Bothalia 16: 173 (1986c). 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.!).

Thallus small, in complete or incomplete rosettes, up to 10 mm across; glaucous green, margins and dark purple flanks densely ciliated; 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, 1,0—3,0 (—4,0) mm long, 0,6—0,8 mm wide, 0,5 mm thick and in section as wide as thick to 1,5 times wider than thick; apex obtuse, shortly emarginate. Groove apically 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 striated, usually one of margins more deeply inflexed, appearing thicker. *Scales* small, not quite reaching thallus margins, purple or partly hyaline, cells oblong, 4- or 5(-6)-sided, 60 x 25 μm. Plate 1A.

Dorsal epithelium unistratose, cells globose to nearly conical, hyaline, 30—40 x 20—30 μm, occasionally some larger; air pores small, 3- or 4-sided. *Assimilation tissue* 250 μm thick, almost 1/2 the thickness of thallus, in vertical columns of 6 or 7(8) isodiametric cells, 25—30 x 25 μm, enclosing narrow 3- or 4(5)-sided air canals; storage tissue occupying ventral 1/2 of thallus, cells irregularly arranged, round or angular, up to 30 μm wide. Fig. 3A—F.

Dioicous. Antheridia with prominent hyaline necks, about 125 μm long, scattered along groove in male thalli. Archegonia with purple necks, crowned by several cilia. *Sporangia* up to 3 per lobe, each with 100—170 spores, overlying dorsal tissue bulging and turning purple, with 1 or 2 cilia, but sometimes none remaining. *Spores* 80—92 μm in diameter, 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 areolae across diameter, 7,5 μm wide, some adjacent areolae occasionally confluent, areolar 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 areolae, 5 μm wide. *Chromosome number*: n = 8 (Bornefeld 1984; 1989). Plate 4E, F.

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, central and

eastern Transvaal, but is rarely found in Swaziland, Natal, Namibia and Botswana. Map 3. Its range extends northwards into Mozambique, Malawi, Angola and Tanzania. Map 46.

Riccia microciliata is distinguished from the other southern African ciliated 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 areolar walls smooth, never granulate. Under adverse conditions, small perennating bulbils are formed from the apices of the thalli, thus enabling the plants to survive.

Vouchers: *S.M. Perold* 102, 1026 (PRE); *I.M. Retief* 252 (PRE); *Smook* 4267 (PRE); *Volk* 81/130 (M; PRE).

4. **Riccia natalensis** *Sim*, The Bryophyta of South Africa: 9 (1926); S. Arnell: 18 (1963a); Volk & Perold: 169 (1986c). Type: Natal, Scheepers' Nek, *Sim* 8228 (PRE, lecto.! selected here; BOL, isolecto.!).

Thallus 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 ciliated; 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, 5,0—10,0 (—12,0) mm long, 2,0—4,0 mm wide, 0,5—0,7 mm thick and in section 4—6 times wider than thick; apex rounded, shortly emarginate. Groove deep and narrow apically, shallow and wide proximally. Thallus margins raised, tumid, shortly winged in older parts, with numerous cilia. 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 x 160 μm, hyaline, cells isodiametric, thin-walled, not persistent.

Dorsal epithelium unistratose, cells globular or mammillate, 40—50 x 50—75 μm, hyaline, soon collapsing and cup-like; air pores triangular or 4-sided. *Assimilation tissue* 250—350 μm thick, almost 1/2 the thickness of thallus, in vertical or laterally sloping columns of 6—8(—10) cells, isodiametric or short-rectangular, 37—50 x 40—50 μm; air canals narrow, 4-sided, toward margins wider, 6-sided; storage tissue 1/2 the thickness of thallus, cells rounded, irregularly arranged, up to 50 μm wide. Fig. 4A—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, each containing 100—200 spores, bulging dorsally, overlying epithelium sometimes blotched with purple, without cilia. *Spores* 95—125 μm in diameter, 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 both spore faces: distal face convex to slightly flattened, 8 or 9 rounded or angular areolae across diameter, 10—15 μm wide, areolar walls low, smooth, projecting at nodes; proximal face with triradiate mark not clearly or only partly defined, 10—13 rounded areolae on each of 3 facets, up to 10 μm wide, sometimes adjacent ones only partly separated or confluent, areolar walls low, smooth, slightly raised at nodes. *Chromosome number*: n = 9 (Bornefeld 1984). Plate 5A, B.

Riccia natalensis is endemic to southern Africa and is infrequently collected on damp, loam-rich soil or black clay in the grassland biome of central and southeastern Transvaal, eastern Orange Free State and Natal. It has not been found in the more arid western parts of the country. Map 4.

The specimen, *Sim* 8228, is here designated as lectotype (not holotype as in Volk & Perold (1986)); 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 areolae and pale straw colour.

In his key, Arnell (1963a) did not place *R. natalensis* with the other ciliated species (Volk & Perold 1986), but with *R. albomarginata* Bisch. (28) and *R. concava* Bisch. (No. 36), where the dorsal epithelium consists of free, multi-celled 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. 34) could be taken for cilia and to Gottsche *et al.* (1846), who classified *R. albomarginata* (No. 28) in their section 'Ciliatae' (See notes under those species).

Vouchers: *Germishuizen* 2888 (PRE); *J.M. Perold* 30, 38 (PRE); *S.M. Perold* 103, 307 (PRE).

5. **Riccia mammifera** *Volk & Perold* in Bothalia 16: 176 (1986c). Type: Transvaal, Farm Klipfontein, Distr. 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-CH 4511 (PRE, para.!).

Thallus 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, (5,0—)7,0—10,0 μm long, 1,0—3,0 mm wide, 0,6—1,1 mm thick and in section 2—3 (—4) times wider than thick; apex broad, truncate or rounded, emarginate. Groove wide to nearly flat. Thallus margins tumid and raised, rounded to slightly attenuate, with projecting cells. Flanks sloping obliquely upward and outward, violet toward apex, otherwise green; ventral face rounded to flat, green. *'Cilia'* in the form of enlarged marginal cells, vertical or slanting, apices rounded to pointed, thin-walled, smooth, hyaline, up to 150 μm long and 60 μm wide at base, only conspicuous at apical margins, generally absent from proximal margins. *Scales* small and inconspicuous, not reaching margin of thallus, 315 x 225 μm, toward apex dark violet with hyaline margins, proximally entirely hyaline, cells 5-sided, 50 x 45 μm, smaller at margins, cell walls straight.

Dorsal epithelium unistratose, cells dome-shaped or mammillate, 30—50 x 50 μm, hyaline, fragile and soon collapsing; air pores 3— or 4(-)5-sided. *Assimilation tissue* 300—550 μm thick, 1/2 the thickness of thallus, in closely packed vertical columns of 8—10 isodiametric cells, 25—30 x 25 μm; air canals narrow, 4- or 5-sided; storage tissue occupying ventral 1/2 of thallus, cells variable in size, up to 60 μm wide. Fig. 4G—L.

Monoicous. Antheridia numerous, with necks projecting about 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, each containing 220—270 spores. *Spores* 80—115 μm in diameter, triangular-globular, polar, straw-coloured to brown, semitransparent; wing smooth, slightly sinuate, about 5 μm wide, broader at marginal angles, notched or with a pore; ornamentation reticulate and similar on both faces: distal face markedly convex, with 8—12, mostly hexagonal areolae across diameter, up to 10 μm wide, areolar walls thin, raised into stout, truncate tubercles at nodes; proximal face with triradiate mark inconspicuous to prominent, apex sometimes nodular, up to 25 rounded areolae on each of 3 facets, 5,0-7,5 μm wide, areolar walls low, only slightly raised at nodes, or forming irregular, vermiculate ridges and few discrete areolae. *Chromosome number*: n = 9 (Bornefeld 1984). Plate 5C, D.

To date, this endemic species, *R. mammifera*, is known from only two localities in the drier, savanna area of the northern and central Transvaal, where it grows on temporarily wet, clayey soil on the banks of small streams. Map 2.

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 'Ciliatae' 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 also present in *R. atromarginata*, but not previously seen in a southern African species.

Originally it was thought (Volk & Perold 1986) that the above collections could perhaps be specimens of *R. coronata*, of which the type and only specimen, *Sim* 8730, from Mooi River, 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. 32) (Volk & Perold 1985).

Voucher: *S.M. Perold 841* (PRE)

Group 'Squamatae'

Thallus margins smooth. *Scales* generally large.

6. **Riccia sorocarpa** *Bisch.* in Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum 17: 1053 (1835); Steph.: 335 (1898); Frye & Clark: 19 (1937); Müller: 457 (1952); S. Arnell: 285 (1956); S. Arnell: 20 (1963a) Campb.: 227 (1977); Na-Thalang: 95 (1980); Jovet-Ast: 315 (1986). Type: Schriesheim bei Heidelberg, *Bischoff* (HEID., holo., fide Jovet-Ast: 315 (1986)).

Thallus 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, 3,0—6,0 mm long, 1,1—1,5 (—1,8) mm wide, 0,5—0,6 mm thick and 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, hardly overlapping each other, rounded, fragile, hyaline, 425 x 250 μm, extending to thallus margins, cells in body of scale 4- or 5-sided, 50-75 x (25—) 37—45 μm, smaller, and wider than long at margin.

Dorsal epithelium bistratose, toward apex and groove cells of upper layer rounded to pyriform, 37—45 x 27 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) x 32 μm; marginal row of cells somewhat larger, hyaline, top cell rounded, intact, extending slightly above dorsal cells; air pores from above small, 4-sided. *Assimilation tissue* 150—200 μm thick, 1/3—2/5 the thickness of thallus, consisting of about 5 cells, 22—45 x 22—32 μm, in vertical columns and enclosing narrow air canals; storage tissue occupying ventral 3/5—2/3 the thickness of thallus, cells closely packed, round to oval, 50 μm in diameter. Fig. 5A—G.

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, each containing about 300 spores. *Spores* 80—100 μm in diameter, 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 areolae across diameter, areolae 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 areolae 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 areolae, occasionally some small, shallow depressions, densely granulose, sometimes granules joining to form short, low, irregular ridges. *Chromosome number*: n = 8 (Na-Thalang 1980; Jovet-Ast 1986). Plate 5E, F.

Riccia sorocarpa is cosmopolitan in distribution. Map 47. In southern Africa it has been infrequently collected on soil overlying weathered rock outcrops at seepages or on damp earth banks in the eastern Transvaal, Natal, Lesotho, northwestern and southwestern Cape, sometimes at high altitudes. Map 5.

The thickened dorsal cell walls provide the most useful diagnostic character for separating this species from the other southern African species of *Riccia* and it can always be recognized by this. The spores, ornamented with numerous granules on the proximal face and with larger central areolae and tall spinous processes at the nodes on the distal face, are also quite distinct and readily distinguished from those of other species.

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.

Vouchers: *S. Arnell* 303 (PRE); *Lambert* 2 (PRE); *Oliver* 8875 (PRE); *S.M. Perold* 307a, 1058a (PRE).

7. **Riccia atropurpurea** *Sim*, The Bryophyta of South Africa: 11 (1926); S. Arnell: 28 (1963a). Type: Natal, Edendale Falls, *Sim* 8112 (PRE-CH 1023) (PRE, lecto.!, selected here).

Thallus 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, 5,0—10,0 mm long, 0,8—1,5 (—2,0) mm wide, 0,5—0,8 mm thick and in section 1,5—2,0(—2,5) times wider than thick; apex somewhat wedge-shaped to more 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 upward and outward, 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, fragile, rounded, imbricate, up to 800 x 550—650 μm, projecting about 60 μm above thallus margins, with hyaline border of 5 or 6 cell rows above brown to deep violet-red base, cells in body of scale hexagonal to oblong-hexagonal, 45—70 x 40—50 μm, marginally smaller, short-rectangular.

Dorsal epithelium bistratose, hyaline, upper layer of cells globose, 22—25 (—35) x 25—37 μm, occasionally covered with fine deposit of salts, soon collapsing and cup-shaped, second layer of cells short-rectangular, 27—35 x 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, 1/2 the thickness of thallus, consisting of vertical columns of 5—8 short-rectangular cells, 30—50 x 25—30 μm, enclosing narrow 4-sided air canals; storage tissue occupying ventral 1/2 of thallus, cells rounded, irregularly arranged, about 50 μm wide. Fig. 6A—H.

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, each containing 100-200 spores, overlying dorsal tissue becoming white and disintegrating, often exposing a row of sporangia in longitudinal hollow. *Spores* 75-105 (—120) μm in diameter, subglobular but generally polar, wing and triradiate mark absent, periphery crenate or papillate, reddish when young, colour deepening to dull, dark brown, opaque; ornamentation reticulate and the same on both faces, with 10—12 (—14) areolae, 7,5—12,5 μm wide, across diameter on distal face, rounded or angular, areolar walls low, smooth, sometimes slightly sinuous, raised at nodes and projections more pronounced over centre; proximal face mostly with flattened contact marks left by sibling spores when still in tetrads, each facet with 25—30 areolae. *Chromosome numbers*: n = 8 (Bornefeld 1984); 16 (Bornefeld, 1989; the latter diploid karyotype is reported by Bornefeld to be eudiploid, i.e. doubling of each of the chromosomes in the basic set of 8 and regarded by him to be unique in *Riccia*).

In the Flora area, *R. atropurpurea* is common and frequently found in Namibia, Botswana, throughout Transvaal, in Swaziland, Natal, Transkei and Orange Free State on shallow, fine sandy or clayey soil overlying granite, quartzite or sandstone outcrops . It has not so far been collected in the Cape, except at Augrabies. Map 6. *Riccia atropurpurea* is also known from collections in Ghana, Nigeria, Angola, Uganda, Tanzania, Malawi and Zimbabwe. Map 48.

The specimen, *Sim* 8112 (PRE-CH 1023), is selected as lectotype 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, 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 they 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. *Riccia atropurpurea* is similar to the tropical African species, *R. lanceolata*, which also has hyaline thallus margins, but its spores are winged and with 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 patterns of spore ornamentation appear to be intermediate between the two species. Jones made the same observation in notes on *Gittins* 24 (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. 12), but this is hardly so, as the latter soon turns brown dorsally, is decidedly smaller and has shiny black scales; the spore ornamentation is also different.

Riccia atropurpurea sometimes forms small round perennating bulbils ventrally, thus enabling it to propagate vegetatively or to survive adverse conditions.

Vouchers: *Glen* 1377 (PRE); *Nicholas* 2159 (PRE); *S.M. Perold* 170, 206 (PRE); *Van Rooy* 1831 (PRE).

8. **Riccia okahandjana** *S. Arnell* in Mitteilungen der botanischen Staatssammlung München 16: 268 (1957); S. Arnell: 32 (1963a). Type: Namibia: Bez. Otjiwarongo: Okosongomingo, *Volk* 11944 (PRE-CH 4233) (PRE, lecto.!, selected here).

Thallus medium-sized, in crowded gregarious patches or in rosettes 15—30 mm across; green to bluish 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, 5,0—8,0 (—10,0) mm long, (1,2—) 1,5—1,8 mm wide, 0,8—1,0 mm thick and in section 1,5 times to twice wider than thick; apex rounded, shortly emarginate. Groove narrow and deep apically, 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, imbricate, 400—600 x 350—450 μm, projecting 100—250 μm above thallus margins, rounded to oblong, shiny black, often hyaline toward base and partly covering the next more apical scale, giving flanks a somewhat 'striped' appearance when dry, cells in body of scale oblong-hexagonal, 65 x 30 μm, walls mostly straight to slightly sinuous, margin crenate and cells smaller, 25—37 x 25 μm. Plate 1B.

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 x 20—25 μm, soon collapsing; second layer of cells also without chloroplasts, 32—45 x 32—50 μm; air pores mostly triangular, small. *Assimilation tissue* 350 μm thick, 1/3 to almost 1/2 the thickness of thallus, cells quadrangular to short-rectangular, 25—37 x 22—25 μm, in columns of 6 or 7(8), enclosing narrow, 4-sided air canals; storage tissue occupying ventral part of thallus, cells up to 50 μm wide, rounded, irregularly arranged. Fig. 7A—H.

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, each with about 150 spores, causing slight bulging of overlying dorsal tissue, which gradually disintegrates, leaving clean-edged, deep, round hollows filled with spores. *Spores* 92—110 (—120) μm in diameter, 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 areolae; 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 6C, D.

In the Flora area *R. okahandjana* is common and widespread, occurring in Namibia, Botswana, throughout Transvaal, Swaziland, Natal, Zululand, Transkei, Orange Free State, northern and eastern Cape on shallow soil overlying granite, quartzite, basalt or sandstone or on clayey soil. Map 7. *Riccia okahandjana* has also been found in Angola, Zimbabwe, Malawi, Tanzania and Uganda (leg. *Wood* 1190a Herb. Jones!). It was recently reported from the Arabian Peninsula (Frey & Kürschner 1988). Map 49.

Arnell (1957) cited 15 specimens collected by Volk, not indicating which particular one he regarded as the type. The specimen, *Volk* 11944 (PRE-CH 4233), is selected as lectotype, because it closely matches the protologue.

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. 9), *R. limbata* (no. 10) and *R. angolensis* (no. 11) and larger than those of *R. nigrella* (no. 12). Although some specimens of *R. limbata* are of a similar size, its distribution is confined to the southwestern, western and northwestern Cape and it frequently develops purple blotches dorsally, which are quite rare in *R. okahandjana*. Occasionally some specimens, notably *S.M. Perold* 739 and 2594, have scales with a wide hyaline border. On transverse 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-CH 4510 (PRE); *Leistner* 3560 (PRE); *S.M. Perold* 110 (PRE); *Smook* 4571 (PRE); *Volk* 987 (PRE).

9. **Riccia congoana** *Steph.* in Bulletin l'Herbier Boissier 6: 328 (1898); Jones: 226 (1957); Perold: 193 (1986b). Type: Fr. Equatorial Africa (=Congo), Forêt de Ceseles, *M. de F. Voz* s.n. (G, holo.!).

R. rhodesiae S. Arnell in Botaniska Notiser 105: 313 (1952); *S. Arnell*: 29 (1963a). Type: Zimbabwe (=S. Rhod.), Victoria Falls, on soil nr Trolley Junction, *S. Arnell* 1291 pp (S!; BOL!; PRE!).

R. nigrosquamata E.W. Jones in Transactions of the British Bryological Society 3: 222 (1957). Type: Tanzania (=Tanganyika), Lighthouse Island, Dar-es-Salaam Harbour, *Jones* 699 (BM, holo.; Herb. Jones, iso.!).

R. berriei E.W. Jones in Transactions of the British Bryological Society 3: 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. aegyptiaca S. Arnell in Botaniska Notiser 116: 9 (1963b). Type: Egypt (Egyptian-Sudanese border), Gebl. Elba Distr., Wadi Aideib, *M. Kassas* s.n. (S, holo.!; CAI, iso.).

R. limbatoides, nom. prov., O.H. Volk in Vegetatio 55: 58 (1984). Namibia (=South West Africa), Grootfontein, Farm Gaikos, *Volk* 00747 (M, PRE!).

Thallus 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, 6,0—12,0 (—15,0) mm long, (2,0—) 3,0—4,0 (—5,0) mm wide, (0,65—) 0,75—0,90 (—1,0) mm thick and in section 3—5 times wider than thick; apex rounded, obtuse, slightly emarginate. Groove apically narrow and deep with convex sides, proximally shallow to almost flat. Thallus margins acute, attenuate, overhanging. Flanks sloping obliquely upward and outward; ventral face green, slightly rounded to convex. *Scales* large, stiff, imbricate, crescent-shaped to rounded, borne mostly on ventral side of wings of thallus, 750—900 x 800 μm, projecting 200—250 μm beyond thallus margins, black or deep purple-red, shiny but sometimes duller, base often hyaline, cells in body of scale long-rectangular or 5- or 6-sided, 75—85 x

25—50 μm, smaller at crenate margins. Plate 1C.

Dorsal epithelium unistratose, cells globose or dome-shaped, 30—40 x 30—35 μm; hyaline, upper cross walls soon collapsing: air pores mostly 4-sided. *Assimilation tissue* 250—300 μm thick, nearly 1/2 the thickness of thallus, consisting of vertical columns of 6 or 7(8) cells, 45—55 x 35—45 μm, enclosing narrow air canals; storage tissue occupying ventral 1/2 of thallus, cells angular to round, variable in size, up to 60 μm wide. Fig. 8A—G.

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, each containing 250—300 spores, overlying tissue disintegrating and spores lying free in long, broad hollows. *Spores* 80—135 μm in diameter, subglobular, usually apolar, without wing and triradiate mark, yellowish brown to reddish brown, semitransparent; ornamentation regularly reticulate, with 6—8(—10) angular areolae across diameter, 10,0—15,0 (—17,5) μm wide, areolar 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 1986). Plate 6E, F.

In southern Africa, *R. congoana* occurs on sandy red soil, on black clay, on dolomitic or calcareous soil in Namibia, Botswana and in northern, eastern, western and southern Transvaal and in Swaziland. Map 8. In the rest of Africa, *R. congoana* is known from Sierra Leone, Nigeria, Angola, Zaire, Egypt, Sudan, Tanzania, Malawi, Zambia, Zimbabwe. It was also recently reported from Saudi Arabia (Frey & Kürschner 1988). Map 50.

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, generally crescent-shaped scales and by the subglobular, apolar spores with angular, thin-walled areolae. Few of the plants from the Flora area were, however, found to have sporangia.

The type specimen of *R. rhodesiae*, *S. Arnell* 1291, is a mixed collection, consisting mostly of *R. atropurpurea* Sim (no. 7), 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 *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*. His memory may have failed him, or else his own inaccuracies (Perold 1986b) could have misled him. *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 itself become a synonym, namely 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.

Vouchers: *Glen* 1423 (PRE); *Hardy* 6446 (PRE); *S.M. Perold* 130, 394 (PRE); *Volk* 00978 (M, PRE).

10. **Riccia limbata** *Bisch.* ex *Krauss* in Flora 29: 315 (1846); Gott. *et al.*: 606 (1846); Steph.: 326 (1898); Sim: 12 (1926); S. Arnell: 23 (1963a); Na-Thalang: 92 (1980). Type: Cape, CBS, in locis humidis ad latera Montium Tafelberg, Duyvelsberg et Leuvenberg, *Krauss* s.n., Julio 1838 (G(G13163), holo.!).

R. capensis Steph. in Denkschriften der Akademie der Wissenschaften, Wien 88: 724 (1913). Type: Cape, Gnadenthal bei Caledon, *Brunnthaler* s.n., Oct. 1909 (G(G13334), holo.! fide Grolle: 226 (1976); W (fide S. Arnell: 312 (1952), 'only sand in specimen packet').

Thallus 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, 10,0—12,0 (—15,0) mm long, 1,8—2,5 (—3,0) mm wide, 0,6—1,0 mm thick and in section 2,5—4 times wider than thick; apex somewhat wider, rounded, shortly emarginate. Groove narrow and deep toward apex, gradually flattening out over rest of thallus, disappearing altogether at base. Thallus margins acute, shortly attenuate. Flanks obliquely sloping upward and outward; ventral face gently rounded, green and streaked with purple or entirely purple. *Scales* large, 1 000—1 100 x 600—850 μm, oblong to rounded, appressed, stiff, projecting about 200 μm above thallus margins, imbricate, shiny, dark purple to black, toward basal margins hyaline to pale violet and fragile, cells in body of scale oblong-hexagonal, up to 87 x 30 μm, often with sinuate walls, cells in lighter coloured part short-hexagonal to rectangular, 20—45 x 15—25 μm, walls straight.

Dorsal epithelium bistratose apically and toward groove, hyaline, top layer of cells globose or mammillose, 35—40 x 25—30 μm, evanescent, subdorsal cells more or less barrel-shaped, 30—45 x

37 μm, ultimately forming the uppermost layer; air pores triangular, small. *Assimilation tissue* 250—400 μm thick, less than 1/2 the thickness of thallus, cells in vertical columns of 6 or 7(8), short rectangular, 37—55 x 35—40 μm, enclosing narrow 4- or 5-sided air canals; storage tissue occupying remainder of thickness of thallus, cells angular, closely packed, about 50 μm wide. Fig. 9A—H.

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, each with about 170 spores. *Spores* 90—125(—130) μm in diameter, 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 areolae 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, areolar walls faint, visible only with light microscope and not with SEM. *Chromosome number*: n = 8 (Bornefeld 1989); n = 16 (Na-Thalang 1980). Plate 7A, B.

In southern Africa *R. limbata* only occurs in the winter rainfall shrublands of the northwestern, western and southwestern 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 9. The species has recently also been reported from Australia by Na-Thalang (1980) (see Chapter 8).

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 most reliably, by its quite large spores, up to 130 μm in diameter, and ornamented on the nearly smooth proximal face by fovea and on the distal face, by spiralling ridges surrounding the central areolae. The spores illustrated on SEM micrographs by Na-Thalang (1980), appear to be more coarsely ornamented on the proximal face than most of the southern African ones. It is sometimes quite difficult to distinguish between sterile plants of *R. limbata* and *R. angolensis* (no. 11), 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 Transvaal and in South West Africa (Namibia); he was clearly referring to *R. okahandjana* (no. 8). Best's (1990) report of *R. limbata* from Zimbabwe (*Best* 2736) obviously falls into this category.

Vouchers: *S. Arnell* 597 (PRE); *Duthie* PRE-CH 1038 (PRE); *Garside* 6276 (PRE); *Oliver* 8858 (PRE); *S.M. Perold* 1427 (PRE).

11. **Riccia angolensis** *Steph.* in Bulletin l'Herbier Boissier 6: 323 (1898); S. Arnell: 24 (1963a). Type: Angola, Dist. Huilla, de Serra de Oiahoia prope Humpata, *Welwitsch* 255, Mais 1860 (BM, holo.!).

R. pseudolimbata S. Arnell in Mitteilungen der Botanischen Staatssammlung München 6: 270 (1957). Syntypes: South West Africa/Namibia, Bez. Marienthal, Haribes, feuchte schattige Uferböschung, *Volk* 12409 (M), 12412, 12413, 12462 p.p. (M, PRE).

Thallus medium-sized, in crowded, gregarious, occasionally overlying patches, or scattered; bright green to yellow-green, often with some purple colouration, 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 irregularly shaped, quickly narrowing toward base, 8,0—10,0 (—12,0) mm long, 2,0—3,0 (—4,0) mm wide, 0,5—0,75 (—1,0) mm thick, and in section 4(—5) times wider than thick; apex subacute to rounded, emarginate. Groove apically narrow and deep, proximally wider and shallower, dorsal face flat to slightly concave. Thallus margins acute to shortly attenuate. Flanks sloping obliquely upward and outward; ventrally slightly rounded to flattish, green, occasionally flecked with violet. *Scales* large, crescent-shaped to rounded, 600—850 x 375—550 μm, appressed, mostly borne ventrally, projecting about 200 μm beyond thallus margins, imbricate apically, more distantly spaced proximally, shiny, deep purple-red to black, base often partly or mostly hyaline more proximally, cells in body of scale oblong or oblong-hexagonal, 85—100 (—135) x 27—35 μm, walls sinuate, at margins cells small, 20—25 x 22—30 μm.

Dorsal epithelium bistratose when young, upper layer of cells hyaline, dome-shaped to globose, occasionally mammillose to broadly conical, 32—42 x 45—60 μm, soon collapsing, subdorsal cells isodiametric to wider than long, 37—50 x 55—67 μm, sides slightly bulging; air pores triangular, small. *Assimilation tissue* 250—350 μm thick in section, almost 1/2 the thickness of thallus, cells short-rectangular, 45 x 35—40 μm, in columns of 6 or 7(8) cells, enclosing narrow, 4-sided air canals; storage tissue occupying ventral 1/2 of thallus, cells

irregularly arranged, 50—75 μm wide. Fig. 10A—G.

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, each containing about 400 spores, dorsally bulging, overlying tissue gradually thinning and disintegrating, leaving spores exposed in shallow hollows. *Spores* 72—82 (—95) μm in diameter, 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, 10—12 irregularly shaped, deep-set areolae across diameter, usually arranged in more or less concentric rings, central areolae 7,5 μm wide, walls raised into tall projections at nodes, marginal areolae smaller and with lower projections; proximal face with triradiate mark distinct, sometimes interrupted, coarsely papillate, areolae irregular in shape and size, 2,5—7,5 μm wide, complete or incomplete, walls slightly raised at nodes, towards wing sometimes lightly sprinkled with papillae. *Chromosome number*: n = 8 (Bornefeld 1984). Plate 7C, D.

This species was originally reported from Angola. Map 51. In the Flora area it is relatively rarely collected in Namibia, Botswana, central Transvaal and in the Orange Free State and only once in Natal. It grows on clayey or on sandy, alluvial soil, having a clear preference for damp places such as seepages and riverbanks. Map 10.

Riccia angolensis differs from the other black-scaled species of *Riccia* from southern Africa, by its generally rather thin thallus 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. 10) (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 areolae 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: *Hansen* 3459 (PRE); *S.M. Perold* 1275 (PRE); *E. Retief* 1235 (PRE); *Smook* 5897 (PRE); *Volk* 5049 (M, PRE).

12. **Riccia nigrella** *DC* in Lam. & DC in Flore Française 6: 193 (1815); Lindenb.: 466 (1836); Nees: 390, 417 (1838); Gott. *et al.*: 605 (1846); Camus: 212 (1892); Steph.: 334 (1898); Howe: 28 (1899); Boulay: 210 (1904); Casares-Gil: 220 (1919); Frye & Clark: 21 (1937); Müller: 465 (1952); Na-Thalang: 93 (1980); Jovet-Ast: 323 (1986); Perold & Volk: 43 (1988b). Type: France, Dept. de l'Héraut, in Sylvula Grammont prope Monspessulanum, *Bouchet* 1807 (PC, holo., fide Jovet-Ast: 323 (1986); G(G23307), iso.!).

R. pearsoni(i) Steph. in Bulletin l'Herbier Boissier 6: 335 (1898). Type: North Wales, Barmouth, *Pearson* May 1885 (S!).

R. capensis auct. non Steph., S. Arnell in Botaniska Notiser 105: 312 (1952); S. Arnell: 28 (1963a). Types: Cape Province, Peninsula, Lion's Head above Fresnaye, *Arnell* 59 (S); Wynberg, cultivated ground, Park Hotel, *Arnell* 162 (BOL!).

Thallus 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 5,0 mm, rarely to 8,0 mm long, 0,5—1,0 mm wide, 0,5—0,6 mm thick and 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* semilunar, appressed, imbricate, 550 x 450 μm, not projecting above thallus margins, shiny violet-black, occasionally dark-coloured and hyaline cells alternating irregularly at mostly smooth margin, cells in body of scale rectangular or short hexagonal, about 52 x 25 μm, smaller at margin.

Dorsal epithelium unistratose, cells short-rectangular or subquadrate, upper surface nearly flat to slightly rounded, persistent, hyaline or mostly with metachromatic contents, 25—35 x 25—32 μm; air pores generally triangular, small, 7,5 μm wide. *Assimilation tissue* 250—325 μm thick, 1/2 the thickness of thallus, cells mostly isodiametric, 25—30 x 20—25 μm, 6—10 in compact vertical rows, rarely a few cells enlarged, up to 62 x 32 μm, with hyaline or brownish contents (idioblasts); air canals narrow, mostly 4-sided; storage tissue occupying ventral 1/2 of thallus, cells closely packed, angular, up to 30 μm wide, ventral epidermal cells often brown or violet. Fig. 11A—F.

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, each containing 160—230 spores, forming overlying clumps when capsules disintegrate. *Spores* 62—87 μm in diameter, 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 generally incompletely reticulate, somewhat dissimilar on the 2 faces: distal face with 10—12 incomplete, irregularly shaped areolae across diameter, or vermicular with thickened, short, sinuous ridges, often roughened with fine granules or papillae; proximal face with triradiate mark distinct, its arms generally wider at juncture with wing, about 30 small areolae on each of 3 facets, ridges thick, slightly raised at nodes. *Chromosome number*: n = 8 (Na-Thalang 1980; Bornefeld 1984; Jovet-Ast 1986). Plate 7E, F.

In the Flora area, *R. nigrella* occurs quite rarely in the summer rainfall parts of the central and southern Transvaal, Natal, Orange Free State and Lesotho, but it is fairly common in the winter rainfall areas of the southwestern and northwestern Cape Province, extending to the southern part of Namibia. It grows on shallow, sandy soil, overlying rock outcrops. Map 11. *Riccia nigrella* is nearly cosmopolitan in its distribution and is found in all countries bordering the Mediterranean as well as in Wales, Cornwall, the Channel Islands, the Macaronesian Islands, North America and in Australia. Map 52.

Riccia nigrella can be distinguished from the other southern African species with shiny black 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. It bears some resemblance to a small *R. macrocarpa* (no. 13) (see note under that species), which is also brown dorsally, and occasionally a few idioblasts are present in the inner tissues of *R. nigrella* as well. Its dorsal and ventral epithelial cells frequently contain hyaline or brownish metachromatic substances which stain blue with dilute aqueous solutions of Toluidine blue (Perold & Volk 1988). 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).

The species is able to survive and propagate vegetatively by forming small, round perennating bulbils.

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 transverse sections of the thalli of his collections at the Cape, seemed to him (incorrectly, as has lately transpired), to be similar to Stephani's figures of *R. capensis* in the latter's unpublished Icones Hepaticarum. 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, on transverse section, the rectangular to quadrate epithelial cells, indicate clearly that he was referring to *R. nigrella*. *R. capensis* Steph. has now been placed in synonymy under *R. limbata* Bisch. (Perold & Volk 1988b).

Vouchers: *Arnell* 150 (PRE);; *Duthie* 5340 (BOL); *Garside* 6650 (BOL); *S.M. Perold* 150 (PRE); *Smook* 4892a (PRE).

13. **Riccia macrocarpa** *Lev.* in Goiran, Bollettino della Società botanica italiana 5: 114 (1894); Steph.: 343 (1898); Müller: 442 (1952); Jovet-Ast: 318 (1986); Sèrgio: 223 (1991). Type: Italy, Toscane, Poggio Santo Romolo, leg. *Levier* s.n., 30 March 1888 (PC, syn.; S, isosyn.)

R. campbelliana Howe in Memoirs of the Torrey Botanical Club 7: 26 (1899); Frye & Clark: 20 (1937); Ladyzhenskaja: 316 (1967); Perold & Volk: 37 (1988a). Type: Calif., nr Stanford Univ., on hills above Mission Dolores, *D.H. Campbell* s.n. May 1, 1896 (NY, lecto.!, fide Grolle: 225 (1976)).

Thallus medium-sized, in crowded gregarious patches or 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 8,0 mm long, 1,0—1,5(—2,0) mm wide, 0,7—0,8 mm thick and in section nearly as wide as thick, to twice wider than thick; apex rounded and obtuse, emarginate. Groove deep, sides raised and convex, flatter proximally. Thallus margins acute, shortly winged, slightly undulating. Flanks sloping upward and outward, bronze-brown; ventral face rounded, green, occasionally flecked with red and brown. *Scales* fragile, inconspicous, imbricate, 750 x 450 μm, not projecting above thallus margins, cells hyaline at mostly smooth margin, rest of scale with groups of brown and different shades of violet cells, interspersed with single or groups of hyaline cells, 4 or 5(6)-sided in body of scale, about 65 x 40 μm, smaller at margin.

Dorsal epithelium unistratose, cells hyaline, subglobose when young, 30—45 x 35—50 μm, becoming flatter and wider laterally, brown and collapsed at margins and proximally; air pores triangular or rectangular, 7—12 μm wide. *Assimilation tissue* 325—400 μm thick, 1/2 the thickness of thallus, consisting of vertical columns of 6—10 cells, 50—60 x 35—50 μm, topmost cells soon losing their chloroplasts, some cells, (idioblasts), differ from the rest by their larger size and contents; air canals 4- or 5-sided, up to 20 μm wide; storage tissue occupying lower 1/2 of thallus, cells rounded or angular, tightly packed, up to 55 μm wide, usually with some scattered idioblasts. Fig. 11G—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, up to 500

μm wide, each containing about 200 spores, overlying, bulging tissue turning brown. *Spores* 85—110 (—120) μm in diameter, triangular-globular, polar, pale straw-coloured to brown, semitransparent; wing 5 μm wide, notched at marginal angles, margin mostly smooth; ornamentation on both faces vermicular to irregularly and incompletely reticulate: distal face with 10—15 incomplete areolae across diameter, 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 1988). Plate 8A, B.

New to southern Africa, *R. macrocarpa* is known from only a few localities in the grasslands of central Transvaal, eastern Orange Free State and northern Cape, where it is found on shallow soil overlying granite, quartzite or sandstone rock outcrops. Map 11. It has also been reported from southern Europe, Macaronesia, North Africa, Turkey, Israel, Western Siberia, North America and possibly South America. Map 53. There is, however, some doubt whether *Sleumer* 1755 (LIL 19853) from Argentina, has correctly been referred here (as *R. campbelliana*) (Perold & Volk 1988a). *R. campbelliana* was recently placed in synonymy with *R. macrocarpa* (Sèrgio 1991).

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 section 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 with sinuous, vermicular ridges on both faces is also a distinguishing character.

Although small plants of *R. macrocarpa* bear a superficial resemblance to *R. nigrella* (no. 12), they can still be readily identified by the usually wider and longer branches, by the thinner, slightly attenuate margins and by the epithelial cells that are not persistent. Sporangia are also rather rare, whereas *R. nigrella* frequently sporulates, producing masses of overlying spores.

Vouchers: *S.M. Perold* 888 (PRE); *S.M. Perold & Germishuizen* 1307 (PRE); *Van Rooy & S.M. Perold* 634, 637 (PRE).

14. **Riccia pottsiana** *Sim*, The Bryophyta of South Africa: 10 (1926); S. Arnell: 30 (1963a). Type: Orange Free State, Bloemfontein, near Eagle's Nest, *G. Potts* 7003, March 1917 (BOL, lecto.!, selected here).

Thallus 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) mm long, (0,7—)0,9—1,1 mm wide, 0,5—0,6 mm thick and in section almost as wide as thick to twice wider than thick; apex rounded, shortly emarginate. Groove apically narrow and 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, very regular, imbricate, rounded, about 500 x 250 μm, extending to margin of thallus or slightly above, dark purplish red, generally with entirely or partly hyaline/white borders, cells in body of scale oblong or oblong-hexagonal, 42—55 x 25—32 μm, walls bulging slightly, smaller at margins.

Dorsal epithelium unistratose, cells globose or mammillose, 37—45 x 30—40 μm, hyaline, intact near groove, collapsed toward margins; air pores small, mostly 4-sided, occasionally triangular. *Assimilation tissue* 300—450 μm thick, more than 1/2 the thickness of thallus, consisting of 8—10 short-rectangular to slightly bulging cells, 25—30 x 20—25 μm, in vertical columns and enclosing narrow air canals; storage tissue generally occupying less than 1/2 the thickness of thallus, cells rounded, closely arranged, up to 50 μm wide. Fig. 12A—H.

?Monoicous. Antheridia not seen. Archegonia with purple necks, along proximal part of groove. *Sporangia* bulging dorsally, containing about 320 spores each. *Spores* 60—78 μm in diameter, 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 two faces, reticulate: distal face convex, with 14—16 small, deep areolae across diameter, 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 areolae, 2,5 μm wide, walls lower and smoother than those on distal face. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 8C, D.

Riccia pottsiana is a rare, endemic species and only known from a few collections in the Orange Free State and central Cape. It grows on shallow soil overlying weathered sandstone outcrops. Map 13.

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 of the bottle-green to dark green thalli and the generally bicoloured scales. The spores of *R. pottsiana* are small with numerous, small, deep areolae, 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 reticulated. He named this species in honour of Prof. George Potts, for many years professor of Botany at the

University College of OFS, Bloemfontein (Gunn & Codd 1981).

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 is here selected from other original material in Sim's herbarium.

A rather puzzling observation by Sim, that this species is related to *R. concava*, concludes his description. *R. concava* (no. 34) 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, however, must have mistaken another species for *R. concava* (Perold 1989e).

Vouchers: *Duthie* 5450, 5452, 5463a (BOL); *S.M. Perold* 285 (PRE); *Smook* 6962b (PRE).

15. **Riccia runssorensis** *Steph.* in Bulletin l'Herbier Boissier 6: 330 (1898); S. Arnell: 271 (1957); S. Arnell: 32 (1963a). Type: Uganda, Mt. Ruwenzori, Kivani, leg. *Scott Elliott* 5,20 (G(G13176) holo., fide Na-Thalang: 86 (1980); BM!)

Thallus 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 more or less symmetrically furcate, closely to moderately divergent; ovate to oblong, narrow toward base, 7,0—9,0 mm long, segments 3,0—4,0 mm long, 1,2—1,6 mm wide, 0,7—0,9 mm thick and in section 1,5 times to nearly twice wider than thick; apex rounded, shortly emarginate. Groove narrow and deep apically, gradually becoming shallower and disappearing toward base. Thallus margins acute. Flanks sloping steeply upward and outward; ventral face rounded, green, often with faint, violet-red, transverse bands of vestigial scales. *Scales* rounded, imbricate, 500—800 x 350—550 μm, projecting less than 100 μm above thallus margins, shiny, very dark red to almost purple, 1 or 2 rows of cells at margin hyaline, cells in body of scale generally 5-sided, up to 80 x 30—50 μm, smaller at margin.

Dorsal epithelium unistratose, hyaline, cells mammillose to pyriform, 25—40 x 30 μm, soon collapsing toward margins and proximally; airpores generally triangular, occasionally 4-sided. *Assimilation tissue* 250—430 μm thick, less than 1/2 the thickness of thallus, consisting of vertical columns of 5—8 rectangular cells, 40—55 x 35—42 μm, enclosing narrow, mostly 4-sided air canals; storage tissue occupying ventral part of thallus, cells hexagonal or rounded, 35—55 μm wide. Fig. 13A—G.

Monoicous. Antheridia with hyaline necks, at intervals along groove. Archegonia numerous, in 1 or 2 rows, necks purple. *Sporangia* serially arranged along basal part of thallus, bulging dorsally, each containing about 130 spores. *Spores* 80—105 μm in diameter, subglobular to globular, apolar, ruby-red, colour deepening to almost black, opaque; wing and triradiate mark absent, periphery with prominent truncate projections, characteristically cogwheel-like in profile; ornamentation regularly reticulate, (6—) 8—10 rounded or angular areolae across diameter of spore, 10—12 μm wide, areolar 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 8E, F.

In southern Africa, this species is fairly rare but widespread and has been collected on damp, clayey soil at the edge of vleys, or on shallow soil overlying dolerite outcrops in Namibia, Botswana, northern, eastern and southern Transvaal, Orange Free State and the northern and central Cape. Map 14.

The type specimen of *R. runssorensis* is from the Ruwenzori Mountains in southwestern Uganda and it has also been collected in Angola. It is only briefly referred to by Jones (1957). Map 54.

Riccia runssorensis may be confused with *R. atropurpurea* (no. 7) which is similar in size, and is sometimes mixed with it. On growing actively, *R. runssorensis* is a bright, clear green, however, 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 areolar nodes, than any of the other species with apolar spores (see note under *R. rosea* (no. 16)). *R. rosea* is a more robust plant, and its reddish pink scales are larger and have a wider hyaline edge, which projects 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 has not been accepted here. *R. macrospora* is a larger plant, 7—12 mm long and 3—4 mm wide, with the thallus margins attenuate and the spores 120(—150) μm in diameter; the chromosome number n is reported to be 48.

Vouchers: *Glen* 1403 (PRE); *S.M. Perold* 219, 782 p.p., 785 (PRE); *Volk* 5374 (BOL).

16. **Riccia rosea** *Volk & Perold* in Bothalia 16: 181 (1986d). Type: Transvaal, Farm Valschspruit, 19 km N of Bronkhorstspruit, on hilltop, *S.M. Perold* 324 (PRE, holo.!); *Volk* 81/023 (M, PRE, para.!).

Thallus 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 12,0 mm long, 1,0—2,5 mm wide, 0,8—1,0 mm thick and in section as wide as thick, to 2,5 times wider than thick; apex rounded, shortly emarginate. Groove narrow and deep, becoming shallow proximally. Thallus margins acute. Flanks steep to ascending obliquely, reddish pink; ventrally rounded, green, often with narrow violet transverse bands. *Scales* wavy, closely imbricate, rounded, 800—900 x 500—750 μm, projecting about 175 μm above thallus margins, reddish or rose-pink, with hyaline margins one to several cell rows wide, cells 4- or 5(7)-sided, 65—100 x 40—50 μm, marginally smaller.

Dorsal epithelium in one or two layers, top cells 35 x 35—55 μm, soon collapsing, subdorsal cells becoming echlorophyllose; air pores mostly triangular. *Assimilation tissue* 375—450 μm thick, 1/2 the thickness of thallus, consisting of 7 or 8 short-rectangular cells, 60—70 x 40—50 μm, in vertical columns; air canals narrow, 3- or 4-sided; storage tissue occupying ventral 1/2 of thallus, cells rounded, 55—60 μm wide, irregularly arranged. Fig. 14A—G.

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, each containing about 200 spores, overlying dorsal surface bulging, soon disintegrating, seldom developing purple blotches. *Spores* 92—105 μm in diameter, subglobular to globular, apolar, without wing and triradiate mark, light brown to brown, semitransparent; ornamentation regularly reticulate with 9—11 well-defined, rounded or angular areolae across diameter, up to 10 μm wide, areolar walls up to 5 μm high, raised at nodes. *Chromosome number*: n = 8 (Bornefeld 1984). Plate 9A, B.

Probably endemic to southern Africa, *R. rosea* is found in Namibia, Botswana, northern, central, eastern and southern Transvaal, northern and central Orange Free State, on shallow sandy soil overlying granite, quartzite or sandstone outcrops or between rotting roots of grasses. Map 15. The range of *R. rosea* extends further northward into central Africa and it is known from Uganda, Tanzania, Zaire, Angola and Zambia. Map 55.

This species can be recognized by the near-white to pale green dorsal surface of the dry, and the older parts of the wet thallus, which seldom develop any purple colouration; by the large, wavy scales, hyaline at the apex, but soon developing pink to reddish bases, whereas the margins remain hyaline and by the prominent antheridial necks in male plants. In the specimens, *D. Fourie* 23c and 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 areolar nodes of *R. rosea* spores are intermediate in length between the very prominent truncate projections of *R. runssorensis* (no. 15) and the low tubercles of *R. atropurpurea* (no. 7). 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).

17. **Riccia albolimbata** *S. Arnell* in Mitteilungen der Botanischen Staatssammlung München 16: 264 (1957); S. Arnell: 25 (1963a); Perold: 17 (1989b). Type: South West Africa/Namibia, Farm Voigtland, bei Windhoek, gegen Ondekaremba, *Volk* 11419 (M, holo.; PRE, iso.!).

R. albosquamata S. Arnell in Mitteilungen der Botanischen Staatssammlung München 16: 266 (1957); S. Arnell: 25 (1963a). Type: South West Africa/Namibia, Damaraland: Neitsas, Grootfontein, am Rande einer Kalkpfanne, *Volk* 452 p.p. (M!).

Thallus 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 8,0 mm long, 1,5—2,2(—3,0) mm wide, 0,8—1,1 mm thick and in section 2—2,5 times wider than thick; apex rounded, emarginate. Groove narrow and deep apically, soon disappearing, proximally flat to somewhat concave. Thallus margins acute to subacute. Flanks generally sloping obliquely upward and outward, green or brownish to dark red; ventrally flat to slightly rounded, green. *Scales* large, undulating, imbricate, 800—900(—1200) x 600 μm, projecting about 150 μm above thallus margins, hyaline to white, base occasionally flecked with brown or dark red, cells in body of scale hexagonal or oblong-hexagonal, 55—100 x 35—55 μm, marginally smaller, surface often encrusted with calcium carbonate deposits. Plate 1D.

Dorsal epithelium unistratose, cells dome-shaped or globose, hyaline, mostly covered with a film of fine calcium carbonate granules, 42—48 x 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, almost 1/2 the thickness of thallus; cells in columns of 6—10, vertical or sloping somewhat laterally, short-rectangular, 50 x 40—45 μm; air canals 4—5 (—6)-sided; storage tissue occupying ventral 1/2 of thallus, cells angular, mostly 55 μm wide. Fig. 15A—H.

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, disintegrating soon and leaving several capsules exposed, each containing 300—450 spores. *Spores* 82—105 μm in diameter, triangular-globular, polar, yellow-brown to dark brown, semitransparent to opaque; wing narrow, 3,0—5,0 μm wide, with pore at marginal 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 areolae across diameter, 5,0—7,5 (—10,0) μm wide, areolar walls thick or thin, raised at nodes, often only central areolae 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 9C, D.

This species is probably endemic to southern Africa and widely distributed in Namibia, throughout Transvaal, Orange Free State, northeastern, northern and central Cape. It is quite rare in Natal. Map 16. It grows on calcrete, loam or shallow soil overlying rock outcrops. A few specimens have been collected in Kenya and Tanzania. Map 56.

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 *R. argenteolimbata* (no. 18), 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 that species). In Arnell's (1963a) key to the *Riccia* species, *R. albomarginata* (no. 28) has been listed twice on p. 14, at nos 7 and 11, whereas *R. albolimbata* has been left out. At 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).

18. **Riccia argenteolimbata** *Volk & Perold* in Volk *et al.* in Bothalia 18: 155 (1988). Type: South West Africa/Namibia, Marienhof (Dunroamin), *Volk* 00910 (M, holo.!); Hatsamas, *Volk* 00762 (M, para.).

Thallus 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, 2,0—7,0 mm long, 0,7—1,2(—2,0) mm wide, 0,6—0,9 mm thick and 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 face rounded, green, apically with arched, narrow brown bands across. *Scales* stiff, closely imbricate, 600—800 x 500 μm, projecting about 100 μm above thallus margins, white entirely or only marginally, base mostly silvery mauve, proximally dark grey-brown, cells in body of scale hexagonal or nearly isodiametric, appearing thick-walled, 50—90 x 25—30 μm, smaller at margin. Plate 1E.

Dorsal epithelium in regular, honeycomb pattern, bistratose, upper layer of cells intact only when young, globose, hyaline, 20—35 x 30—40 μm, capped with calcium deposits, soon collapsing; second layer of cells without chloroplasts, short rectangular, 25—37 x 22—32 μm, upper transverse and lateral walls thicker above, thinning out below; air pores mostly triangular, some quadrangular, small. *Assimilation tissue* 300—450 μm thick, 1/2 the thickness of thallus, compact cells rectangular, 40—50 x 32—37 μm, in columns of 8—10, enclosing very narrow, 4-sided air canals; storage tissue occupying ventral 1/2 of thallus, cells 45 μm wide, angular. Fig. 16A—F.

Dioicous. Antheridia in male thalli with short hyaline necks. Archegonia in female thalli with dark purple necks. *Sporangia* usually single, bulging slightly dorsally, each containing 200—450 spores, rarely sporulating. *Spores* 80—120(—130) μm in diameter, globular to subglobular, apolar, wing and triradiate mark absent, periphery tuberculate, reddish brown to almost black, semi-opaque to opaque; ornamentation reticulate with 12—15(—16)

round to angular areolae across diameter, 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 9E, F.

Riccia argenteolimbata is apparently endemic to southern Africa and in the Flora area, is found on fine greyish soil overlying calcrete, crystalline limestone or dolomite in Namibia, Botswana, northwestern and southwestern Transvaal, Orange Free State and the northern Cape Province. Map 17. It has also been collected in Tanzania and Kenya. Map 57.

This 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.

Specimens *Volk* 881 and 883, which Arnell (1957, 1963a) identified as *R. albosquamata*, contain thalli of *R. argenteolimbata* and *R. albolimbata* (no. 17). His description of *R. albosquamata*, however, as well as its type specimen, *Volk* 452 p.p., and most definitely the latter's winged and therefore, polar spores, do not correspond with those of *R. argenteolimbata*. Arnell appears to have been uncertain about the distinguishing characters of the two white-scaled species and misidentified them several times. *R. argenteolimbata* has therefore been described as a new species (Volk *et al.* 1988) and *R. albosquamata* is treated as a synonym of *R. albolimbata* (Perold 1989b). (See note under *R. albolimbata*).

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. 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. Several karyotypes are known for *R. argenteolimbata*.

Vouchers: *Henderson* 659 (PRE); *S.M. Perold* 737 (PRE); *E. Retief* 1493a (PRE); *Smook* 4487 (PRE); *Volk* 81/164 (M, PRE).

19. **Riccia albornata** *Volk & Perold* in Volk *et al.* in Bothalia 18: 160 (1988). Type: Cape, ca. 10 km westl. Kenhardt, an der Strasse nach Kakamas, *Volk* 81/081 (M, holo.!).

Thallus medium-sized to large, in crowded gregarious patches, not in rosettes; green, shiny, towards 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, 5,0—9,0(—12,0) mm long, 1,5—2,0(—4,0) mm wide, 1,0—1,5 mm thick and in section 1,5—2,5 or more times wider than thick; apex rounded, obtuse, emarginate. Groove deep apically, 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, frilly, imbricate, 1 250 x 750 μm, projecting up to 100 μm above thallus margin, apically hyaline, proximally white, lime-encrusted, sometimes bases reddish purple, cells in body of scale 4- or 5(6)-sided, 75—85(—100) x 35—50 μm, at margin smaller and brick-shaped.

Dorsal epithelium unistratose, cells globose or mammillate, surface occasionally dusted with fine calcium carbonate deposits, 30—40(—50) x 40—60 μm, hyaline, soon collapsing, a single cell often spanning two columns of assimilation cells beneath; air pores rectangular, toward margins wider and 5- or 6-sided. *Assimilation tissue* 1/2 the thickness of thallus, cells short-rectangular, 40—50 x 30—37 μm, in vertical columns of 6—8(—10); air canals up to 80 μm wide, mostly 6-sided; storage tissue occupying ventral 1/2 of thallus, cells mostly 50 μm wide. Fig. 16G—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 when ripe and leaving capsules exposed in hollow, each containing about 300 spores. *Spores* 85—115 μm in diameter, 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 areolae across diameter, 2,5 μm wide, areolar walls thick, raised into processes at nodes and frequently anastomosing to form short, convoluted ridges; proximal face with triradiate mark distinct, 30—40 small areolae on each of 3 facets. *Chromosome number*: n = 15 (Bornefeld in Volk *et al.* 1988). Plate 10A, B.

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, northwestern, central and southwestern Cape Province. Map 18.

Vegetatively *R. albornata* is not easily distinguished from *R. albolimbata* (no. 17), but it never grows in rosettes; the scales are generally larger and frillier, the dorsal epithelial cells somewhat larger and the wider air canals enclosed by six columns of cells. The spore ornamentation is markedly different with numerous small, irregular areolae 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 and central Cape.

Vouchers: *Duthie* 5149 (BOL); *Oliver* 1463 (PRE); *S.M. Perold* 1800 (PRE); *Smook* 6961 (PRE); *Volk* 84/667 (M, PRE).

20. **Riccia montana** *Perold* in Bothalia 19: 9 (1989a). Type: Cape, Witteberg Mountains, basalt cliffs at top of Jouberts Pass, 10 km E of Lady Grey, *Van Rooy* 2712 (PRE, holo.!).

Thallus medium-sized, gregarious, not in rosettes; light green to green, finely spongy and 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 8,0 mm long, 1,7—2,0(—2,5) mm wide, 0,6—0,75 mm thick and in section 2,5 to 3 times wider than thick; apex rounded to somewhat keeled, emarginate. Groove narrow and deep along most of length of dorsal face, proximally flat to slightly concave. Thallus margins acute. Flanks almost vertical distally to sloping obliquely outward and upward basally, green; ventrally rounded, green. *Scales* wavy at apex, soon appressed to flanks, imbricate, 850 x 500 μm, hardly projecting above thallus margins, hyaline or whitened with calcium deposits, sometimes flecked with red toward base, cells in body of scale 4- or 5(6)-sided, 50—85(—90) x 40—45 μm, smaller at margin. Plate 1F.

Dorsal epithelium unistratose, cells hyaline, globose, covered with fine film of calcium deposits, 20—30 x 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, 20—45 μm across, wider towards thallus margins, often only partly aligned with air canals below. *Assimilation tissue* 300—350 μm thick, 1/2 the thickness of thallus, consisting of vertical columns of 6—10 cells, 50—65 x (37—)42—50 μm; air canals 5- or 6-sided; storage tissue occupying lower 1/2 or more of thickness of thallus, cells angular, tightly packed, up to 50 μm wide. Fig. 17A—H.

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, each containing up to 450 spores, bulging conspicuously dorsally, overlying tissue not turning white, but shrinking and disintegrating. *Spores* 70—85 μm in diameter, 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 areolae across diameter, about 7,5 μm wide, areolar walls thick, 5 μm high, extending partly onto wing, with raised papillae at nodes; proximal face with triradiate mark distinct, to less clearly defined, areolae often incomplete, irregularly ridged, or with complete, angular areolae, raised at nodes. *Chromosome number*: n = 9 (Bornefeld pers. comm). Plate 10C, D.

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 Natal, where it is found on black, humus-rich soil, overlying basalt outcrops. Map 19.

This 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. 20) and *R. argenteolimbata* (no. 18) 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).

21. **Riccia alboporosa** *Perold* in Bothalia 19: 12 (1989a). 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.!).

Thallus medium-sized, gregarious or single, 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 7,0 mm long, 1,8—3,5(—4,0) mm wide, 0,8—1,2 mm thick and in section 2—3 times wider than thick; apex rounded, emarginate. Groove apically deep and wide, flattening out proximally. Thallus margins raised and blunt. Flanks sloping obliquely outward and upward, green; ventral face gently rounded, green. *Scales* mostly inconspicuous, appressed to flanks, imbricate, 550 x 350 μm, hardly extending to thallus margins, heavily encrusted with calcium salts, cells in body of scale mostly hexagonal, up to 85 x 37 μm, marginally smaller, brick-shaped.

Dorsal epithelium unistratose, cells hyaline, dome-shaped in and near dorsal groove, but soon collapsing and becoming heavily encrusted with

thick calcium deposits, wedge-shaped from above, 60—75 x 50 μm wide at broadest part, generally 5 or 6(—7) cells radially arranged around each air pore, part of which form the roof over wide air canals below; air pores 5- or 6(7)-sided, wide, regularly spaced. *Assimilation tissue* 400 μm thick, 1/2 the thickness of thallus, topmost cells generally somewhat thicker-walled, often 2 under each dorsal cell, soon losing their chloroplasts as overlying dorsal cells collapse, air canals 50—80 μm wide, enclosed by columns of 6—8 rectangular cells, 45—50 x 37—45 μm; storage tissue occupying lower 1/2 of thickness of thallus, cells 50—75 μm wide. Fig. 18A—G.

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, each containing 400—500 spores. *Spores* 75—88 μm in diameter, triangular-globular, polar, yellow-brown, semitransparent; wing 5 μm wide, slightly wider at perforated marginal angles, margin mostly smooth; ornamentation reticulate, but dissimilar on 2 faces: distal face with 11—13 areolae across diameter, 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 areolae, 3 μm wide, sometimes adjacent ones confluent, ridges low. *Chromosome number*: n = 10 (Bornefeld 1989). Plate 10E, F.

This species is endemic to, and only known from three localities in the arid shrublands of the northwestern Cape Province, where it grows on fine sandy or brackish soil overlying tillite rocks. Map 19.

Riccia alboporosa is easily recognized by the widely, but regularly spaced air pores, encircled by dorsal epithelial cells, the inner parts of which rapidly become white on drying. It differs from the other white-scaled species by the inconspicuousness of its scales which are heavily encrusted with calcium salts, by the puffy appearance of the dorsal surface in the dry plant and by the finely reticulated spores.

Vouchers: *Oliver* 8849 (PRE); *S.M. Perold* 1772, 1775 (PRE); *Magill* 3905 (F; PRE).

22. **Riccia bicolorata** *Perold* in Bothalia 20: 188 (1990b). Type: Cape, Victoria West, 48,6 km NE of, Farm Kalkfontein, common in damp areas around bushes, *Smook* 6990a (PRE, holo.!).

Thallus 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(—5,0) mm long, 1,0—1,3(—1,5) mm wide, 0,6—0,8 mm thick and in section 1,5 times to nearly twice wider than deep apically, soon becoming wide and shallow. Thallus margins subacute. Flanks steep to sloping slightly obliquely, green; ventral face rounded, green. *Scales* rounded, appressed to slightly wavy, imbricate, 500 x 300 μm, projecting about 100 μm beyond thallus margins, base deep purple and shiny, margins dull white, encrusted with calcium deposits, cells in body of scale short-hexagonal, up to 62 x 42 μm, marginal row smaller.

Dorsal epithelium unistratose, hyaline, cells globose to conical or mammillose, 25—55 x 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, 1/3—1/2 the thickness of thallus, consisting of vertical columns of 6—8(—10) cells, 45 x 42 μm, enclosing air canals which widen laterally; storage tissue occupying ventral 1/2—2/3 of thickness of thallus, cells about 55 μm wide. Fig. 19A—F.

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 serially arranged, bulging dorsally, containing 180—190 spores each. *Spores* 77—93 μm in diameter, triangular-globular, polar, light brown to brown, semitransparent, wing about 5 μm wide, thin, slightly undulating, notched or perforated at angles, margin smooth; ornamentation reticulate, rather different on the two spore faces: distal face with mostly 10 incomplete areolae across diameter, 5,0—7,5 μm wide, cross walls often undeveloped and radial walls thickened, fading out toward margin, papillae projecting from nodes, especially over centre; proximal face with triradiate mark rather poorly defined, dotted with granules, facets with incomplete areolae, walls sprinkled with granules and raised into papillae at the nodes. *Chromosome number*: n = 16 (Bornefeld pers. com.). Plate 11A, B.

Endemic to southern Africa, the species is so far only known from a few collections in the shrublands of the northwestern, central, southern and eastern Cape, where it is found on alkaline soil, sometimes in association with other *Riccia* species, such as *R. alboporosa* (no. 20), *R. albornata* (no. 19) and *R. pulveracea* (no. 38). Map 21.

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 border along the thallus margins. In young plants the primal branches are closely associated and 'butterfly'-shaped, often tearing apart along the middle, as growth continues. *Riccia bicolorata* is somewhat similar to *R. argenteolimbata* (no. 18), but the latter has a more compact thallus, triangular air pores and apolar spores. *R. pottsiana* (no. 14) also bears some similarity to *R. bicolorata*, bt 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).

2. Section Pilifer

Pilifer *Volk* in Mitteilungen der Botanischen Staatssammlung München 19: 455 (1983). Type species: *R. albomarginata* Bisch. ex Krauss.

Pteroriccia Schust. pro gen. in Phytologia 56: 72 (1984). Type species: *R. villosa* Steph.
Pteroriccia (Schust.) Schust. pro subgen. in Phytologia 57: 412 (1985). Type species: *R. villosa* Steph.
Micantes Volk & Perold pro sectione in Bothalia 16: 187 (1986). Type species: *R. hirsuta* Volk & Perold.

Thalli medium-sized to quite large; terricolous. *Scales* generally large, hyaline, sometimes base partly red or violet, lateral, very rarely ventral, 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.

23. **Riccia villosa** *Steph.* ex Brunnthaler in Denkschriften der Kaiserlichen Akademie der Wissenschaften 88: 724 (1913); S. Arnell 19: (1963a); Volk & Perold: 120 (1984). Type: Kapland, Karoo bei Matjiesfontein, auf sandigem Boden, *Brunnthaler* s.n., XI 1909 (G(G13342), holo.!),

Thallus 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 8,0 mm long, 1,8—2,5 mm wide, 1,5 mm thick and in section up to about 1,6 times wider than thick; apex slightly narrowed, rounded. Groove narrow at apex, 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, imbricate, triangular-acuminate, up to 1 800 μm from base to apex and 1 000 μm across base, projecting about 500 μm above thallus margins, hyaline, with deep purple base, margins denticulate apically, sometimes ending with a narrow caducous terminal cell; cells mostly oblong-hexagonal, larger toward base, up to 110 x 40 μm, walls straight. Plate 2A.

Dorsal epithelium consisting of free-standing tapering pillars, about 450 μm long, almost 1/3 the thickness of thallus, composed of 4 or 5(6) fragile, hyaline cells, 2—3 times longer than wide, 45—130 x 25—50 μm; air pores obscured by cell pillars, small, generally 4-sided. *Assimilation tissue* 250—400 μm thick, less than 1/3 the thickness of thallus, consisting of 6 or 7(8) cells, 37—50 x 25—45 μm, in vertical columns enclosing narrow air canals; storage tissue, occupying ventral 1/3 of thallus and consisting of polygonous cells, 40 μm in diameter, sometimes with numerous oil droplets. Fig. 20A—E.

?Dioicous. Antheridial necks not seen, hidden between dense dorsal cell pillars. Archegonia with purple necks, about 60 μm long. *Sporangia* single or 2 or 3 close together along median part of thallus, dorsally bulging and overlying tissue blotched with purple, each with about 350 spores. *Spores* 85—110(—115) μm in diameter, triangular-globular, polar, brown to very dark brown or black and opaque, wingless; ornamentation papillate or vermiculate; 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 similar sculpturing, but ridges not in obvious spirals, triradiate mark not prominent, each of its three arms terminating at a marginal pore. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 11C, D.

This 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 northwestern, southwestern and southern Cape. Map 21.

Riccia villosa is easily distinguished from other species in section *Pilifer* by its large, triangular scales with apically denticulate margins. *Riccia hirsuta* (no. 24) 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. 8) (see note under that species), but the latter's spores are light brown, its scales semilunar and black, and its dorsal epithelium not multicellular. Most plants of *R. villosa* are sterile; only four of the many that were examined had sporangia, propagation usually being by bulbils.

Schuster (1984) initially placed *R. villosa* in a new monotypic genus, *Pteroriccia*, but later (Schuster 1985) changed it to subgeneric rank to include all those species, where the dorsal cells are free-standing, multicellular uniseriate hairs and the assimilation tissue is compact, i.e. lacking large polyhedral air chambers. In this revision, Schuster's genus and subgenus, *Pteroriccia*, instituted for the reception of this species, have not been accepted (Perold 1986a), although, in the long term, it may be advisable to do so.

Vouchers: *Brusse* 5217 (PRE); *Compton* 5428 (BOL); *Germishuizen* 4783 (PRE); *Oliver* 8039 (PRE); *S.M. Perold* 504 (PRE).

24. **Riccia hirsuta** *Volk & Perold* in Bothalia 16: 187 (1986e); Volk & Perold: 23 (1990). Type: Cape, Kamiesberg plateau, north of Leliefontein, towards Draaiklip, on sandy, periodically moist soil, *Oliver* 8040 (PRE, holo.!).

Thallus medium-sized to large, scattered, not in rosettes; dorsally furry and shiny, green to greyish green over centre, whitish along margins; when dry, margins partly inflexed, dorsally concave, grey, matted. *Branches* simple or once or twice symmetrically furcate, medium divergent, oblong to obovate, up to 10,0 mm long, 2,0—4,0 mm wide, 1,5—2,0 mm thick and in section as wide as thick to twice wider than thick; apex truncate. Groove short, wide and shallow, obscured by thick pelt of hairs. Thallus margins subacute, shortly winged to overhanging. Flanks steep to sloping obliquely outward and upward, green, occasionally flecked with reddish purple; ventral face slightly rounded to flat, pale green. *Scales* triangular, large, up to 1 500 μm high and 650—1 200 μm wide at base, projecting above thallus margins, overlapping, hyaline, occasionally with reddish purple cells at base, basal cells small, larger in body of scale, oblong-hexagonal, 180 x 50 μm, outer marginal row narrow, long-rectangular, elongated, up to 250 μm long, apices split into several loose cellular strands, variously bending and twisting. Plate 2B.

Dorsal epithelium free-standing, very tall, tapering cell pillars, about 1 000 μm long, almost 1/2 the thickness of thallus, composed of (2—)4—7 thin-walled, hyaline cells, 4—5 times longer than wide, 150—375 x 42—70 μm; air pores 4-sided, closely spaced, obscured by tall, dense dorsal hairs. *Assimilation tissue* 300—400 μm thick, 1/6—1/5 the thickness of thallus, consisting of 5 or 6(7) cells, 40—62 x 35—50 μm, in vertical columns, enclosing 4—8-sided air canals, widening proximally; storage tissue occupying ventral 1/3 of thallus, cells 50—55 μm wide, angular. Fig. 21A—G.

?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, containing about 650 spores each. *Spores* 95—125(—130) μm in diameter, 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 two faces: distal face with 3—5(6) large central areolae across, 25—38 μm wide, mostly partly subdivided into smaller areolae 12 μm wide, often with a papilla in the middle, occasionally areolae 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 Volk & Perold 1986e).Plate 11E,F.

Riccia hirsuta is endemic to southern Africa and has to date only been found in a very restricted area in Namaqualand, north of Leliefontein. It grows on moist, sandy or clayey soil, overlying the edges of granitic rock outcrops near seepages. Map 22.

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, yet rather similar species, the other taxon being *R. tomentosa* (no. 48), which, however, has well-spaced, circumscribed air pores, tall, polygonal air chambers and papillose spores in permanent tetrads, but is also equipped with very tall, shiny, dorsal hairs 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 reassigned to section *Pilifer* Volk, with section *Micantes* Volk & Perold (where it had previously been classified), sunk under section *Pilifer*. *R. tomentosa* is placed in subgenus *Pannosae*.

Vouchers: *S.M. Perold* 2099—2101, 2182 (PRE).

25. **Riccia simii** *Perold* in Bothalia 20: 36 (1990a). Type: Cape, Perie 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); Volk: 453 (1983). Type: not designated.

Thallus 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, medium to widely divergent; oblong to obovate, up to 12,0 mm long, segments 4,0—5,0 mm long, 1,8—2,5 mm wide, 0,9—1,3(—1,5) mm thick and in section twice wider than thick; apex acute. Groove narrow and deep apically only, soon disappearing and dorsally flat. Thallus margins subacute. Flanks steep to proximally sloping obliquely upward and outward, green, sometimes flecked with violet; ventral face gently rounded to flat, green. *Scales* nearly semicircular, large, about 1 500 x 600—900 μm, projecting 200—500 μm above thallus margins, hyaline, closely imbricate, wavy, margins smooth, cells somewhat striate, in body of scale long-hexagonal or long-rectangular, 80—110(—125) x 30—35(—40) μm, at margins with generally 2 rows of smaller, brick-shaped cells.

Dorsal epithelium free-standing, 4- or 5-celled, gradually tapering, fine pillars, basally somewhat thicker-walled, hyaline, up to 250(—350) μm long, 1/4—1/3 the thickness of thallus, apical cells 25—50 x 18—20(—25) μm, often slightly bent, tips rounded, intermediate cells 45—75(—80) x 25—35 μm, basal cells 62—80 x 30—38 μm, mostly equally long; air pores small, 4(—8)-sided, obscured by tall cell pillars. *Assimilation tissue* about 350 μm thick, 1/3 the thickness of thallus, consisting of vertical columns of up to 8 cells, 40 x 25 μm, enclosing narrow 4- or 5-sided air canals; storage tissue, 1/3 the thickness of thallus, cells rounded to angular, closely packed, up to 50 μm wide. Fig. 22A—F.

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, each with about 370 spores. *Spores* 70—105(—120) μm in diameter, 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 areolae usually complete, occasionally all complete, variable in size, 5—10 μm wide, irregularly shaped, rounded or elongated, adjacent areolae 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 areolae, 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 12A, B.

The distribution of this endemic species, *R. simii*, ranges from the Orange Free State to Transkei, eastern, central, southern and southwestern Cape. It grows on shallow soil overlying dolerite or sandstone outcrops. Map 22.

Sim (1926) reported this species (as *R. albomarginata* (no. 28)) from Transvaal and Natal, but this has not been verified. Plants from Namibia that Arnell (1957, 1963a) identified as *R. albomarginata*, have been reassigned to another species, *R. albovestita* (no. 31) (see note under that species).

Riccia simii can be distinguished from other species in section *Pilifer* by the large, prominent, hyaline, wavy, closely imbricate scales, up to 1 500 μm long and projecting as much as 500 μm beyond the thallus margins. The dorsal face is velvety and covered with fine cellular hairs, which are usually relatively thick-walled at the base and less fragile than is usual for cell walls in this section; the basal cells are more or less 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. 28)).

Vouchers: *Duthie* 5115 (BOL); *S.M. Perold* 1304 (PRE); *Smook* 3908 (PRE); *Van Rooy* 1823 (PRE); *Volk* 81/289a (M, PRE).

26. **Riccia vitrea** *Perold* in Bothalia 20: 178 (1990c). 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.!).

Thallus medium-sized to rather large, in crowd

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 9,0 mm long, segments up to 4,0 mm long, 1,2—1,8(—2,3) mm wide, (0,9—)1,2—1,5 mm thick, in section as wide as thick, about 1,5 times wider than thick; apex acute, thick and fleshy. Groove from apex to about midway 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, imbricate, 1 250—1 750 x 600—850 μm, rounded, margins mostly smooth, projecting about 200 μm above thallus margins, hyaline to pale cream, base sometimes reddish purple, cells in body of scale oblong-hexagonal, up to 150 x 50 μm, walls straight to rather bulging, at margins cells smaller, wider than long, in 1—4 rows.

Dorsal epithelium free-standing, 4- or 5(6)-celled, fragile, hyaline pillars, uniformly wide to somewhat wider toward base, 320—450(—500) μm long, 1/3 the thickness of thallus, cells 2(—3) times longer than wide, top cell long-conical to bent, (60—)75—92 x 25—37 μm, lower cells 62—125(—150) x 25—55 μm; air pores 4- or 5(6)-sided, obscured. *Assimilation tissue* (350—)400—500 μm thick, about 1/3 the thickness of thallus, consisting of up to 10 cells, 32—45(—50) x 28—32 μm, in vertical columns, enclosing narrow air canals; storage tissue occupying ventral 1/3 of thallus, cells closely packed, up to 50 μm wide. Fig. 23A—F.

?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, containing about 550 spores each. *Spores* 72—100(—110) μm in diameter, 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 two spore faces: distal face with up to 16, rather irregular areolae across diameter, 5 μm wide, walls thin, granular, raised at nodes, but frequently thickened and linked up to form short radiating ridges, with areolae confluent, especially toward the centre; proximal face with triradiate mark well to poorly defined, areolae small, generally very incomplete, often only coarse granules or low papillae at the nodes, intervening walls absent or very low. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 11C, D.

This species is so far only known from a few localities in the dry shrublands of Namaqualand, where it grows on coarse-grained soil overlying granite rock outcrops. Map 23.

Riccia vitrea can be recognized by the large, billowing, hyaline to pale cream-coloured scales and by the tall dorsal cell pillars, similar to those in *R. villosa* (no. 23) and *R. simii* (no. 25) (=*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).

27. **Riccia namaquensis** *Perold* in Bothalia 20: 180 (1990f). Type: Cape, Carolusberg, Hester Malan Res., near old mine, flat granitic outcrop, at seepage (-CA), *S.M. Perold* 1420 (PRE, holo.!)

Thallus 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, up to 8,0 mm long, 1,8—2,3(—2,5) mm wide, 1,2—1,4(—1,6) mm thick, in section generally 1,5 times to twice wider than thick; apex rounded, emarginate, somewhat keeled below. Groove apically 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, 1 100—1 350 x 650 μm, wavy, closely imbricate, margins smooth, projecting 150—250 μm above thallus margins, hyaline, but appearing white, base sometimes with purple blotches, cells in body of scale about 65—112 x 50 μm, smaller at margins, 45 x 50 μm. Plate 2E.

Dorsal epithelium in free-standing, 3- or 4(5)-celled pillars, densely crowded, hyaline, 200—350(—400) μm long, up to 3/10 the thickness of thallus, cells longer than wide, top cell variable, often conical, 65 x 50—60 μm at base, rarely small and rounded, 30 x 25 μm, second cell 50—67 x 40—52(—60) μm, very occasionally also small and rounded, like some top cells, third and fourth (basal) cells up to 100 x 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, 3/10 the thickness of thallus, with vertical columns of 6—8(—10) cells, 37—52 x (30—)37—45 μm wide, separated by narrow air canals; storage tissue occupying ventral 2/5 of thallus, cells angular, closely packed, up to 60 μm wide. Fig. 24A—F.

?Monoicous. Antheridia in one or two rows along midline of thallus, necks hyaline. Archegonia scattered, necks purple. *Sporangia* mostly present toward base, dorsally bulging, with 600—700 spores each. *Spores* 65—78(—85) μm in diameter, 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 two faces: distal face with (12—)14—16 crowded areolae across diameter, up to 5 μm wide, some adjacent areolae toward the centre incompletely separated, walls irregular, raised papillae at nodes; proximal face with triradiate mark distinct, sprinkled with fine granules, each facet with about 50 small areolae, sometimes incomplete, walls low, often granulate. *Chromosome number*: n = 9 (Bornefeld pers. com.). Plate 12E, F.

This species is known only from the dry shrublands of the northwestern Cape, where it grows on shallow, coarse-grained to clayey soil, overlying granitic outcrops, and occasionally also at seepages. Map 24.

Riccia namaquensis has large, closely imbricate, hyaline scales, which appear white, as several layers are superimposed; the dorsal cell pillars at 250—400 μm long, are intermediate in length between the lower, bulging cells of both *R. furfuracea* (no. 37) and *R. concava* (no. 34) and the taller cells of *R. vitrea* (no. 26), 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. 28)) and *R. parvo-areolata* (no. 30). *Riccia namaquensis* can, however, be distinguished from both by generally 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).

28. **Riccia albomarginata** *Bisch. ex Krauss*, Flora 29: 135 (March 1846); Gott. *et al.*: 604 (Oct. 1846); Steph.: 329 (1898) based on Zeyher's specimen only; Perold: 31 (1990a). Type: In locis humidis circa urbem Capstad, *Krauss* s.n., p. p. 1838 (specimen in middle of herbarium sheet BM, lecto.!; W, isolecto.!).

Thallus 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, 5,0—7,0 mm long, terminal segments 1,0—3,0 mm long, 0,7—1,8 mm wide, 0,6—1,1 mm thick and in section as wide as thick to twice wider than thick; apex rounded, emarginate. Groove deep toward apex, 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* rounded, imbricate, fragile, 700—800 x 400 μm, projecting about 150 μm above thallus margins, hyaline, some basal cells occasionally with purple colouring, cells in body of scale hexagonal, 60—80(—100) x 40 μm, smaller at margin, cell walls straight, sometimes faintly yellow stained.

Dorsal epithelium free-standing, 3- or 4(5)-celled, fragile, hyaline pillars, 130—200(—230) μm long, 1/5 the thickness of thallus, cells longer than wide, top cell conical, or uniformly wide, sometimes bent, 45—65 x 20—30 μm, lower cells 42—60 x 32—37 μm, basal cells 25—37 x 30—40 μm; air pores small, 4- or 5-sided, obscured. *Assimilation tissue* 250—350 μm thick, 1/3 the thickness of thallus, consisting of 7 or 8 cells, 32—47 x 32 μm, in vertical columns enclosing narrow air canals; storage tissue occupying ventral 1/3 of thallus, cells rounded, mostly 37 μm wide. Fig. 25A—F.

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, containing about 300 spores each. *Spores* 75—95(—105) μm in diameter, triangular-globular, polar, brown to dark brown, semitransparent to opaque; wing 5—7 μm wide, wider at perforated marginal angles, margin more or less smooth to faintly crenulate; ornamentation reticulate, somewhat similar to dissimilar on the two faces: distal face with about 14 irregular areolae across diameter, 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 areolae on each facet, walls thick, convoluted,

raised at nodes, otherwise mostly smooth. *Chromosome number*: not known. Plate 13A, B.

The distribution of *R. albomarginata* appears to be confined to a few areas in the northwestern and southwestern Cape where it grows on coarse, gravelly soil, overlying granitic or sandstone outcrops. Map 25. 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. It clearly is a duplicate of one of the following collections held at PRE: *Sim* 9068, 9069, 9070, 9072, all of which I have 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 have 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 Vienna identifies Krauss as the collector, but Krauss (March 1846) described only one species, 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 (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. 31). The specimens previously assigned to *R. albomarginata* have now been referred to *R. simii* sp. nov. (no. 25) (Perold 1990a). This species is characterized by large, wavy, hyaline scales and is mostly found in the summer rainfall areas of the eastern Cape, Transkei and Orange Free State.

Vouchers: *S.M. Perold* 1930, 1979, 2118, 2382 (PRE).

29. **Riccia ampullacea** *Perold* in Bothalia 20: 168 (1990b). Type: Lesotho, Sani Pass, mountain slopes W of Border Post, on soil in small cave, *Van Rooy* 3573 (PRE, holo.!).

Thallus 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 8,0 mm long, 1,5—2,5 mm wide, 0,6—0,9(—1,1) mm thick and in section 2—2,5 times wider than thick; apex rounded, shortly emarginate. Groove present toward apex only, otherwise dorsal face concave. Thallus margins acute. Flanks sloping obliquely outward and upward, green; ventral face slightly rounded to flat, green. *Scales* large, rounded, imbricate, margins mostly smooth, hyaline, occasionally dark red toward base, 1 000—1 100 x 500 μm, projecting above thallus margins, cells in body of scale 5- or 6-sided, 100—125 x 45 μm, smaller and brick-shaped at margin.

Dorsal epithelium in free-standing 3- or 4-celled, fragile, hyaline pillars, 200—250 μm long, 1/4 the thickness of thallus, cells longer than wide, top cell conical, 45—67(—80) x 30—37 μm, lower cells often somewhat constricted in middle, 50—80(—110) x 35—52 μm; air pores small, about 25 μm wide, 4- or 5-sided. *Assimilation tissue* 300—400 μm thick, 1/3—1/2 the thickness of thallus, consisting of 7 or 8 cells, 37—42(—50) x 25—35 μm, in vertical columns, enclosing 4—6(—8)-sided air canals; storage tissue occupying ventral 1/3 of thallus, cells mostly 50 μm wide, round or angular. Fig. 26A—F.

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, containing about 480 spores. *Spores* 90—95(—105) μm in diameter, 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 areolae 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 areolae less than 5 μm wide, walls granulate, raised at nodes, sometimes anastomosing into short, semiradiating ridges. *Chromosome number*: n = 16 (Bornefeld 1989). Plate 13C, D.

Riccia ampullacea appears to be restricted to summer rainfall, alpine heath-grassland localities in the Drakensberg of the Orange Free State, Lesotho and Natal and the Witteberg of the eastern Cape Province, where it is infrequently collected in damp places on humus-rich soil overlying basalt outcrops. Map 26.

This species is rather similar to *R. parvo-areolata* (no. 30) as both have wide, concave thalli when dry, with large, hyaline scales and dorsal cell pillars consisting of three or four elongated cells. However, in *R. ampullacea* 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 spore ornamentation differs in generally having thick radiating ridges on the distal face and its distribution is also different.

Vouchers: *Van Rooy* 2724, 2971, 3045, 3240 (PRE).

30. **Riccia parvo-areolata** *Volk & Perold* in Bothalia 15: 117 (1984). Type: Cape, near Doringbaai, W of Vredendal, Kliphoek Farm, gravel on sandstone, *J.M. Perold* 23 (PRE, holo.!).

Thallus medium-sized, scattered or in loose patches, never in rosettes; not quite velvety, furry, tangled or matted proximally, slightly glistening, light green to glaucous green; 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, medium divergent, broadly oblong-obovate, up to 10,0 mm long, 2,5—4,0(—5,0) mm wide, 1,2 mm thick and in section 2—4 times wider than thick; apex slightly keeled to roundly truncate and shortly emarginate. Groove only apically present, soon flattening out, even becoming somewhat convex dorsally. Thallus margins subacute. Flanks sloping obliquely upward and outward distally, steeper proximally, green; ventral face slightly rounded, green, sometimes flecked with violet. *Scales* apically prominent, semicircular, imbricate, up to 1 200 x 600 μm, projecting slightly above thallus margins, hyaline, base flecked with mauve, margins mostly smooth, cells elongated, 5- or 6(7)-sided, straight-walled, mostly 110 x 50 μm, smaller at margin. Plate 2C.

Dorsal epithelium free-standing, uniseriate hairs, not tapering, about 200 μm long, 1/6 the thickness of thallus, consisting of 3 or 4 fragile, inflated, hyaline cells, slightly longer than wide, size variable, 25—75 x 25—65 μm, apical cell bluntly conical or mammillate 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, 1/2 the thickness of thallus, consisting of vertical columns of 8—12 cells, 37—50 x 45 μm, enclosing air canals, centrally narrow, 4-sided, laterally widening and 5- or 6-sided; storage tissue occupying ventral 1/3 of thallus, cells generally 55 μm wide, often with oil droplets. Fig. 27A—E.

?Dioicous. Antheridial necks not seen, obscured by dorsal cell pillars. Archegonia with purple necks, scattered along central part of thallus. *Sporangia* bulging dorsally, each containing 400—900 spores; when ripe, spores lying free in the decaying thallus. *Spores* 70—80(—90) μm in diameter, 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 areolae across diameter 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 three facets with 45—50 small, round areolae with granulate walls. *Chromosome number*: n = 8 (Bornefeld 1984; 1989). Plate 13E, F.

Riccia parvo-areolata is endemic to, and known from only a few collections in the southwestern Cape growing on damp, shallow, sandy loam. Map 27.

Riccia parvo-areolata can be distinguished from other species in section *Pilifer* mainly by the finely areolate and granular ornamentation of its spores and by the variously shaped, but generally conical or mammillate 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 pronouncedly concave, when it can easily be confused with *R. concava* (no. 34). However, *R. concava* is 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; most often living material is required, as the dorsal cell pillars 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 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).

31. **Riccia albovestita** *Volk* in Mitteilungen der Botanischen Staatssammlung München 17: 245 (1981). 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 Volk & Perold in Bothalia 15: 531 (1985). 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 Volk & Perold in Bothalia 16: 23 (1986b). 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.!).

Thallus medium-sized, scattered, in incomplete rosettes about 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 10,0 mm long, 1,5—2,3(—3,0) mm wide and 0,8—1,0 mm thick, in section twice wider than thick; apex slightly narrowed, subacute to rounded, emarginate. Groove deep and narrow apically 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 outward and upward, green, toward base occasionally flecked with dark red; ventral face almost flat to gently rounded, green. *Scales* semi-circular, large, 1 000—1 350(—1 500) x 500—750 μm, conspicuous at apex, more proximally appressed to flanks and hardly reaching thallus margins, imbricate, hyaline, base often wine-red to reddish purple, cells in body of scale oblong-hexagonal, 90—110 x 35—40 μm, smaller at margin and nearly isodiametric, 35 x 30—40 μm, occasionally a few conical cells projecting from margin of apical scales.

Dorsal epithelium free-standing, short, tapering pillars, 120—220 μm long, 1/6—1/5 the thickness of thallus, composed of 3 or 4 fragile, hyaline cells, top cell smallest, mostly longer than wide, 45 x 35 μm, conical, mammillate or occasionally globular, central and basal cells shorter than wide, 45—75 x 45—95 μm, lateral walls bulging; air pores 4-sided to polygonal, partly obscured by dorsal cells and by occasional globular, single-celled outgrowths at bases of pillars. *Assimilation tissue* 400—500 μm thick, 1/2 the thickness of thallus, consisting of cells up to 55 x 45 μm, in vertical columns of 8—10, enclosing 4—8-sided air canals which widen upwardly; storage tissue occupying ventral 1/3 of thallus, cells closely packed, rounded or hexagonal, 50 μm wide. Fig. 27F—K.

Dioicous. Antheridia along groove, necks colourless, about 500 μm long. Archegonia scattered along the centre, necks purple-brown. *Sporangia* bulging dorsally, containing 250—500 spores each. *Spores* 60—80(—90) μm in diameter, 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 two faces: distal face with 4—6(—7) large, complete or incomplete central areolae, 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 areolae, 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 14A, B.

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 and southern Transvaal, Orange Free State and northern, central, eastern and southwestern Cape. It is therefore far more widespread than Volk (1981) originally thought, and not confined to Namibia. Map 28.

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; sometimes the bases are a deep wine red. The short free-standing dorsal pillars are generally three- or four-celled and markedly tapering, with the basal cell the widest. The spores are mostly rather smallish, light brown and usually incompletely reticulate with larger, partly subdivided areolae 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. 28), presumably because of the loose dorsal cell pillars and the large hyaline scales. Arnell's (1963a) illustrations of the spores of *R. albomarginata* were drawn from one of these specimens (Volk 1981).

Two species subsequently described as new, *R. duthieae* (Volk & Perold 1985) and *R. sarcosa* (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).

32. **Riccia alatospora** *Volk & Perold* in Bothalia 15: 534 (1985). Type: Cape, Stellenbosch, Platklip, on moist sand in hollows on granite outcrop, June 1929 *Duthie* 5004 (BOL, holo.!); PRE-CH 1007 (PRE, iso.!).

Thallus 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 smallish pinkish red scales. *Branches* once or twice symmetrically furcate, terminal segments short, variously divergent; obcuneate to obovate, base narrow, 3,5(—5,0) mm long, 0,9—1,5(—2,0) mm wide, 0,6—1,2 mm thick, in section 1,5 times to twice wider than thick; apex obtuse, shortly

emarginate. Groove narrow and deep at apex, soon shallow and wide, dorsal face becoming flat to slightly convex. Thallus margins subacute. Flanks sloping obliquely outward and upward, steeper proximally, green; ventral face gently rounded to almost flat, green. *Scales* present at apex and distal flanks, absent proximally, mostly rounded, imbricate, 550 x 450 μm, hardly extending to thallus margins, pinkish red with hyaline more or less smooth margins, cells oblong-hexagonal or 5-sided, straight-walled, up to 80 x 25 μm, smaller at margin.

Dorsal epithelium in free-standing cell pillars, tapering, 120—160 μm long, 1/6—1/5 the thickness of thallus, consisting of 2 or 3 fragile, hyaline cells, longer than wide, 35—75 x 30—70 μm, apical cells conical, occasionally mammillate; air pores 4—6-sided, enlarging proximally. *Assimilation tissue* 300—600 μm thick, 1/2 the thickness of thallus, consisting of vertical columns of 7 or 8 cells, 30—45 x 37 μm, enclosing 4—6—8-sided air canals, up to 80 μm wide; storage tissue 1/3 the thickness of thallus, with rounded, irregularly arranged, thin-walled cells, 55 μm wide. Fig. 28A—F.

Dioicous. Antheridia scattered, necks colourless, up to 150 μm long. Archegonia along centre of thallus, necks purple. *Sporangia* dorsally bulging, containing about 150—200 spores each. *Spores* 90—110(—125) μm in diameter, 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 areolae up to 40 μm across with thick crenulate walls 12 μm high, partially or completely subdivided into smaller areolae by low ridges, all surrounded by an outer row of smaller areolae, walls raised at nodes; proximal face with triradiate mark distinct, its arms thin and high, each facet with about 30 smallish complete or incomplete areolae, up to 12,5 μm wide, walls raised into spinous thickenings at nodes. *Chromosome number*: n = 8 (Bornefeld). Plate 14C, D.

This endemic species is very rare and only known from two localities: one in the northwestern Cape and the other in the southwestern Cape, where it is found on damp sand or soil overlying granite. Map 29.

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. 33), 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 to enable one to recognize the particular species he was referring to. 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. 28), *R. concava* (no. 34) and *R. villosa* (no. 23), the other 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).

33. **Riccia hantamensis** *Perold* in Bothalia 19: 157 (1989c). 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.!).

Thallus 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 10,0 mm long, terminal segments generally short, 1,5—3,0 mm long, 2,5—3,8 mm wide, 0,7—1,2 mm thick and in section 3—3,5 times wider than thick; apex rounded to truncate, emarginate. Groove apically deep, soon flattening out and disappearing about 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* small, up to 800 x 250 μm, fragile, hyaline, ventrally situated, inconspicuous, partly overlapping to somewhat spaced, only present toward apex, cells mostly short- or long-hexagonal, up to 75 μm long, smaller at more or less smooth margin. Plate 2D.

Dorsal epithelium in free-standing cell pillars, tapering, 135—160 μm long, 1/7—1/5 the thickness of thallus, consisting of 3 or 4 fragile, thin-walled, hyaline cells, mostly shorter than wide, 40—58 x 48—80 μm, apical cells small, rounded to conical, basal cells wide and bulging at sides; air pores 3- or 4(5)-sided, wider proximally. *Assimilation tissue* about 350 μm thick, 1/2 the thickness of thallus, consisting of cells 50 x 35 μm, arranged in vertical

columns 8 cells high and 1 or 2 cells wide, enclosing 4—6—8-sided obliquely sloping air canals, up to 100 μm wide; storage tissue 1/6—1/4 the thickness of thallus, cells rounded, about 85 μm wide. Fig. 29A—G.

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, about 700 μm wide, containing 900—1200 spores each. *Spores* 60—80(—85) μm in diameter, 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 areolae, 15—20 μm wide, some with central boss and often partly subdivided, outer row(s) of areolae 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, areolae on each of 3 facets angular, 5—10 μm wide, walls raised at nodes, often irregular and incompletely separating areolae. *Chromosome number*: n = 9 (Bornefeld 1989, as *R. alatospora* var. *hantamensis*). Plate 14E, F.

This extremely rare and endemic species in section *Pilifer*, is so far only known from one locality (which is the type locality and its environs) in the northwestern Cape which has succulent Karoo vegetation. It grows on clayey soil on the bank of a small stream. Map 29.

Riccia hantamensis is closely related to, but distinguished from *R. alatospora* (no. 32) (see note under that species), on account of the much more robust size of the 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. 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).

34. **Riccia concava** *Bisch.* ex *Krauss*, Flora 29: 135 (March 1846); Gott. *et al.*: 604 (Oct. 1846); Steph.: 325, 378 (1898); Sim: 12 (1926); S. Arnell: 22 (1963a); Perold: 161 (1989d). Type: Cape, in locis humidis in kloof inter M. Tafelberg et Leuwenberg, *Krauss* s.n., Julio 1838 (G(G8979) holo.!), ex Herb. Musci. Palat. Vindob.; (S, iso.!) fide Grolle: 226 (1976).

Thallus 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, 6,0—10,0 mm long, 3,0—4,0 mm wide, 0,9—1,2 mm thick and in section 3—4 times wider than thick; apex rounded, emarginate. Groove narrow and deep apically, 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* semicircular, imbricate, 900—1 200 x 600 μm, not or hardly projecting beyond thallus margins except at apex, where they do, hyaline, cells elongated, 4- or 5(6)-sided, up to 160 x 50—65 μm, margins smooth, cells smaller and brick-shaped.

Dorsal epithelium free-standing, 3- or 4-celled, fragile, hyaline pillars, 180—260 μm long, 1/5 the thickness of thallus, cells generally shorter than wide, not tapered but apical cell smallest, globose or conical, frequently collapsed, 34—42 x 45—60 μm, second cell 50—62 x 85 μm wide, lateral walls bulging, basal cell rectangular, 50—75 x 68—75 μm; air pores small, 4- or 5-sided, obscured by bulging dorsal cells. *Assimilation tissue* 450 μm thick, 1/2 the thickness of thallus, consisting of vertical columns of 6—8 short-rectangular cells, up to 55 x 43 μm, enclosing narrow 4- or 5-sided air canals; storage tissue 1/4—1/3 the thickness of thallus, cells round or angular, up to 60 μm wide. Fig. 30A—H.

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, each with about 350 spores. *Spores* 75—100 μm in diameter, 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 areolae across diameter 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 areolae on each facet, walls raised at nodes. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 15A, B.

Although fairly common, the distribution of *R. concava* is restricted to the shrublands of the northwestern, western, southwestern and southern Cape Province. It grows on sandy, well-drained soil overlying granite. Map 30.

Arnell (1961, 1963a) reported *R. concava* from the Canary Islands; although his collections from there (*Arnell* UPS 20635—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 reporting it 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 apical 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. *R. concava* can be confused with *R. parvo-areolata* (no. 30), 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, nor did Krauss or Gottsche *et al.* for that matter. However, Bischoff, who named the plant, observed (in litt.) that the small scales of the dry plant, when superficially observed, could be taken for cilia. Possibly he 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).

35. **Riccia elongata** *Perold* in Bothalia 21: 167 (1990b). Type: Transvaal, 5 km NE of Kriel on road to Vandijksdrift, near disused bridge, on dry slope, *S.M. Perold* 2018 (PRE, holo.!)

Thallus 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 8,0 mm long, segments 1,0—4,0 mm long, 1,1—2,0 mm wide, 0,8—1,1(—1,2) mm thick and in section, as wide as thick to twice wider than thick; apex acute. Groove narrow and deep toward apex, soon becoming wide and shallow. Thallus margins subacute. Flanks steep to somewhat obliquely sloping upward and outward, green; ventral face rounded, green. *Scales* large, imbricate, rounded with mostly smooth margins, projecting about 200 μm above and beyond thallus margin, hyaline, base occasionally with some purple-red cells, 850—1 100 x 500—600 μm, cells in body of scale long-hexagonal or oblong-rectangular, 125—150 x 42—60 μm, smaller at margin.

Dorsal epithelium free-standing, 3- or 4-celled, fragile, hyaline pillars, up to 200 μm long, 1/5 the thickness of thallus, top cells smallest, globose, occasionally conical or mammillate (35—)40—50(—60) x 45—65 μm, other cells larger, with bulging lateral walls, 58—80(—100) x 40—75 μm; air pores small, generally 4-sided, occasionally triangular. *Assimilation tissue* 350 μm thick, 1/3 the thickness of thallus, about consisting of 6 cells, 35—47 x 37—40 μm, in vertical columns, and enclosing narrow, 4- or 6(7)-sided air canals; storage tissue occupying ventral 1/2 of thallus, cells tightly packed, angular, about 65 μm wide, containing starch granules. Fig. 31A—G.

?Monoicous. Antheridia not seen. Archegonia only seen in sections, immature. *Sporangia* bulging dorsally, singly along middle of proximal part of thallus, containing about 250 spores each. *Spores* 70—85(—90) μm in diameter, triangular-globular, polar, light brown, semitransparent; 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 areolae across diameter, 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 areolar walls, areolae 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 15C, D.

Riccia elongata is a rare, endemic species and has so far been found at only a few localities in eastern Transvaal where it grows on soil on gentle slopes or at rock outcrops near seepages. Map 31.

This 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. 25) 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. 34), *R. furfuracea* (no. 37) and *R. trachyglossum* (no. 36), but these species frequently develop purple colouration 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).

36. **Riccia trachyglossum** *Perold* in Bothalia 21: 172 (1990e). Type: Lesotho, Sani Top, mountain slopes west of Border Post, on soil bank of small pond in bog, *Van Rooy* 3539 (PRE, holo.!).

Thallus 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 5,0 mm long, 1,0—2,0 mm wide, 0,7—0,9 mm thick and in section 1,5 times to twice wider than thick; apex keeled. Groove apically present, its sides raised, tumid. Thallus margins subacute. Flanks rather steep to sloping obliquely, green; ventral face gently rounded to almost flat, green. *Scales* rounded, imbricate, projecting slightly above thallus margin, hyaline, 750 x 500—550 μm, cells in body of scale long-rectangular to short-hexagonal, 112—137(—187) x 42—65 μm, smaller toward base, at mostly smooth margin, brick-shaped to irregularly shaped.

Dorsal epithelium in free-standing, 2- or 3(4)-celled fragile, hyaline pillars, about 180 μm long, 1/5—1/4 the thickness of thallus, apical cell globose, rarely conical, 32—45 x 47—55 μm, lower cells with sides bulging 55—75(—100) x 47—65 μm; air pores 4-sided. *Assimilation tissue* 350 μm thick, 1/3—1/2 the thickness of thallus, consisting of 6 or 7 cells, 50—65 x 58—62 μm, in vertical columns, enclosing narrow, (3—)4(—5)-sided air canals; storage tissue occupying ventral 1/3—1/2 of thallus, cells 37—55 μm wide, angular, closely packed. Fig. 32A—F.

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, each containing about 580 spores. *Spores* 70—87(—92) μm in diameter, triangular-globular, polar, light brown, semitransparent; wing 5 μm wide, rather wider at perforated angles, margin finely crenulate; ornamentation reticulate, dissimilar on two faces: distal face with 8 angular or irregular areolae across diameter, 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 areolae, 3—5 μm wide, walls thin, irregular. *Chromosome numbers*: n = 16, 17 (Bornefeld pers. comm.). Plate 15E, F.

Riccia trachyglossum is so far only known from the alpine heath-grassland in Lesotho, at altitudes of about 2 500—3 000 m above sea level; it grows on soil banks in bogs. Map 33.

This species is distinguished from others in section *Pilifer*, which also have globose to bulging dorsal cells (e.g. *R. concava* (no. 34), *R. elongata* (no. 35) and *R. furfuracea* (no. 37)), by its somewhat smaller size, rather low hyaline scales, raised, tumid 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).

37. **Riccia furfuracea** *Perold* in Bothalia 21: 176 (1990c). Type: Cape, Klein Roggeveld, SW of De Kom, damp east slope with dense, short scrub, *Oliver* 8957a (PRE, holo.!)

Thallus 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 scurfy, yellowish green to glaucous-green 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 8,0 mm long, (1,1—)1,5—1,8(—2,0) mm wide, 0,9—1,2 mm thick and in section 1,5 times to twice wider than thick; apex bluntly wedge-shaped. Groove deep toward apex, sides convex, flattening out about 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* mostly semi-circular, large, 750—1 200 x 500—625 μm, conspicuous, projecting up to 125 μm above thallus margins, imbricate, hyaline, base often partly purple red, cells 50—85 x 37—42 μm, oblong-hexagonal in body of scale, one or two rows of smaller cells at more or less smooth margin.

Dorsal epithelium free-standing, thin-walled, hyaline, 2 or 3-celled, pillars 75—150(—180) μm long, 1/10—1/7 the thickness of thallus, not tapering, cells generally shorter than wide, topmost cell mammillate or round, rarely conical, 32—47 x 40—52 μm, basal cells 37—40(—50) x 50—62(—75) μm, cells frequently collapsed toward margins and proximally; air pores small, 3- or 4(occasionally 5)-sided. *Assimilation tissue* 350—450 μm thick, less than 1/2 the thickness of thallus, consisting of short-rectangular cells (37—)50—62 x 32—40(—45) μm, in vertical columns, enclosing narrow, mostly 4-sided air canals; storage tissue occupying ventral 1/2 of thallus, cells angular to rounded, up to 55 μm wide, with numerous starch granules. Fig. 33A—E.

?Monoicous. Antheridia with hyaline necks in a row along groove. Archegonia scattered, with purple-brown necks. *Sporangia* about 700 μm wide, bulging dorsally, single along middle of proximal part, containing 300—450 spores each. *Spores* 70—78(—88) μm in diameter, 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 two spore faces: distal face with (6—)7—9(—10) areolae across diameter, 7—8 μm wide, areolar 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, areolae generally poorly defined, incomplete, walls indistinct, low. *Chromosome number*: not known. Plate 16A, B.

Riccia furfuracea is a recently described endemic species. It is known from the shrublands of the northwestern and southwestern Cape and grows on shallow soil overlying granitic rock outcrops, at seepage areas or on stream banks. Map 32.

It can be distinguished from other species in section *Pilifer* by its very low dorsal cell pillars, composed of only two(or three), mostly wider than long cells. The top cell is often mammillate. From above it is not very obvious that the cells are in free-standing pillars, and 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 areolae on the proximal face.

Vouchers: *Oliver* 8910, 8921 (PRE); *S.M. Perold* 1476, 1515, 1854 (PRE).

38. **Riccia pulveracea** *Perold* in Bothalia 21: 185 (1990d). 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.).

Thallus 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 6,0 mm long, 1,1—1,3(—1,5) mm wide, 0,9 mm thick and in section slightly wider to 1,5 times wider than thick; apex rounded, slightly emarginate. Groove apically deep and sharp, soon shallow and wide. Thallus margins subacute. Flanks steep, green; ventral face rounded, green. *Scales* almost semilunar, wavy, imbricate, 750—925 x 400—600 μm, projecting 100—200 μm above thallus margins, conspicuous toward apex, hyaline, sometimes basal and scattered cells higher up reddish purple, cells in body of scale long-hexagonal, 50—65(—80) x 25—35 μm, smaller and brick-shaped at mostly smooth margin. Plate 2F.

Dorsal epithelium generally two-celled, low, free-standing, hyaline pillars 70—105 μm long, 1/10 the thickness of thallus, top cell globose to markedly mammillose, small, 35—55 x 37—42 μm, basal cell 35—47 x 37—52 μm, soon collapsing, appearing powdery; air pores mostly 4-sided, small. *Assimilation tissue* 300—400 μm thick, less than 1/2 the thickness of thallus, consisting of cells (25—)32—46 x 30—37 μm, in vertical columns of 8—10, and enclosing narrow, 4-sided air canals; storage tissue occupying ventral 1/2 of thallus, cells angular, 45—55 μm wide. Fig. 34A—F.

?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, about 470 spores present in each. *Spores* 75—92 μm in diameter, 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 smooth; ornamentation different on the 2 faces: distal face with 12—14 rather irregularly shaped areolae across diameter, 2,5—5,0(—7,5) μm wide, cross walls often incomplete and adjacent

areolae 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 areolae forming an open network, the walls low, granular to verruculose. *Chromosome number*: not known. Plate 16C, D.

Riccia pulveracea is endemic to southern Africa and is so far only known from the Orange Free State and central and eastern Cape Province, where it grows on alkaline soil in between karroid bushes. Map 33.

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. 34) by Duthie.*R. pulveracea* is a smaller plant, however, with shorter, more delicate dorsal pillars. The spore ornamentation is rather different as the proximal face has fewer areolae with thicker walls and it is quite coarsely granular; the distal face occasionally also has 3—5 short radiating ridges, but the areolae lack a central nodule, as is sometimes found in *R. concava* (no. 34).

Riccia furfuracea (no. 37), *R. elongata* (no. 35) and *R. trachyglossum* (no. 36) 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).

2. Subgenus **Ricciella**

Ricciella *(A. Braun) Reichenb.*, Der Deutsche Botaniker Herbarienbuch: 23 (1841), (fide Grolle: 426 (1983). Lectotype species: *R. fluitans* L.).

Spongodes (Nees) Volk, Mitteilungen der Botanischen Staatssammlung München 19: 456 (1983). Type species: not designated.

Thalli smallish to large; terricolous, rarely aquatic. *Scales* small, ventral, mostly evanescent.

Dorsal epidermis chlorophyllose; air pores scattered, soon enlarging, often becoming cavernous. *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.

1. Section **Spongodes**

Spongodes *Nees*, Naturgeschichte der Europäischen Lebermoose 4: 391 (1838). Lectotype species: *R. crystallina* L. emend. Raddi fide Grolle: 248 (1976).

Thalli medium-sized to large, rarely heterothallic with small male gametophytes; terricolous. *Scales* small, ventral, evanescent.

Dorsal epidermis chlorophyllose; air pores soon large, cavernous. *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'.

Group 'Crystallina'

Thalli mostly in rosettes or partial rosettes; becoming cavernous.

39. **Riccia crystallina** *L. emend. Raddi* in Opuscoli Scientifici di Bologna 2: 351, 353 (1818); Steph.: 369 (1898); Sim: 14 (1926); Jovet-Ast: 459 1964); Jovet-Ast: 82 (1966); Jovet-Ast: 340 (1986);

Na-Thalang : 107 (1980). Type: not designated.

R. plana Tayl. in Hooker, London Journal of Botany 5: 414 (1846); Steph.: 368 (1898); Duthie & Garside: 111 (1937); Hässel: 223 (1962); S. Arnell: 40 (1963a). Type: Australia, Swan River, *Drummond* s.n. 1843 (K, holo.; MEL, iso.).

Thallus 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 toward base becoming slightly spongy; when dry, bluish grey, finely spongy, margins raised, not inflexed. *Branches* 2 or 3 times dichotomously furcate, shortly to rather more deeply divided, often crowded and overlapping laterally to moderately divergent; obcuneate, 5,0—7,0 mm long, (2,0—)3,0—4,0 mm wide, 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 at apex, shallow. Thallus margins rounded, obtuse. Flanks sloping obliquely, green; ventral face gently rounded to flat, green. *Scales* hyaline, minute, difficult to detect, ventrally present near apex only.

Dorsal epidermis with component cells almost globular, shiny, single or tiered in pairs, laterally rather loosely connected, 50—60 μm wide; walls of air chambers not visible from above, air pores apically small and obscured, but soon widening as air chambers enlarge, eventually leaving them more exposed. *Assimilation tissue* 400—600 μm thick, 2/3—3/4 the thickness of thallus, air chambers apically narrow, slit-like, toward base wide, polygonal, bounded by one-layered plates of chlorophyllose cells; storage tissue 1/4—1/3 the thickness of thallus, cells 50—60 μm wide, in about 4 layers. Fig. 35A—F.

Monoicous. Antheridia in two lateral rows along dorsal face of lobes, necks colourless, up to 200 μm long. Archegonia along middle of lobes, necks purple-brown, up to 250 μm long. *Sporangia* abundant, bulging slightly ventrally, crowded, 600—800 μm wide, containing about 400 spores each. *Spores* 65—80(—85) μm in diameter, triangular-globular, polar, pale yellow to light brown, semi-transparent, polar; 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 both spore faces: distal face highly convex, occasionally slightly indented over centre, with 8—10 usually complete, round or oval areolae across diameter of spore, 7,5—10,0 μm wide, areolar walls thin and low, raised at nodes into spinous or truncate processes, up to 7,5 μm high, the tips often bifid or even trifid; proximal face with triradiate mark distinct, its arms up to 5,0 μm high, but often interrupted for short sections, dotted with granules, each facet with about 20 rounded or angular areolae, 5,0—7,5 μm wide, walls thin and low, raised at nodes into spinous processes, granular or divided at the tips. *Chromosome number*: n = 8 (Mehra 1977; Jovet-Ast 1986; Bornefeld 1989). Plate 16E, F.

Although Micheli (1729) had clearly distinguished between two species, Linnaeus (1753) united into one species '*Riccia minima et minor*' and named the combination *R. crystallina*. There is no type specimen in the Linnean herbarium in London, but a Dillenian element, presumably seen by Linnaeus, has been shown to be *R. cavernosa* (Koponen *et al.* 1977). Micheli's specimens have not been traced at FI. Raddi (1818) published a highly acceptable emendation of the two species and cited Micheli's drawings, Tab. 57, Figs. 3 and 7, but they are rather poor, and it has not yet been decided whether or not to select one of Raddi's own collections from Pisa, as a neotype of *R. crystallina*.

Riccia crystallina is a subcosmopolitan species. Map 58. It is widely distributed in southern Africa, but has been fairly rarely collected, except in the south-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 34.

This species can be distinguished from *R. cavernosa* (no. 40) by the finer, compact texture of the thallus, its crystalline appearance and glaucous-green colour. Its spores are highly ornamented, somewhat 'prickly' in appearance, and have eroded wing margins; they are easily identified and should not be mistaken for those of other species. It is, however, uncertain exactly what species Sim (1926) had in mind; Duthie & Garside (1936) remarked that his 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. The caption, however, states 'four spores before separation', which could possibly imply that they separated later, although the description refers to 'the spores mostly remaining three to four together'. No collectors are cited, but *Garside* 6 (PRE-CH1064 (PRE)), a bequest from Sim's herbarium, and numbered 8337 by him, was identified as *R. crystallina*, although the spores remain permanently in tetrads, thus certainly placing it in *R. curtisii*! Duthie's enclosed note reads: 'Possibly a mixture of *R. crystallina*? and *R. curtisii*. The only spores seen adhered in tetrads and is characteristic of *R. curtisii*'. *R. 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. Arnell* 189 (BOL); *Duthie* 5006 (BOL); *Koekemoer* 103a (PRE); *Morley* 308 (PRE); *S.M. Perold* 455 (PRE).

40. **Riccia cavernosa** *Hoffm. emend Raddi* in Opuscoli Scientifici di Bologna 2: 353 (1818); Jovet-Ast: 459 (1964); Jovet-Ast: 82 (1966); Jovet-Ast: 342 (1986); Na-Thalang: 108 (1980); Vianna: 71 (1981). Type: Allemagne. In terra limosa, ad piscinas. (Herb. Hoffm., not at MW, fide Jovet-Ast: 342 (1986)).

R. cavernosa Hoffm. in Deutschlands Flora, Crypt. 2: 95 (1795).

Ricciella rautanenii Steph. in Bulletin l'Herbier Boissier 6: 378 (1898); Duthie & Garside: 20 (1939); S. Arnell: 40 (1963a). Type: Hereroland, Tsoachaub River, *Rautanen* (G).

Thallus 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 cavernous; when dry, margins not inflexed, yellowish, spongy. *Branches* repeatedly dichotomously furcate, shortly to deeply divided, nearly parallel or crowded and overlapping; oblong-obovate or obcuneate, (2,0—)4,0—8,0 mm long, 1,5—2,5(—4,0) mm wide, up to 1,0 mm thick and in section 1,5—2,5(—4) times wider than thick; apex obtusely rounded, shortly emarginate. Groove generally only apically present, shallow. Thallus margins rounded, obtuse. Flanks obliquely sloping, ventral face rounded, green. *Scales* absent or evanescent.

Dorsal epidermis gently domed over each air chamber, cells 4- or 5 (6)-sided, walls slightly bulging, up to 80 x 55 μm, radially arranged around rapidly enlarging air pores, soon becoming cavernous, some scattered conical cells projecting vertically, about 60 x 37 μm, generally somewhat obscuring young air pores. *Assimilation tissue* up to 800 μm thick, 4/5 the thickness of thallus, air chambers 65—150 μm wide, generally uniseriate, appearing multi-seriate because of obliquely sloping cavities, surrounded by unistratose plates of chlorophyllose cells 50—100 x 50—60 μm; storage tissue 1/4 the thickness of thallus, cells mostly in 5 rows, 50—95 μm wide, some with chloroplasts. Fig. 35G—M.

Monoicous. Antheridia 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, up to 1 000 μm wide, containing a variable number of spores, on average about 350, but sometimes less and occasionally twice as many. *Spores* 85—110(—115) μm in diameter, triangular-globular, polar, reddish brown or almost black, semitransparent to opaque; wing 5 μm wide, somewhat broader at marginal angles, sometimes notched or with pore 5 μm wide, margin finely crenulate or serrulate, occasionally erose; ornamentation with irregular ridges, complete areolae 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 areolae, quite variable. *Chromosome number*: n = 8 (Na-Thalang 1980; Jovet-Ast 1986; Bornefeld 1989). Plate 17A, B.

Riccia cavernosa is a cosmopolitan species. Map 59. It is also widely distributed in southern Africa, where it is found on alluvial mud or on damp, sandy soil in Namibia, Botswana, northern, eastern, western and southern Transvaal, Natal, Orange Free State, northern, central, northwestern, southwestern, southern and eastern Cape Province. Map 35.

It 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; however, 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.

Vouchers: *Acocks* CH3602 (PRE); *Kock* 934 (PRE); *S.M. Perold* 363 (PRE); *Schelpe 3907* (PRE); *Volk* 81/228 (M, PRE).

41. **Riccia cupulifera** *A.V. Duthie* in Transactions of the Royal Society of South Africa 24: 116 (1937); S. Arnell: 39 (1963a). Type: Cape, Stellenbosch, *A.V. Duthie* 5007 (BOL, syn.!).

Plants heterothallic, 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; male plants much smaller, simple or furcate, somewhat lighter green to yellow-green; walls of inner polygonal air chambers clearly visible through dorsal epidermis, which soon becomes pitted and cavernous; when dry, greenish yellow and slightly wrinkled, spongy, margins not inflexed. *Branches* in female thalli, 2 or 3 times dichotomously furcate, shortly to deeply divided, almost overlapping or closely to moderately divergent; oblong to obcuneate, up to 7,0 mm long, 2,0—3,5 mm wide, 0,7—1,0(—1,5) mm thick, in section about 3 times wider than thick; apex rounded, truncate or emarginate. Groove apically short and shallow, otherwise flat. Thallus margins obtuse, rounded. Flanks slightly bulging to somewhat obliquely sloping, ventral face rounded to flat, green. *Scales* minute, ventral toward apex,

evanescent, rarely observed. Plate 3A.

Dorsal epidermis slightly domed over each air chamber, cells polygonal, variable in size, 60—130 x 50—75 μm, radially arranged around air pores, 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 marginal cells, becoming as wide as air chambers proximally. *Assimilation tissue* 500—800 μm thick, 2/3—4/5 the thickness of thallus, air chambers polyhedral, uniseriate, narrow in younger parts of thallus, wider proximally, separated by one-layered plates of chlorophyllose cells; storage tissue 1/3—1/5 the thickness of thallus, cells up to 50 μm wide, in 3 or 4(5) layers. Fig. 36A—F.

Dioicous. Antheridia very numerous, in a row along middle of mostly small male thalli, necks hyaline, about 200 μm long. Archegonia scattered along median area of female plants, necks purple. *Sporangia* up to 700 μm wide, bulging dorsally, each containing about 450 spores, from above dark spore mass visible through overlying tissue, which gradually shrinks away, exposing cup-like hollows which become confluent along the middle of the older thalli with large numbers of liberated spores at the bottom. *Spores* 90—115(—122) μm in diameter, triangular-globular, polar, light brown to darker brown, semitransparent; wing thick and 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 areolae on both spore faces, which are similar to rather dissimilar: distal face often highly convex, with 12—13 small areolae or fovea across diameter, 2,5—5,0 μm wide, walls high and 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 about 35 small, deep, rounded areolae, less than 5 μm wide, sometimes adjacent ones confluent, walls thickened and raised, especially at nodes, granulate to papillate. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 17C, D.

Riccia cupulifera is endemic to southern Africa, and widespread in the shrublands of the northwestern and southwestern Cape, rare in the Orange Free State and only found once in Transvaal. Map 36.

It grows on damp, sandy soil or on mud, and can be distinguished from *R. crystallina* (no. 39) and *R. cavernosa* (no. 40), the other two rather similar species with spongy thalli, by being dioicous and heterothallic, by the characteristic 'butterfly'-shaped 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. Arnell* 303 (PRE); *Duthie* 5488 (BOL); *Oliver* 8053 (PRE); *S.M. Perold* 591 (PRE); *Schelpe* 7787 (BOL).

Group 'Vesiculosa'

Thalli rarely in rosettes; mostly large and succulent.

42. **Riccia bullosa** *Link* ex *Lindenb.* in Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum XIV (supplement): 119 (1829); Lehm.: 371 (1829); Lindenb.: 441 (1836); Nees: 391, 433 (1838); Gott. *et al.*: 609 (1846); Steph.: 377 (1898); Sim: 13 (1926); S. Arnell: 42 (1963a); Perold (1991, in press). Type: Cape, terrestris, ad montem tabularem versus montum Leonio, *Ecklon* s.n. (STR, lecto.!).

R. crassa Nees ex Lindenb. in Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum XIV (supplement): 119 (1829) nom. inval.

R. montaguensis S. Arnell in Botaniska Notiser 105: 308 (1952); S. Arnell: 44 (1963a). Types: Cape Province, Montagu, Bath Kloof, near the caves, *S. Arnell* 714 (BOL!; PRE!), 741 (BOL!).

Thallus medium-sized to large, in crowded, gregarious patches or scattered; apically light green, soon turning straw-coloured, deeply grooved, laterally swollen to bloated, with small polygonal domed areas, transversely wrinkled, becoming proximally pitted and spongy; when dry, rather deflated and with folds across, sides not inflexed, margins scalloped. *Branches* once, occasionally twice dichotomously furcate, sometimes simple, shortly to deeply divided, moderately to widely divergent; broadly ovate to oblong, 5,0—15,0 mm long, 3,5—5,5 mm wide, 1,5—2,5 mm thick, in section 2—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* hyaline, vestigial, in pairs, ventrally toward apex only.

Dorsal epidermis forming a domed roof over each air chamber, cells 4—6-sided, 62—75 x 35—40 μm, air pores ringed by 6 or 7 wedge-shaped, smaller and often thinner-walled

cells, 37 x 17 μm, breaking down with age and exposing air chambers. *Assimilation tissue* 1 000—1 500 μm thick, occupying 3/5 of thickness of thallus, air chambers tall, mostly in one layer, vertical or sloping obliquely, 175—250 μm wide, narrower toward centre and apex, separated by chlorophyllose plates, one cell thick; storage tissue 2/5 the thickness of thallus, cells angular, closely packed, 65—75 μm wide, containing starch granules. Fig. 37A—F.

Dioicous. Antheridia in one or two crowded rows along slightly raised central ridge in groove, hyaline necks protruding from small pits, up to 500 μm long. Archegonia in a row along groove, purple necks about 300 μm long. *Sporangia* up to 1 100 μm wide, crowded together, bulging dorsally, overlying tissue thinning and disintegrating, containing about 700 spores each. *Spores* (100—)130—150(—160) μm in diameter, 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 areolae across diameter, 10—15 μm wide, sometimes larger and incompletely separated by low, fragmentary ridges radiating from central pillar, areolar 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 areolar walls, each of three facets with 13—18(—25) rounded areolae, 10—15 μm wide, often incompletely separated and adjoining ones confluent. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 17E, F.

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 and southern Cape as well as the Drakensberg mountain range of Natal and Lesotho. Map 37.

It can be distinguished from other species in the subgenus by its large, rather bloated, straw-coloured or yellow-green thalli. *Riccia garsidei* (no. 43), although closely related, is often larger, almost white when dry, with many exposed air chambers; its spores have fewer and larger areolae. *Riccia volkii* (no. 44) (see note under that species) is less robust and swollen, with narrowly winged, smaller spores and with its distribution restricted to the summer rainfall areas.

Riccia bullosa was originally supposed to also grow in Portugal (Nees 1838), not Spain as mentioned 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 (Tab. 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 1991, in press).

Arnell (1952) described a new species, *R. montaguensis*, although admitting that it was very similar to *R. bullosa* in habit and colour, but somewhat smaller. Gametophytes of *R. montaguensis* were closely examined and found to be indistinguishable from those of *R. bullosa*, which can vary considerably in size from rather small to large. The supposedly smaller spores, which Arnell reported to have a diameter of 80 μm, were found to be rather larger at 100—130 μm (see also Garside's note on herbarium sheet of specimen, *S. Arnell* 714 (BOL)). The ornamentation on the distal face is incomplete, with some large areolae containing a central papilla and low, radiating ridges. Spores from all the sporulating material of this species at BOL and many recent collections at PRE have been measured and photographed and they exhibit a continual gradation in size and also in the completeness or incompleteness of the ornamentation, so that a broader circumscription of *R. bullosa*, which includes these variations, is necessary. *Riccia montaguensis* Arnell is therefore included in the synonymy of *R. bullosa*.

Sim's (1926, p. 13) note under *R. bullosa*, that *R. capensis* (Brunnthaler 1913) (see note under *R. limbata* (no. 10)) '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) from O'Kiep, Namaqualand, which Sim cites, has been placed under *R. schelpei* (no. 50), but the Pole-Evans collection from Premier Mine, Transvaal has not been traced. Judging by its distribution it is most probably a specimen of *R. volkii* (no. 44).

Vouchers: *Magill* PRE-CH 4509 (PRE); *Morley* 272 (PRE); *Oliver* 8777 (PRE); *S.M. Perold* 467 (PRE); *Van Rooy* 3541 (PRE).

43. **Riccia garsidei** *Sim*, The Bryophyta of South Africa: 13 (1926); S. Arnell: 41 (1963a). Type: Cape, Stellenbosch Flats, *Garside* 2 (PRE-CH 1059) (PRE, holo.!).

Thallus medium-sized to large or very large, in gregarious patches or scattered; glaucous to pale olive or buff, very succulent; when dry, light smokey grey to white, honeycombed, sides not inflexed. *Branches* simple or once symmetrically furcate, mostly shortly divided, moderately to widely divergent; elliptical-oblong to broadly ovate, 10,0—12,0(—15,0) mm long, (4,0—)6,0(—8,0) mm wide, 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 toward apex, 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 x 15—35 μm, air pores ringed by 6 or 7 smaller cells, variable in shape, 20—25 x 12 μm, soon rupturing, completely exposing air chambers below. *Assimilation tissue* up to 1 800 μm thick, occupying 2/3 the thickness of thallus, air chambers very tall, mostly in one layer, vertical to obliquely sloping laterally, gradually widening upward, eventually 350—450 μm wide, shape mostly hexagonal when viewed from above, enclosed by unistratose, chlorophyllose cell plates; storage tissue occupying ventral 1/3 of thallus, cells up to 75 μm wide, angular, closely packed. Fig. 39A—F.

Dioicous. Antheridia in one (or two) rows, along centre of branches, a hyaline neck protruding from each quite large hollow. Archegonia serially arranged, thin purple necks obscured. *Sporangia* up to 1 800 μm wide, quite deeply embedded below midline, mostly crowded together, each containing about 1 350 spores. *Spores* (118—)120—130(—135) μm in diameter, triangular-globular, polar, golden brown 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 areolae across diameter, 12,5—20,0 μm wide, areolar 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 about 18 areolae, usually more than 15 μm wide, adjacent ones sometimes confluent, areolar walls up to 5 μm high, some meeting along arms of triradiate mark and marginally extending across wing. *Chromosome number*: not known. Plate 18A, B.

This species is endemic to southern Africa and has been collected in the southwestern and southern Cape on gravelly or clayey soil. Map 38.

Riccia garsidei is closely related to *R. bullosa* (no. 42), but can be distinguished from it by its almost white colour when dry, the larger size 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 areolae.

Vouchers: *Duthie* 5002, 5075, 5475 (BOL); *Marais* 5464a (BOL); *Wilman* 663 (BOL).

44. **Riccia volkii** *S. Arnell* in Mitteilungen der Botanischen Staatssammlung München 16: 271 (1957); S. Arnell : 42 (1963a). Type: SWA/Namibia, Otjiwarongo: Kleiner Waterberg, am Rand der Wannen im roten Sandstein, Boden kalkfrei, *Volk* 1029 (M, holo.; PRE, iso.!).

Thallus 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 dichotomously furcate, shortly to deeply divided, moderately to widely divergent; broadly ligulate to lingulate, up to 9,0 mm long, segments 2,0—6,0 mm long, 2,5—3,5 mm wide, 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, hyaline, vestigial or absent. Plate 3B.

Dorsal epidermis a slightly domed to flat covering over each air chamber, partly chlorophyllose, cells 5- or 6-sided, mostly isodiametric, 50—60 μm; air pores small, surrounded by 6 or 7(8) radially arranged, smaller cells, 12—25 x 20 μm, widening as air chambers increase in size. *Assimilation tissue* 650 μm thick, 1/2—3/5 the thickness of thallus, consisting of one layer of almost vertical air chambers, up to 150 μm wide toward margins, narrower in centre, separated by unistratose plates of chlorophyllose cells, 55—75 x 37 μm; storage tissue 2/5—1/2 the thickness of thallus, cells about 55 μm wide, angular, closely packed. Fig. 39A—F.

Dioicous. Antheridia in one or two rows along groove, hyaline necks emerging from small pits. Archegonia with purple necks up to 250 μm long, median, female plants hardly to slightly wider. *Sporangia* mostly 900 μm wide, bulging dorsally, 2 or 3 linearly arranged toward base, overlying tissue disintegrating, with about 300 spores in each. *Spores* (88—)90—100(—112) μm in diameter, 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 areolae across diameter, 10—15 μm wide, sometimes 2 adjacent areolae confluent, with slight constriction where cross wall failed to develop, areolar 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 about 15 rounded areolae, up to 10 μm wide, sometimes confluent or with slight constriction. *Chromosome number*: n = 8 (Bornefeld 1984, 1989). Plate 18C, D.

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, central, eastern and southern Transvaal and the Orange Free State. Map 38.

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. 42) and of *R. garsidei* (no. 43), but the branches are narrower and more delicate, sometimes forming a rosette. The smaller, narrow-winged spores with poorly defined, triradiate mark and rounded areolae 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).

45. **Riccia rubricollis** *Garside & Duthie* ex *Perold* in Bothalia 21: 51 (1991a); S. Arnell: 35 (1963). Type: Cape, Knysna, Belvidere, on turf in shady places, not far from lagoon, Sept./Oct. 1929, *Duthie* 5014 (BOL, lecto.!; PRE, isolecto.!).

Thallus 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* once or twice symmetrically or asymmetrically furcate, rarely simple, and then apically bilobed, moderately to widely divergent, oblong or somewhat linear, up to 12,0 mm long, segments 2,5—6,0 mm long, 2,8—3,0 mm wide, 0,7—1,0 mm thick medianly, at sporangia up to 1,5 mm thick, thinner toward winged margins, in section 2—4 times wider than thick; apex tapered, ventrally keeled. Groove only apically 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 cover over large air chambers, cells oblong-hexagonal or 5-sided, 62—80 x 50 μm, walls up to 10 μm deep; air pores apically small, about 30 μm wide, surrounded by slightly curved, narrow, elongated cells, soon disintegrating and air pores rapidly enlarged, leaving air chambers exposed. *Assimilation tissue* 400—750 μm thick, occupying more than 1/2 to most of thickness of thallus, air chambers 5- or 6-sided, elongated, mostly in one layer, generally 12 across width of thallus, sloping laterally and widening toward the top, up to 200—250 μm wide, enclosed by unistratose, chlorophyllose cell plates; storage tissue less than 1/2 the thickness of thallus, cells empty, angular, 30—70 μm wide, smaller below. Fig. 40A—F.

Dioicous. Antheridia in a row along midline of branches, when mature bulging dorsally, with conspicuous, mostly dark purple necks, up to 300 μm long and 25 μm wide. Archegonia 3 or 4 serially arranged toward base, necks purple, thin, hidden. *Sporangia* up to 1 100 μm wide, deeply imbedded, not bulging dorsally or protruding ventrally, but eventually opening to upper surface, containing about 620 spores each. *Spores* 92—100(—105) μm in diameter, 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 areolae across diameter, central ones larger, 20—25 μm wide, smaller toward margin, about 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, areolae up to 12 μm wide, mostly incomplete, walls slightly raised at nodes. *Chromosome number*: not known, as living material not available. Plate 18E, F.

Riccia rubricollis is only known from Knysna in the southern 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. 47), *Fossombronia* sp. and *Pleuridium* sp. (Map 40).

The species is easily recognized by the conspicuous single row of deep purple antheridial necks along the midline of the more or less linear, apically tapering branches of the male plants. Stolons, as frequently seen arising along the entire ventrally keeled face of *R. purpurascens*, are here confined to the thickened perennating tips of some branches. 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. Arnell (1963a) described it under the name, *R. rubricollis*, but without a Latin description and without citing a type specimen. These have now been done (Perold 1991), after Duthie's specimens, following a

thorough search, were relocated at BOL. Although more robust and fleshy, *R. rubricollis* is clearly related to *R. purpurascens*, because of its somewhat linear habit, but is not classified together with it and *R. stricta* (no. 46) 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 areolae on the distal face of the spores are wider.

Voucher: *Duthie* 5406 (BOL)

2. Section **Ricciella**

Ricciella *(A. Braun, pro gen.) Bisch.*, Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum 17: 1068 (1835). Lectotype species: *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, sparingly furcate. *Scales* very small to small, ventral, mostly only toward apex, single or split, without central appendage.

Dorsal epidermis chlorophyllose, air pores small, surrounded by smaller companion cells, not becoming cavernous. *Assimilation tissue* with polyhedral air chambers enclosed by unistratose walls.

Sporangia bulging and opening ventrally; vertical or oblique. *Spores* smallish, areolar walls thick or partly thick.

46. **Riccia stricta** *(Lindenb.) Perold* in Bothalia 22: 197—206 (1990g). Type: Cape, Philipstown, ad arborum truncos (!?), *Ecklon* s.n. (BM, lecto.!).

R. fluitans L. var. δ Lindenb. in Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum 18: 85 (1836).

R. fluitans L. var. δ Nees, Naturgeschichte der Europäischen Lebermoose 4: 440 (1838).

R. fluitans L. var. ?ε *stricta* Gott. *et al.*, Synopsis hepaticarum: 610 (1846). Type: Cape, Philipstown, *Ecklon* (BM!).

R. tenerrima Steph. Icones Ined. Type: Natal, dist. Alexandra, Sta. Dumisa, leg. *Rudatis* (Herb. Münch.).

R. stricta A.V. Duthie ined. fide S. Arnell: 37 (1963a).

? *Ricciella stricta* (Gott. *et al.*) Trev. in Memorie de Reale Istituto Lombardo Ser. 3,4: 62 (1877).

Thallus small to medium-sized, in dense, tangled masses; bright green, often with purple streaks along margins; when dry, flattened to almost unchanged, but groove more pronounced and longer, light green. *Branches* repeatedly symmetrically or asymmetrically furcate, moderately to widely divergent; linear or strap-shaped, 15,0—20,0 mm long, segments 5,0 mm or more long, (0,3—)0,5—0,8(—1,2) mm wide, 0,25—0,35(—0,5) mm thick and in section 1—3(—4) times wider than thick; apex slightly narrowed and somewhat tapering, occasionally bulbous. Groove only visible at apex 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 segment, apically single, soon splitting into two halves, obtusely triangular, concave, hyaline, occasionally somewhat purple, small, up to 250—500 x 150—400 μm, cells 4- or 5(6)-sided, isodiametric, 50—65 μm wide, 1 or 2 rows toward apex wider than long. Plate 3C.

Dorsal epidermis forming flat cover over elongated air chambers, cells long-hexagonal, 42—65 x 25 μm, smaller and isodiametric at margins, about 25 μm, air pores small, up to 17 μm wide, surrounded by ring of 5 or 6 smaller companion cells, partly overlying slightly thicker-walled epidermal cells. *Assimilation tissue* 100—500 μm thick, less than 1/2, to most of thickness of thallus, air chambers in 1 or 2 layers medianly, uniseriate laterally, up to 65 μm wide, enclosed by chlorophyllose plates, one cell thick, cells isodiametric, 25—40 μm; storage tissue occupying ventral part of thallus, cells rounded, about 25 μm wide. Fig. 41A—G.

Monoicous. Antheridia near apex and more proximally, single, at intervals medianly along branches, necks hyaline, conspicuous, 150—200 μm long, at the base surrounded by low, hyaline, conical cells, 37—50 x 30 μm. Archegonia median,

up to 3 per segment, serially arranged, sometimes interspersed between antheridia, obliquely orientated, neck purple, 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, subspherical, up to 600 μm wide, abundantly supplied with rhizoids, containing about 270 spores each. *Spores* (50—)62—70(—75) μm in diameter, triangular-globular, polar, light brown, semitransparent; 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—6 large, deep areolae across diameter of spore, 17—20 μm wide, in centre a pillar or boss, from which several low ridges radiate outward, sometimes forming a network, areolar 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 areolae, some incomplete, often subdivided by faint radiating ridges, walls thin, raised at nodes. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 19A, B.

Riccia stricta is known from central, eastern and southern Africa. Map 60. In the Flora 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, central, eastern and southern Transvaal, Natal, Orange Free State, Lesotho, Transkei and central, southwestern, southern and eastern Cape. Map 39.

Lindenberg (1836) and Nees (1838) both stated that *R. fluitans* var. ?δ *stricta* was collected by Ecklon at the Cape (Philipstown and Krakakamma). Gottsche *et al.* (1846), however, recognized it as an additional taxon, *R. fluitans* var. ?ε *stricta* (var. ?δ). *R. fluitans* L. var. δ *minor*, leg. Wallich is from Nepal, according to them, whereas the previous authors regarded the Indian species as *R. fluitans* var. *Y minor*, collected at Malabar by Belanger. Ecklon's specimen was reported by Gottsche *et al.* to be from Promontorio Bonae Spei (southwestern Cape), whereas Philipstown (locality on specimen label) is in the central Cape. *Riccia* species are not known to occur on tree bark either, as they had reported. *R. fluitans* L. var. ?ε *stricta* (var. ?δ) is now elevated to specific rank as *R. stricta* (Perold 1990f).

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 the 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 areolae containing a central boss on the distal face and, on the proximal face, a prominent triradiate mark.

R. fluitans L. *sensu stricto* is thought not to occur naturally in southern Africa (Perold 1990f).

Vouchers: *Glen* 1832 (PRE); *Magill* 5039 (PRE); *Mauve & Venter* 5077 (PRE); *S.M. Perold* 2455 (PRE); *Van Zinderen-Bakker* 7472 (BOL).

47. **Riccia purpurascens** *Lehm.* in Linnaea IV: 371 (1829); Lindenb.: 451 (1836); Gott. *et al.*: 611 (1846); Steph.: 363 (1898); Sim: 15 (1926); S. Arnell: 36 (1963a); Perold: 203 (1990g). 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. & Lindenb. in Novarum & Minus Cognitarum Stirpium Pugillus 4: 23 (1832); Trev.: 62 (1877).

Thallus 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, thin and flat. *Branches* repeatedly and irregularly furcate, narrowly to moderately divergent; linear, 9,0—17,0 mm long, segments 1,0—5,0 mm long, 1,5—2,0 mm wide, 0,4—0,6 mm thick medianly over keeled ventral part, lateral wings up to 0,3 mm thick, in section 3—5(—7) times wider than thick; apex narrowed, shortly emarginate. Groove distinct toward apex, 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, frequently giving rise to stolons. *Scales* toward apex only, ventral, spaced and split into 2 halves, up to 3 pairs, hyaline, difficult to detect. Plate 3D.

Dorsal epidermis forming flat cover over large air chambers, cells oblong-hexagonal or 5-sided, up to 110 x 35—60 μm, at apical margin rectangular, smaller, 45 x 30 μm; air pores small, surrounded by 4 or 5 radially arranged, thin-walled cells, 17—35 x 12—15 μm, partly overlying slightly thicker-walled epidermal cells. *Assimilation tissue* 300-400 μm thick, occupying most of thickness of thallus, air chambers polyhedral, in 2 layers medianly, uniseriate laterally, enclosed by chlorophyllose plates, one cell thick; storage tissue confined to central keeled part, mostly only 1—4 layers of cells, angular, 50—62 μm wide. Fig. 42A—F.

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, about 50 μm long. Archegonia single or in pairs, sometimes adjacent, median, vertically orientated, necks short, brownish purple with hyaline tip, opening into a depression, base surrounded by conical cells, 30—40 μm long. *Sporangia* up to 550 μm wide, thallus widening and bulging ventrally with surrounding tissue thicker, mostly 6 layers of cells, and containing up to 580 spores each. *Spores* (65—)70—80(—88) μm in diameter, triangular-globular, polar, yellow to bright brown, semitransparent; wing thick and up to 7,5 μm wide, at marginal angles 2 small pores, one on either side of each arm of triradiate mark, margin finely crenulate; ornamentation incompletely reticulate and different on 2 spore faces: distal face with 4—6 large, angular, mostly incomplete areolae across diameter, 20 μm wide, usually subdivided by secondary ridges or a central pillar into smaller areolae, 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 areolae, mostly short broken walls, straight or curved, edged with tall uneven spines, warty papillae or low granules. *Chromosome number*: n = 8 (Bornefeld 1989). Plate 19C, D.

Endemic to southern Africa, *R. purpurascens* has been collected in the northwestern, southwestern and southern Cape, which are winter rainfall areas. Map 40. It grows on damp, sandy soil or on mud. It is not nearly as widespread as *R. stricta* (no. 46), which occurs mostly in summer rainfall regions; only in the southwestern and southern 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*. So must also be *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*, the wing also wide, but with two small pores at each marginal angle; the areolar walls on both spore faces and the triradiate mark on the proximal face are much roughened with granules, papillae or even spines.

Vouchers: *S. Arnell* 332 (BOL); *McLaughlin* PRE-CH 4197; *S.M. Perold* 634a, 1770 (PRE).

3. Subgenus **Thallocarpus**

Thallocarpus *(Lindb.) Jovet-Ast*, Revue bryologique et lichénologique 41: 452 (1975). Type species: *R. curtisii* (James ex Aust.) Aust.

Thallocarpus Lindb.: 377 (1874).
Cryptocarpus Aust.: 231 (1870).
Angiocarpus Trev.: 444 (1877).

Plants heterothallic; terricolous. *Scales* absent.

Dorsal epidermis chlorophyllose, cavernous, in one stratum. *Assimilation tissue* with polyhedral air chambers.

Sporangia immersed. *Spores* remaining coherent in tetrads, ornamentation with slender spinules or stout spines.

48. **Riccia curtisii** *(James ex Aust.) Aust.* in Bulletin of the Torrey Botanical Club 6: 305 (1879); Steph.: 369 (1898); Haynes: 284 (1920); Duthie & Garside: 122 (1936); Frye & Clark: 32 (1937); Hässel: 218 (1962); S. Arnell: 36 (1963a); Jovet-Ast: 452 (1975); Vianna: 76 (1981). Type: North Carolina, Society Hill, leg. *Curtis* s.n., 1853; on moist ground, South Carolina, Ravenel, leg. *Curtis* s.n., 1849 (Hb. Sulliv.).

Riccia spongosa S. Arnell, Botaniska Notiser 105: 310 (1952); S. Arnell: 38 (1963a). Type: Cape, George, Wilderness, forest-path 1/2 mile east of the hotel, *S. Arnell* 1393 (BOL, holo.!).

Cryptocarpus curtisii Aust. in Proceedings of the Academy of Natural Sciences Philadelphia 21: 231 ('Dec. 1869', 1870) nom. illeg.

Thallocarpus curtisii (Aust.) Lindb. in Notiser Sällskap pro Fauna et Flora Fennica Förhandlingar 13: 377 (1874); Aust.: 21 (1875); McAllister 43: 117 (1916).

Angiocarpus curtisii (Aust.) Trev. in Memorie de Reale Istituto Lombardo Ser. 3,4: 444 (1877).

Plants heterothallic, female thalli smallish to medium-sized, scattered or crowded, in incomplete or complete rosettes, up to 10 mm, rarely to 20 mm across; light green to yellowish green; dorsally pitted and spongy, intact toward apex; when dry, margins not inflexed, dull green, cavernous; male thalli much smaller, frequently partly overgrown by female thalli; yellowish to partly reddish brown, often with some purple colouration. *Branches* in female plants once to several times dichotomously furcate, shortly to deeply divided, almost overlapping to narrowly divergent; oblong or quite variable, 2,0—8,0 mm long, 2,0—4,0 mm wide, up to 1,0 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 x 75—80 μm, but quite variable in size and shape, around air pores rather smaller, 80—90 x 62—75 μm, unmodified and regularly arranged; air pores small and inconspicuous at apex, rapidly enlarging, becoming almost as wide as air chambers, irregularly polygonal to oblong. *Assimilation tissue* up to 750 μm thick, 3/4 the thickness of thallus, air chambers polyhedral, sloping, much enlarged proximally, separated by unistratose walls composed of chlorophyllose cells 87 x 55 μm; storage tissue restricted to ventral part, 1/4 or less, of thickness of thallus, in 3—5 rows of cells, about 60 μm wide. Fig. 43A—E.

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 also about 200 μm long, base purple. *Sporangia* up to 700 μm wide, mostly containing 64 spore tetrads each. *Spores* in tetrads, (100—)105—115(—125) μm in diameter, yellow-brown to tan-brown, semitransparent; wingless; usually only three spores of tetrad visible, occasionally all four, joined by narrow band or ridge; ornamentation reticulate, variously developed, with small, deep, round areolae or fovea, 2,5—3,5 μm wide, extending to connecting band, the areolar 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 19E, F.

In the Flora area, *R. curtisii* is fairly rare; it has been collected at seepages on soil derived from granitic rock in the shrublands of the northwestern Cape, on cultivated soil in a wheatfield and on garden paths in the southwestern and southern Cape. Map 41.

This species is quite widely distributed and is known from North and South America, southern Africa and from India. Map 61.

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.

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*. Perold (1989e) compared SEM micrographs of the spore tetrads of both species: in *R. compacta* the tetrads are joined together at a groove, not a band or a ridge, the papillae at the sides of the convex faces are without fovea at their bases and there is no reticulum here; the spinules in the centre are smooth and slender and without granules. There appears to be a fair amount of variation, however, as *Arnell* 301 and *S.M. Perold* 641 could be referred to both species by these criteria. Moreover, SEM examination of spores from a North American specimen of *R. curtisii*, *Severun Rapp* s.n., 1931 (PRE), showed it to have larger, conical spines, lacking a basal reticulum and with the ornamentation differing more widely from southern African *R. curtisii* spores than *R. curtisii* and *R. compacta* spores differ from each other. 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, therefore remains unresolved.

Arnell (1952, 1963a) described another new species with tetrad spores from southern Africa, *R. spongosa*. It is doubtful, however, whether the only collection ever made, *Arnell* 1393, truly warrants this status, as the spores appear to be rather young (Perold 1989e) and, therefore, misleading in their so-called differences. Garside expressed a similar view in a note found with this specimen. *Riccia spongosa* is now regarded by me as a synonym of *R. curtisii*.

Vouchers: *S. Arnell* 12 (BOL); *Duthie* 5018 (BOL); *Duthie* 5486 (BOL); *S.M. Perold* 474, 479 (PRE).

49. **Riccia perssonii** *S.A. Kahn* in Svensk botanisk tidskrift 49: 433 (1955); S. Arnell: 37 (1963a); Jovet-Ast: 149 (1967a); Jovet-Ast: 449 (1975). Type: Bangladesh (=East Pakistan), Dacca, growing on shaded soft mud along the edge of a pond, *Kahn* 1 (Dacca Univ.)

Plants heterothallic, small to medium-sized in female plants, scattered, reported to form rosettes up to 11 mm across; light green; dorsally spongy.

Branches once or twice, sometimes up to 3 times dichotomously furcate, shortly to deeply divided, moderately divergent; oblong or variable, 2,0—4,0 mm long, 0,5—1,3 mm wide, about 0,3 mm thick, in section 2—4 times wider than thick; apex rounded to acute; male thalli much smaller, once dichotomously furcate. 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, separated by chlorophyllose, unistratose cell plates; storage tissue consisting of only a few layers of cells. Fig. 44A, B.

Dioicous. Antheridia with hyaline necks, 125 μm long, basally surrounded by conical cells, in 1 or 2 rows along middle of branches. Archegonia with purple necks, in rows. *Sporangia* single, at base of branches or several together in centre of thalli, about 500 μm wide and containing up to 64 spore tetrads each. *Spores* in tetrads, (90—)95—102(—110) μm in diameter, tan-brown, semitransparent; wingless; all four 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 areolae 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 1975). Plate 20A, B.

In the Flora area *R. perssonii* has only been collected twice in the far northern part of Namibia, on lime-free, damp, black, clayey soil. Map 41. It is possible that the Stephens specimen from neighbouring Botswana (Chobe), reported by Duthie & Garside (1937) under *R. curtisii* (no. 48), 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.

Except for Bangladesh, *R. perssonii* is also known from the north-central and north-eastern African countries, Chad and Sudan respectively (Jovet-Ast 1967, 1975), and from southern Africa. Map 62.

Both 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. Subsequently, Kahn (1957) described another species, *R. arnellii*, also from Bangladesh, with both tetrahedral and rhomboidal spore tetrads.

Vouchers: *Smook* 7612 p.p. (PRE); *Volk* 2059 (M, PRE).

4. Subgenus Pannosae

Pannosae *(Perold) Perold*, subgen. nov. Holotype species: *R. tomentosa* Volk & Perold.
Pannosae Perold, pro sectione in Volk & Perold in Bothalia 20: 28 (1990).

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* (Volk & Perold 1990), made for the reception of *R. tomentosa* on account of its tetrad spores and placed under subgenus *Thallocarpus*, is now elevated to the rank of subgenus *Pannosae* (Perold) Perold. There are several important differences which separate *R. tomentosa* from the other two species, *R. curtisii* and *R. perssonii*, in subgenus *Thallocarpus*: the dense hair-like cellular outgrowths from the dorsal epidermis, which does not become cavernous, 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.

50. **Riccia tomentosa** *Volk & Perold* in Bothalia 20: (1990). Type: Cape, Pedroskloof, on road to Rooifontein, 2 km beyond Willem Stone Bridge, sandy soil, *S.M. Perold* 1495 (PRE, holo.).
Thallus large to very large, in crowded, gregarious patches or scattered; dorsally shaggy-haired or

tomentose, silvery to dusty grey; when dry, hairs matted, whitish, deeply concave toward centre, margins erect or scarcely inflexed to somewhat reflexed proximally. *Branches* simple or symmetrically to asymmetrically furcate, moderately divergent; oblong to ovate-oblong, up to 18,0 mm long, 2,0—4,0(—5,0) mm wide, narrower proximally, 3,0—4,0 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 upward and outward, green, toward lower, ventral parts occasionally reddish purple; ventral face rounded to flat, light green. *Scales* large, triangular, imbricate, hyaline, 1 500 μm long, base up to 1 200 μm wide, apically divided into loose filamentous strands, one cell wide, 4 or 5 cells and up to 1 000 μm long, cells in body of scale 5-sided, 112 x 25—42 μm, cell walls straight to slightly sinuous, smaller at base, and at one side of scale, a row of long-rectangular cells, 180 x 40 μm. Plate 3E.

Dorsal epidermis over air chambers slightly domed, with outgrowths of free-standing, straight or bent hair-like cell pillars, up to 2 700 μm long, 5/7 the thickness of thallus, composed of (2—)5—14 cells, 50—270 x 50—100 μm, tapering upwards from broad base, thin-walled, hyaline; air pores spaced, circumscribed by 5 or 6(7) radially arranged, wedge-shaped cells, some intervening cells lacking contact with an air pore. *Assimilation tissue* ± 500 μm thick, 1/8—1/6 the thickness of thallus, with sloping, elongated, polyhedral air chambers 37—62(—112) μm wide, separated by plates of isodiametric cells; storage tissue 1/8—1/6 the thickness of thallus, cells about 50 μm wide, angular, with small spaces between. Fig. 45A—F.

Dioicous. Antheridia and archegonia difficult to observe, as obscured by dense dorsal hairs. *Sporangia* bulging dorsally, overlying tissue tinged with mauve, mostly 800 μm wide, containing up to 300 spore tetrads each. *Spores* in tetrads, 115—145 μm in diameter, 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 verruculate, 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 in Volk & Perold 1990). Plate 20C, D.

This species is rarely collected and is endemic to the arid shrublands of Namaqualand, northwestern Cape where it is found on reddish brown, coarse, sandy soil, overlying clay. Map 42.

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 and 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. 24) (See note under that species).

On account of its tetrad spores, which it shares with *R. curtisii* (no. 48) and *R. perssonii* (no. 49), *R. tomentosa*, section *Pannosae* (Volk & Perold 1990), was initially also referred to subgenus *Thallocarpus*, but the marked differences in the morphology of *R. tomentosa* indicate that it would be more properly placed in a subgenus on its own. Section *Pannosae* has 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).

5. Subgenus Chartacea

Chartacea *Perold*, in Volk & Perold in Bothalia 16: 29 (1986). Holotype species: *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, areolar walls granulate or almost smooth.

51. **Riccia schelpei** *Volk & Perold* in Bothalia 16: 29 (1986b). Type: Cape, Hester Malan Res., Carolusberg (W), seepage area, *Schelpe* 7775 (BOL, holo.!; PRE, iso.!).

Thallus medium-sized to large, in gregarious patches

or scattered; green, somewhat shiny to greasy, dorsally reticulate with outlines of air chambers faintly visible from above; 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 12,0 mm long, 3,0—6,0 mm wide, 1,5—2,0 mm thick and in section 2—3 times wider than thick; apex rounded, emarginate, keeled below. Groove deep toward apex, its sides convex and steeply sloping, more proximally shallow and wide. Thallus margins winged, acute, attenuate. Flanks sloping steeply upwards and outwards and abruptly into undulating wing; ventral face slightly convex, greenish. *Scales* large, imbricate, up to 1 500 x 300—500 μm, projecting slightly above thallus margins, hyaline with some scattered purple cells at base, cells in body of scale oblong, 5- or 6-sided, 110 x 50 μm, cell walls straight, smaller at mostly smooth margin. Plate 3F.

Dorsal epidermis unistratose, cells variously shaped, polygonal, 35—70 x 30—50 μm, hyaline, thick-walled, 5—8 radially arranged around each air pore, with superimposed ring of smaller, roundish, 15—20 μm wide, fragile cells which reduce diameter of pores to 5—20 μm. *Assimilation tissue* 750—1 300 μm thick in section, 1/2—2/3 the thickness of thallus, with wide polyhedral, sloping air chambers enclosed by chlorophyllose plates, one cell thick, cells isodiametric, about 55 μm wide; storage tissue occupying ventral 1/3—1/2 of thallus, cells rounded, up to 70 μm wide. Fig. 46A—F.

Monoicous. Antheridia with short, hyaline necks. Archegonia with hyaline tips above purple-brown bases, opening into 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, each containing 600—800(—1 000) spores enclosed in a red-brown sac, which later disintegrates. *Spores* 90—115 μm in diameter, 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 areolae across diameter, 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 areolae, about 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 20E, F.

This species is endemic to the arid shrublands of the northwestern and southwestern Cape, where it is quite rare. It is found on decomposed granite, at seepages or at margins of flat rock outcrops. Map 43.

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. The spores of some collections, notably *S.M. Perold* 535, have smoother areolar walls than most of the others examined. A note by Duthie, found with a specimen of *R. schelpei*, *Giffen* 3 (PRE-CH 1056), which had previously been identified as *R. bullosa* (no. 42) (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. ciliifera*, but spores different'.

Vouchers: *Oliver* 8041 (PRE); *S.M. Perold* 1480, 1946, 2178 (PRE); *C.M. van Wyk* 2524 (PRE).

2. RICCIOCARPOS

Ricciocarpos *Corda* in Opiz, Beiträge zur Naturgeschichte 12: 651 (1829) (orth. var.: *Ricciocarpon* Corda mut. Corda 1830, *Ricciocarpus* Corda mut. Dum. 1874); Howe: 26 (1899); Müller: 44 (1952); Hässel: 205 (1962); S. Arnell: 12 (1963). Holotype species: *R. natans* (L.) Corda.

Hemiseumata Bisch. ex Lindley: 57 (1847). Type species: *Riccia natans* L.

Hemiseuma Bisch.: 1040, 1071 (1835). Type species: *Riccia natans* L.

Thallus 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 14,0 mm long, 3,0—7,0

mm wide, less than 1,0 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* 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 layers of large, superimposed, polyhedral air chambers; storage tissue reduced, only 3 or 4 layers of cells; rhizoids mostly absent in aquatic form, smooth and tuberculate in land form. Oil cells present.

Monoicous. *Sporangia rare*, immersed in ridge along groove toward base. *Spores* smallish, triangular-globular, polar, black, opaque, granulate-areolate, 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); Howe: 33 (1899); Schiffn. in Engl. & Prantl: 15 (1909); Massalongo: 831 (1912); Casares-Gil: 235 (1919); Macvicar: 30 (1926); Frye & Clarke: 39 (1937); Müller: 414 (1952); Hässel: 205 (1962); S. Arnell: 12 (1963a); Campb.: 121 (1975); Vanden Bergh.: 183 (1972). Type: Britain, Suffolk, 'in stagnis, circa Hadley', leg. *Buddle* (OXF, holo. fide Grolle 87: 229 (1976); H-SOL, iso. fide Isoviita 89: 23 (1970) Xerox copy! Lichen no. 18. tab. 78. fig. 18, Dillenius : 536 (1741).

Riccia natans L., Systema Naturae: (Ed. 10) 1339 (1759); Lindenb.: 121 (1829); Nees: 319, 419 (1838); Gott. et al.: 607 (1846); Sim: 15 (1926).

R. capillata Schmidel, Icones Plantarum et Analyses Partim: 276 (1797).

R. velutina Wilson in Hooker, Icones Plantarum 3: t 249 (1839).

Ricciocarpus velutinus Steph. in Bulletin l'Herbier Boissier 6: 758 (1898); Ladyzhenskaja: 3 (1943).

Thallus large, gregarious, occasionally in dense mats or in partial rosettes, 20—30 mm across; olive-green to yellowish green, tinged with purple along margins, firm and somewhat leathery, convex, reticulate; when dry, deflated, otherwise little altered, sides not inflexed. *Branches* 2—3 times dichotomously furcate, shortly to deeply divided, hardly divergent; obcordate, up to 14,0 mm long, 3,0—7,0 mm wide, less than 1,0 mm thick in centre, rapidly thinning toward margins, in section 4—8 times wider than thick; apex rounded, emarginate. Groove very pronounced throughout, dividing near apex, containing central raised ridge, obscured by highly convex sides of groove almost meeting 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* in several rows, in dense bunches of ribbons, ventral, pendant in aquatic form, violet to reddish black, linear-lanceolate to tapering, up to 10 mm long, 375—600 μm wide, cells oblong-hexagonal, 80—125 x 25 μm, with occasional, smaller, scattered, specialized oil cells in interior, margins toothed, with dark, conical cells 17—27 μm long.

Dorsal epidermis covering air chambers persistent, cells hexagonal to polygonal, up to 50 x 15—27 μm, air pores 5- or 6-sided, about 50 μm wide, surrounding cells not differentiated, thin-walled. *Assimilation tissue* occupying most of thickness of thallus, air chambers in several layers, superimposed, polyhedral, 60—450 μm wide, separated by unistratose plates of cells, 35 x 15 μm, occasionally with scattered oil cells; storage tissue only 3—4 layers of cells ventrally. Fig. 47A—F.

Monoicous. Antheridia along ridge in central groove, hyaline necks about 100 μm long. Archegonia also along groove, but apparently not together with antheridia. *Sporangia* infrequent, single or up to 3 in series, immersed, the position marked by a slight elevation. *Spores* (55—)60—67(—75) μm in diameter, triangular-globular, polar, black, opaque; wing narrow, margin crenulate; ornamentation granulate-areolate: distal face with poorly defined, 6—8 areolae across diameter of spore, the entire surface thickly covered with granules; proximal face without defined triradiate mark, areolae absent, sprinkled with granules and papillae. *Chromosome number*: n = 9 (Siler 1934; Müller 1952; Jovet-Ast 1974; Bornefeld 1987). Plate 21A, B.

In the Flora area *Ricciocarpos natans* is known from East Caprivi, Botswana, Natal, Zululand and Transkei. It floats on still water, often in association with *Lemna* and *Azolla*, or becomes stranded on mud at the margins of pool or vleis. Map 43. *Ricciocarpos natans* is cosmopolitan and although rare, it is found in all parts of the world, even in Alaska. Map 63.

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

Müller (1952) treated *R. lutescens* Schweinitz as a species of *Riccia*.

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

Insufficiently known species

Riccia coronata Sim, The Bryophyta of South Africa: 9 (1926). Type: Natal, Mooi River, *Sim* 8730. This was the only specimen of this species and cannot 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 *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 species. 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 Volk, in Nova Hedwigia 39: 117 (1984). Type: 30 km nördlich von Tsumeb an der Hauptstrasse nach Angola, *Volk* 81/153a p.p. (M). Only sterile, cultured specimens have been examined, but 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 introduced. It is therefore excluded from the Flora.

CHAPTER 8

DISCUSSION AND NOTES ON PHYLOGENETIC CRITERIA

The aim in this chapter is to examine some of the pertinent ideas concerning the phylogeny as well as the relationships of the Ricciaceae. These have been gleaned from the literature and are augmented by personal observations and speculations. Together they may form a basis upon which the construction of a phylogeny of the family could be attempted sometime in the future. In formulating phylogenetic schemes, palaeobotanical, phytogeographical, morphological, cytological and biochemical criteria are of particular significance and will be considered in that order.

A. Palaeobotanical criteria

The fossil record of possible precursors of the Ricciineae, and indeed of all the hepatics, is meagre. This is in spite of the fact that their dorsiventral thalli could have been rather readily covered by sediments, so that they should be reasonable candidates for preservation, provided the appropriate kind of sedimentation occurred in the right situation at the right time (Lacey 1969). Their failure to become preserved could, however, mainly be ascribed to their softness of texture, with the cell walls containing only small amounts of cellulose, which leads to their early decay. An added problem is that there are major difficulties in recognizing and interpreting properly those fragments that have been preserved (Krassilov & Schuster 1984).

In studying fossil remains, it should also be borne in mind that, because of the paucity of the fossil record, one cannot be sure how long evolution had progressed before the fossils present today, were laid down in the rocks. As Miller (1979) remarks, 'the time of evolution and the time of appearance in the fossil record must be kept conceptually distinct'.

The fossil records of possible ancestors to the Ricciineae (plus some other hepatics) are here briefly referred to and are chronologically arranged according to the geological time it is claimed they were fossilized.

According to Schuster (1984), the discovery of the earliest hepatic, *Pallaviciniites devonicus* (Hueber) Schust., suggests that Hepaticae of the order Metzgeriales, to which it belongs, already existed by Devonian times. The separation of the subclasses Jungermanniidae and Marchantiidae must then predate the middle Devonian and the origin of the Ricciineae can possibly be sought at a somewhat later date.

Ricciellopsis, a fossil genus, was described from the middle Devonian in the Ukraine by Istchenko & Schljakov (1979). The plant grew in a rosette and had spherical bulges, which are inferred to have been sporangia, but Grolle (1983), regards any evidence of it having ricciaceous or even bryophytic relationships as rather questionable. Schuster (1966) notes that there is no sound evidence of the existence in the Paleozoic era of any plants assignable to the Marchantiales. On the other hand, Jovet-Ast (1987) regards some Carboniferous fossil species assigned to the form-genus *Thallites*, for example *T. willsii* Walton and *T. lichenoides* (Matthew) Lundblad, as possibly related to the Ricciineae.

From the Permian, there are apparently no fossils known that resemble *Riccia*. Although not a member of the Ricciineae, it may be of interest to mention here the first undisputed Marchantialean records, namely the Mid-Triassic South African plant, *Hepaticites cyathodoides*, from the Upper Umkomaas Valley in Natal, which was reported and described by Townrow (1959) and again as *Marchantites cyathodoides* (Townrow) Anderson by H.M. Anderson (1976), who explored additional sites at Little Switzerland in Natal and at Dordrecht in the eastern Cape. The latter author also described another species of *Marchantites*, namely *M. tennantii* (H.M. Anderson 1976), from the Molteno formation at Dordrecht.

Another early, but rather ambiguous Mesozoic

fossil, *Naiadita lanceolata* Buckm. emend. Harris, was shown to agree in most features with liverworts and was tentatively compared with the living genus *Riella* of the order Sphaerocarpales. It is probably to be regarded as an ancient and anomalous single case, where leaf elaboration occurred in the Marchantioids (Schuster 1984).

Lundblad (1954) described specialized *Riccia*-like spore tetrads from the early Mesozoic era, the Rhaeto-Liassic period in Sweden, as *Ricciisporites*, but later, she (Lundblad 1959) changed her mind about these spore tetrads having a truly demonstrable affinity to the extant *Riccia curtisii*. Another taxon, *Ricciopsis florinii*, also described by Lundblad (1954), appeared to be more convincing in its relationship to the Ricciineae (Schuster 1984), but the septate walls of its rhizoids, contradict such an affinity. Grolle (1983) excludes the genera *Ricciisporites* Lundblad, and *Ricciopsis* Radczenko as respectively, hardly or certainly not bryophytic. A further *Ricciopsis* species, *R. algoaensis* Gianniny & Wiens (in Anderson & Anderson 1985) was described from Lower Cretaceous rock slabs in the Algoa Basin, eastern Cape. The thalli are dichotomously branched, in small, completely or incompletely formed rosettes, which are 9 mm across and occupy extensive gregarious patches. *Marchantites dunbrodiensis* Gianniny & Wiens (in Anderson & Anderson 1985) was reported from the same locality. There are several other Cretaceous records from elsewhere, but these are of no particular concern here.

Starting with the Triassic, the list of Marchantioid fossils becomes progressively longer as time passes. It seems that at least 12 species, referred to *Marchantiolites* Lundblad, *Ricciopsis* Radczenko, *Marchantites* (Brongniart) Walton and *Preissiites* Knowlton, are reasonably well known from the Triassic times to the Eocene. It would appear that by the Jurassic the Marchantiales began to diversify into modern suborders (Krassilov & Schuster 1984), and that by the start of the Cretaceous, some 135 million years ago, all extant orders must have existed. None of the above fossils can, however, actually be interpreted as ancestral to the Ricciineae. Nevertheless, by Jurassic or even Triassic times, the evolution of very specialized types such as *Ricciopsis*, indicates that the warm-wet regime of the early Carboniferous, followed by the cool-wet regime during the Carboniferous-Permian glaciations, succeeded by the warm-dry regime of the early Mesozoic, stimulated the relatively late evolution of a taxon such as the Ricciineae, which has large durable spores and lacks elaters, as they had become ineffective (Krassilov & Schuster 1984). Certainly, by the late Tertiary (Miocene and Pliocene), species referable to modern Ricciaceae already existed (Jovet-Ast 1986).

B. Phytogeographical criteria

A search of the relevant literature has provided information about the movement of tectonic plates, climatic changes and present day disjunct distribution patterns, that are referred to in the following paragraphs. For the sake of completeness, a brief outline of likely past events is given.

The continents have 'drifted' around the world for at least 2 500 million years, maybe even for as long as 3 500 million years. The supercontinent, Pangaea, came into existence after North America had collided with Eurasia and was then joined by the South American, African, Indian (including Australia) and Antarctic plates. Pangaea is thought to have existed 180—300 million years ago, after which it divided into two parts: Laurasia in the north and Gondwana in the south, separated by the Tethys Sea.

Gondwana, which mainly comprised South America, Africa, India, Australia and Antarctica, existed for about 50—60 million years. During the Ordovician-Silurian and Carboniferous-Permian, major areas of Gondwana became glaciated, but with relatively warm intervals. During the Jurassic, massive and successive lava flows covered large parts of the supercontinent. Thereafter, Gondwana became fractured and its component parts were centrifugally rafted to their present positions (Seyfert & Sirkin 1979).

During the late Jurassic to the early Cretaceous, the South Atlantic between South America and Africa widened gradually and opened eventually into the North Atlantic which had originated from the Western Tethys. Along the bulge of Africa, the two continents appear to have remained in tenuous contact for a long time, however.

From about the middle Cretaceous and onwards, Africa moved north, revolving slowly counter-clockwise and pushing the Arabian-Iranian plate in front of it until this united with south-central Asia. Seemingly, Africa must have migrated far enough northward for most of its cool-adapted Gondwanan taxa to die out even in its southernmost section (Schuster 1982). In the east, the Madagascar/India subcontinent had separated from Africa toward the end of the Cretaceous. In the

early Palaeocene, i.e. the earliest part of the Tertiary Period, India broke away from Madagascar and moved rapidly northward, where it collided with the Asian landmass, causing the rise of the Himalayas.

In the south, Antarctica provided a land bridge between Australia and South America until about 50 million years ago, when Australia started drifting north-eastward. Antarctica separated 30—25 million years ago and shifted south-westward over the south pole (Du Toit 1937). It became subject to increasing glaciation and extinction of its flora.

With the continents changing their positions, especially in latitude, they inevitably experienced a change in climate. The northward moving landmasses of North America, Europe and Asia passed from the tropics and subtropics into the temperate and cold zones. South America, Africa, India and Australia, also moving north, experienced the opposite by changing from generally colder to warmer conditions. It is known that southern African, when situated at latitude 15 degrees south, in the late Cretaceous, had a cool temperate flora, but fossil pollen sequences from the southwestern Cape indicate that during the Miocene, subtropical vegetation and climates existed in these regions (Coetzee 1983).

The climatic changes were, however, not limited to temperature only. Of equal importance were the changes in humidity caused by the changing wind regime and ocean currents as a result of the changes in the relative positions of the continents (Frakes 1979).

The glaciation of Antarctica had a drastic effect on the climate of the Southern Hemisphere. The introduction of cold water to the west coast of southern Africa by the Benguela Current, in addition to other factors such as the uplift and mountain elevation along the eastern parts of the subcontinent during the Miocene, Pliocene and Pleistocene, increased the summer drought in the west and contributed to the formation of deserts and the expansion of savannas in the interior (Coetzee 1978). During the interglacials, as at present, winter rains appeared in the western and southwestern Cape and created new habitat conditions (Von Breitenbach 1986).

Continental drift and sea-floor spreading (global plate tectonics), as well as other factors, offer some explanation for past climatic changes and also for disjunct and inconsistent distribution patterns of modern liverwort communities. The intercontinental relationships exist mostly at the higher taxonomic levels, such as families, whereas the lower taxa, i.e. genera and species, are more often confined to particular continents. Many of these present taxa developed in isolation after the continents had moved too far apart for genetic interaction, even if the possibility of long-distance dispersal of spores by air or ocean currents is taken into account. Van Zanten (1984) expresses the opinion, however, that spores of the Marchantiales (as well as those of Anthocerotales and *Fossombronia*) can probably survive the hazards of long-distance aerial transport, but the large size of the spores of many of these species would probably seriously hamper their transport. Long-range transport of smaller spores in the climatological belts of the earth has been shown, but aerial transport across the equator occurs very infrequently, if at all (Van Zanten & Pócs 1981). Engel & Schuster (1973) conclude that transport by ocean currents is only a very slight possibility for bryophyte spores.

By examining the distribution patterns of modern Ricciaceae from southern Africa and elsewhere (for maps see Part 2 of the dissertation), it is hoped to shed more light on the past history of the family.

Cosmopolitan or subcosmopolitan species are considered first. *Ricciocarpos natans* (Map 63) and several species of *Riccia*, e.g. the mesophytic *R. cavernosa* (Map 59) and *R. crystallina* (Map 58) as well as the xerophytic *R. nigrella* (Map 52), *R. sorocarpa* (Map 47) and *R. trichocarpa* (Map 44) are found almost world-wide. They are quite possibly very old species which existed before the continents separated and may be of Pangaean origin as it is unlikely that they all managed to disperse effectively over the immense distances that separate them nowadays. Although *R. crozalsii* (Map 45) is restricted to the southwestern Cape in the flora area, it is otherwise also widespread and is known from East and North Africa, the Mediterranean countries, Macaronesia, England, Australia, New Zealand and India.

Other species are apparently mostly restricted to Africa south of the Sahara, namely *R. albolimbata* (Map 56), *R. angolensis* (Map 51), *R. argenteolimbata* (Map 57), *R. atropurpurea* (Map 48), *R. congoana* (Map 50), *R. microciliata* (Map 46), *R. okahandjana* (Map 49), *R. rosea* (Map 55), *R. runssorensis* (Map 54) and *R. stricta* (Map 60). As southern Africa is much more species-rich with regard to the genus *Riccia*, than the rest of Africa, it seems likely that most of these species evolved here, and then by short-distance dispersal effected by

animals or other agents, step-wise migrated northward, perhaps via the mountains along the eastern part of the subcontinent. If this route was followed, it must have been after the Miocene, as there is geological evidence that there were no high mountains here in the early Tertiary (Lind & Morrison 1974). *Riccia okahandjana* has even penetrated to Arabia. *Riccia congoana*, referred to as a palaeotropical taxon by Frey & Kürschner (1988), has a pan-African distribution and has now also been collected in Saudi Arabia. If it is eventually proven to be conspecific with *R. billardieri*, it would, therefore, also be widespread toward the East i.e. India, Malaysia and Australia. Accordingly, it could be surmised that this species, now disjunct between tropical Africa and India, may already have existed in the Jurassic, when India and continental Africa were still connected. Little is known about the species of the interconnecting island, Madagascar, however; only *R. fluitans* (Jovet-Ast 1948), *R. cavernosa* (Jovet-Ast 1964), *R. trichocarpa* (Jovet-Ast 1986) and *R. atromarginata* Lev. var. *jovet-astii* (Rauh & Buchloh 1961) have been reported from there.

Interestingly enough, two of the species that occur in Africa, *R. frostii* (Mauritania, Sudan, Egypt), and *R. membranacea* (Ghana, Nigeria, Shaba, Sudan, Tanzania), also occur in North and South America, but are absent from southern Africa. Other African species such as *R. lanceolata*, *R. nigerica* and *R. discolor*, but with the very recently discovered exception of outliers of *R. moenkemeyeri* (Perold in press), are also unknown in southern Africa.

North African *Riccia* species are mostly the same as those in the Mediterranean region, *R. bifurca*, *R. bicarinata*, *R. gougetiana*, R. *lamellosa* among others. They are apparently of Laurasian origin and their migration route southward was probably through the former Tethys Sea, especially at the Tetuan-Gibraltar gap (Schuster 1972).

A peculiar distribution pattern is that of *R. macrocarpa* (Map 53), which appears to be a Northern Hemisphere species, known from North America, countries around the Mediterranean and from Western Siberia, i.e. a Circum-Tethyan species (Frey & Kurschner 1988), but it has now been collected at a few southern African sites as well. Two of the rare species that retain their spores in permanent tetrads, *R. curtisii* and *R. perssonii* also have highly disjunct distributions. *Riccia curtisii* (Map 61) has been reported from the Cape, Argentina, Brazil, North America and India and is most probably of Gondwanan origin, with subsequent migration to North America after the latter was joined by South America in the late Pliocene. *Riccia perssonii* (Map 62) has been collected in northern Namibia, Chad, Sudan and Bangladesh. If one ruled out wind dispersal because of the immense distances and also the large size of the spores in these *Riccia* species, one would have to consider dispersal by birds, which may be a possibility in the case of *R. macrocarpa*, as many of our birds migrate over Africa to Europe and Siberia and return again. However, this would certainly not explain the distribution of *R. curtisii* and *R. perssonii*. Presumably they are both very old species with a Gondwanan distribution pattern and may have been more continuously widespread in earlier times, but have only survived as relicts. It could also be inferred that some of the sites they now occupy, were 'rafted' to their present positions. Schuster (1984) believes that in phylogenetically old species (with slow rates of evolution), continental drift may provide the explanation for disjunct ranges, whereas long-range dispersal is mostly operative in phylogenetically young species

A list of Cape endemics includes the following: *R. alboporosa*, *R. albornata*, *R. bicolorata*, *R. cupulifera*, *R. purpurascens*, *R. rubricollis*, *R. schelpei*, *R. tomentosa*, as well as a number of species in section *Pilifer*, e.g. *R. alatospora*, *R. albomarginata*, *R. concava*, *R. furfuracea*, *R. hantamensis*, *R. hirsuta*, *R. namaquensis*, *R. villosa*, *R. vitrea* and others. There can be little doubt that these species are of relatively recent origin and must have evolved in isolation, without enough time having elapsed for them to have spread widely. Some species are highly diversified, but others in section *Pilifer* are closely related, which is taken to be an indication of their youthfulness. They probably developed in response to drastic climatic, orographic and vegetation changes that occurred in the area after the break-up of Gondwana, particularly since the glaciation of Antarctica. This resulted in a Mediterranean type of climate with summer drought and winter rains in the comparatively recent past. A Cape floristic element, with a high degree of endemism, is also found in higher plants, which is characterized by a large number of species as well as many endemics (Goldblatt 1978).

Riccia limbata is another species from the winter rainfall areas of the Cape. It has also been reported from Australia. After examining some of the collections from Australia, I have, however, wondered whether they were correctly referred by

Seppelt (1974) and by Na-Thalang (1980), but Seppelt (pers. com.) does not appear to agree with me. If correctly placed, this probably is the sole example of a seemingly 'endemic' southern African *Riccia* species (here strictly confined to the western Cape), that we also share with Australia. An interesting explanation for this kind of disjunct distribution pattern was suggested by Dr H.F. Glen, NBI, in that formerly, sailing ships used soil from Paarden Island, Cape, as ballast and sometimes stranded on the Australian West coast. Plants contained within the soil, would have succumbed to the salinity of the ocean, but perhaps some spores could have survived. On the other hand, one could argue that the Australian plant is a vicariant species, or that it was formerly widespread across Antarctica, which served as a landbridge between southern Africa and Australia (*Monocarpus*, for example, is a genus found only in these two areas). In my experience, however, the endemic *Riccia* species from the Cape have narrowly restricted distributions.

In the summer rainfall areas of southern Africa, there are rather fewer endemic *Riccia* species. These are *R. mammifera*, *R. montana*, *R. natalensis*, *R. pottsiana*, *R. volkii*, as well as a number of species in section *Pilifer*, namely, *R. albovestita*, *R. ampullacea*, *R. elongata*, *R. simii*.

Riccia ampullacea, *R. montana* and *R. trachyglossum* may be regarded as examples of the evolution of endemic taxa in mountains. *Riccia bullosa* is known from the Drakensberg mountains of Natal and Lesotho as well as fom the Cape.

Species in section *Pilifer* are thought to be strictly endemic to southern Africa, but there appear to be two exceptions: a) some specimens from the Canary Islands, that were incorrectly assigned by Arnell (1961) to *R. concava* (Perold 1989d); b) another species in this section that was recently reported by Jovet-Ast (1986) from Iles Crozet, southeast of the Cape. If they evolved in southern Africa, as seems likely, how did they get to these places?. This is a question raised by Jovet-Ast (1986) herself. Wind dispersal to the Crozet Archipelago is a possibility, as the northwesterly winds can reach gale force in winter, or else it could have been introduced (to either of these localities) by birds or by passengers disembarking from boats (Jovet-Ast 1986). Schuster (1982) reckons that Iles Crozet (and Tristan da Cunha) were recently deglaciated and both are geologically relatively young. According to Jovet-Ast (1987), members of section *Pilifer* are either very ancient, but incapable of vast dispersion, or else relatively young, appearing after the break-up of Gondwana and could not reach the other continents. I would certainly subscribe to the latter view.

In making phytogeographical pronouncements, it is difficult to distinguish between disjunctions that may be due to long-distance dispersal and those due to interruption of a previously more continuous range (Poynton 1983). Some can only be explained by continental 'rafting' (with very slow evolution, or none at all), whereas other disjunct species may be relicts that survived in refugia. Therefore, lack of knowledge about geological events, especially the positioning of the plates and the timing of their breakup, coupled with the inadequacy of the fossil record, prevents one from expressing anything more than speculative views. What is certain, however, is that southern Africa, with 51 species of *Riccia*, 75% of which are probably endemic, is to be regarded as a major centre of diversity and of endemism.

On Map 64 three adjacent grids in the western and southwestern Cape (winter rainfall region) with more than 10 endemic *Riccia* species per geographical degree square are identified; in the southern Orange Free State (summer rainfall region) there is only one grid. This grid, however, includes Bloemfontein, where more intensive collecting has probably taken place than in most other areas. It is possible that uneven collecting could produce artefacts. Regardless of that, the species in the two regions are quite different, so that one must conclude that there are two centres of diversity in southern Africa, one in the winter rainfall area, and another in the summer rainfall area.

C. Morphological criteria

Because the fossil record is so meagre, phylogenetic speculations have to be based on evidence provided by the intensive study of extant plants. A resumé of morphological and physiological characters of the Ricciaceae is therefore given. As there is no consensus as to which characters are derived (apomorphic) and which are primitive (plesiomorphic), certain assumptions would have to be made. It is also difficult to assess the direction of evolution, and it must be borne in mind that all characters did not evolve at the same rate. Schuster (1984) states that 'in order to determine the direction of evolution it is necessary to try to determine the presumed nature of the ancestral type or types', an exercise which will be attempted further on in this chapter.

Ecologically the Ricciaceae are pioneers: some have radiated into mesic or xeric open terrestrial areas, whereas others have colonized temporary water habitats. Hygrophytic Ricciaceae could perhaps be regarded as more primitive than xerophytic ones, on the basis of the evolutionary tendency from water to land. Those that are aquatic may have become secondarily so. Species of *Riccia* are adapted to a wide range of habitats, and must generally survive under nutrient-poor conditions, as they are weakly competitive. Most are perennial xerophytes, able to persist for shorter or longer periods, whereas others are annual or even ephemeral.

a. Vegetative Gametophyte

The life cycle of the Ricciaceae, as of all bryophytes, involves an alternation of generations with dominant, free-living gametophytes. This is a primitive character common to the bryophytes and it is likely that the initial reaction of the gametophyte on becoming progressively more terrestrial, may have been toward a prostrate applanate form, i.e. toward a thallus (Schuster 1984). The thallus condition is therefore presumed to be derived and not ancestral. The plants remain small because, with progressive adaptation of the gametophyte to a land environment, selection would place limits on how large they became (Schuster 1984). Growth of the thallus is by a cuneate apical cell with four cutting faces (Crandall-Stotler 1981) and branching is dichotomous, which is a primitive feature, or else, it may even be revertant in the Ricciaceae. The growth form is usually in partial or complete rosettes. Most species are homothallic, but a few are markedly heterothallic, namely *R. cupulifera*, *R. curtisii* and *R. perssonii*. This is also regarded as primitive. Hybridization has not been found, which shows the Ricciaceae to be a stable group (Jovet-Ast 1986).

The thallus is histologically complex with a dorsal epidermis or epithelium and a ventral epidermis. They enclose two layers: (a) an upper assimilation tissue layer with chlorophyllose cells which surround air canals or air chambers, these opening via dorsal pores; (b) a lower storage tissue layer in which the cells contain starch. In the archaic relict from Australia, *R. caroliniana*, the assimilation tissue is, however, ventrally situated. Species with a compact anatomy are regarded as further advanced than the more primitive hygrophils with loose air chambers. The assimilation tissue, which functions in gaseous exchange, has developed from the apex by internal schizogenous cell wall separation. There are, however, no morphologically distinct tissues for water uptake and conduction, nor can these plants control water loss. Instead, we often find a combination of physiological drought resistance adaptations linked with structural adaptations to delay water loss (Schuster 1984), or to increase water uptake and retention.

b. Adaptations to xeric conditions

Many species of *Riccia* are able to suspend metabolism or aestivate during drought, when the tissue water diminishes. In the dry state, some are very heat-tolerant and are able to withstand temperatures in excess of 80 degrees centigrade. When rain does eventually fall their unique protoplasmic properties enable them to revive quickly (referred to as 'la faculté de reviviscence' by Jovet-Ast (1987)) and to resume normal life processes even after years of desiccation (Volk 1984).

The evolutionary development of such poikilohydric features, in which they have little control over rates of water uptake and loss, but can tolerate severe desiccation, can be regarded as one of the dominant trends in the phylogeny of xerophytic *Riccia* species. To delay water loss, even, as Watson (1964) rather dramatically expresses it, 'holding tenaciously that minimum quantity of water which is necessary for survival', there has been thickening of the walls of the subepithelial cells in *R. sorocarpa* (Bischler & Jovet-Ast 1981) and to a certain extent, this has also occurred in *R. atropurpurea* and in *R. argenteolimbata*.

Volk (1984) has shown experimentally that water is not taken up by the dorsal surface of the thallus, as it is not wettable in most species, but species such as *R. garsidei* (and the proximal parts of *R. bullosa*) have large open air cavities, whereby they can increase their water uptake. To retain water temporarily, the hollow 'cups' left by the collapsed dorsal cells in many species serve as tiny reservoirs (Bischler & Jovet-Ast 1981). In members of section *Pilifer*, most of which are well adapted to xeric conditions, the cells in the loose dorsal pillars become distended with water when wet; possibly they then also act as small reservoirs, and do not only retard transpiration or insulate the plants against intense light. Another device that may aid the survival of some species or diminish climatic stress, is the breakdown of the cells of the dorsal epithelium, except in the groove. The assimilation tissue thus lies in direct contact with the atmosphere, or it can take up water over its whole surface

(Bischler & Jovet-Ast 1981), after removal of the water repellent dorsal epithelium. Shiny or crystalloid crusts occurring on the upper thallus surface of some species, e.g. *R. albolimbata* (and *R. alboporosa*), could reflect light, thus reducing the heat endured by the thalli (Volk 1984).

Many xerophytic species have developed large ventral scales, between which water can circulate by capillarity and even be stored for short periods. Some species grow in dense stands and are able to retain water for longer periods than scattered colonies. It is also presumed that species in dense stands form a more stable community and that this is a significant evolutionary strategy which evolved rather later (Schuster 1984). Speeding up of the life cycle, as in *R. sorocarpa* where it can be completed in as little as three weeks, is an adaptation to the unpredictable nature of some habitats (Schuster 1984).

Thus, if it is assumed that those species which have adapted well to xeric conditions and to intense light are more advanced, the hygrophilous species must of necessity be more primitive or else revertant, if they had earlier acquired the characters for adaptation to a xeric environment, but now occupy moist habitats (Nehira 1987).

c. Dorsal air pores

The dorsal air pores in many species of section *Riccia* from drier localities, are 3- or 4-sided, but in *R. nigrella* and *R. argenteolimbata* they are almost exclusively 3-sided. Volk (pers. comm.) regards the latter as derived, as they are formed by a denser packing together of the cell columns and are transposed across the width of one half cell. In species with less compact assimilation tissue, the pores are larger and 4—6- or even 7-sided (e.g. *R. albolimbata*), whereas species in subgenus *Ricciella*, which are generally hygrophyllous or even aquatic (probably secondarily so), have pores which are frequently encircled by a ring of thin-walled, smaller companion cells, partly overlying the somewhat thicker-walled epidermal cells (section *Ricciella*). These are referred to as protostomata by Jovet-Ast (1987), and because they are raised, she regards them as derived, as opposed to species in section *Spongodes*, where the pores are simple and enclosed by mostly unmodified, but sometimes rather smaller epidermal cells.

In some Marchantiales species, the receptacles bear compound pores, but their thalli have simple pores. Because the reproductive system is evolutionary conservative, it has sometimes been interpreted that the compound pores are 'primitive' and that simple pores are 'reduced'. Schuster (1984) says, however, that it is more likely that the compound pore is an adaptation of the elevated and hence more exposed carpocephalum. This serves to illustrate different ways in which the same structures can be interpreted.

d. Ventral scales or cilia

The ontogeny of ventral scales has not been adequately studied (Schuster 1983). They may be vestigial as in *R. purpurascens* or occur ventrally in a single median row as in *R. stricta*. In other *Riccia* species they are in two ranks. Many xerophytic species have developed large ventral scales, either pigmented as in *R. limbata*, or bleached as in *R. villosa* and *R. albolimbata*, or they have cilia, as in *R. trichocarpa*. Scales and cilia arch over the dorsal face as the sides of the thalli turn up and roll inward, with the dorsal epithelium and pores eventually hidden and protected between the two connivent flanks. This is a further adaptation to hot, arid conditions and hence is derived.

e. Rhizoids

Ventrally both genera have dimorphic rhizoids, smooth as well as tuberculate, as opposed to the monomorphic rhizoids presumably found in the ancestral form.

f. Asexual reproduction

Various forms of asexual reproduction have evolved, to allow survival for protracted dry periods. These are bulbils or turions as in *R. atropurpurea* and *R. argenteolimbata*, or subterranean stolons ventrally attached to the thallus by a pedicle as in *R. purpurascens* and *R. rubricollis*. The bulbils and stolons can regenerate when the thallus has died. Many species can regenerate from the protected apical cells, or indeed from any other cells of the thallus. Taxa that are able to propagate by asexual means as well, have an advantage over those that can only propagate by sexual means. The ability to maintain populations by asexual propagation may have been crucial in allowing survival under marginal climatic conditions, during periods of climatic stress.

g. Sexuality and sexual reproduction

Water is required for fertilization to take place, this being a relict of the amphibious ancestral type. Since

the motile spermatozoids are waterborne, fertilization could happen more readily if male and female gametangia were juxtaposed, than if they were located in separate plants. Monoicous taxa, e.g. *R. okahandjana* certainly produce sporophytes more readily than dioicous ones, e.g. *R. rosea*, *R. argenteolimbata* and *R. villosa*. It has been suggested that monoicous taxa predominate in deserts or semi-deserts, i.e. regions unfavourable for fertilization.

There are apparently strong tendencies for an increase in bisexuality when comparing generalized taxa with specialized ones. Regarding sexuality in *Riccia*, Longton & Schuster (1984) report that 85% of species are bisexual, but in southern African taxa, the figure is definitely lower at about 60%. It therefore appears that in southern Africa, there is a higher percentage of more generalized, dioicous taxa, despite the rather low rainfall in most of the country.

Schuster (1984) maintains that in the Hepaticae there is a direct relationship between primitiveness and unisexuality, with species of stenotypic and/or primitive orders like Monocleales and Sphaerocarpales being unisexual. The spores of unisexual taxa are also supposed to be less effectively dispersed than bisexual taxa, although ineffective dispersal may be partially overcome by the wide range of phenotypic, gametophytic plasticity in *Riccia*. However, if a species is unisexual, but frequently produces gemmae, e.g. *R. argenteolimbata*, then its potential for sexual reproduction should be enhanced, but need not necessarily be realised.

Sexual reproduction is the norm in most species of *Riccia*, but it makes additional demands on the gametophyte. Antheridia are initiated by four androgonial initials and the neck of the archegonia consists basally of six neck cell rows. The gametangia are produced in a simple acropetal arrangement, which is an unspecialized trait. Sometimes the acropetal sequence of archegonia or antheridia is interrupted, the gametangia being separated by regions of sterile tissue, e.g. in *R. purpurascens* (Perold 1990). There is no sharp periodicity in gametangium and/or sporophyte development. In many species both sex organs and sporophytes are produced in continuous acropetal sequence, but in the monoicous species, *R. congoana*, male and female gametangia are seldom produced simultaneously and sporophyte production is rare. It may be that this mainly central African species, which frequently sporulates in the tropics, is in the Transvaal near the fringes of its range and that its fertility is reduced. On the other hand, self-fertilization may be prevented since male and female gametangia are temporarily separated, but still a 'late' archegonium can be fertilized by an 'early' antheridium, as does occasionally happen.

Obligate self-fertilization would result in minimum levels of genetic diversity between individuals within a population, but the short-term advantages of high spore production may outweigh the long-term benefits of diversity, when the environment is stable. In the face of long-term environmental change, uniformity and an incapacity to change, would of course, put such a self-fertilizing population at risk of extinction (Schuster 1984).

Originally it was thought that hepatics with highly complex sporophytes are derived and that those with simple sporophytes, such as the Ricciaceae, where the seta is lacking and the capsule enclosed by the gametophyte, are primitive. Schuster (1984) points out that simple economy would dictate that less 'effort' should go into the sporophyte and that it should make fewer demands on the 'host' gametophyte, and not become progressively more elaborate. In the Ricciaceae the sporophyte is reduced to its basic function of spore production, i.e. it is simply 'a bag of spores'. The Ricciaceae are therefore better adapted and have become an end point of evolution in the Hepaticae.

The internalized sporophyte is protected against desiccation. In xerophytic species the capsule generally projects dorsally and in hydrophytic or aquatic species it usually juts out ventrally, so that when the spores are liberated, they can be dispersed by water. Nutrition of the spores takes place through the delicate, unistratose capsule wall, as there are no nurse cells. The capsule wall has no thickenings, is cleistocarpic and dehiscence lines are lacking. The spores are freed when the capsule wall disintegrates and after the partial decay of the surrounding gametophyte tissue.

h. Spores

The spores have become increasingly larger and this state seems to have been selected for under xeric conditions, as they would have considerable food reserves to draw on, when germination occurs. Elaters can have little or no effect in loosening up such large spores, or in their subsequent dispersal, should elaters indeed play a role here. They have therefore become obsolete and are totally eliminated.

A highly ornamented thick and rigid spore coat, which is usually brown in colour and so increases their tolerance against radiation, has developed. It also enables the spores to tolerate frost as well as long, dry periods when germination cannot occur. According to Schuster (1984), the evolution of larger spores does not appear to restrict wide dispersal of such taxa. Even if it did, as Van Zanten (1984) maintains, the durability of the spores may cancel out any potential loss in dispersibility due to their increased size and mass.

In southern African *Riccia* species there seems to be no close correlation between the size of the spores and the number of spores produced per capsule. Small species like *R. microciliata*, *R. nigrella* and *R. pottsiana*, which have spores ranging in diameter from 60—90 μm, produce 100—170, 160—230 and about 320 spores per sporangium respectively. In *R. alatospora*, also a small species, 150—200 spores, which are 90—110(125) μm in diameter, are produced and in the related, but larger species, *R. hantamensis*, the spores are smaller at 60—85 μm, and 900—1 200 per capsule were counted. In other larger species, such as *R. congoana*, with a spore size of up to 135 μm in diameter, the spore production is 250—300 per capsule; in *R. bullosa* with a spore size of up to 150 μm, about 700 are produced. In the permanently tetrad-bearing species, *R. curtisii*, 64 tetrads measuring 100—125 μm across, were counted, while in the larger thalli of *R. tomentosa*, up to 300 tetrads of 115—145 μm across, were found. In the sometimes aquatic species, *R. stricta*, which is also rather on the small size, although elongated, about 270 spores of 50—70 μm diameter are formed. It does not produce many sporangia either, so that one cannot deduce that increased sporophyte production would make up for the relatively fewer spores produced per capsule. Generally speaking, it would appear that species with larger thalli produce a larger number of spores per capsule, irrespective of the size of the spores.

Spores can remain viable for years and according to Schuster (1984), increased duration of viability seems to be a modern adaptation. In *R. albovestita* the spores were able to germinate six years after collection. As discussed before, spores may be dispersed by wind, water or animal agents and the roughened wall could be of importance for overland dispersal over short distances during heavy rainfall, because of a 'rolling' effect (Berrie 1975). The protuberances on the spore wall are also presumed to aid spore dispersal by sticking to animals' fur or birds' feathers, or perhaps to the feet of both.

Jovet-Ast (1987) is of the opinion that the smooth spores of *R. crustata* and *R. albida*, which lack ornamentation, must be quite primitive. As more advanced, she regards those with reticulate ornamentation, although the archaic relict from Australia, *R. caroliniana*, has this type of ornamentation. Possibly this serves to illustrate that 'synchronised' evolution of the sporophyte and the gametophyte did not occur. Jovet-Ast (1987) regards the papilla-like, sinuous ornamentation in *R. villosa* spores as most advanced. Tetrad spores which have spiny projections (echinule), she thinks are primitive, because the species that belong here are primitive in other features. Inoue (1960) also considered the permanently united tetrad a primitive spore type, but Schuster (1966) thinks that tetrads in *Sphaerocarpos* and *Riccia* are strictly a derived feature, because they are exceedingly specialized and occur in very derived groups.

In a transmission electron microscopical (TEM) study of the spore-wall of 14 species of *Riccia*, Thaithong (1982) showed that there is a basic similarity of the intine layer, but variations in the exine, such as the thickness of the layers, the size of the granules and their density and the gaps between laminae are quite evident. In the subgenera *Riccia* and *Ricciella*, some species of each subgenus have the same exine structure and Thaitong suggests that this points to the possibility that these species in the former subgenus may have evolved from the latter subgenus or vice versa.

i. Spore germination and sporeling development

Spore germination in the Ricciaceae is exogenous and is initiated by dehiscence of the spore wall on the convex distal face, followed by the formation of a germ pore between the areolae and the emergence of a germ filament through the pore. The filament enlarges into a germinative tube and at its tip, it produces a quadrant which has four cells in two tiers. More cells are formed at the top of the quadrant, producing a plate, which elongates into a column. The germ rhizoid is produced from the basal cell of the filament, when it consists of a few cells. On the basis of differences in germ rhizoid formation, Inoue (1960) recognized seven different patterns: the Ricciaceae belongs to the *Stephensoniella* type and is characterized by the absence of a septum between the germ rhizoid and the germ tube. Duthie & Garside (1937) interpreted the 'quadrant' type of embryo as derived by modifi-

cation of the filamentous type.

The pattern of sporeling development is supposed to be an important factor in phylogenetic studies, but there is actually limited phylogenetic linkage; variation can occur even within the same genus (Schuster 1984).

When sporelings are produced during a wet period, subsequently followed by a dry one, the sporelings will die if they are not resistant to drought. Only if they are drought-tolerant, may they be able to survive. Drought-tolerance of sporelings may thus influence the effectiveness of species dispersal, but data on the drought-tolerance of liverwort sporelings are scarce (Van Zanten & Gradstein 1988).

The morphology of the Ricciaceae has here been surveyed in some detail in order to demonstrate its significance in evolutionary decisions and its importance in discussions of ricciaceous origins and inter-relationships. However, morphology depends on complex interactions of genetic, epigenetic, physiological and ecological factors; and phylogenetic derivations based on morphology may not be linear (Bischler 1988). Indeed, Schuster (1984) says, we must conceive of a 'bush-type' phylogeny, not a 'tree-type'.

D. Cytological criteria

The cells of the Ricciaceae are mostly thin-walled; only in a few rare species, such as *R. sorocarpa*, *R. atropurpurea* and *R. argenteolimbata* has there been a thickening in the walls of the subdorsal cells and in *R. schelpei* of the dorsal cells. The cells of the epithelium, in the relevant species where they can be uni- or bistratose or pillared, are echlorophyllose, whereas the epidermal cells in the other species and the assimilation tissue cells in all species, contain numerous chloroplasts. The storage tissue cells generally contain starch granules. Oil cells are present in *Ricciocarpos natans*, but are absent in all the subgenera of *Riccia*. Two species, *R. macrocarpa* and sometimes *R. nigrella*, contain idioblasts, but their function is not known.

a. Nuclear cytology

It has generally been accepted that traditional means of assessing evolution within the bryophytes include determination of the chromosome number, as well as karyotype analysis. The chromosome number has mostly been regarded as a critical factor with regard to the phylogeny of the Marchantiales, and some recently established numbers may need to be verified.

In the Ricciaceae the basic, haploid chromosome number is n=8 or multiples of 8 (16, 24) (Jovet-Ast 1970). In southern African species, as far as can be ascertained, nearly 60% have only n=8 chromosomes, but numbers of 9, 10, 12, 15, 17 and 20 have also been recorded, with some species having several different karyotypes (Bornefeld 1984, 1989). Tatuno (1959) considered the basic number of n=8 to be primitive, but Schuster (1966) expressed the opinion that, in view of the very specialized morphological and biological features of *Riccia*, this judgement should be challenged.

Chromosome formulae in liverworts owe their terminology to Tatuno (1941), who distinguished between V chromosomes with median centromeres, J chromosomes which are acrocentric and I chromosomes which are telocentric. Thus the basic formula is as follows: 1I + 2J + 4V + 1m (the latter is a microchromosome). Bornefeld (1984), however, chooses to refer to the chromosomes in the Ricciaceae as A, BB, CC, DD and E, and regards them as derived from an ancestral set of A B C D E by three-fold aneuploidy, which he interprets as the most primitive in the Marchantiales (Bornefeld 1987b). He arranges the chromosomes according to size, i.e. from large to small, starting with A, the largest chromosome. Homologous chromosomes are, however, not necessarily of the same size.

An added refinement to distinguish between chromosomes is to measure the length of each chromosome and to compare it to that of the A chromosome, as was done by Bornefeld (1984). According to Bornefeld (1984), in all those instances where chromosome numbers are a multiple of 8, this is not accomplished by diploidy or polyploidy of the original chromosome set, except for the sole example of *R. atropurpurea* (n=16), where this is indeed so, and this is then referred to as eudiploidy. For the heterogeneous multiplication of different chromosomes, which results in a multiple set of the original 8 chromosomes, the term 'nothopolyploidy' is used. Bornefeld postulates that polyploidy is further derived (or advanced) than the haploid set and that eupolyploidy is further derived than nothopolyploidy. He also believes that most bryophyte species are aneuploid to various degrees and only exceptionally are they haploid. Newton (1983), among others, clearly states that categorical evidence that most hepatics are basically haploid,

seems to be wanting, but that they are basically diploid, is controversial, although it remains the more plausible of the two alternatives.

Chromosome numbers have been determined by Bornefeld (1989) for most of the southern African *Riccia* species. Polyploidy appears to occur naturally in several of our species, but does not confer distinct morphological characteristics on the plants. *R. argenteolimbata* is an extreme example, as it has five chromosome numbers and six karyotypes (Volk *et al.* 1988), none of which can be distinguished in the morphology of the plants. These data obviously do not support the use of chromosome numbers for the taxonomic differentiation of *Riccia* species. The genetically different forms can be told apart only in living material, and then solely by chromosome number. Such studies can, however, show the incipient differentiation processes and may supply data for judging the future evolution of a taxon (Szweykowski 1982).

Newton (1990) remarks that, polyploidy in bryophytes appears to present an effective barrier to sexual reproduction between the original and the derived chromosome number. In self-fertilizing species with diploid or polyploid gametophytes, recombination of alleles is possible in the sporophytes, when the gametes involved are heterozygous at one or more loci (Schuster 1984). In some bryophytes doubling of the chromosome number may lead to a shift from dioicy to monoicy, according to Smith (1978), but in the Ricciaceae this change in sexuality has not been observed. *R. argenteolimbata* is dioicous in spite of 'doubling' or even 'trebling' of its basic chromosome number, whereas *R. rosea* which has n=8 chromosomes, is also dioicous. Neither of them frequently produce spores, however.

Chromosome numbers in southern African *Riccia* species do not appear to provide conclusive insights regarding their phylogeny or relationships. Greater emphasis on the study of the molecular composition and structural conformation of the chromatin itself, particularly as it relates to differential expression as euchromatin and heterochromatin could, however, provide valuable information in this respect (Newton 1983), but has not yet been done.

E. Biochemical criteria

Knowledge of the chemical compounds present in the Ricciaceae is necessary to understand their biological properties and can also shed new light on whether individual taxa are primitive or advanced. However, biochemical information does not always fit in with interpretations of bryophyte evolution based on more traditional criteria. Suire & Asakawa (1979) thus report a primitive flavonoid pattern in *R. crystallina* (naringenin and apigenin) which is otherwise considered by some to be a much reduced and therefore advanced taxon. Other members of the genus, e.g. *R. fluitans*, as well as *Ricciocarpos natans*, are reported to have more advanced flavonoids (luteolin derivatives). Suire & Asakawa (1980) suggest that these findings may indicate that the Ricciaceae is an ancient group or else heterogeneous, or it may be that their flavonoid biosynthesis is capricious. Flavonoid chemistry is nevertheless regarded as a valuable indication of the level of biochemical sophistication reached by a species. Quite a number of species in the Marchantiales have already been investigated for flavonoids (as well as terpenoids and aromatics). Flavonoids probably occur in all the members of the order. In the only southern African *Riccia* species in which flavonoids have so far been investigated, *R. stricta*, Markham (pers. comm.) found a wide range of these compounds, most of which he (Markham *et al.* 1978) had reported for *R. fluitans*; in fact, there were no components by which *R. stricta* could be distinguished chemically from *R. fluitans*.

Terpenoids are exclusive to hepatics with oil cells, so that they are absent from the genus *Riccia*, but they have been reported as sesquiterpene lactones in *Ricciocarpos natans* by Wurzel & Becker (1989).

Lunularic acid has been reported (Huneck 1984) in a few *Riccia* species, namely *R. angolensis*, *R. ciliifera*, *R. fluitans* and *R. gangetica*. Lunularic acid, a non-polymerised phenolic compound, is apparently only found in liverworts, and according to Suire (1975), it links the metabolism of the hepatics to that of the algae.

Kohn *et al.* (1988) investigated the presence of acetylenic fatty acids in 12 *Riccia* species. Their presence was apparently found to be a genus-specific character in the species examined. In *Ricciocarpos natans* acetylenic fatty acids were absent, but the fatty acid pattern was very similar to that of the Marchantiaceae and also resembled that of the Oxymitraceae, another member of the Ricciineae. These acetylenes are long-chain fatty acids with a characteristic arrangement of triple and double bonds and it is hypothesised that their presence in *Riccia*, *Monoclea forsteri* and certain mosses, indicates that these taxa have not evolved too far from a common ancestor. On the other hand, it is

clear that the above data, when interpreted as phylogenetic trends, do not support the same affinities as those based on the morphology.

The enzymes, malate dehydrogenase and peroxidase, were electrophoretically surveyed by Dewey (1988) in North American specimens assigned to 16 *Riccia* species. Using starch gel as the conducting medium, distinct allozymes could be identified by isozyme banding patterns, which appeared to be species-specific. Zymograms thus provide an additional phenotypic character, but the electrophoretic data obtained by Dewey in this study did not permit phylogenetic inferences to be drawn within the subgenus *Riccia*.

Immunochemical assays by Hartung *et al.* (1987) showed that abscissic acid is produced by several species of the Marchantiales; among them five *Riccia* species were investigated. The authors expressed the view that the level of ABA-like immunoreactivity could be an indication of the biosynthesis of stress-induced substances.

Other chemical compounds that have so far been identified in a few species of the Ricciaceae, are the following: chlorophyll a and chlorophyll b; the carotenoids, and carotenes, lutein and epoxylutein; phytosterols, including stigmasterol and sitosterol, and the enzymes ascorbic acid, oxidase and catalase.

On the basis of chemical evidence, Asakawa *et al.* (1980) concluded that the Ricciaceae is one of most isolated families among the Marchantiales, suggesting that its origin is probably different. Unfortunately, information on the ultra-structure of the Ricciaceae, other than the spores studied by Thaitong (1982), is not yet available; it can, however, be expected to contribute significantly to the systematics and phylogeny of the family.

■ ■ ■ ■ ■

In an attempt to construct a phylogeny of the southern African Ricciaceae, the following table (Table 2, page 86) has been drawn up to try and pinpoint primitive characters (on the left) as opposed to those that are advanced (on the right). The assignment of traits to 'primitive' or 'advanced' status is tentative, but is still problematical and sometimes even rather arbitrary. Unfortunately there is also no way of telling to what extent the evolutionary processes of convergence, parallelism and divergence have distorted the developmental pattern as it appears in the modern representatives of the family. Generally speaking, convergence is a major consideration in phylogenetic speculation of this kind. This is due to the low number of character states for each given character, as well as the strong tendency toward reduction displayed by the Ricciaceae.

On the basis of the more primitive characters in the family (and other groups), it is here postulated that the ancestor of the Ricciineae, which may have originated in the Permian, would have occupied damper, terrestrial localities than the more specialized xeric taxa that evolved later. This hypothetical ancestor would have been a short-lived annual and fairly delicate, living in scattered colonies with the growth form prostrate, applanate, the branching probably dichotomous and the assimilation tissue spongy and ventrally situated, as in the Australian relict, *R. caroliniana*. The rhizoids would probably have been monomorphic (smooth), the air pores compound, and scales absent or vestigial; oil cells would have been present, the sexual condition dioicous, with some degree of gametophytic heterothally; the gametangia would be acropetally arranged and the sporophyte probably not entirely sunken into the gametophyte, but with marked reduction of the seta; elaters would be present but non-functional, the spores would probably be in tetrads, and less than 50 μm in diameter, with the wall beginning to darken and thicken; the ornamentation would be smooth to faintly reticulate and the spores would probably not be viable for long. In this exercise at attempting to postulate a hypothetical ancestor of the Ricciaceae, it would, however, be fitting to recall Schuster's (1984) comment that 'a *Riccia*-like ancestor is fiction'. Evidence for making any of the above assumptions is lacking and thus they are merely speculative.

As the present intuitive, subjective and anecdotal approach to phylogeny is unsatisfactory, the classificatory value of a cladistic analysis should be explored in the future and the methodology compared with the traditional phenetic approach. With the current state of our knowledge, however, it does not appear to be possible to construct a reliable phylogenetic classification of the Ricciaceae. There are still too many unanswered questions concerning the cytogenetics, chemistry, ultrastructure and even the taxonomy of the species from all the different continents.

Another subject for future study would be the investigation of isozymes in species of section *Pilifer* and their separation by starch gel electrophoresis, as was done by Dewey (1988) in some species of section *Riccia*. Quite a number of collections at BOL and PRE that belong to section

Pilifer, have not been identified and it is certain that there are more species in this section, than those already described. It is very difficult, however, to distinguish between them vegetatively. The shape, size and number of cells in the dorsal pillars are most important specific characters, but they collapse on drying out and can only rarely be reconstituted well enough to make adequate observations.

Unfortunately the spore ornamentation, such a useful diagnostic character in species of other sections, here displays a spectrum of variation which makes it less reliable. The scales in all these species are hyaline and with rare exceptions, are rounded. These species also appear to be particularly sensitive to environmental conditions. The large number of structurally quite closely related species suggest recent, active evolution, with some of them still in the process of speciation.

Table 2.—**Postulated direction of character evolution in the Ricciaceae**

In a few instances further evolutionary modifications are suggested and are preceded by a question mark (partly after Vitt, Classification of the Bryopsida. In: R.M. Schuster (editor), New Manual of Bryology 2: 723).

Character	Polarity of character states: Primitive	Advanced
Gametophytic:		
habit	prostrate	thalloid
growth form	rosettes	linear
branching	dichotomous	?unbranched
habitat	mesic	xeric
duration of life	annual	perennial
life style	scattered colonies	dense stands
assimilation tissue position	ventral	dorsal
assimilation tissue composition	loose	compact
dorsal pores	compound	simple
rhizoids	monomorphic	dimorphic
scales	absent	present
oil cells	present	absent
chromosome number (n)	8	multiples of 8
polyploidy	absent	present
flavonoids	simple	advanced
asexual propagulae	absent	present
sexual condition	dioicous	monoicous
heterothally	present	absent
arrangement of gametangia	acropetal	?grouped
periodicity of gametangia	absent	?present
Sporophytic:		
sporophyte size	partly reduced	much reduced
sporophyte position	dorsal, with short seta	sunken into thallus, seta lost
capsule wall	thickening of cell walls	thin, unistratose
capsule dehiscence	by dehiscence lines	cleistocarpous
elaters	present	absent
spore size	smaller than 50 μm	larger than 50 μm
spore-wall thickness	thin	thick
spore ornamentation	smooth	reticulate
spore composition	tetrads	monads
spore shape	globular	polar, triangular-globular

CHAPTER 9

CONCLUSIONS

- The Ricciaceae is the most widespread family of all the liverworts and is known from every continent except Antarctica.

- It belongs to the order Marchantiales and is distinguished from other members of the order by its simplified thalli and reduced sporophytes.

- It is regarded as a taxonomically difficult family because the morphological simplicity of the plants offers few diagnostic characters, some of which are subject to environmental modification.

- *Riccia* spores are large, thick-walled and highly ornamented with significant differences between most species.

- In southern Africa the family Ricciaceae is represented by two genera, five subgenera and 52 species, almost three quarters of which are endemic. As far as is known, there is thus greater species-richness over here, than in any other area.

- A suite of characters that generally determines the subgeneric placing of a taxon, relates to the composition of the dorsal cells of the thallus, whether echlorophyllose and homogeneous, in one/two strata or in free-standing multicellular pillars, with the air pores numerous, small intercellular spaces; the dorsal cells can also form a chlorophyllose epidermis interrupted by larger, well-spaced and defined air pores. Other important characters at this level are the composition of the assimilation tissue, whether compact or spongy, and the spore assemblage, whether single or coherent in permanent tetrads. Characters important at the specific level are the presence or absence of cilia or of scales, the colour, size, shape and stance of the latter, as well as the spore ornamentation.

- The greatest concentration of species occurs in two separate areas, one in the western Cape which has winter rain, and the other in the southern Orange Free State which has summer rain. The species in the two areas are quite different so that there are two centres of diversity.

- Species in the western Cape are often narrow endemics, whereas most of those in the Orange Free State extend further northward, frequently even into tropical Africa.

- The stimulus for intensive speciation occurred during periods of aridity, particularly in the western Cape, which experienced a drastic change in climate, to that of a Mediterranean type with winter rain and summer drought, after the glaciation of Antarctica.

- Responses to arid conditions are the ability to revive after long periods of drought and to resume metabolism on wetting, the development of large ventral scales in many species, occasional thickening of some cell walls, the compact composition of the assimilation tissue and presumably the development of free-standing dorsal cell pillars which characterize section *Pilifer*.

- The Ricciaceae may have originated in the Triassic, but where is not known, as fossil evidence is meagre.

- Some species of the Ricciaceae are cosmopolitan or subcosmopolitan and are presumably of Pangaean origin. Others evolved in isolation after the land masses separated in the Jurassic.

- The disjunct distribution pattern of some species may be explained by earlier land connections which have since been obliterated, by continental drift, by long- range spore dispersal or else by step-wise dispersal.

- The large size of the spores could place serious constraints on long range dispersal by wind, but birds or human agents may also be responsible. In short- range dispersal water and animals may play a role.

- The identification of some disjunct species needs to be checked as there is some doubt that *R. limbata* also grows in Australia. It may be a vicariant species. The presence in Australia of *R. runssorensis*, placed in synonymy by Na-Thalang (1980) under *R. macrospora*, is not accepted in this study either.

- Multiple chromosome numbers are found in several species, without this being reflected in the morphology. Due to the small number of characters by which taxa can be differentiated, some species may be less closely related than their morphological features suggest and evolution in the family may actually centre around their biology.

- Biochemical studies have been too few to allow an unambiguous placement of the Ricciaceae.

- With the current state of our knowledge, it is not possible to construct a reliable phylogenetic classification of the Ricciaceae, which, however, appears to represent an endpoint of evolution in the Marchantiales, because of the very reduced sporophytes.

CHAPTER 10

SPECIMENS EXAMINED

For each species, all specimens studied are listed and are held at PRE, unless otherwise indicated. Herbarium acronyms follow Vitt *et al.* (1985). Specimens are alphabetically arranged by the collector's name and then numerically for each collector. Quarter-degree grid references (based on Edwards & Leistner 1971) are given for every collection. This is followed by the country of origin (in parenthesis) for specimens from the rest of Africa, north of the FSA region. Distribution records and collections from the African Islands, including Madagascar, are meagre and have been excluded.

R. alatospora
Duthie 5004, type, 3318DD (BOL, PRE); 5324, 3318DD (BOL). *Naudé* s.n., 3318DD (BOL). *Oliver* 8058, 3318DD. *S.M. Perold* 468, 3318BB; 1425 p.p., 2918CA; 1426, 2918CA.

R. albolimbata
M.J.A.W. Crosby 1029, 3025BD. *Duthie* 5110, 3125AC (BOL); 5438, 3125AC (BOL); 5441 p.p., 2925CB (BOL); 5445, 2925CB (BOL); 5449, 2925CB (BOL); 5469, 3023DA (BOL); 5507, 2926AA (BOL); 5519, 2926AA (BOL). *Germishuizen* 4910, 2825AC. *Glen* 1400, 2330AD; 1404, 2330AD. *Henrici* PRE-CH 3741 p.p., 2926AA. *Herman* 289, 2925AB; 304, 2924CB. *Hoffmann* PRE-CH 4516, 1813AA. *Koekemoer* 501, 2624DC; 504 p.p., 2723DA; 505, 2823AC; 506, 2822DB. *Long & Rae* 920, 2016AA (E). *MacDonald* 77/82, 2823DC. *Magill* 6487 p.p., 2823BC; 6490 p.p., 2823BC; 6499, 2824DA. *S.M. Perold* 217, 2628CC; 222, 2527CA; 228, 2527CA; 339, 2428DB; 398, 2530BC; 454, 2527CD; 699, 2730CB; 719, 2329AD 725, 2329AB; 733, 2229CA; 737, 2228DB; 759, 2228DB; 770, 2228DA; 781, 2228CC; 793, 2228CD; 794, 2228CD; 795, 2228CD; 803, 2229DD; 950, 3025CB; 951, 3025CB; 1206, 2627AD; 1365 p.p., 2728CC; 1366, 2728CC; 1369, 2727BD; 1380, 2624DD; 1382, 2624DB; 1445, 2917DD; 2024, 2724AA. *Pócs* 89010/AH p.p., 0335BA (Tanzania) (EGR, PRE). *Potts* PRE-CH 1010, 2926AA; PRE-CH 1036 p.p., 2926AA. *Reid* 140, 3027AA. *E. Retief* 1459, 1917CA. *Smook* 2929, 3025DA; 3517, 2923DD; 4231, 2327BD; 6583 p.p., 2726DC; 6584 p.p., 2726DC; 7395, 2328BB. *Smook & Harding* 810, 3022CC. *Stephansen* 5393, 2229xx. *Thompson* 277 p.p., 2828DD. *Toelken* 5558, 2118DA. *Townsend* 80/183, grid unknown (Kenya) (Herb. Townsend); 82/14, 2528CA (Herb. Townsend); *Ubbink* 1156, 2627CA (PUC); 1291, 2627CA (PUC). *A.E. van Wyk* 5753 p.p., 2725BB. *Venter* 12197, 2430BB; 21457, 2724AD. *Vogel* T136, 2531CB (MJG). *Volk* 452 p.p., type of *R. albosquamata*, 1918BC (M); 881 p.p., 2017CA (M, PRE); 883 p.p., 2017CA (M, PRE); 01254 p.p., 2416DD (M); 11080, 2217CD (M, PRE); 11419, type, 2217AD (M, PRE); 11705, 2317BC (M, PRE); 11946, 2116DA (M, PRE); 11967, 2116DA; 12744, 2516BC (M, PRE); 81/041, 2827AC (M, PRE); 81/115, 2116AA (M, PRE); 81/146, 1918AC (M, PRE); 81/151, 1918AC (M, PRE); 81/156, 2017AA (M, PRE); 81/164, 1816DC (M, PRE); 81/174, 1816DC (M, PRE); 81/200, 2316BA (M, PRE); 81/210, 2825CA (M, PRE); 81/225, 2827AC (M, PRE); 81/265, 2217CD (M, PRE); 81/289, 2926AA (M, PRE); 84/653, 2827AC (M, PRE); 84/690, 2117DB (M, PRE); 84/703, 1918AD (M, PRE); 84/717, 2116CD (M, PRE); 84/721, 2116CD (M, PRE). *Vorster* s.n., 2430BC. *Wilman* 5517, 2823xx (BOL).

R. albomarginata
Krauss s.n., July 1838 p.p., type, 3318CD (BM, W). *S.M. Perold* 538, 3218BD; 1424 p.p., 2918CA; 1425 p.p., 2918CA; 1610 p.p., 3017BB; 1756 p.p., 3119AC; 1891, 3219AA; 1930, 3218BB; 1979, 3219AC; 2040, 2918CA; 2115 p.p., 3017BD; 2118 p.p., 3018CA; 2122, 3018CA; 2124 p.p., 3018AC; 2357, 3219AC; 2382, 3218BD; 2383 p.p., 3218BD. *C.M. van Wyk* 1489, 3119AC. *Zeyher* s.n., grid unknown, G13117 (G).

R. alboporosa
Magill 3905, 3118DB (F, PRE). *Oliver* 8849, 3119AB; 8854, type, 3119AD. *S.M. Perold* 1772, 3119AD; 1775, 3119AD; 2317, 3119AD.

R. albornata
Duthie 5149, 3125AC (BOL). *Fellingham* 746 p.p., 3420AD. *Levyns* 5532, grid unknown (BOL). *Morley* 362, 3319DA; PRE-CH 4525, 3319DA; PRE-CH 4526, 3319DA. *Oliver* 1463, 3218BB (BOL); 8854 p.p., 3119AD. *S.M. Perold* 1445, 2917DD; 1800, 3119AB; 1801, 3119AB; 2541, 3124AB; 2542, 3124BA. *Russell* s.n., 3121BB. *Smook* 3351, 3024CC; 6837, 3023BC; 6862 p.p., 3023BC; 6928, 3023CD; 6961, 3123AA; 6990, 3123AA. *Smook & Harding* 810, 3022CC. *Steyn* 5487, 3222BC (BOL). *Volk* 81/081, type, 2921AC (M, PRE); 84/667, 2820CB (M, PRE).

R. albovestita
M.J.A.W. Crosby 520, 2728CA. *Du Preez* 2105, 2926AC. *Duthie* 5182, 3319DD (BOL); 5193, 3319DD (BOL). *Koekemoer* 102, 2827CD; 103 p.p., 2827CD. *J.M. Perold* 35, 2927AB; 39, 2927AB; 44, 2927AB. *S.M. Perold* 342, 2629AB; 784, 2228CD; 955, 2926AC; 1317, 2827DC; 1319, 2927BA; 1347, 2827BD; 2026, 2724AA; 2463, 2628BA; 2464, 2628BA; 2465, 2628BA; 2473, 2629AB. *Retief & Germishuizen* 218, 3125BC. *Retief & Reid* 294, 3222DB. *Smook* 4036, 3326BA; 6583, 2726DC. *Van Rooy* 2419, 3026BB. *Volk* 00484, 2314BC (M); 01164 p.p., type, 2217CD (M); 12462 p.p., 2417DA (M); 81/070, 3224AC (M, PRE); 81/272, 3224AC (M, PRE); 81/273, 3224AC (M, PRE); 81/274 p.p., 3224AC (M, PRE); 81/292, 2827AC (M, PRE); 84/646, 3224AC (M, PRE). *Zietsman* 943, 2826DC.

R. ampullacea
Du Preez 2106 p.p., 2927AC. *Van Rooy* 2724, 3027CB; 2971, 2828DC; 3045 p.p., 2828DC; 3050, 2828DC; 3164 p.p., 2928BD; 3207, 2928BD; 3240, 2928BD; 3573, type, 2929CB; 3635, 2929CA.

R. angolensis
Hansen 3459, 2525CA. *Magill* 6371 p.p., 25290CB. *Mendes* 742, 1414CA (Angola) (LISU); 1474, ? 1513xx (Angola) (LISU). *Pearson* 9852, 2115DC. *S.M. Perold* 1275, 2729CD; 1276, 2729CD; 1354, 2828AC; 2466, 2628BA. *Potts* PRE-CH 1036 p.p., 2926AA; 7029, 2926AA (BLFU). *E. Retief* 1235, 3222DB; 1543 p.p., 2217CA. *Schinz* s.n., grid unknown (Angola) (BM). *T.R. Sim* 8644 p.p., 2930CB (BOL). *S.L.* PRE-CH 1044, 2930CB. *Smook* 5897, 3026BB. *Tidmarsh* 10436, 2926AA. *Volk* 863, 2217AD; 5049, 2217CB; 5058, 2217CA; 5313, 2417DA; 12412, 2417DA; 12462, 2417DA; 81/091, 2216DA (M, PRE); 81/261, 2317CA (M, PRE). *Welwitsch* 255, type, ? 1513AB (Angola) (BM).

R. argenteolimbata
Braggins 91/184, NE0036BA (Kenya). *Gibbs Russell & Smook* 5240, 2116AA. *Hardy* 4868, 2716DA; 6586 p.p., 2418DD. *Henderson* 659, 2123BD. *Hoffmann* PRE-CH 4514, 2017AA. *Kreiner* 5, 1914DB. *Long & Rae* 834, 1921CC (E); 842, 1921CC (E); 921, 2014AA (E); 946, 2316AD (E). *Magill* 4955, 2231CB. *S.M. Perold* 339 p.p., 2428BB; 727, 2329AB; 728, 2329AB; 737 p.p., 2228DB; 766, 2228DA; 767, 2228DA; 769, 2228DA; 772, 2228DA; 793 p.p., 2228DC; 794, 2228DC; 957, 2827AC. *Pócs* 87072/A, 0639CD (Tanzania) (EGR). *Pócs & Orban* 89156/APP, 0336BC (Tanzania) (EGR, PRE). *Pócs et al.* 90051/K p.p., 0337AB (Tanzania) (EGR, PRE). *Potts* 7003 B-E, 2926AA (BLFU). *Smook* 4231, 2327BD; 4487, 2922BC; 5118, 1916AA; 5138, 1916BA; 5140 p.p., 1916BA; 5159, 1917AB. *E. Retief* 1422 p.p., 1915AA; 1493 p.p., 1916AA. *A.E. van Wyk* 5753 p.p., 2725BB. *Volk* 00453, 2017AA (M); 00454, 1917DC (M); 00462, 2016CA (M); 00469, 2116DA (M); 00507, 2118DB (M); 00591, 2217DC (M); 00744, 1916CB (M); 00749, 1916CB (M); 00752, 2217CA (M); 00761, 2217DC (M); 00762, 2217DC (M); 00764, 2217DC (M); 00765, 2217DC (M); 881 p.p., 2016CA (M, PRE); 883 p.p., 2016CA (M, PRE); 00910, type, 2116BD (M); 00912, 1915BB (M); 00975, 1916CD (M); 00977, 2016AA (M); 01291, 2317BB (M); 01389, 1815CC (M); 5116, 1916AC (M); 5135, 2016AA (M); 5137, 2014BA (M); 5170, 2116DA (M); 5268, 2417BA (M); 6169, 2117DB (M); 6212 p.p., 2118DB (M); 6386, 2416BB (M); 6439, 2416BB (M); 6856, 2416BD (M); 6860, 2416BB (M); 11906 p.p., 2116CA (M); 81/146, 1918AC (M, PRE); 81/151 p.p., 1916DB (M, PRE); 81/156, 1916AB (M, PRE); 81/164, 1816DD (M, PRE); 81/170, 1916CA (M, PRE); 81/172, 1915BA (M, PRE); 81/174, 1816AA (M, PRE); 81/177 p.p., 1916DC (M, PRE); 81/200, 2316BA (M); 81/210 p.p., 2825CA (M, PRE); 81/265 p.p., 2217CD (PRE); 84/692, 2017AA (M); 84/705, 1918AC (M); 84/713, 2014CC (M); 84/721, 2017AA (M); 85/773, 2017AA (M); 85/775, 2017AA (M); 85/853, 2116AA (M); 86/922, 2118DB (M); 86/930, 2017AA (M); 86/933, 2017AA (M); 86/934, 2017AA (M).

R. atropurpurea
Anderson PRE-CH 13444, 2528CB. *Boughey* s.n., grid unknown (Ghana) (Herb. Jones). *Chadwick* 293, 2431AB. *M.J.A.W. Crosby* 1109, 2724AA. *Een* 1 p.p., 0234BD (Tanzania) (Herb. Een). *Fourie* 23 p.p., 2229DC; 32, 2229DC. *Gibbs Russell & Smook* 5246, 2116AA; 5266 p.p., 2016AD. *Glen* 1377, 2430DA; 1386, 2430AB; 1405, 2330AD; 1406, 2330AD; 1425, 2230BC; 2468, 2526BB. *Hardy* s.n., 2531DD. *Hardy, Retief & Herman* 5293, 2427BA. *E.W. Jones* 457, NE0703DD (Nigeria) (Herb. Jones); 685, 0637DC (Tanzania) (Herb. Jones). *Kemp* 764, 2632AA. *Koekemoer* 263, 3030CB. *Leistner* 3555 p.p., 2528CA; 3559, 2528CA. *Long* 12439, 2127AB (E). *Long & Rae* 827, 2021xx (E). *Magill* 3618, 2329BD; 3619, 2329BD; 3636, 2229DD; 4933, 2331AD; 4935, 2331AA; 4996, 2230DB; 5040, 2331DD; 6407, 2722AB. *Mendes* 1365, grid unknown (Angola) (LISU); 1422 p.p., 1513BA (Angola) (LISU); 1635, 1615CA (Angola) (LISU). *Morley* PRE-CH 13506, 2217AD. *Nicholas* 2159, 2528CA. *J.M. Perold* 46, 2528CA. *S.M. Perold* 70, 2529CB; 89, 2529CB; 91, 2529CB; 92, 2529CB; 93, 2529CB; 94, 2529CB; 104, 2529CB; 106, 2529CB; 107, 2529CB; 108, 2529CB; 109, 2529CB; 111, 2528CA; 123, 2528CA; 124, 2528CA; 133, 2628DC; 136, 2528DC; 141, 2528DC; 145, 2528DC; 146, 2528DC; 170, 2528CA; 171, 2528CA; 172, 2528CA; 180, 2527DD; 181, 2627CB; 186, 2727AB; 187, 2727AB; 190, 2727AB; 191, 2727AB; 193, 2727AB; 1917, 2727AB; 198, 2727AB; 199, 2727AB; 200, 2727AB; 201, 2727AB; 203, 2727AB; 204, 2727AB; 205, 2727AB; 206, 2727AB; 207, 2628CC; 208, 2628CC; 209, 2628CC; 210, 2628CC; 214, 2628CC; 215, 26268CC; 216, 2628CC; 232, 2527AD; 233, 2527AD, 237, 2527AB; 238, 2527AB; 239, 2527AB; 240, 2527AB; 241, 2527AB; 242, 2527AB; 244, 2527AB; 259, 2627BB; 269, 2528CA; 278, 2527DA; 279, 2527DA; 280, 2527DA; 283, 2527BC; 299, 2829DC; 305 p.p., 2930AA; 311, 2829DC; 318, 2528DB; 319, 2528DB; 337, 2428CB; 345, 2629AB; 384, 2530BB; 391, 2530BD; 395, 2530BD; 396, 2530BD; 397, 2530BD; 409, 2430DB; 410, 2430DB; 415, 2430DB; 426, 2530AB; 431, 2529CC; 436, 2428BD; 437, 2428BD; 460, 2628AB; 722, 2329AD; 723, 2329AD; 724, 2329AD; 730, 2229CA; 740, 2228DB; 742, 2228DB; 743, 2228DB; 754, 2228DB; 755, 2228DB; 764, 2228DA; 765, 2228DA; 768, 2228DA; 775, 2228CD; 776, 2228CD; 782, 2228CD; 783, 2228CD; 787, 2228CD; 789, 2228CD; 790, 2228CD; 796, 2228DC; 799, 2229DC; 800, 2229DC; 811, 2428CA; 821, 2428CA; 822, 2428CA; 823, 2428CA; 824, 2428CA; 825, 2428CA; 826, 2428CA; 827, 2428CA; 832, 2427DB; 836, 2428AC; 840, 2428AB; 843, 2328CD; 845, 2328CD; 877, 2427DC; 878, 2427DC; 879, 2527BC; 880, 2527BC; 881 p.p., 2527BC; 886, 2527CC; 890, 2526DD; 959 p.p., 2528BA; 964, 2529AB; 976, 2429DC; 988, 2429DD; 989, 2429DD; 1013, 2530DC; 1014, 2530DC; 1027, 2530DC; 1028, 2530DC; 1069, 2630DA; 1087, 2729BB; 1202 p.p., 2627CA; 1204, 2627AD; 1208, 2627AB; 1210, 2428CD; 1215, 2528AD; 1240, 2728BC; 1241, 2728BC; 1285, 2828BD; 1286, 2828BD; 1305, 2828CB; 1317 p.p., 2827DC; 1352, 2828AC; 1365 p.p., 2728CC; 1370, 2528DC; 1376, 2528DD; 1378, 2528CB; 2003, 2531AB; 2005, 2531AB; 2007, 2530BD; 2435, 2528AD; 2438, 2329DC; 2440, 2329DD; 2469, 2628BB; 2480, 2629AB; 2649 p.p., 1535AD (Malawi). *Pócs & Geissler* 86165/A, 0636DD (Tanzania) (EGR, PRE). *Pócs et al.* 88099/B p.p., 0637DC (Tanzania) (EGR). *Potts* 7002, 2926AA (BLFU); 7004, 2926AA (BLFU). *Reid* 1023, 2732BA. *E. Retief* 1240, 2530DB. *I.M. Retief* 254, 2331CC. *T.R. Sim* 8112, type, 2930CB (BOL, PRE); PRE-CH 1022, 2930CB (BOL, PRE); PRE-CH 1024, 2930CB (BOL, PRE); PRE-CH 1025, 2930CB; PRE-CH 1030, 2628DA; PRE-CH 1837, 2028AD (Zimbabwe). *Smook* 4197, 2328CC; 4267 p.p., 2327BC; 4787, 2526AD; 4803, 2528CB; 4861 p.p., 2530AB; 4892, 2630AD; 5815, 2926DC; 6417, 2729CB; 6583 p.p. 2726DC; 7031, 2725BB; 7032, 2427CB; 7033, 2427CB; 7359, 2329AA; 7430 p.p., 2329AA. *Van Rooy* 1831, 3129BA. *Van Rooy & Perold* 638, 2528CB; 665, 2529CB. *Volk* 931, 1915DB; 2766, 2315DB; 81/011, 2529CB (M, PRE); 81/013, 2529CB (M, PRE); 81/017, 2529CB (M, PRE); 81/022, 2528DC (M, PRE); 81/033, 2727AB (M, PRE); 81/102, 2216CA (M, PRE); 81/112, 2116AA (M, PRE); 81/131, 1918AD (M, PRE); 81/137, 1918AD (M, PRE); 81/214, 2827AC (M, PRE); 81/234, 2628CC (M, PRE); 81/235, 2628CC (M, PRE); 81/250, 2527AD (M, PRE); 81/253, 2525DD (M, PRE); 81/257, 2317AD (M, PRE); 84/645, 2930AA; 84/662, 2820CB; 84/666, 2820CB; 84/700, 1918AD; 84/701, 1918AD; 84/704, 1918AD; 84/710, 2016CC; 84/715, 2216AA. *Wood* 1190, 0031BD (Uganda) (Herb. Jones).

R. bicolorata
Koekemoer 300, 3321AD; 477, 3322DB. *Oliver* 8849 p.p., 3119AB. *S.M. Perold* 1443, 2917DD; 1772 p.p., 3119AD; 2318, 3119AD; 2554, 3421BA. *Smook* 3215 p.p., 3025CA; 6990 p.p., type, 3123AA.

R. bullosa
S. Arnell 714, type of *R. montaguensis*, 3320CC (BOL, PRE); 741, type of *R. montaguensis*, 3320CC (BOL). *Duthie* PRE-CH 1055, 3318DD; 5486 p.p., 3318DD (BOL); s.n. 2/12/1936, 3318DD (BOL); s.n. 20/9/1937, 3318DD (BOL); s.n. 10/1937, 3318DD (BOL). *Ecklon* s.n., type, 3318CD (STR). *Ellis* PRE-CH 13467, 3017AC; PRE-CH 13473, 2828DD; PRE-CH 13474, 2828DD. *Esterhuysen* 26141, 2929AB. *Garside* 3, 3318DD. *Koekemoer* 284, 3320CA; 319, 3219CD. *Lam & Meeuse* 4287 p.p., 3418AA (L). *Magill* 4317, 2929CC; 4401 p.p., 2929CB; 4588, 2828DC; PRE-CH 4509, 2929CB. *Morley* 215, 3318DD; 272, 3318AD; 306, 3319CC. *Oliver* 1466, 3219AB (BOL); 1475, 3319AD (BOL); 1476, 3319CA (BOL, PRE); 7324, 2828DB; 8038, 3018AC; 8777, 3324BB; 8876, 3119BD; 8926, 3120CC; 9555, 3018CB. *S.M. Perold* 467, 3318DD; 510, 3218DC; 536, 3218BD; 555, 3219AC; 562, 3219AC; 566, 3319AD; 1471, 3018AA; 1600, 3017BB; 1615, 3018AC; 1821, 3119BD; 1872, 3119CB; 1874, 3119CB; 1881, 3219AA; 1897, 3219AA; 1919, 3218BB; 1924, 3218BB; 1945, 3219AA; 2097, 3018AC; 2170, 3018AA; 2320, 3119AC; 2335, 3119BD; 2388, 3218BD; 2396, 3218BD; 2400, 3219CA; 2523, 2929CB; 2527, 2929CB; 2528 p.p., 2929CB. *Schelpe* 7690, 2828DA (BOL, PRE); 23856, 2828DD (BOL). *Stirton* 9175, 3219AC. *Thompson* 266, 3028CC; 267, 3028CC; 277, 2828DD; 278, 2828DD. *Van Rooy* 1086, 2828DB; 2995, 2828DC; 3133, 2828DC; 3135, 2828DC; 3136, 2828DC; 3142, 2828DC; 3462, 2929CA; 3535, 2929CB; 3541, 2929CB; 3578, 2929CB; 3579, 2929CB. *leg. unknown* s.n., 3419BA (BM).

R. cavernosa
Acocks PRE-CH 3602, 2824DB. *Anderson* PRE-CH 4507, 2824DB. *Arnold* 4323, 2717DA. *Barker & Reid* 8, 2127DA. *Barnard* PRE-CH 1070, 2820CB. *Bedford* 5411, 3226CA (BOL). *Best* 2672, 1830AA (Zimbabwe) (MO). *Brueckner* s.n., 2824DB (BOL). *Burtt-Davy* PRE-CH 1048, 2627DB. *Buys* 5059, 3225BA (BOL). *Camerik* 189, 2326BB. *Condy* 11, 2330DC. *Garabedian* PRE-CH 1063, 2028BD (Zimbabwe). *Germishuizen* 4943, 2825AC. *Glen* 1802, 2430AD. *Hall* 24858, 1713xx (BOL). *Hilliard & Burtt* 10751, 3224AB. *Junod* PRE-CH 141, 1836CA (Mozambique); PRE-CH 1068, 2532BA (Mozambique). *Koch* 934, 2315CA. *Koekemoer* 367, 2717DA; 368, 2717DA; 369, 2717DA. *Le Roux* PRE-CH 4495, 2917DB. *Lübenau-Nestlé* SA128, 3322CC (Pte. Herb.). *Matthews* s.n., 2820AD (PU). *Oliver* 7309, 2330BD; 9003, 2817AA; 9173, 2816BB; 9488, 3019CC. *Ortendahl* 565, 2719AA. *J.M. Perold* 32, 2927BC. *S.M. Perold* 353, 2629BA; 363, 2629BC; 453, 2527CD; 849, 2328CD; 893, 2527AC; 895, 2527CD; 1395, 2917DB; 1517, 3018AB; 1626, 3018CA; 1807, 3019CD; 1858, 3119CB; 1877, 3219AA; 2023, 2724AA; 2025, 2724AA; 2029, 2820CB; 2428, 3220DA; 2432, 3220DA. *Phillipson* PRE-CH 13482, 3227CA. *Pocs et al.* 87206/P, 0836DA (Tanzania) (EGR, PRE). *I.M. Retief* 174, 2431AA. *Schelpe* 3907, 2229BB (Zimbabwe) (BM, BOL); 7779, 2917DB (BOL); s.n., 3420CA (BOL). *Shearing* 178, 3121DC. *T.R. Sim* 7432, 2930CB. *Smith* 1429, 1922CD; 3605, 1921AC. *Smook* 4786, 2526AD; 5275, 2216DB. *Smook & Harding* 777, 2921CC. *Stephens* 5416, 2217CA (BOL). *Strange* 238, 0136BD (Kenya) (BM). *Van der Merwe* 1416, 2820CB. *Van Hoepen* 1909, 2819DA; 2023, 2819DA. *Van Putten* s.n., 3218BA (BOL). *Van Vuuren* 1767, 2531AD; 1773, 2330CA; 1788, 2531BB; 1800, 2330CA. *Venter* 12198, 2430BB. *Viviers* s.n., 3221DD (BOL). *Volk* 12229, 2018CA; 12446, 2417DA; 81/191, 2217CA (M, PRE); 81/192, 2217CA (M, PRE); 81/211, 2825CA (M, PRE); 81/228, 2827AC (M, PRE). *Wagener* PRE-CH 4496, 2329CD. *Wager* 26, 3322CD; PRE-CH 237, 2028BA (Zimbabwe). *Welwitsch* 257, 1512AA (Angola) (BM).

R. concava
S. Arnell 12 p.p., 3318CD (BOL); 67 p.p., 3318CD (BOL). *Betzler* 139, 2817CD. *Duthie* 5005, 3318DD (BOL); 5407, 3220BC (BOL); 5417 p.p., 3318DD (BOL); 5468, 3319AC (BOL); 5470, 3318DB (BOL). *Garside* 6108, 3318DD (BOL); 6128, 3318CD (BOL). *Krauss* s.n. July 1838, type, 3318CD (G). *Moll* 6025, 3217DD. *Morley* 214, 3318DD. *Oliver* 8949, 3220DA; 8957 p.p., 3220DA. *S.M. Perold* 470, 3318DD; 478, 3318DD; 485, 3318AD; 899, 3322BC; 1414, 2917DB; 1415, 2917DB; 1431, 2918CA; 1432, 2918CA; 1438, 2917DD; 1447, 3017BB; 1454, 3017BB; 1455, 3017BB; 1460, 3018AA; 1465, 3018AA; 1466, 3018AA; 1493, 3018AA; 1500, 3018AB; 1501, 3018AB; 1604, 3017BB; 1773, 3119AD; 1788, 3119AC; 1791, 3119AC; 1792, 3119AC; 1795, 3119AB; 1798, 3119AB; 1888, 3219AA; 2054, 2917DB; 2057, 2917DB; 2091, 3017BB; 2094, 3017BB; 2103, 3017BD; 2104, 3017BD; 2105, 3017BD; 2113, 3017BD; 2115, 3017BD; 2148, 3018AA; 2172, 3018AA; 2173, 3018AA; 2185, 3119AC; 2195, 3119AC; 2312, 3119AC; 2313, 3119AC; 2316, 3119AC; 2362, 3219AC; 2426, 3220DA; 2427, 3220DA. *C.M. van Wyk* 1493, 3119AC.

R. congoana
S. Arnell 1291, type of *R. rhodesiae*, 1825BD (Zimbabwe) (BOL, PRE, S); 1332, 1825BD (Zimbabwe) (PRE, S). *Brusse* 4195, 1917CA. *Dudley* 1930 p.p., 1535AA (Malawi). *Een* s.n., 0234BD (Tanzania) (Herb. Een, S). *Glen* 1378, 2430DA; 1401, 2330AD; 1402, 2330AD; 1423, 2230BC; 1428, 2230BD. *Gittins* 12 p.p., NE0232CD (Uganda)(Herb. Jones); 22 p.p., NE0232CD (Uganda) (Herb. Jones). *Godfrey* G-H1652, 2531AB (NY). *Hardy* 6446, 2230BC. *Herman* 176, 2427DC. *Hoffmann* PRE-CH 4513, 2016BC. *E.W. Jones* 699, type of *R. nigrosquamata*, 0639CD (Tanzania) (BM, Herb. Jones); 712, 0639CD (Tanzania) (BM); 1154, NE0704CD (Nigeria) (Herb. Jones, NY); 1168, NE0703DD (Nigeria) (Herb. Jones, NY); 2252, 0736CA (Tanzania) (Herb. Jones). *Kassas* s.n. type of *R. aegyptiaca*, grid unknown (Egypt) (S, CA). *Kemp* 1273, 2632AA. *Kreiner* 4, 1914DB. *Loveridge* 1217, ? 1730DB (Zimbabwe) NY). *Magill* 3640, 2229DD; 3644, 2229DD; 4952, 2231CB; 4999, 2230DB; 5028, 2231CC. *Mendes* 112, grid unknown (Angola) (LISU); 668, 1313DB (Angola) (LISU); 670, 1313DB (Angola) (LISU); 1474, 1513BA (Angola) (LISU); 1559, grid unknown (Angola) (LISU); 1571, grid unknown (Angola) (LISU). *Mott* 870, 2425DB. *S.M. Perold* 130, 2528CA; 173, 2527DD; 174, 2527DD; 175, 2527DD; 394, 2530BD; 732, 2229CA; 738, 2228DB; 744, 2228DB; 746, 2228DB; 747, 2228DB; 757, 2228DB; 762, 2228DB; 763, 2228DA; 771, 2228DA; 778, 2228CD; 779, 2228CC; 797, 2229CB; 2592, 2526CC; 2658, 1133BB (Malawi); 2686 p.p., 1433BB (Malawi). *Pócs* 8603/A, 0337AB (Tanzania) (EGR, PRE); 89105/A, 0637AB (Tanzania) (EGR, PRE). *Pócs & Kayambazinthu* 87041/W, 0831AC (Tanzania) (EGR, PRE). *Pócs & Hall* 8654/L, ? 0737xx (Tanzania) (EGR, PRE). *Pócs & Murphy* 89135/E, 0637DC (Tanzania) (EGR, PRE); 89136/E, 0637DC (Tanzania)(EGR, PRE). *Pócs & Orban* 89139/A, 0437BA/BB (Tanzania) (EGR, PRE); 89155/A, 0336BC (Tanzania) (EGR, PRE); 89161/A, 0637AB (Tanzania)(EGR, PRE). *Pócs & Persson* 88007/AE, 0636DD (Tanzania) (EGR, PRE). *Pócs & Schippers* 8688/C, 0336BA (Tanzania) (EGR, PRE). *Pócs et al.* 88099/A, 0831AC (Tanzania) (EGR, PRE); 90051/J, 0337AB (Tanzania) (EGR, PRE). *I.M. Retief* 248, 2331CC; 249, 2331CC. *Smook* 5118 p.p., 1916AA; 5139, 1916BA. *Stirton* 6810, 2531BD. *Thompson* 291, 2527CA. *Van der Schyff* 3460 p.p., 2531AA. *Volk* 693 p.p., 2117DB; 722, 1915CC; 747, 1918CA (M, PRE); 978, 2016AA; 987, 2017AC. *Vorster* PRE-CH 13536, 2430BA. *Voz* s.n., type, grid unknown, Congo (G).

R. crozalsii
S. Arnell 33, 3418AB (BOL); 49, 3418AB (BOL); 51, 3418AB (BOL); 67, 3418AB (BOL); 69 p.p., 3418AB (BOL); 231, 3318DD (BOL); 356, 3418AB (BOL); 802 p.p., 3320CC (BOL); PRE-CH 3920, 3418AB; PRE-CH 3921, 3418AB; PRE-CH 3927 p.p., 3418AB; PRE-CH 4125, 3418AB; PRE-CH 4126, 3418AB; PRE-CH 4127, 3418AB; PRE-CH 4128, 3418AB; PRE-CH 4129, 3418AB; PRE-CH 4130, 3418AB; PRE-CH 4135 p.p., 3418AB. *Duthie* PRE-CH 1021, 3318DD; 5018, 3318DD (BOL); 5024, 3319AC (BOL); 5064, 3318DD (BOL); 5076, 3319AC (BOL); 5117, 3318DD (BOL); 5333, 3319AC (BOL); 5436, 3318DD (BOL); 5469, 3319AC (BOL). *Garside* PRE-CH 1065, type of *R. africana*, 3318DD. *Malherbe*

& Davies 5373, 3219AC (BOL); 5374, 3219 AC (BOL). *Morley* 222, 3318 DD; 275, 3319AB; 305, 3319CC; 313, 3319CC. *S.M. Perold* 473, 3318DD; 589, 3320CC; 596, 3419BB; 612, 3419BA; 634, 3319CC; 643, 3418CD; 1149 p.p., 3318DD; 1920, 3218BB. *Pócs & Kabuta* 8682 p.p., 0336BA (Tanzania) (EGR). *C.M. van Wyk* 1492, 3318DD. *Wager* PRE-CH 1027 p.p., 3318CD.

R. crystallina
S. Arnell 150 p.p., 3418AB (BOL); 189, 3418AB (BOL); 1143, 3418AB (BOL). *Duthie* 5006, 3318DD (BOL); 5052, 3423AA (BOL); 5192, 3318DD (BOL); 5216, 3318DD (BOL); 5306, 3318CD (BOL); 5309, 3423AA (BOL); 5313, 2821AC (BOL); 5420, 3318DD (BOL); 5515, 2824BA (BOL). *Duthie & Garside* 5529, 3318CD (BOL). *Koekemoer* 103 p.p., 2827CD. *Malherbe & Davies* 5376, 3219AC (BOL). *Morley* 308, 3318DB. *Oliver* 8912, 3119DD; 8957 p.p., 3220DA. *J.M. Perold* 38 p.p., 2927AB. *S.M. Perold* 364, 2629BC; 455, 2527CD; 487, 3318BD; 894, 2527CD; 1837, 3119DD; 1851, 3119DD; 2433, 3220DA; 2522, 2929CB; 2528 p.p., 2929CB. *Pócs & Kabuta* 8682/P p.p., 0336BA (Tanzania) (EGR). *Schelpe* 4808, 2016BC (BOL). *Smith* PRE-CH 1068, 2925CB; PRE-CH 1069, 2925CB. *Stephens* PRE-CH 1057 p.p., 3125AB. *leg. unknown*, s.n., 3419BA (BM).

R. cupulifera
Armstrong 5310, 3423AA (BOL). *S. Arnell* 187, 3418AB (BOL); 303, 3418AB (BOL, PRE); 591, 3418AB (BOL, PRE); 605, 3418AB. *Duthie* 541, 3318DD; 5007, type, 3318DD (BOL); 5010, 3423AA (BOL); 5018 p.p., 3318DD (BOL); 5321, 3318DD (BOL); 5323, 3319AC (BOL); 5431, grid unknown (BOL); 5523, 3318AD (BOL); 5524, 3318DD (BOL). *Lübenau-Nestlé* SA34, 3318AD (Pte. Herb.); SA35, 3318AD (Pte. Herb.). *Morley* 277, 3319AB; 303, 3419BA; 311, 3318DB. *Oliver* 8043, 3018AC; 8053, 3218BB. *J.M. Perold* 38 p.p., 2927AB. *S.M. Perold* 357, 2629AA; 479, 3318DD; 486, 3318BD; 488, 3318BD; 490, 3318BD; 501 p.p., 3218DC; 591, 3320CC; 597, 3419BB; 609, 3419BA; 641 p.p., 3318DB; 1172, 3419 BA; 1179, 3318DB; 1397, 2917DB; 1418, 2918CA; 1628, 3018CA; 1754, 3119AC; 1961, 3219AC; 1982, 3219AC; 1984, 3219CD; 2371, 3219AC.

R. curtisii
S. Arnell 7, 3418AB (BOL, PRE); 12 p.p., 3418AB (BOL); 301, 3418AB (BOL); 773, 3320CC (BOL); 776, 3320CC (BOL); 786, 3320CC (BOL); 1393, 3322CD. *Duthie* 5018 p.p., 3318DD (BOL); 5486 p.p., 3318DD (BOL). *Garside* 6, 3318DD. *S.M. Perold* 474, 3318DD; 479 p.p., 3318DD; 641, 3318BD; 2182, 3018AC; 2395, 3218BD. *C.M. van Wyk* 1495, 3318DD.

R. elongata
S.M. Perold 424, 2530AB; 1058, 2630AD; 2018, type, 2629AB; 2476, 2629AB. *Smook* 4912, 2630 AD.

R. furfuracea
Oliver 8910, 3119DD; 8921, 3120CC; 8957 p.p., type, 3220DA. *S.M. Perold* 1398 p.p., 2917DB; 1400, 2917DB; 1465 p.p., 3018AA; 1476, 3018AA; 1489, 3018AA; 1515, 3018AB; 1854, 3119BD; 1869, 3119CB/CD; 1870, 3119CB/CD; 1879, 3219AA; 1890, 3219AA; 1892, 3219AA; 1895, 3219AA; 2033, 2917DB; 2034, 2917DB; 2035, 2917DB; 2045, 2917DB; 2049, 2917DB; 2140, 3018AA; 2155 p.p., 3018AA; 2156 p.p., 3018AA; 2171, 3018AA; 2176, 3018AA; 2180, 3018AA; 2319 p.p., 3119AC; 2322 p.p., 3119AC; 2425, 3220DA; 2429, 3220DA.

R. garsidei
S. Arnell 307, 3318CD. *Garside* 2, type, 3318DD. *Marais* 5464, 3318DB (BOL). *Wilman* 663, 3118DC (BOL). *leg. unknown* 5002, 3318DD (BOL); *leg. unknown* 5075, 3319AC (BOL); *leg. unknown* 5473, 3319AC (BOL).

R. hantamensis
Germishuizen 4034, 3119BD. *S.M. Perold* 1830, type, 3119BD; 2338, 3119BD.

R. concava
S. Arnell 12 p.p., 3318CD (BOL); 67 p.p., 3318CD (BOL). *Betzler* 139, 2817CD. *Duthie* 5005, 3318DD (BOL); 5407, 3220BC (BOL); 5417 p.p., 3318DD (BOL); 5468, 3319AC (BOL); 5470, 3318DB (BOL). *Garside* 6108, 3318DD (BOL); 6128, 3318CD (BOL). *Krauss* s.n. July 1838, type, 3318CD (G). *Moll* 6025, 3217DD. *Morley* 214, 3318DD. *Oliver* 8949, 3220DA; 8957 p.p., 3220DA. *S.M. Perold* 470, 3318DD; 478, 3318DD; 485, 3318AD; 899, 3322BC; 1414, 2917DB; 1415, 2917DB; 1431, 2918CA; 1432, 2918CA; 1438, 2917DD; 1447, 3017BB; 1454, 3017BB; 1455, 3017BB; 1460, 3018AA; 1465, 3018AA; 1466, 3018AA; 1493, 3018AA; 1500, 3018AB; 1501, 3018AB; 1604, 3017BB; 1773, 3119AD; 1788, 3119AC; 1791, 3119AC; 1792, 3119AC; 1795, 3119AB; 1798, 3119AB; 1888, 3219AA; 2054, 2917DB; 2057, 2917DB; 2091, 3017BB; 2094, 3017BB; 2103, 3017BD; 2104, 3017BD; 2105, 3017BD; 2113, 3017BD; 2115, 3017BD; 2148, 3018AA; 2172, 3018AA; 2173, 3018AA; 2185, 3119AC; 2195, 3119AC; 2312, 3119AC; 2313, 3119AC; 2316, 3119AC; 2362, 3219AC; 2426, 3220DA; 2427, 3220DA. *C.M. van Wyk* 1493, 3119AC.

R. hirsuta
Oliver 7240 p.p., 3018AC; 8038 p.p., 3018AC; 8040, type, 3018AC. *S.M. Perold* 2099, 3018AC; 2100, 3018AC; 2101, 3018AC; 2182, 3018AC.

R. limbata
S. Arnell 10, 3318CD (BOL); 62, 3318CD (BOL); 68, 3318CD (BOL); 69, 3318CD (BOL); 239, 3318CD (BOL); 711, 3320CC (BOL); 724, 3320CC (BOL); 768, 3320CC (BOL); 784, 3320CC (BOL); 795, 3320CC (BOL); PRE-CH 3927 p.p., 3318CC; PRE-CH 4135 p.p., 3318CD. *Brunnthaler* s.n., October 1909, type of *R. capensis*, 3419BA (G). *Duthie* 5003, 3318DD (BOL); 5204, 3319CB (BOL); 5343, 3319CD (BOL); 5422, 3423AA (BOL); 5471, 3319AD (BOL); PRE-CH 1038, 3318DD; PRE-CH 1040, 3318DD; PRE-CH 1042, 3318DD. *Eaton* s.n., 3318CD (BM, NY). *Garside* 5, 3318DD; *Hampshire* 5419, 3423AA (BOL). *Jordaan* 5354, 3420CA (BOL). *Koekemoer* 301, 3321AD. *Klingmuller* 9041, 3318CD. *Krauss* s.n., July 1838, type, 3318CD (BM, G). *Leighton* 538, 3418BB (BOL). *Magill* 6172, 3320DC. *Malan* s.n., 3318DD (BOL). *Michel* PRE-CH 1026, 3318CD. *Morley* 218, 3318DD; 221, 3318DD; 282, 3319DA; 307, 3319CC. *Naudé* 5337, 3319CB (BOL). *Oliver* 8042, 3018AC; 8858, 3119AC; 8927, 3120CC; 9026, 3318DD; 9205, 3018AA. *S.M. Perold* 466, 3318DD; 469, 3318DD; 519, 3219CA; 583, 3319DA; 587 p.p., 3319DA; 588, 3320CC; 595, 3419BB; 613, 3419BA; 644, 3318CD; 1173, 3419BA; 1427, 2918CA; 1602, 3017BB; 1614, 3018AC; 1867, 3119CB; 1868, 3119CB; 1878, 3219AA; 1889, 3219AA; 1896, 3219AA; 1944, 3219AA; 2098, 3018AC; 2348, 3218BD; 2394, 3218BD; 2415, 3319AC. *Pieterse* 11, 3318CD. *Stirton* 9453, 3418AB. *Van der Merwe* s.n., 3319CB (BOL). *C.M. van Wyk* 2521, 3320AB. *Volk* 86/912, 3018AA (M, PRE). *Wager* PRE-CH 1027, 3318CD. *Wilms* 2550, 3318CD (BM). leg. unkown, s.n., 3419BA (BM).

R. macrocarpa
M.J.A.W. Crosby 1110, 2724AA. *S.M. Perold* 69, 2529CB; 80, 2529CB; 81, 2529CB; 888 p.p., 2527CC. *Perold & Germishuizen* 1307, 2828CB. *Van Rooy & Perold* 634, 2529CB; 637, 2529CB; 642, 2529CB. *Volk* 81/010, 2529CB (M, PRE). (Extra African records of *R. macrocarpa* (=*R. campbelliana*) specimens examined are listed in Volk & Perold 1988a).

R. mammifera
S.M. Perold 447, type, 2529CA; 841, 2328CD. *Wagener* PRE-CH 4511, 2529CA.

R. microciliata
Chadwick 293 p.p., 2431AB. *Glen* 1405 p.p., 2330AD; 1411 p.p., 2330CD. *Kemp* 1272, 2632AA. *Long* 12434, 2127AB (E, PRE). *Mendes* 698, 1313DB (Angola) (LISU). *S.M. Perold* 95,

2529CB; 102, 2529CB; 243, 2527AB; 308, 2829DB; 383, type, 2530BB; 426 p.p., 2530AB; 435, 2428BD; 748 p.p., 2228DB; 751, 2228DB; 818, 2428CA; 844 p.p., 2328CD; 1026, 2530DC; 1217, 2528AD; 2645 p.p., 1535AD (Malawi); 2683 p.p., 1433BB (Malawi); 2689, 1434AA (Malawi). *Pócs* 88012/L, 0636DD (Tanzania) (EGR, PRE). *Pócs & Orban* 89138/D, 0438CD (Tanzania) (EGR, PRE). *Pócs et al.* 90051/L p.p., 0337AB (Tanzania) (EGR, PRE). *I.M. Retief* 252, 2331CC. *H. Sérgio* s.n., 1933AB (Mozambique) (LISU). *Smook* 4267 p.p., 2327BC. *Vogel* T465, grid unknown (M, PRE). *Volk* 81/130, 1918AD (M, PRE); 81/131 p.p., 1918AD (M, PRE); 81/249, 2527AB (M, PRE).

R. montana
Glen 1728, 3028CA/CC. *Jacot Guillarmod et al.* 60, 2929CC. *Oliver* 8354, 3027DD. *J.M. Perold* 31, 2927BC. *S.M. Perold* 2526, 2929CB. *Schelpe* s.n., 2828CB (BOL). *Smook* 3240, 3028CA; 7101, 2928DA; 7308 p.p., 2928DA. *Van Rooy* 2712, type, 3027CB; 2718, 3027CB; 3045, 2828DC; 3046, 2828DC; 3446, 2929CA; 3540, 2929CB; 3566, 2929CB; 3702, 2929CB.

R. namaquensis
S.M. Perold 564, 3219AC; 565, 3219AC; 1420, type, 2918CA; 1421, 2918CA; 1464, 3018AA; 1557, 3018BC; 1558, 3018DC; 1580, 3018BC; 1613, 3018AC; 1614, 3018AC; 1615, 3018AC; 1616, 3018AC; 1753, 3119AC; 1756, 3119AC; 2030, 2918CA; 2036, 2918CA; 2037 p.p., 2918CA; 2039, 2918CA; 2095, 3018AA; 2096, 3018AC; 2102, 3018AC; 2130, 3018AC; 2131, 3018AC; 2132, 3018AC; 2133, 3018AC; 2136, 3018AC; 2137, 3018AC; 2139, 3018AA; 2372, 3219AC; 2373, 3219AC; 2374, 3219AC; 2375, 3219AC; 2376, 3219AC; 2377, 3219AC.

R. natalensis
Germishuizen 2888, 2630AD. *J.M. Perold* 30, 2728CA; 38, 2927AB. *S.M. Perold* 103, 2529CB; 307, 2930AA; 352, 2629BA; 355, 2629BA; 421, 2530AB; 430, 2529CC; 679, 2730AD; 816, 2428CA; 1048, 2630BA; 1057, 2630AD. *Reid* 1107, 2529AD. *Sim* PRE-CH 1009, 2730DC; 8228, type, 2730DC (BOL, PRE). *Smook* 7429, 2329AA. *Van der Bijl* PRE-CH 1134, 2929BC. *Volk* 633/84, 2930AA (M, PRE).

R. nigrella
S. Arnell 26, 3318CD (S); 36, 3318CD (S); 49, 3318CD (S, UPS); 50, 3318CD (BOL); 59, type of *R. capensis* auct. non Steph., 3318CD (S, UPS); 150, 3418AB (BOL, PRE); 162, type of *R. capensis* auct. non Steph., 3418AB; 186, 3418AB (S); 189, 3418AB (BOL); 302, 3418AB (BOL); 792, 3320CC (BOL, PRE, S, UPS); 802, 3320CC (BOL, PRE, S); PRE-CH 4123, 3418AB; PRE-CH 4124, 3320CC. *M.J.A.W. Crosby* 1112, 2724AA. *Duthie* 5340, 3318DD (BOL); 5457 p.p., 2926AA (BOL); 5494 p.p., 2926AA (BOL). *Garside* 6650, 3318CD (BOL). *Germishuizen* 4934, 2825AC. *Glen* 1472, 2917DA; 1585, 2917DA. *Herman* 549, 3124BB. *Koekemoer* 516, 2917DB; 616, 3318CD. *Lambert* 1, 3318CD. *Loxly* 5023, 3318CD (BOL). *Maas Geesteranus* 11910, 2528CA (L). *Oliver* 9203, 3018AA. *J.M. Perold* 35 p.p., 2927AB; 38 p.p., 2927AB. *S.M. Perold* 150, 2528DC; 320, 2528DC; 425, 2530AB; 501, 3218DC; 506, 3218DC; 520, 3219CA; 533, 3218BD; 642, 3318CD; 888 p.p., 2527CC; 956, 2926AC; 1088 p.p., 2729BB; 1147, 3318DD; 1171 p.p., 3419BA; 1274, 2729CD; 1322, 2827DC; 1336, 2827BC; 1340, 2827BC; 1365 p.p., 2728CC; 1456, 3017BB; 1478, 3018AA; 1757, 3119AC; 1882, 3219AA; 1947, 3219AA; 2090, 3017BB; 2117, 3018CA; 2329, 3119AC; 2412, 3319AD; 2470, 2628BB; 2570, 3318DD. *P.K.* 5368, 3318CD (BOL). *T.R. Sim* PRE-CH 1025 p.p., 2930CB. *Smook* 4892 p.p., 2630AD; 3418 p.p., 3024AC; 3544 p.p., 2924BA; 4892 p.p., 2630AD; 6028, 3225AD; 6962 p.p., 3123AA; 7308 p.p., 2928DA. *Thompson* 252, 3226BC. *Van Brakel* 5019, 3418BA (BOL). *Van Rooy* 2414, 3026BB; 2417, 3026BB; 2598, 3027CC. *C.M. van Wyk* 2525, 3320AB. *Vogel* C682, 3319AC (MJG). *Volk* 81/214 p.p., 2827AC (M, PRE); 81/289 p.p., 2926AA (M, PRE). (Extra African records of *R. nigrella* specimens examined are listed in Perold & Volk 1988b).

R. okahandjana
Acocks 5415, 2824DA (BOL). *Anderson* PRE-CH 13443, 2528CB. *Best* 2098, 1731CA (Zimbabwe) (MO). *Bottomley* PRE-CH 271, 2528CA. *Bourell et al.* 2625, 2628AA (MO). *Brueckner* 224, 2824DA (BOL). *Brusse* 4250, 2017AD; 4251, 2017AD; 4500, 2531BB. *Chadwick* 294, 2431AB. *Codd* PRE-CH 3764, 2528CA. *Condy* PRE-CH 13471, 2426DA. *M.J.A.W. Crosby* 1113, 2724AA. *De Winter* PRE-CH 12822, 2528CA. *Duthie* 5502, 2926AA (BOL); 5503, 2926AA (BOL); 5504, 2926AA (BOL); 5442, 2925CB (BOL); 5483, 2926AA (BOL). *Eaton* s.n., 3318CD (NY). *Edwards* 131, 2930CB. *Ellis* PRE-CH 4510, 2732CA. *Fourie* 23 p.p., 2229DC; 24 p.p. 2229DC; 29, 2229DC. *Germishuizen* 5216, 2529BB. *Gibbs Russell & Smook* 5117, 2618CB; 5118, 2618CB; 5246 p.p., 2116AA; 5266, 2016AD. *Giess* 8684, 2115CC; 8685, 2016AB. *Godfrey* GH-1657 p.p., 2531AA (NY). *Glen* 1411, 2330CD; 1424, 2230BC; 2082, 2427BD; 2083, 2427BD; 2101, 2427BD; 2464, 2527AC; 2510, 2628CA; 2540, 2627CD. *Hardy* 4300, 2229DD. *Harrison* 1013, 2823AC. *Hoffmann* PRE-CH 4515, 2016BC. *Kemp* 765, 2632AA. *Koekemoer* 365, 2820CB; 504, 2723DA. *Le Brun* 9230, grid unknown (Zaïre) (BR). *Leistner* 3555, 2528CA; 3557, 2428AB; 3560, 2527DC. *Long* 12435, 2127AB (E); 12437, 2127AB (E). *Long & Rae* 960, 1822BD (E). *Magill* 6416, 2722DC; 6475, 2822CB; 6489 p.p., 2823BC; 6493, 2824AC. *Mauve* 933, 2528CB. *Mendes* 3813, 1413CD (Angola) (LISU). *Miller* 7703, 2028AD (Zimbabwe). *Mogg* 1558, 2528CA. *Morley* PRE-CH 13505, 2217AD. *Mott* 867, 2425DB. *Oliver* 7311, 2329BC. *Onderstall* PRE-CH 13475, 2531CA. *Ortendahl* 567 p.p., 2718BA; 696, 2718BC. *S.M. Perold* 67, 2528CA; 68, 2528CA; 73, 2529CB; 74, 2529CB; 78, 2529CB; 82, 2529CB; 84, 2529CB; 88, 2529AD; 90, 2528CB; 96, 2529CB; 110, 2529CB; 125, 2528CA; 131, 2528CA; 137, 2528DC; 169, 2528CA; 183, 2627DA; 211, 2628CC; 212, 2628CC; 218, 2728BA; 220, 2528CD; 230, 2527CA; 234, 2527AD; 235, 2527AD; 267, 2528CA; 268, 2528CA; 305 p.p., 2930AA; 309, 2828DB; 312, 2929DC; 315, 2828BB; 321, 2528DB; 325, 2528DB; 331, 2428CB; 343, 2629AB; 382, 2530BB; 392, 2530BD; 393, 2530BD; 411, 2430DB; 427, 2530AB; 434, 2428BD; 720, 2329AD; 721, 2329AD; 729, 2229CA; 731, 2229CA; 739, 2228DB; 741, 2228DB; 752, 2228DB; 758, 2228DB; 763 p.p., 2228DA; 777, 2228CD; 780, 2228CC; 788, 2228CD; 791, 2228CD; 798, 2229DC; 802, 2229DC; 809, 2428CA; 812, 2428CA; 813, 2428CA; 814, 2428CA; 844, 2328CD; 887, 2527CC; 891, 2526DD; 953, 2926AC; 959, 2528BA; 961, 2528BB; 970, 2529AB; 977, 2429DC; 1029, 2530DC; 1035, 2530DC; 1041, 2630BA; 1070, 2630DA; 1085, 2630CC; 1088, 2729BB; 1202, 2627CA; 1203, 2627AD; 1205, 2627AD; 1209, 2428CD; 1214, 2528AD; 1239, 2728BC; 1242, 2728BC; 1340, 2827BC; 1342, 2827BC; 1365, 2728CC; 1368, 2727DD; 1988, 2528CA; 2002, 2531AB; 2006, 2530BD; 2012, 2528DA; 2013, 2528DA; 2014, 2528DA; 2028, 2722DD; 2434, 2528AD; 2436, 2329DC; 2437, 2329DC; 2440 p.p., 2329CC; 2471, 2628BB; 2479, 2629AB; 2584, 2525DD; 2594, 2526CA; 2595, 2528BC; 2643, 2429AA; 2649 p.p., 1535AD (Malawi); 2683 p.p., 1433BB (Malawi). *Pócs & Kayambazinthu* 87041/X, 0637DC (Tanzania) (EGR, PRE). *Pócs & Murphy* 89136/H, 0637DC (Tanzania) (EGR, PRE). *Pócs et al.* 88099/C, 0637DC (Tanzania) (EGR, PRE); 90051/K p.p., 0337AB (Tanzania) (EGR, PRE). *Potts* PRE-CH 1032, 2926AA. *E. Retief* 1523, 2017AC. *I.M. Retief*, 251, 2331CC. *Russell* PRE-CH 13545, 2718CB. *H. Sérgio* s.n., 1933AB (Mozambique) (LISU). *T.R. Sim* 9071, 2030BD (Zimbabwe); 9073, 2028AD (Zimbabwe); PRE-CH 1039, 2930CD; PRE-CH 1049, 2532BA (Mozambique); PRE-CH 1066, 2930CD; PRE-CH 1061, 2930CD. *Smith* 1613, 1923BC (MO). *Smook* 4267 p.p., 2327BC; 4571, 2820CB; 4787 p.p., 2526AD; 4861, 2530AB; 4892 p.p., 2630AD; 5081, 2116DD; 5082, 2116DD; 5178, 2016BC; 5189, 2017AD; 5276, 2528CA; 5277, 2731AC. *Story* 3399, 3227CA. *Van Rooy* 1085, 2528CB; 1826, 3129BA; 2334, 2926CD. *Van Rooy & Perold* 635, 2529CB; 636, 2529CB. *A.E. van Wyk* 5752, 2822AB. *C.M. van Wyk* 3043, 3023BC. *Venter* 10479, 2329DD; 12230, 2329CD; 12462, 2724AD. *Volk* 715, 1915DA; 11944, type 2116BD;

1956, 2116DD; 81/018, 2529CB (M, PRE); 81/019, 2529CB (M, PRE); 81/021, 2528DC (M, PRE); 81/030, 2727AB (M, PRE); 81/042, 2827AC (M, PRE); 81/080, 2921AC (M, PRE); 81/083, 2920BB (M, PRE); 81/084, 2820CB (M, PRE); 81/090, 2216DA (M, PRE); 81/095, 2217CA (M, PRE); 81/100, 2116CA (M, PRE); 81/103, 2116AA(M, PRE); 81/111, 2216AA (M, PRE); 81/142, 1918CA (M, PRE); 81/175, 1814BC (M, PRE); 81/181, 2016AA (M, PRE); 81/186, 2217CD (M, PRE); 81/190, 2217CD (M, PRE); 81/201, 2316BD (M, PRE); 81/202, 2316BD (M, PRE); 81/203, 2825CA (M, PRE); 81/213, 2827AC (M, PRE); 81/233, 2628CC (M, PRE); 81/249 p.p., 2527AD (M, PRE); 81/270, 2217CD (M, PRE); 81/288, 2926AA (M, PRE); 84/636, 2929BC (M, PRE); 84/637, 2929BC (M, PRE); 84/652, 2827AC (M, PRE); 84/660, 2820CB (M, PRE); 84/661, 2820CB (M, PRE); 84/663, 2820CB (M, PRE); 84/665, 2820CB (M, PRE); 84/691, 2118BA (M, PRE); 84/693 p.p., 1917CA (M, PRE). *Wagener* PRE-CH 4512, 2626DC. Wager PRE-CH 3843, 2530BD. *Ward* 10726, 2115CC. *Watson* PRE-CH 272, 2528CA. *Welwitsch* 244 p.p., 0915DA (Angola) (BM).

R. parvo-areolata
Duthie 5414, 3418BB (BOL). *J.M. Perold* 14, 3118AB; 15, 3118AB; 19, 3118CD; 22, 3118CD; 23, type, 3118CD; 24, 3118CD; 25, 3118CD; 26, 3118CD. *S.M. Perold* 1726, 3118CD.

R. perssonii
Smook 7612 p.p., 1815BB. *Volk* 2059, 1919BA (M, PRE).

R. pottsiana
Duthie 5147, 3125AC (BOL); 5148, 3125AC (BOL); 5443, 2925CB (BOL); 5444, 2925CB (BOL); 5450, 2925CB (BOL); 5451, 2925CB (BOL); 5452, 2925CB (BOL); 5463 p.p., 2925CB (BOL). *Henrici* PRE-CH 3741, 2925AC. *J.M. Perold* 37, 2927AC. *S.M. Perold* 285, 2728DB; 314, 2828BB; 1361, 2828AB. *Potts* PRE-CH 1017, 2926AA; PRE-CH 1019 p.p., 2926AA; PRE-CH 1020, 2926AA; 7003, type, 2926AA (BLFU, BOL). *Smook* 3338, 3124BB; 7308 p.p., 2928DA. *Volk* 81/203 p.p., 2825CA (M, PRE); 81/204, 2825CA (M, PRE); 81/231, 2827AC (M, PRE).

R. pulveracea
S. Arnell 753 p.p., 3220DA (BOL). *Duthie* 5455, 2926AA (BOL); 5461 p.p., 2926AA (BOL); 5484, 2926AA (BOL); 5485, 2926AA (BOL); 5498, 2926AA (BOL). *Herman* 549 p.p., 3124BA (F, PRE). *Potts* PRE-CH 1047, 2926AA. *Smook* 3339, type, 3124BB (F, PRE); 6962 p.p., 3123AA. *Van Rooy* 2451, 3026BB; 2598, 3027CC.

R. purpurascens
S. Arnell 240, 3318CD; 248, 3318CD; 251, 3318CD; 330, 3318CD; 332, 3418AA (BOL); 401, 3418AA (BOL); 494, 3318CD; 569, 3418AA; 638, 3418AA (BOL); 724, 3320CC (BOL); 725, 3320CC (BOL); 755, 3320CC (BOL); 922, 3318CD (BOL); 1734, 3423AA (BOL). *Barnard* 52344, 3318CD. *Breutel* 34, 3419BA (BM, L). *Duthie* PRE-CH 1125, 3318DD; PRE-CH 1128, 3318DD; 5012, 3318DD (BOL); 5325, 3318DD (BOL); 5381 p.p., 3319AC (BOL); 5382, 3423AA (BOL); 5423, 3423AA (BOL); 5425, 3318AD (BOL); 5434, 3423AA (BOL); 5437, 3423AA (BOL); 5510, 3418AD (BOL). *Eaton* s.n., 3318CD (BM). *Ecklon* s.n., type, 3318CD (BM, G, NY). *Esterhuysen* 19232, 3318CD (BOL); 21718, 3318CD (BOL). *Garside* PRE-CH 1126, 3318DD; 26210, 3318AD (BOL). *Groenewald* 5327, 3319AC (BOL). *Leighton* 537, 3217DD (BOL). *Malan* s.n., 3318DD (BOL). *Malherbe & Davies* 5377, 3219AC (BOL). *McLaughlin* 1211, 3423AA. *Morley* 291, 3419BA; 360, 3319DA. *Oliver* 8778, 3418BB; 9027, 3318DD; 9224, 3419AC; 9433, 3419DB; 9446, 3419DA. *S.M. Perold* 477, 3318DD; 500, 3218DC; 587, 3319DC; 590, 3320CC; 594, 3419BB; 611, 3419BA; 634 p.p., 3319CC; 1755, 3119AC; 1935, 3218BB; 2347, 3218BD; 2386, 3218BD. *Schelpe* 3901, 3318BC. *T.R. Sim* PRE-CH 1498, 3318CD. *Wager* PRE-CH 253, 3318CD. *Wilms* 2549, 3318CD (BM).

R. rosea
Fourie 23 p.p., 2229DC; 24 p.p., 2229DC. *Glen* 1403 p.p., 2330AD. *E.W. Jones* 529 p.p., N0033CA (Uganda) (BM, NY). *Le Brun* 7693 p.p., grid unknown (Zaïre) (BR). *Long* 12438, 2127Ax (E, M). *Maas Geesteranus* 6499, 2926AA (L). *Mendes* 1421, 1513BA (Angola) (LISU). *S.M. Perold* 139, 2528DB; 140, 2528DB; 141, 2528DB; 142, 2528DB; 143, 2528DB; 185, 2727AB; 196, 2727AB; 322, 2528DB; 323, 2528DB; 324, type, 2528DB; 344, 2629AB; 346, 2629AB; 347, 2629AB; 408, 2430DB; 749, 2228DB; 750, 2228DB; 753, 2228DB; 785, 2228CD; 881, 2527BC; 954, 2926AC; 2607, 2528DA. *Pócs* 88012/K, 0636DD (Tanzania) (EGR, PRE). *Pócs & Murphy* 89044/A p.p., ? 0431CD (Tanzania) (EGR, PRE). *Volk* 00930, 1915DB; 01165 p.p., 2217CD; 6334, 2516BC; 12403, 2417DA; 81/020, 2529CB (M, PRE); 81/023, 2528DB (M, PRE); 81/031, 2727AB (M, PRE); 81/032, 2727AB (M, PRE); 81/106, 2216AA (M, PRE); 81/111, 2216AA (M, PRE); 81/116, 2216AA (M, PRE); 81/124 p.p., 1918AD (M, PRE); 81/125, 1918AD (M, PRE); 81/131, 1918AD (M, PRE); 81/132, 1918AD (M, PRE); 81/133, 1918AD (M, PRE); 81/270, 2217CD (M, PRE); 84/693, 1918AD (M, PRE); 84/700 p.p., 1918AD (M, PRE); 84/701 p.p., 1918AD (M, PRE); 84/702 p.p., 1918AD (M, PRE); 84/707, 2016BB (M, PRE); 84/710 p.p., 2016CC (M, PRE); 84/714, 2216AA (M, PRE); 84/715, 2216AA (M, PRE); 84/716, 2216AA (M, PRE).

R. rubricollis
Duthie 5014, type, 3423AA (BOL, PRE); 5406, 3423AA (BOL).

R. runssorensis
Glen 1403 p.p., 2330AD. *Long & Rae* 868, 2121AA (E); 871, 2122BA (E). *Mendes* 697, 1313DB (Angola) (LISU). *Ortendahl* 567 p.p., 2718BA (BOL, PRE). *S.M. Perold* 219, 2728BA; 782 p.p., 2228CD; 785, 2228CD; 1208 p.p., 2627AB; 2004, 2531AB; 2466, 2628BA. *Scott Elliott* 5, 20, type, NE0030CC (Uganda) (BM, G). *Smook* 6962, 3123AA; 7031, 2725BB. *Volk* 672, 2217CD; 00835, 2117AD; 5374, 2417DA; 6150, 2117DB; 6504, 2317BC; 6875, 2317BC; 11500, 2317BC; 81/124 p.p., 2827AC (M, PRE); 81/125 p.p., 1918AD (M, PRE); 81/214, 2827AC (M, PRE); 81/225 p.p., 2827AC (M, PRE); 81/262 p.p., 2629AA (M, PRE).

R. schelpei
Giffen 3, 2917DA. *Oliver* 8041, 3018AC; 9198, 3017BB; 9201, 3018AA; 9487, 3019CC. *S.M. Perold* 535, 3218BD; 1417, 2918CA; 1453, 3017BB; 1480, 3018AA; 1601, 3017BB; 1611, 3018AC; 1946, 3219AA; 2052, 2917DB; 2114, 3017BD; 2134, 3018AA; 2143, 3018AA; 2178, 3018AA; 2327, 3119AC; 2397, 3218BD. *Perry & Manning* 3752 p.p., 3119CA. *Schelpe* 7775, type, 2917DB. *C.M. van Wyk* 2524, 3320AB.

R. simii
M.J.A.W. Crosby 1111, 2724AA. *Duthie* 22, 3322CA; 5115, 3322CA (BOL); 5330, 2826CB (BOL); 5456, 2926AA (BOL); 5461, 2926AA (BOL). *Du Preez* 2106, 2927AC. *Fellingham* 746, 3420AD. *Hitchcock* 5478, 3025CA (BOL). *Koekemoer* 291, 3322BC; 292, 3322CB; 302, 3321AD. *Liebenberg* 7632, 3225AD. *Lübenau-Nestlé* SA129, 3322BC (Pte. Herb.). *Magill* 5911, 3224AA. *Oliver* 8490, 3420BD; 9435, 3419DB. *J.M. Perold* 29, 2828DA; 36, 2927AB; 39, 2927AB; 43, 2927AB; 44 p.p., 2927AB. *S.M. Perold* 505, 3218DC; 949, 3124DB; 1304, 2828CB; 1306, 2828CB; 1318, 2827DC; 1323, 2827DC; 1337, 2826BC; 1341, 2826BC; 1346, 2826BD; 1353, 2828AC; 1360, 2828AB; 1363, 2828AB; 1366, 2727CC; 2535, 2827AA. *Potts* PRE-CH 1011, 2926AA. *T.R. Sim* 338, type, 3227CC. *Smook* 3908, 3224BC; 6028 p.p., 3225AD; 6418, 2729CB; 6631, 2727DC. *Thompson* 257, 3127AB. *Van Rooy* 1708 p.p., 3129BB; 1817, 3129BA; 1818, 3129BA; 1823, 3129AB; 1708 p.p., 3129BB; 2337, 2926CD; 2338, 2926CD; 2403, 3026BB; 2416, 3026BB; 2515, 3027AC; 2602, 3027CC; 2685, 3027CC;

2766, 3027DC. *C.M. van Wyk* 1781, 3420CB. *Volk* 81/051, 2926AA (M, PRE); 81/226, 2826AC (M, PRE); 81/289 p.p., 2926AA (M, PRE); 84/655, 2827AC (M, PRE); 84/730, 2827AC (M, PRE).

R. sorocarpa
S. Arnell 7, 3418AB (BOL); 147, 3418AB (BOL); 186, 3418AB (BOL); 304, 3418AB (BOL); 784, 3320CA (BOL); 826, 3320CA (BOL); PRE-CH 3927 p.p., 3418AB; PRE-CH 4132, 3418AB. *Duthie* 5015, 3318CD (BOL); 5413, 3318DD (BOL). *Koekemoer* 488 p.p., 3321AD. *Lambert* s.n., 3418AB. *Oliver* 8875, 3119BD. *S.M. Perold* 305, 2930AA; 307 p.p., 2930AA; 586, 3319DA; 1058 p.p., 2630AD; 1171, 3419BA; 1822, 3119BD; 1836, 3119DD; 1846, 3119DD; 2529 p.p., 2929CB. *Pócs & Kabuta* 8682/P p.p., 0336BA (Tanzania) (EGR). *Stirton* 9512, 3321AD.

R. stricta
Beesley 22, 0336BC (Tanzania) (BM); 23, 0336BC (Tanzania) (BM, PRE). *Botha & Van Wyk* 1016, 2831CD. *Brandt* 5360, 2331AB (BOL). *Breutel* s.n., 3419BA (L). *Britten* 2785, 3326BC. *Burtt-Davy* PRE-CH 110, 3130AA. *Davy* 17009, 3422BB. *Doidge* PRE-CH 3580, 2929DD. *Drege* s.n., grid unknown (BM). *Duthie* 5022, 3319AC (BOL); 5043, 3423AA (BOL); 5044, 3423AA (BOL); 5143, 3225BA (BOL); 5220, 3423AA (BOL); 5384, 2722DD (BOL); 5386, 3423AA (BOL); 5387, 3423AA (BOL); 5388, 3423AA (BOL); 5389, 3423AA (BOL); 5390, 3423AA (BOL); 5391, 3319AC (BOL); 5477, 3319AC (BOL); 6004, 3423AB (BOL). *Eccles* 25757, 2028BA (Zimbabwe) (BOL). *Ecklon* s.n., type, 3024AD (BM). *Eyles* 1405, 2732BC; 3885, 1831BA (Zimbabwe) (BOL). *Germishuizen* 2922 p.p., 2630CD. *Gerstner* 705, 2732DA. *Giess* 15236, 2016CD. *Glen* 1832, 2230CB; 2029, 2832AB. *Goosens* PRE-CH 3672, 2627CA. *Hendry* PRE-CH 1107, 2531CC. *Herschel* PRE-CH 1089, 2729BD. *Hilliard & Burtt* 8151, 2930DD; 10344, 2930AC. *E.W. Jones* 655, 0438CD (Tanzania) (BM). *Junod* PRE-CH 69, 2330AA; PRE-CH 1049, 2330CA; PRE-CH 1102, 2532DC (Mozambique); 324, 2532DC (Mozambique). *Krauss* 425, grid unknown (BM). *Kuun* 5307, 1725DD (Zambia) (BOL); 5308, 1725DD (Zambia) (BM, BOL). *Lambert* 6, 2931CD. *Long & Rae* 870, 2122BA (E). *Louw* 1621, 2627AC. *Magill* 4626, 2828CB; 5039, 2331DD; 5385, 2732CD; 6592, 2330CC; 7067, 2929CB. *MacLea* 7 p.p., grid unknown (BM). *Mauve & Venter* 5077, 2430DA. *McDonald* PRE-CH 13422, 3226CA. *Meeuse* 9411, 2230CD (NY, PRE). *Mogg* PRE-CH 1078, 2931CA. *Moonsammy* 14, 2930DD. *Naudé* 5429, 3319CB (BOL). *Nicholas* 1194, 2731CD. *Nixon* 109, 2813CD (BOL). *Pegler* 1354, 3228AD (BM, BOL, PRE). *S.M. Perold* 27, 2931CA; 354, 2629BA; 356, 2629BA; 360, 2629AA; 365, 2629BC; 438, 2428BD; 913, 3323CC; 1051, 2630AD; 1071, 2630DA; 1277, 2729CD; 1284, 2828BD; 2455, 2329DD; 2499, 2929CB; 2521, 2929CB; 2528 p.p., 2929CB; 2529 p.p., 2929CB; 2600, 2528DA; 2611, 2331CC. *Pócs* 90069/F, 0337AB (Tanzania) (EGR, PRE). *Potts* 1758, 3226DD (BOL); 1760, 3226DD (BOL). *Rehmann* 7, 2828CC (BM). *Reid* 1106, 2529AD. *Rudatis* 1291, grid unknown (BM). *Schelpe* 4807, 2016BC (BOL). *G.W. Sim* PRE-CH 1087, 2930AC; 8093, 2930AC. *T.R. Sim* 313, 3226CD; 7593, 2930CA; 9041, 3325CD; 9056, 1725DD (Zambia); 9065, 2030BD (Zimbabwe); 9066, 1725DD (Zambia); 9067, ? 2028AD (Zimbabwe); PRE-CH 1072, 2930CB; PRE-CH 1074, 2730DD; PRE-CH 1075, 2930CB; PRE-CH 1083, 2628BA; PRE-CH 1088, 2628AA; PRE-CH 1092, 2929BA; PRE-CH 1103, 2929AB; PRE-CH 1105, 2831DC; PRE-CH 1106, 2930CB; PRE-CH 1109, 2930CB; PRE-CH 1114, 1725DD (Zambia); PRE-CH 1115, 2930CB; PRE-CH 1118, 2930BC; PRE-CH 1120, 2730DD; PRE-CH 1122, 2930CB; PRE-CH 1123, 2730DD. *Symons* PRE-CH 1104, 2832AB. *Taylor* 2611, 0030CC (Uganda) (BM). *Thompson* 260, 2722CA; 295, 2530BA. *Thorne* 49753, 3322CC. *Ubbink* 964, 2627CA (PUC); 1004, 2627AC (PUC); 1154, 2627AC (PUC). *Van der Bijl* 14, 2930DD; 19, 2930DD; PRE-CH 1097, 2930CA; PRE-CH 1112, 2929BD. *Van Rooy* 1167, 2829CA; 2089, 3228BD; 2141, 3128DC; 2201, 3129CD. *B-E. & C.M. van Wyk* 933, 3325BC; 2091, 3325BC; 2093, 3325BC. *Van Zinderen Bakker* 7472, 2926AA (BOL). *Venter* 12199, 2430BB. *Volk* 5313, 2417DA; 01261, 2016DA (M, PRE); 12460, 2016DA (M, PRE). *Wagener* 1, 3423BB; 2, 3423BB. *Wager* 10, grid unknown (Mozambique); 18, 2528CA; 60, grid unknown (Mozambique). *Ward* PRE-CH 5354, 2930DD. *Wells* 57, 2930CB. *West* PRE-CH 3668, 2929BB. *Wirminghausen* 247, 3326BD.

R. tomentosa
Le Roux & Fourie PRE-CH 4494, 2917DB. *Oliver* 9196, 3017BB; 9197, 3017BB. *S.M. Perold* 1495, type, 3018AA; 1556, 3018BC. *Perold & Crosby* 2157, 3018AA; 2158, 3018AA. *Perold & Reid* 1462, 3018AA. *Schelpe* 7784, 2917DB (BOL, PC, PRE).

R. trachyglossum
J.M. Perold 33, 2927BD; 34, 2927BD. *S.M. Perold* 2530, 2929CA; 2531, 2929CA. *Van Rooy* 3539, type, 2929CA.

R. trichocarpa
Braggins 91/185, NE0036AC (Kenya). *M.J.A.W. Crosby* 1108, 2724AA. *Duthie* 5457, 2926AA (BOL); 5494, 2926AA (BOL) ; 5508, 2926AA (BOL). *Gibbs Russell & Smook* 5266 p.p., 2016AD. *Hardy* 6586, 2418DD. *Henderson* 658, 2123BD. *E.W. Jones* 529 p.p., N0033CA (Uganda) (BM, NY). *Long* 12436, 2127AB (E, PRE). *J.M. Perold* 38 p.p., 2927AB. *S.M. Perold* 748, 2228DB; 841 p.p., 2328CD; 844 p.p., 2328CD; 2600 p.p., 2528DA. *Pócs & Kayambazinthu* 87041/Z, 0637DC (Tanzania) (EGR, PRE). *Pócs et al.* 90051/M, 0337AD (Tanzania) (EGR, PRE). *E. Retief* 1403, 1916AA; 1422, 1915AA; 2585, 2525DD; 2593, 2526CC. *Schelpe* 2535 p.p., 0037AB (Kenya) (BM; Herb. Jones). *Smook* 5118 p.p., 1816DD; 6030, 3225AD; 7308 p.p., 2928DA. *Toelken* 5561, 2118DB (BOL, PRE). *Townsend* 77/408 p.p., grid unknown (Kenya) (Herb. Townsend). *Volk* PRE-CH 4210, 2316DA; PRE-CH4211, 1918BC; 00912, 1918BC (M, PRE); 01291, 2417BB (M, PRE); 81/114, 2216AA (M, PRE); 81/143, 1918CA (M, PRE); 81/165, 1816DC (M, PRE); 81/167, 1816DD (M, PRE); 81/172, 1815DC (M, PRE); 81/173, 1815DC (M, PRE); 81/176, 2016AA (M, PRE); 81/261, 2317CA (M, PRE); 81/264, 2217CD (M, PRE); 84/687, 2217 CD (M, PRE); 84/688, 2820CB (M, PRE); 84/689, 2117DB (M, PRE); 84/695, 1918AD (M, PRE); 86/851, 2216AA (M, PRE).

R. villosa
S. Arnell 803, 3320CC (BOL). *Betzler* 033, 2817CD. *Brunnthaler* s.n., XI 1909, type, 3320BA (G). *Brusse* 5217, 3323CB. *Compton* 5428, 3219AC (BOL). *M.J.A.W. Crosby* 1082, 3119AC. *Duthie* 5195, 3218AB (BOL); 5331, 3319DD (BOL); 5398, 3319CB (BOL); 5404, 3220BC (BOL); 5428, grid unknown (BOL); 5430, 3319CB (BOL); 5454, 3219CA (BOL). *Filter* PRE-CH 4489, 2917DB; PRE-CH 4490. 2917DB. *Germishuizen* 4783, 2816DD; 4784, 2816DD. *Glen* 1521, 3320AC; 1580, 3119AC. *Koekemoer* 488, 3321AD; 516 p.p., 2917DB. *Kuun* 5332, 3319DD (BOL). *Leighton* 534, grid unknown (BOL). *Le Roux* PRE-CH 4493, 2917DB. *Levyns* s.n., 3320CB (BOL); 25272, 3321AD. *Lübenau-Nestlé* SA64, 3118DA (Pte. Herb.); SA66, 3119AC (Pte. Herb). *Magill* 6143, 3321AD. *Nel* 5164, 3319DD (BOL). *Oliver* 1467, 3219AB (BOL); 7214, 2917DD; 8039, 3018AC; 8579, 3119AC; 9187, 3017BB; 9199, 3017BB; 9461, 3118DB; 9507, 3018DB. *Page* s.n., 3320CC (BOL). *J.M. Perold* 20, 3118CD; 21, 3319CD. *S.M. Perold* 504, 3218DC; 1430, 2918CA; 1440, 2917DD; 1448, 3017BB; 1513, 3018AB; 1516, 3018AB; 1518, 3018AA; 1605, 3017BB; 1627, 3018CA; 1630, 3017DC; 1728, 3118CD; 1750, 3119AC; 1763, 3119AC; 1787, 3119AC; 1873, 3119CB; 1880, 3219AA; 1898, 3219AA; 1948, 3219AA; 2032, 2917DB; 2085, 2917DD; 2088, 3017BB; 2123, 3018AC; 2177, 3018AA; 2193, 3119AC; 2315, 3119AC; 2321, 3119AC; 2326, 3119AC; 2358, 3219AC. *Perry & Manning* 3752, 3119CA. *Pillans* 10036, 3320BA (BOL). *Schelpe* 4746, 3118DA (BOL); 4871, 2917DB (BOL); 7814 p.p., 2917DD (BOL); 8229, 3019AB. *Slater* 5126, 3318AA (BOL). *Stephens* 5433, 3219AA (BOL);

23885 p.p., 3119AC (BOL); 24726, 3218BB (BOL); s.n., 3218BB (BOL). *Van der Merwe* 5222, 3320CC (BOL); 5481, 3319CB (BOL); 6222, 3320CC (BOL). *C.M. van Wyk* 1488, 3319AC; 2522, 3320AB. *Volk* 84/673, 2917DB (M, PRE); 84/674, 2917DB (M, PRE). *Young* 5133, 3320AB (BOL).

R. vitrea
S.M. Perold 1398 p.p., 2917DD; 1419, 2917DB; 1422, 2917DB; 1423, 2917DB; 1424, 2917DB; 1425 p.p., 2917 DB; 1475, type, 3018AA; 2041, 2917DB; 2043, 2917DB; 2044, 2917DB; 2046, 2917DB; 2047, 2917DB. Schelpe 7776, 2917DB (BOL, PC, PRE).

R. volkii
M.J.A.W. Crosby 463, 2528CD; 1113, 2724AA. *Glen* 1835, 2527AC. *Hardy et al.*, 5280, 2428CB; 5335, 2427BC. *J.M. Perold* 35 p.p., 2927AB; 38 p.p., 2927AC. *S.M. Perold* 97, 2529CB; 135, 2528DC; 184, 2727AB; 195, 2727AB; 433, 2529CC; 817, 2428CA; 837, 2428AC; 1058 p.p., 2630AD; 2472, 2628BB. *Smook* 3316, 3124BB. *Van der Merwe* PRE-CH 231, 2529CD. *Volk* 1021, type, 2017AD; 1029, 2016BC (M, PRE); 81/125, 1918AD (M, PRE); 81/133, 1918AD (M, PRE); 81/230, 2827AC (M, PRE); 84/702 p.p., 1918AD (M, PRE).

Ricciocarpos natans
Gerstner 5038, 2731xx. *Koch* 934, 2315CA. *Peeley* 1653 p.p., 2632CD. *Pienaar & Vahrmeijer* 474, 1724CD. *Smith* 1441, 1922DB. *Tinley* 418, 2632CD. *Wager* 55, 3129DA; PRE-CH 233, 3129DA.

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PART 2

FIGURES, PHOTOGRAPHIC AND SEM MICROGRAPHIC PLATES AND DISTRIBUTION MAPS

INDEX TO ILLUSTRATIONS, PLATES AND DISTRIBUTION MAPS

Genera and species are arranged alphabetically.

(The literature was consulted for the distribution of most cosmopolitan and subcosmopolitan species)

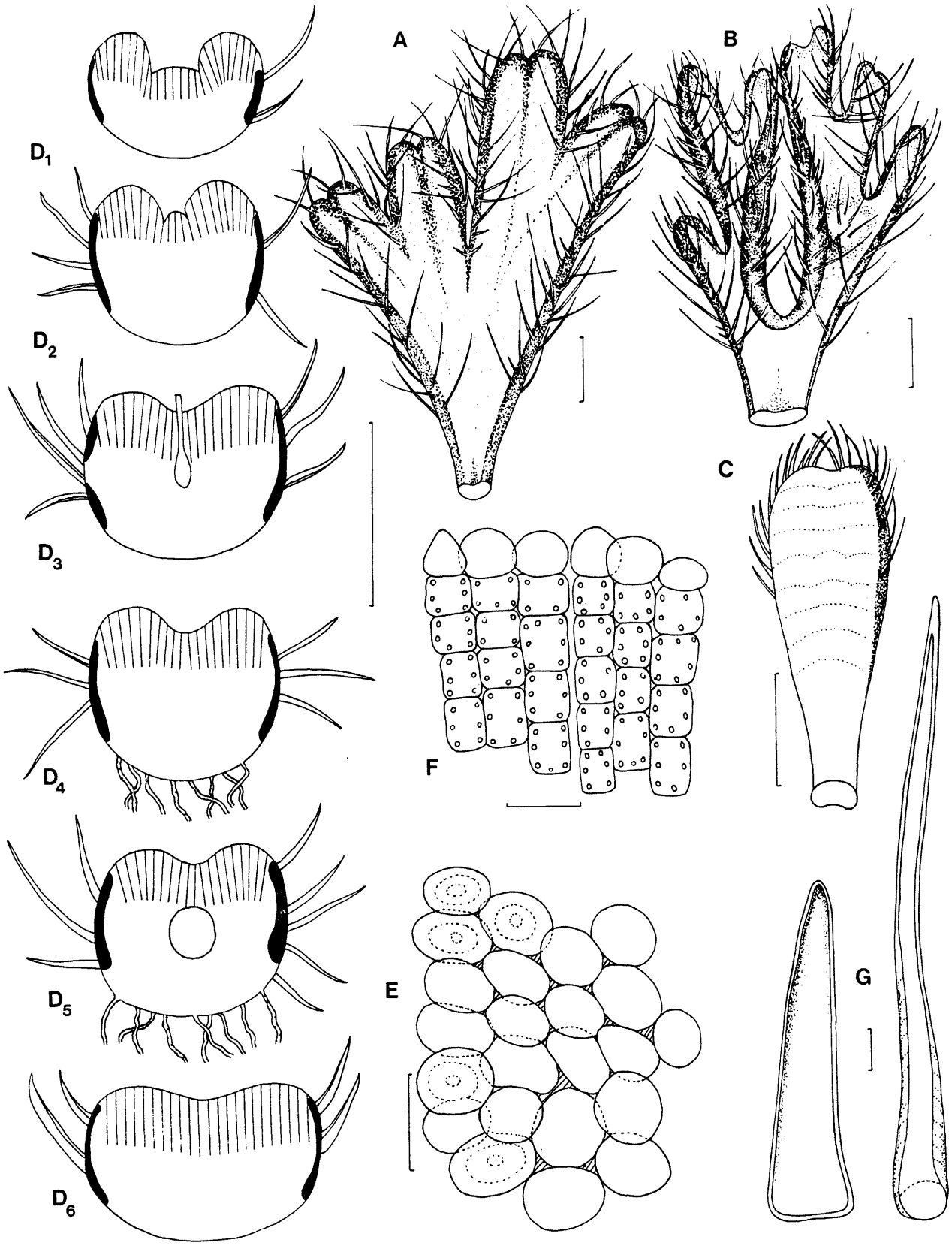


FIGURE 1.---*Riccia trichocarpa* (A--G): A, thallus wet; B, thallus dry; C, ventral face of branch; D, cross sections of branch at different distances from apex to basal part; E, epithelial cells and air pores (hatched), seen from above; F, epithelial and assimilation tissue cells in cross section; G, cilia: short and wide, long and slender. (A--G, *Henderson* 658). Scale bars A--D = 1 mm; E--G = 50 µm.

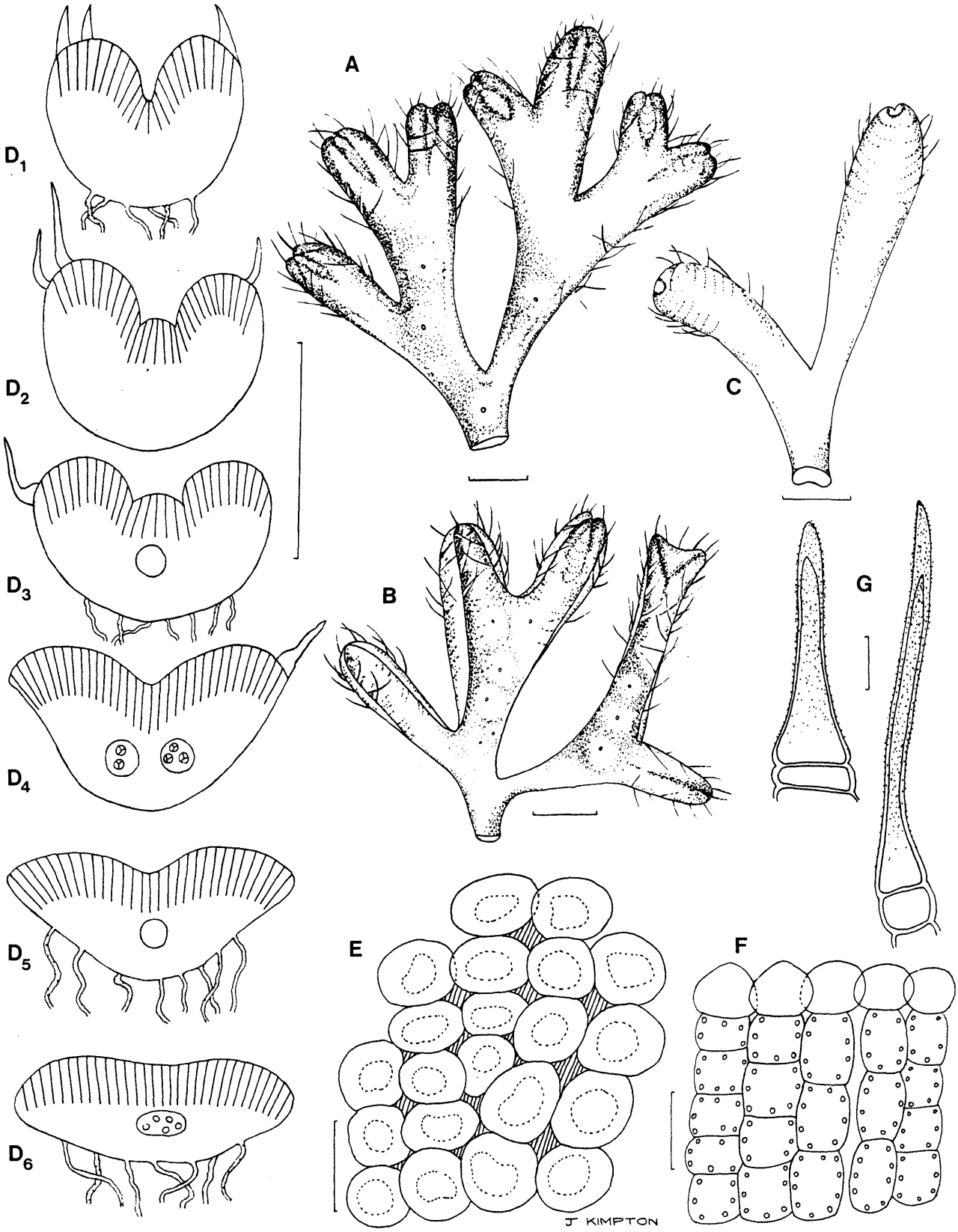


FIGURE 2.---*Riccia crozalsii* (A--G): A, thallus wet; B, thallus dry; C, ventral face; D, cross sections of branch at different distances from apex to basal part; E, epithelial cells and air pores seen from above; F, epithelial and assimilation tissue cells in cross section; G, cilia. (A--G, *S.M. Perold* 473). Scale bars A--D = 1 mm; E--G = 50 µm.

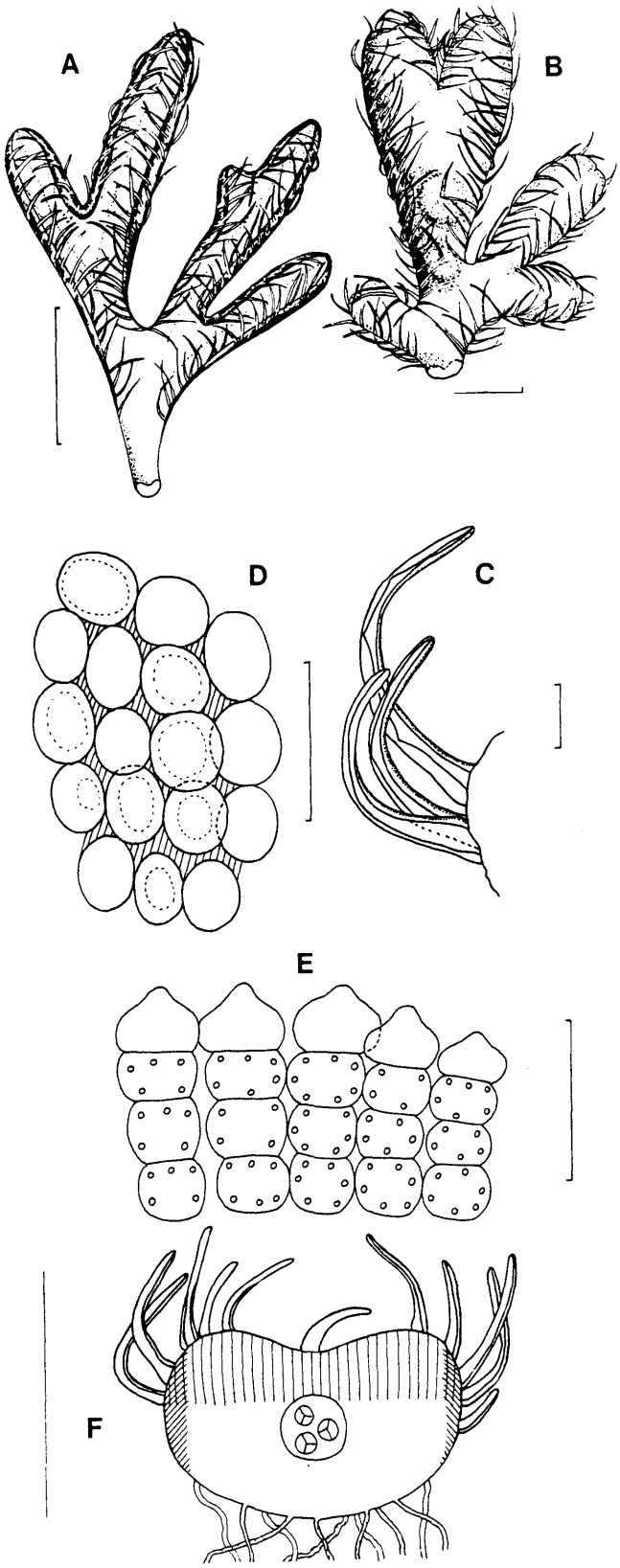


FIGURE 3.---*Riccia microciliata* (A--F): A, thallus dry; B, thallus wet; C, cilia at margin; D, epithelial cells and air pores seen from above; E, epithelial and assimilation tissue cells in cross section; F, cross section of branch. (A--F, *S.M. Perold* 1026). Scale bars A, B, F = 1 mm; C--E = 50 µm.

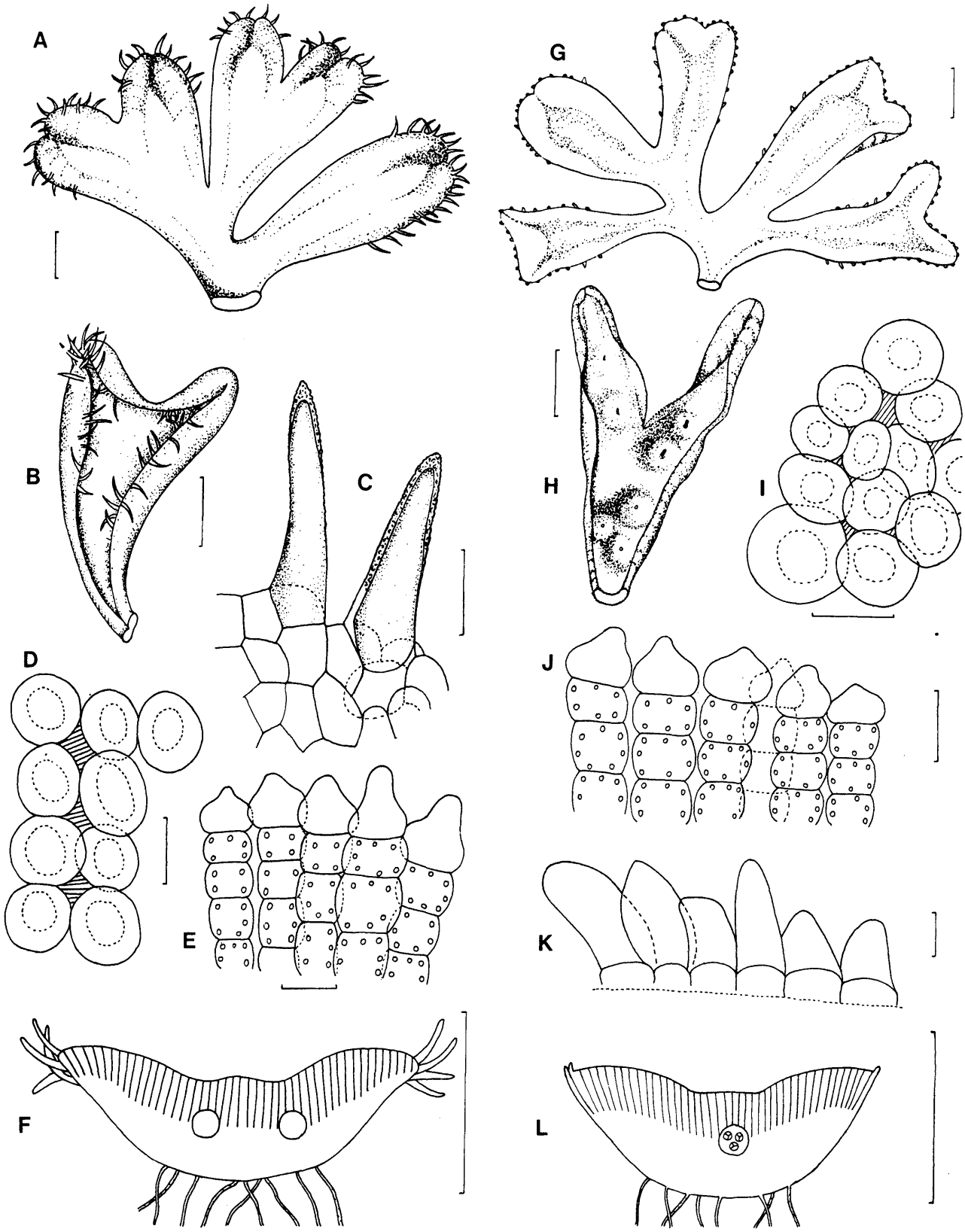


FIGURE 4.---*Riccia natalensis* (A--F): A, thallus wet; B, thallus dry; C, cilia at margin; D, epithelial cells and air pores seen from above; E, epithelial and assimilation tissue cells in cross section; F, cross section of branch. *R. mammifera* (G--L): G, thallus wet; H, thallus dry; I, epithelial cells and air pores seen from above; J, epithelial and assimilation tissue cells in cross section; K, marginal row of short cilia; L, cross section of branch. (A--F, *S.M. Perold* 1048; G--L, *S.M. Perold* 447). Scale bars A, B, F, G, H, L = 1 mm; C--E, I--K = 50 µm.

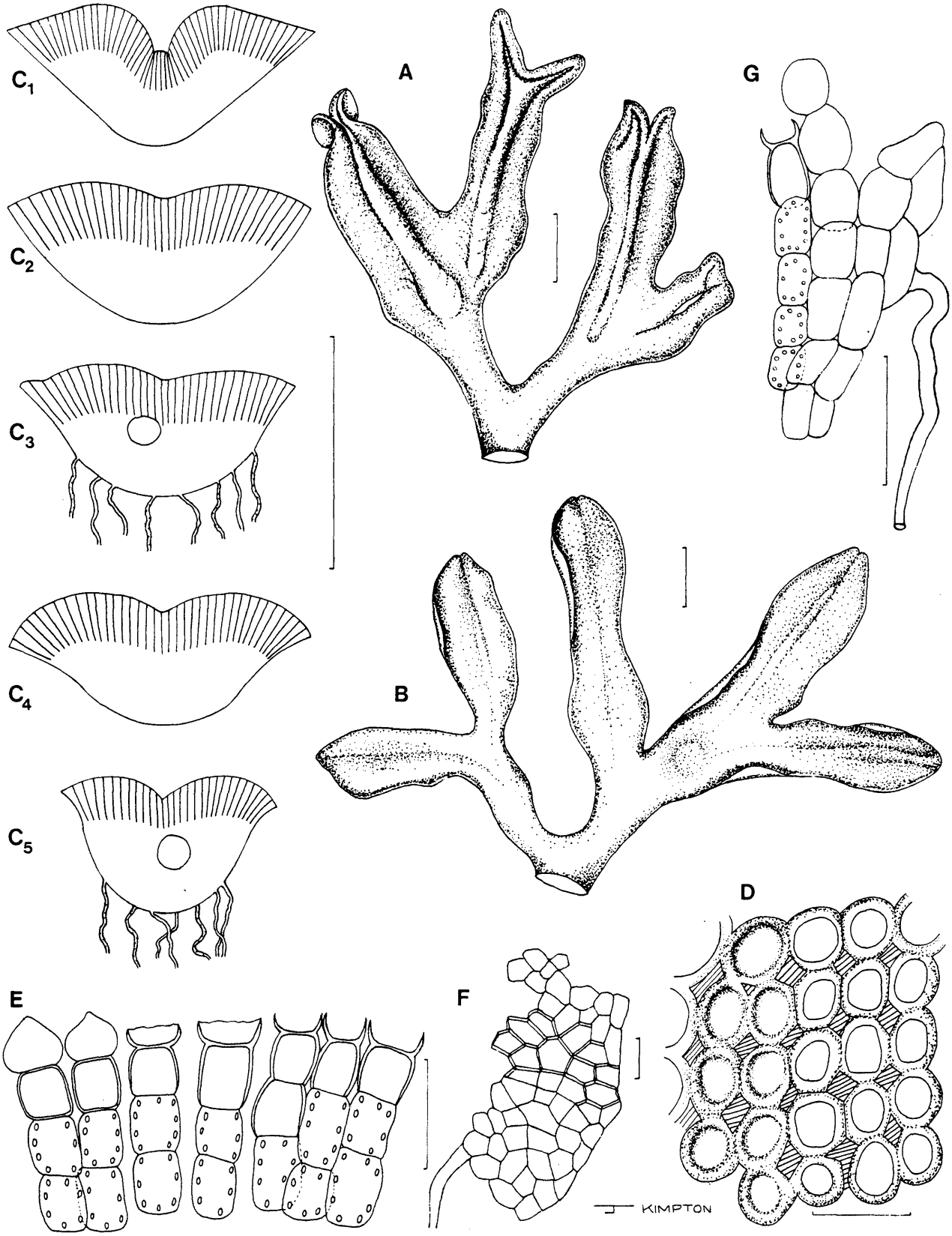


FIGURE 5.---*Riccia sorocarpa* (A--G): A, thallus dry; B, thallus wet; C, cross sections of branch at different distances from apex to basal part; D, epithelial cells and air pores from above; E, partly thick-walled epithelial cells and thin-walled assimilation tissue cells in cross section; F, scale; G, margin of thallus and scale in cross section. (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.

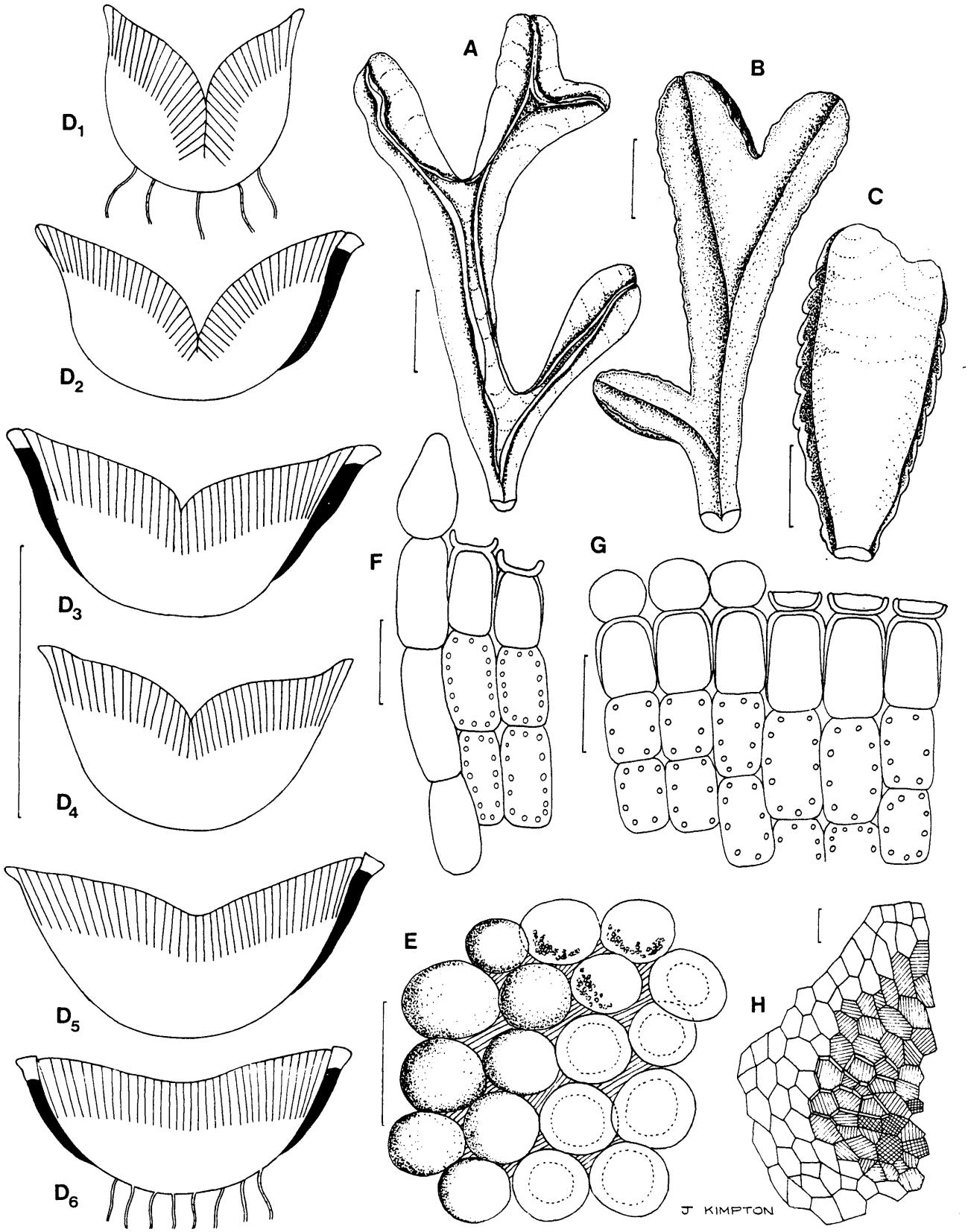


FIGURE 6.---*Riccia atropurpurea* (A--H): A, thallus dry; B, thallus wet; C, ventral face of thallus; D, cross sections of branch at different distances from apex to base; E, epithelial cells as seen from above on left intact, on right collapsed; F, cross section of cells at thallus margin; G, cross section of 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.

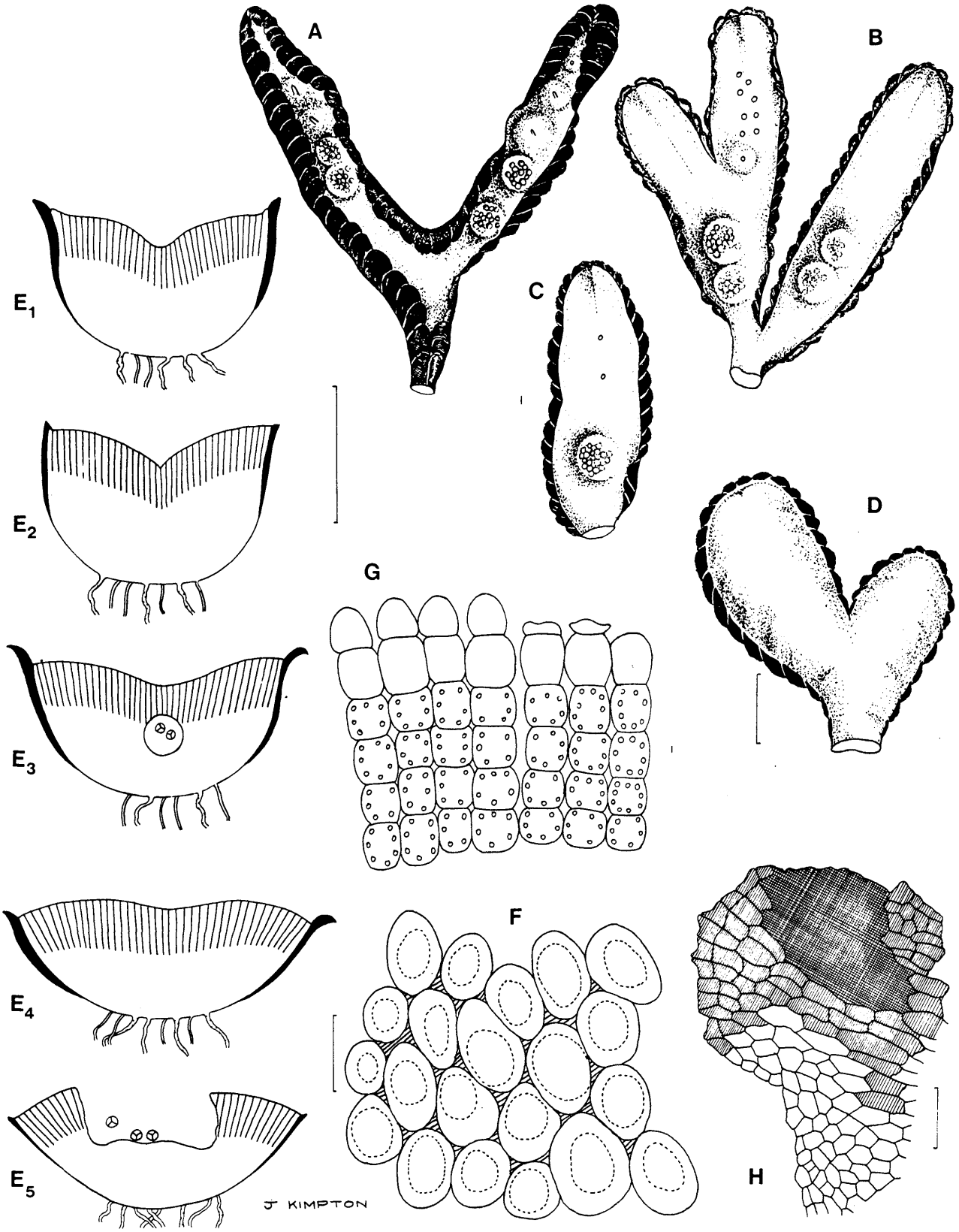


FIGURE 7.---*Riccia okahandjana* (A--H): A, thallus dry; B, C, thalli wet; D, ventral face of thallus; E, cross sections of branch at different distances from apex to base; F, epithelial cells and air pores from above; G, cross section showing epithelial cells, bistratose on the left, top cells collapsing and unistratose on the right; H, scale. (A, B, E, *S.M. Perold* 1041; C, F, G, *S.M. Perold* 1365a; D, *H. Anderson* PRE-CH 13443; H, *S.M. Perold* 315). Scale bars A--E = 1 mm; F, G = 50 µm; H = 100 µm.

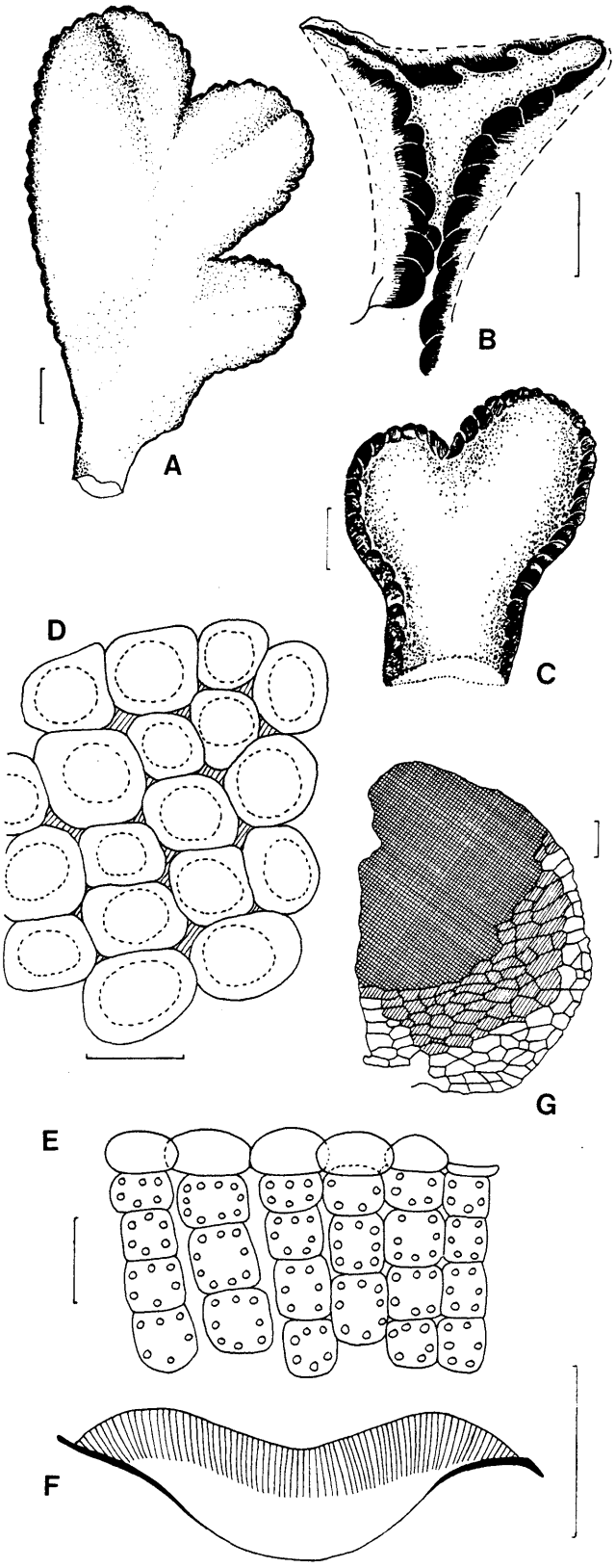


FIGURE 8.---*Riccia congoana* (A--G): A, thallus wet; B, thallus dry; C, ventral face of thallus; D, epithelial cells and air pores from above; E, cross section of epithelial and assimilation tissue cells; F, cross section of branch; G, scale. (A, *S.M. Perold* 747; B, D, E, *S.M. Perold* 763; C, G, *Volk* 00978; F, *Arnell* 1332). Scale bars A--C, F = 1 mm; D, E = 50 µm; G = 100 µm.

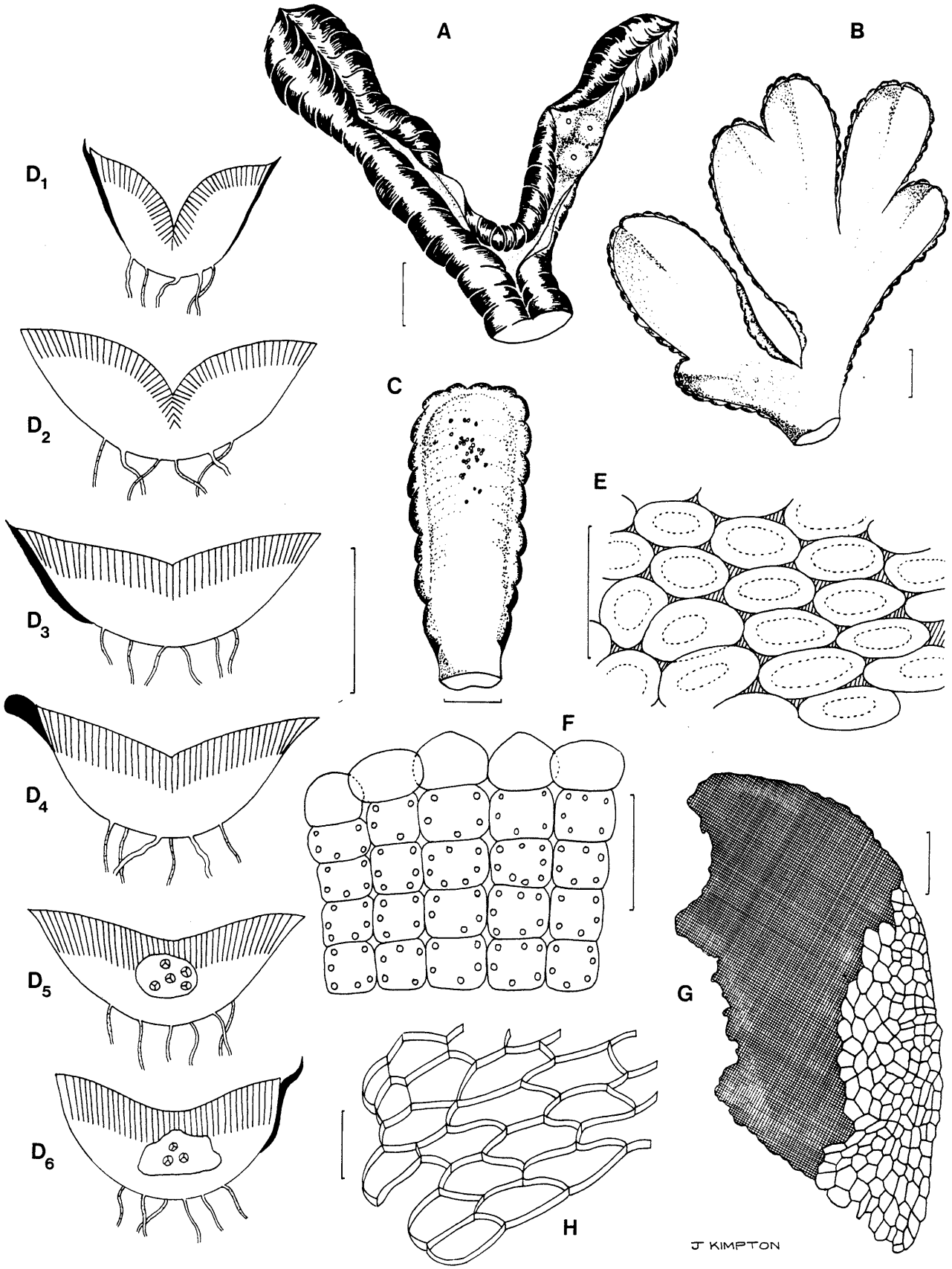


FIGURE 9.---*Riccia limbata* (A--H): A, thallus dry; B, thallus wet; C, ventral face of branch; D, cross sections of branch at different distances from apex to base; E, epithelial cells and air pores from above; F, cross section of epithelial and assimilation tissue cells; G, scale; H, cells in body 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.

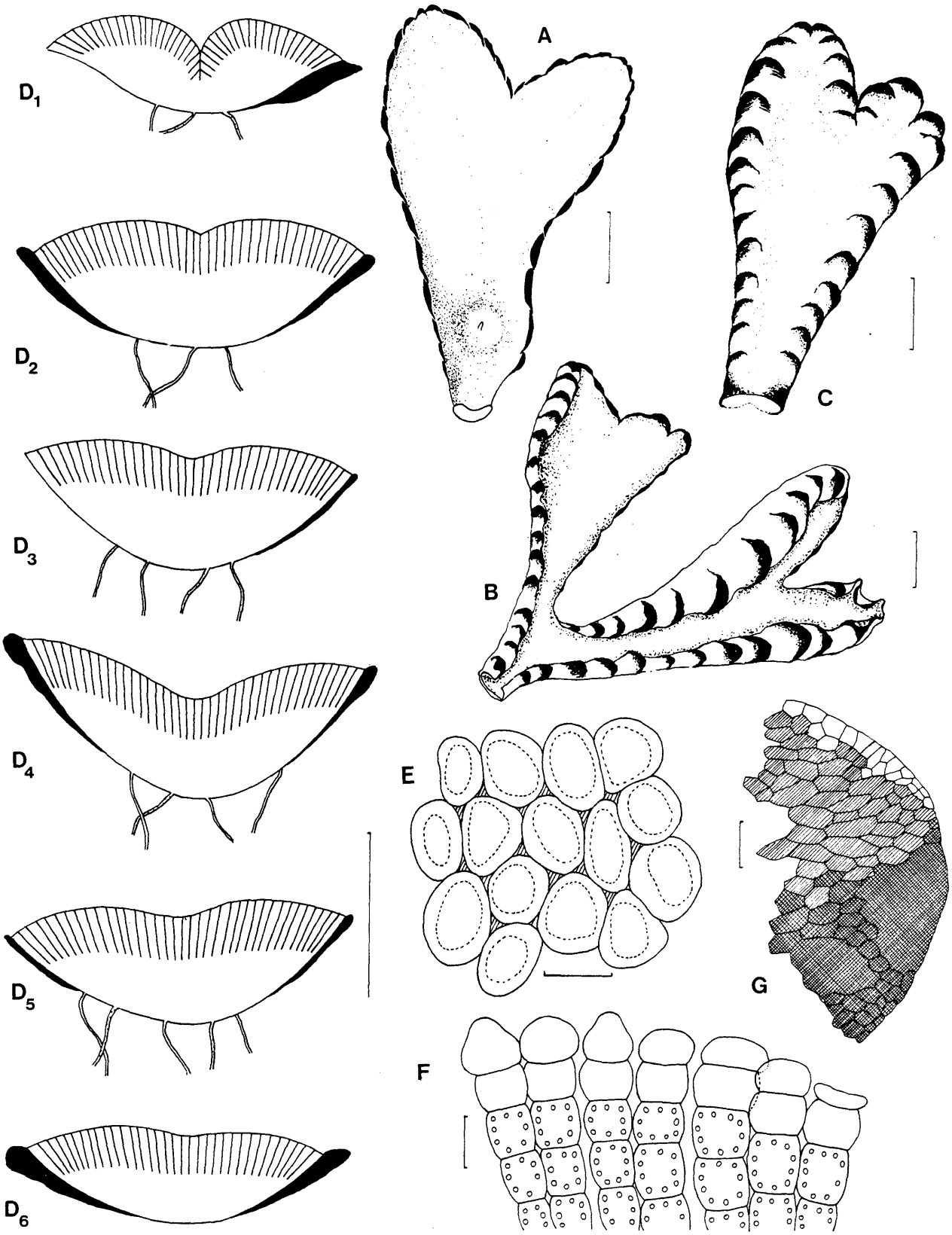


FIGURE 10.---*Riccia angolensis* (A--G): A, thallus wet; B, thallus dry; C, ventral face of thallus; D, cross sections of branch at different distances from apex to base; E, epithelial cells and air pores from above; F, cross section of bistratose epithelial cells, top cells collapsing toward the right; 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.

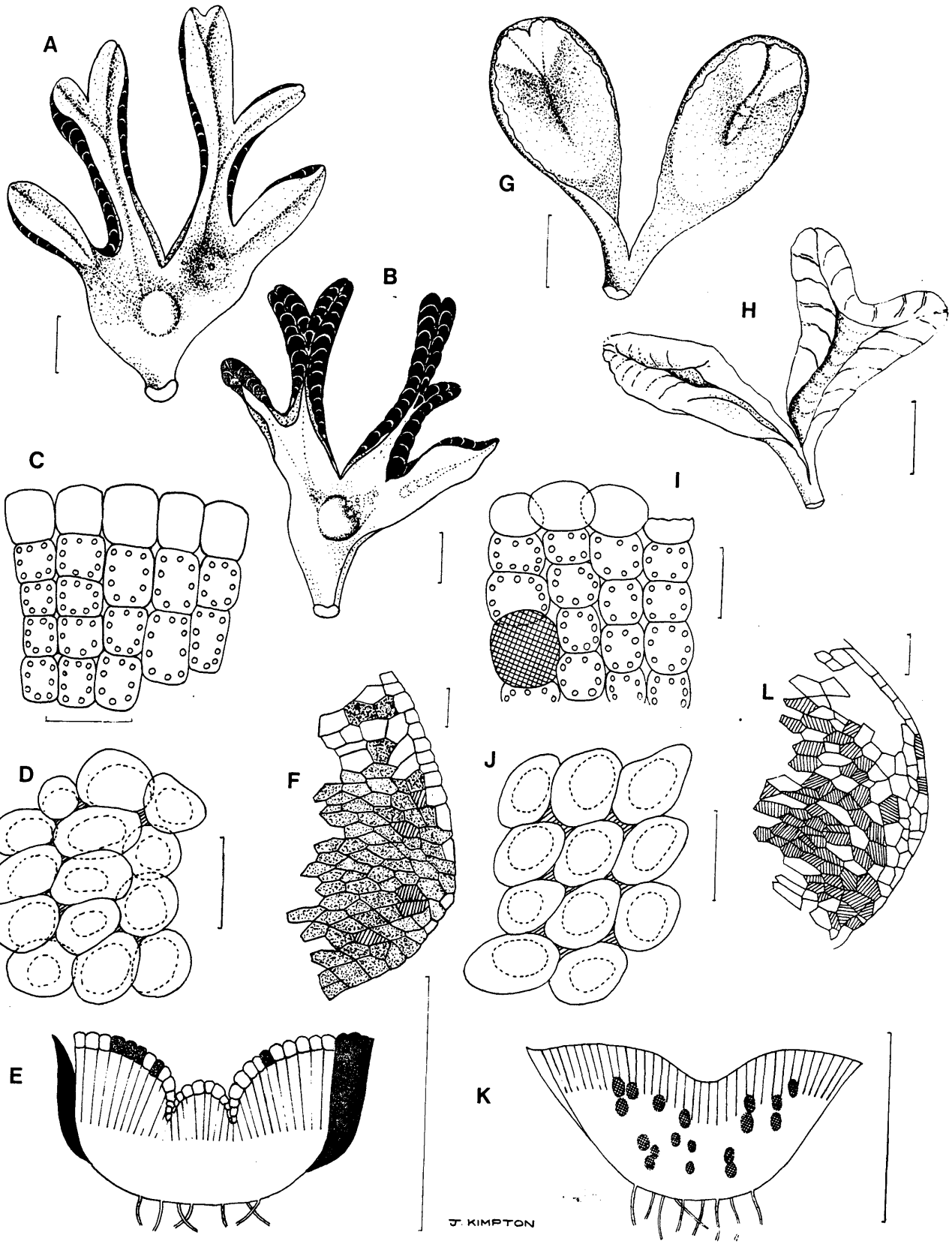


FIGURE 11.—*Riccia nigrella* (A--F): A, thallus wet; B, thallus dry; C, cross section of epithelial and assimilation tissue cells; D, epithelial cells and air pores from above; E, cross section of branch, showing persistent epithelial cells, some with finely granular contents; F, scale. *R. macrocarpa* (G--L): G, thallus wet; H, thallus dry; I, cross section of epithelial and assimilation tissue cells with one idioblast; J, epithelial cells and air pores from above; K, cross section of branch showing some idioblasts (cross 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.

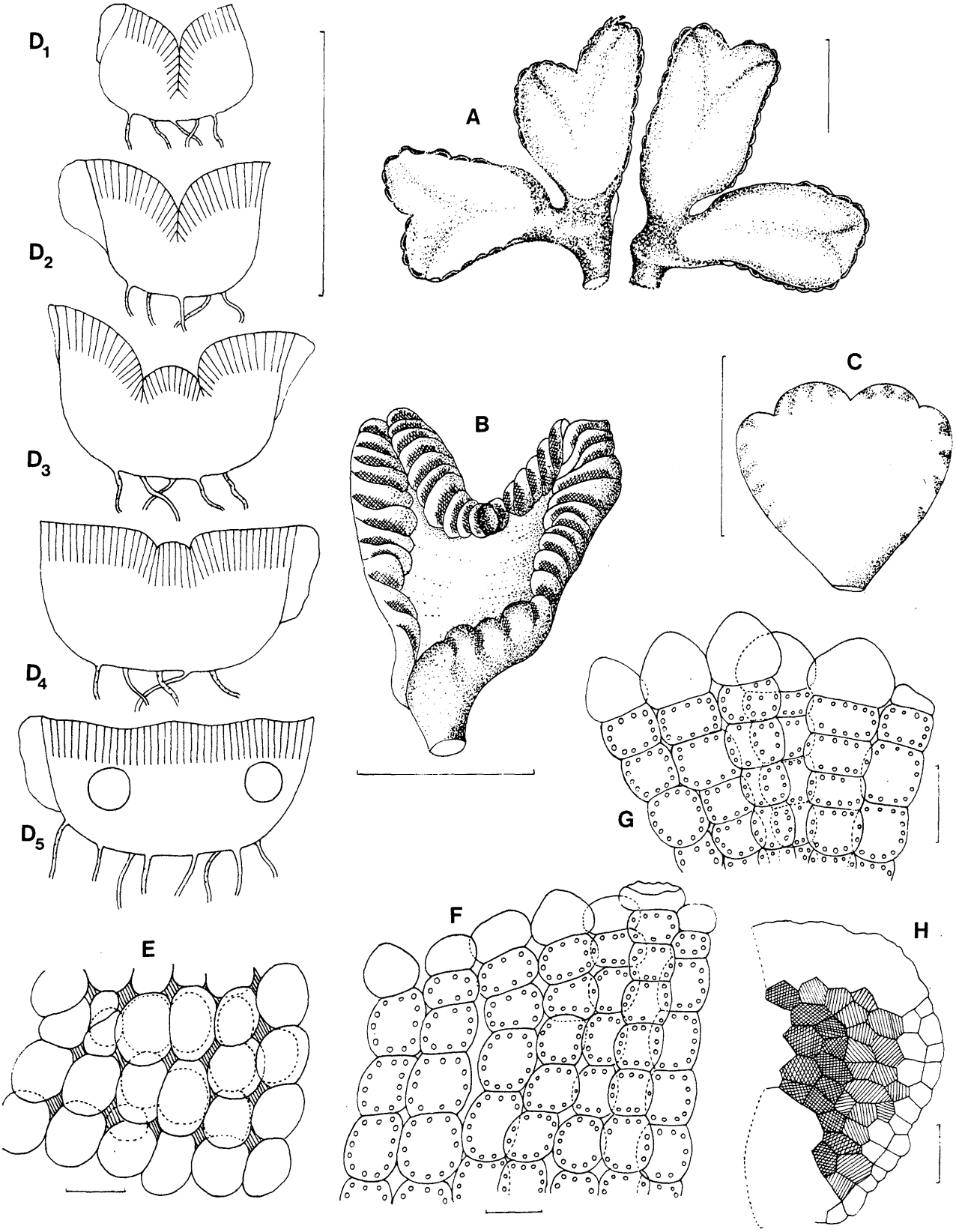


FIGURE 12.---*Riccia pottsiana* (A--H): A, thallus wet; B, thallus dry; C, ventral face of thallus; D, cross sections of branch at different distances from apex to basal part; E, epithelial cells and air pores from above; F, cross section of epithelial and assimilation tissue cells; G, epithelial cells 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.

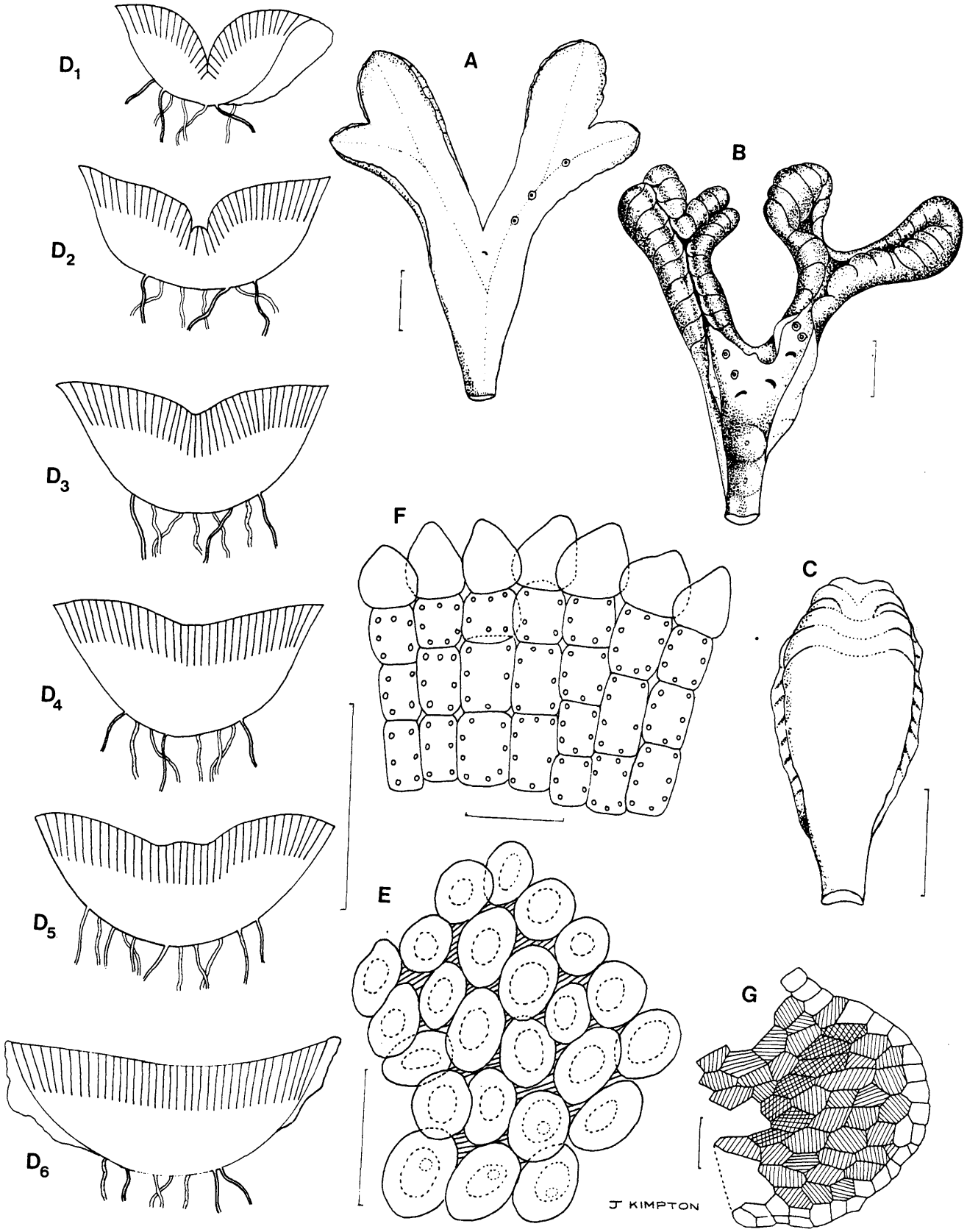


FIGURE 13.—*Riccia runssorensis* (A--G): A, thallus wet; B, thallus dry; C, ventral face of thallus; D, cross sections of branch at different distances from apex to basal part; E, epithelial cells and air pores from above; F, cross section of epithelial and assimilation tissue cells; G, scale. (A, C, *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 = 100µm.

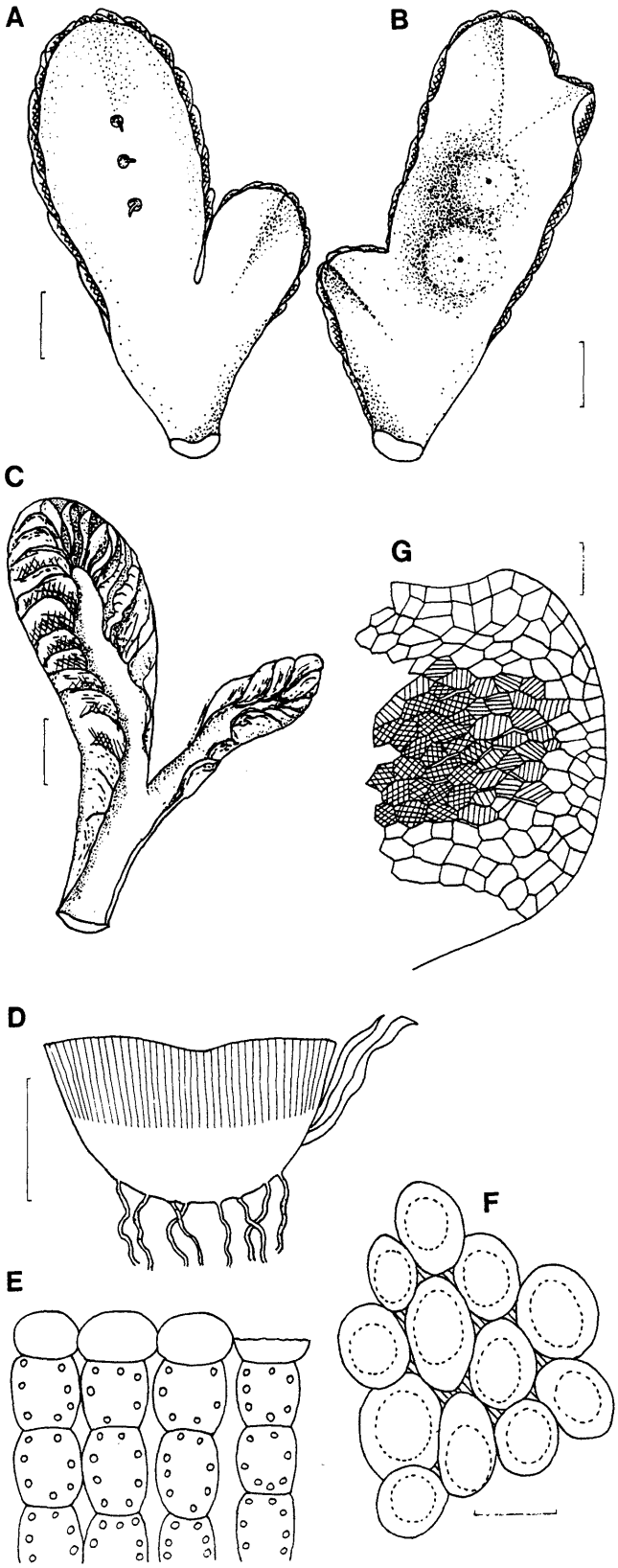


FIGURE 14.—*Riccia rosea* (A–G): A, male thallus wet; B, female thallus wet; C, thallus dry; D, cross section of branch; E, cross section of epithelial and assimilation tissue cells; F, epithelial cells and air pores from above; G, scale. (A, B, *S.M. Perold* 2018a; C, D, G, *S.M. Perold* 346; E, F, *H. Anderson* PRE-CH 13445). Scale bars A–D = 1 mm; E, F = 50 µm; G = 100 µm.

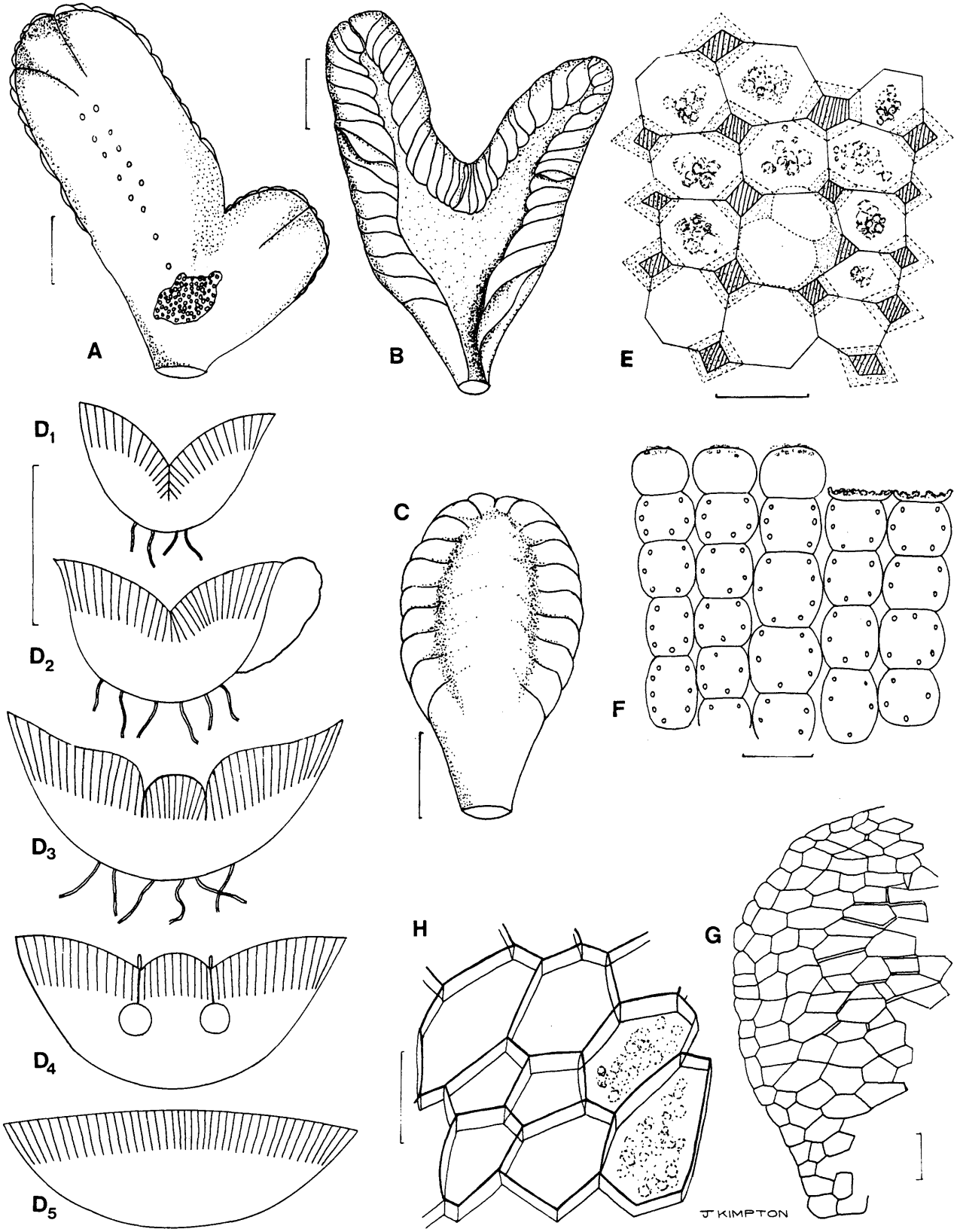


FIGURE 15.---*Riccia albolimbata* (A--H): A, thallus wet; B, thallus dry; C, ventral face of thallus; D, cross sections of branch at different distances from apex to basal part; E, epithelial cells, some with overlying calcium crystals, and air pores (hatched) seen from above, air canals stippled; F, cross section of epithelial cells, intact on the left, collapsed on the right, assimilation tissue below; G, scale; H, enlarged scale cells, on the 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.

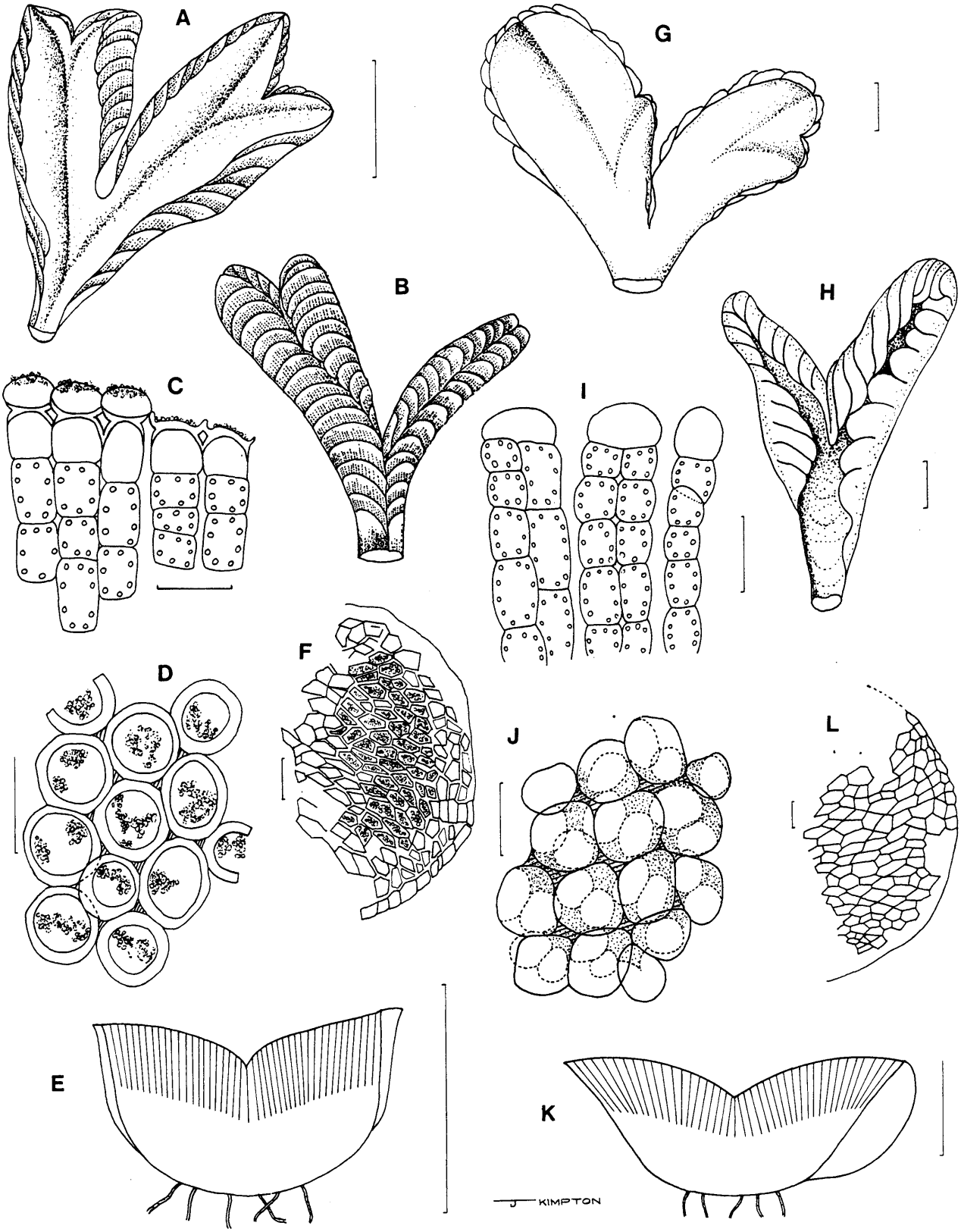


FIGURE 16.---*Riccia argenteolimbata* (A--F): A, thallus wet; B, thallus dry; C, cross section of epithelial cells, partly thicker-walled, on the left intact, on the right collapsed, assimilation tissue below; D, collapsed, thicker-walled epithelial cells with overlying calcium crystals, air pores mostly three-sided, as seen from above; E, cross section of branch; F, scale. *R. albornata* (G--L): G, thallus wet; H, thallus dry; I, cross section of epithelial and assimilation tissue cells; J, epithelial (solid lines) and subdorsal (broken lines) cells, air pores (hatched) overlying air canals (dotted), seen from above; K, cross section of 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.

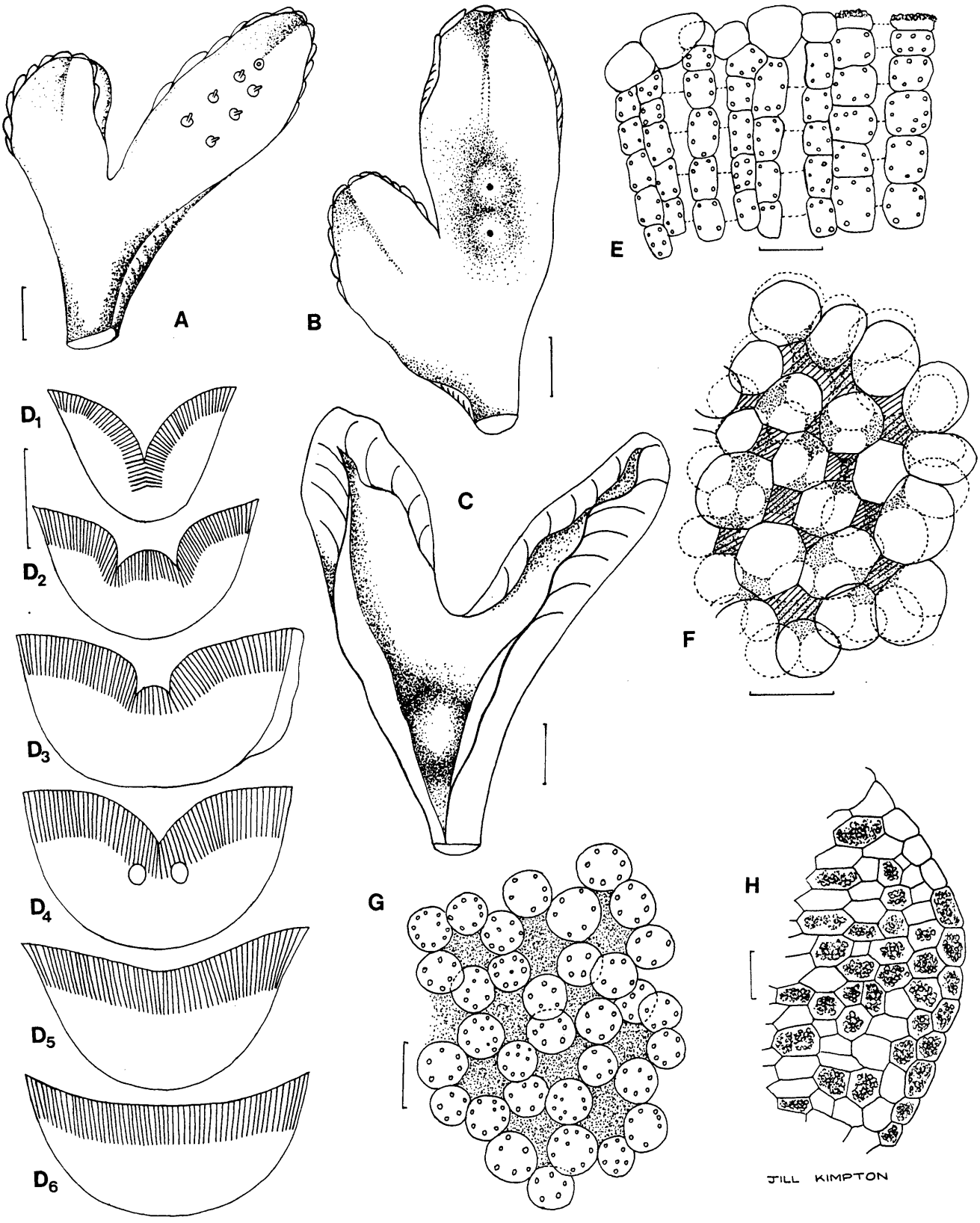


FIGURE 17.---*Riccia montana* (A--H): A, male thallus wet; B, female thallus wet; C, female thallus dry; D, cross sections of branch at different distances from apex to basal part; E, cross section of epithelial and assimilation tissue cells; F, epithelial (solid lines) and subdorsal (broken lines) cells, air pores (hatched) overlying air canals (stippled), seen from above; G, horizontal section 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.

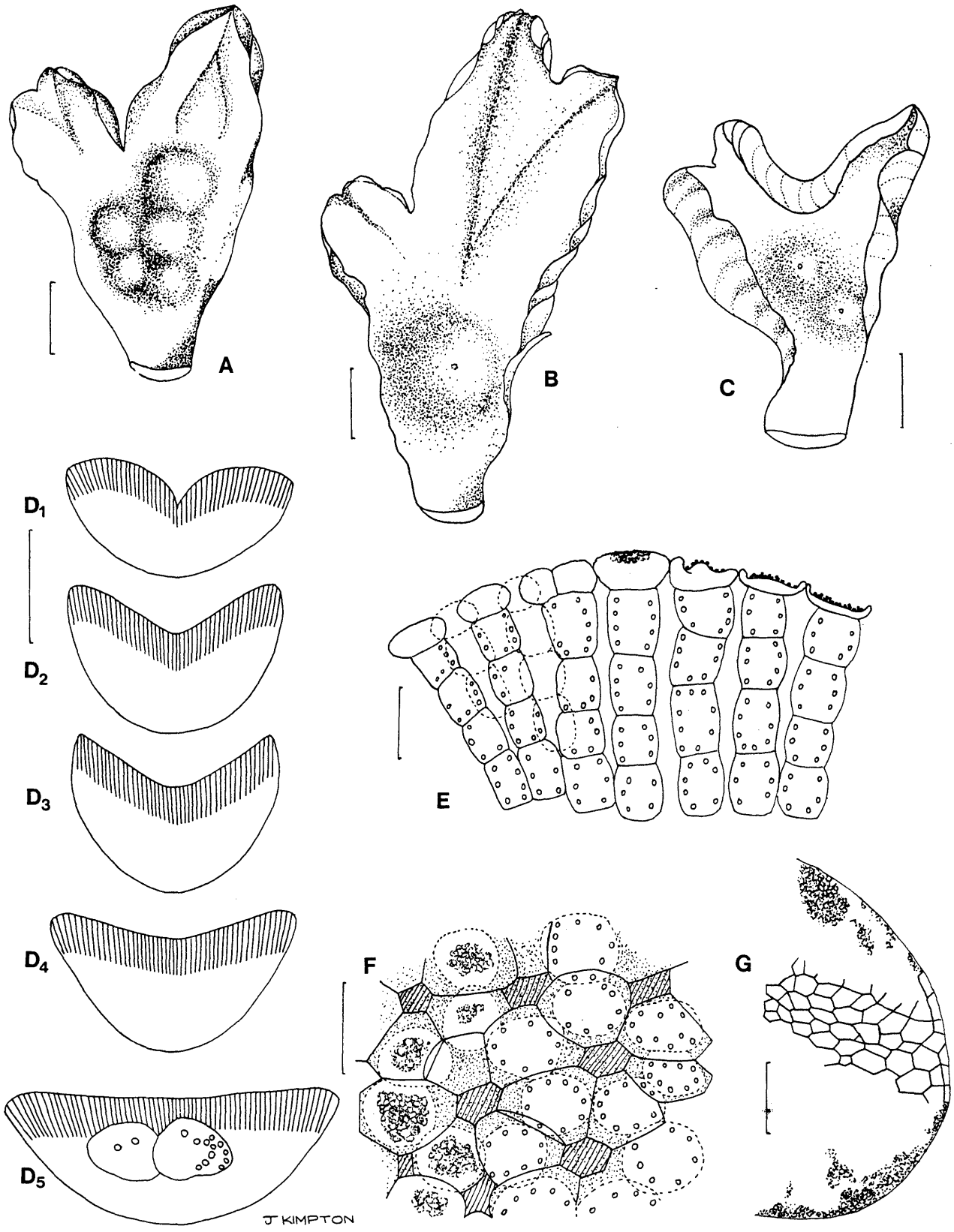


FIGURE 18.---*Riccia alboporosa* (A--G): A, B, thalli wet; C, thallus dry; D, cross sections of branch at different distances from apex to basal part; E, cross section of epithelial cells, intact on the left, collapsed on the right and covered with calcium deposits, assimilation tissue below; F, epithelial (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.

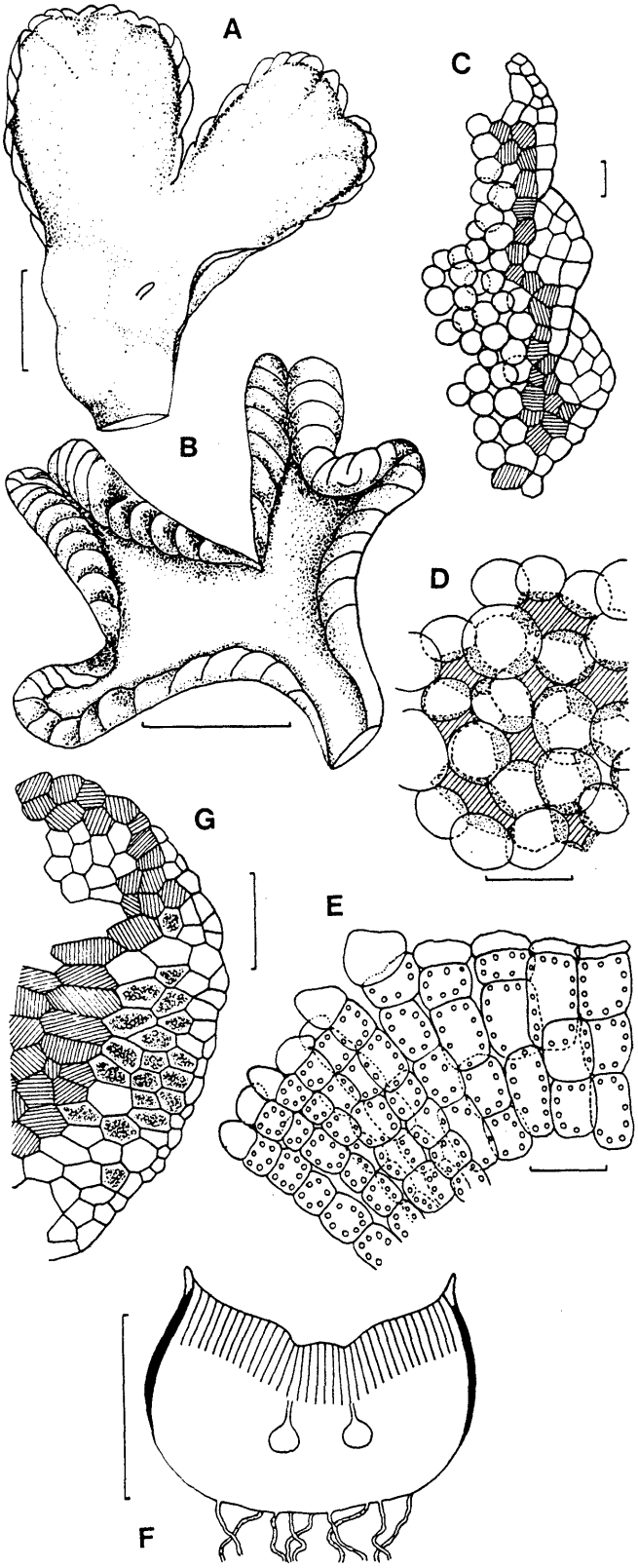


FIGURE 19.---*Riccia bicolorata* (A--F): A, thallus wet; B, thallus dry; C, dark margin of thallus (hatched) and projecting scales seen from above; D, epithelial (solid lines) and subdorsal (broken lines) cells, air pores (hatched) overlying air canals (stippled), seen from above; E, cross section of epithelial cells, intact at groove on left, collapsing to the right, assimilation tissue below; F, cross section of branch; G, scale. (A--G, *Smook* 6990a). Scale bars A, B, F = 1 mm; D, E = 50 µm; C, G = 100 µm.

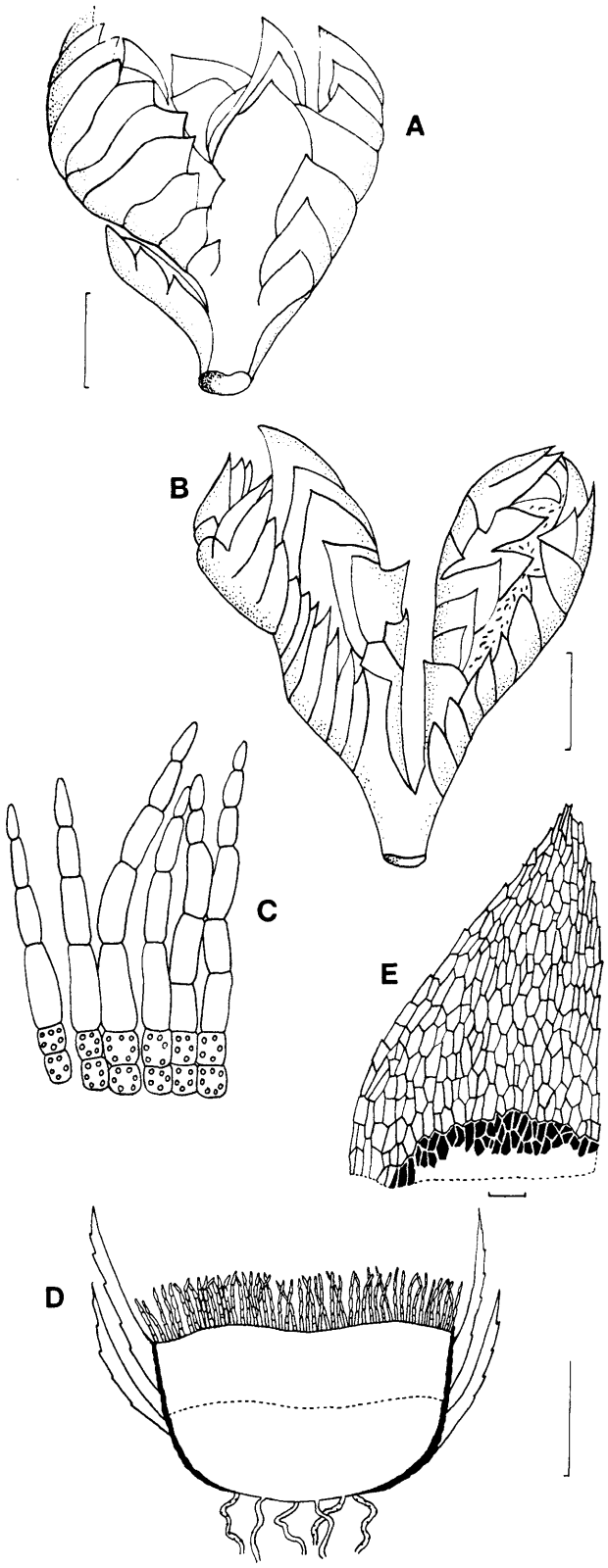


FIGURE 20.---*Riccia villosa* (A--E): A, thallus wet; B, thallus dry; C, cross section of long tapering epithelial cell pillars and assimilation tissue below; D, cross section of branch; E, scale. (A, C, D, *C.M. van Wyk* 2522; B, E, *S.M. Perold* 504). Scale bars A, B, D = 1 mm; C = 50 µm; E = 200 µm.

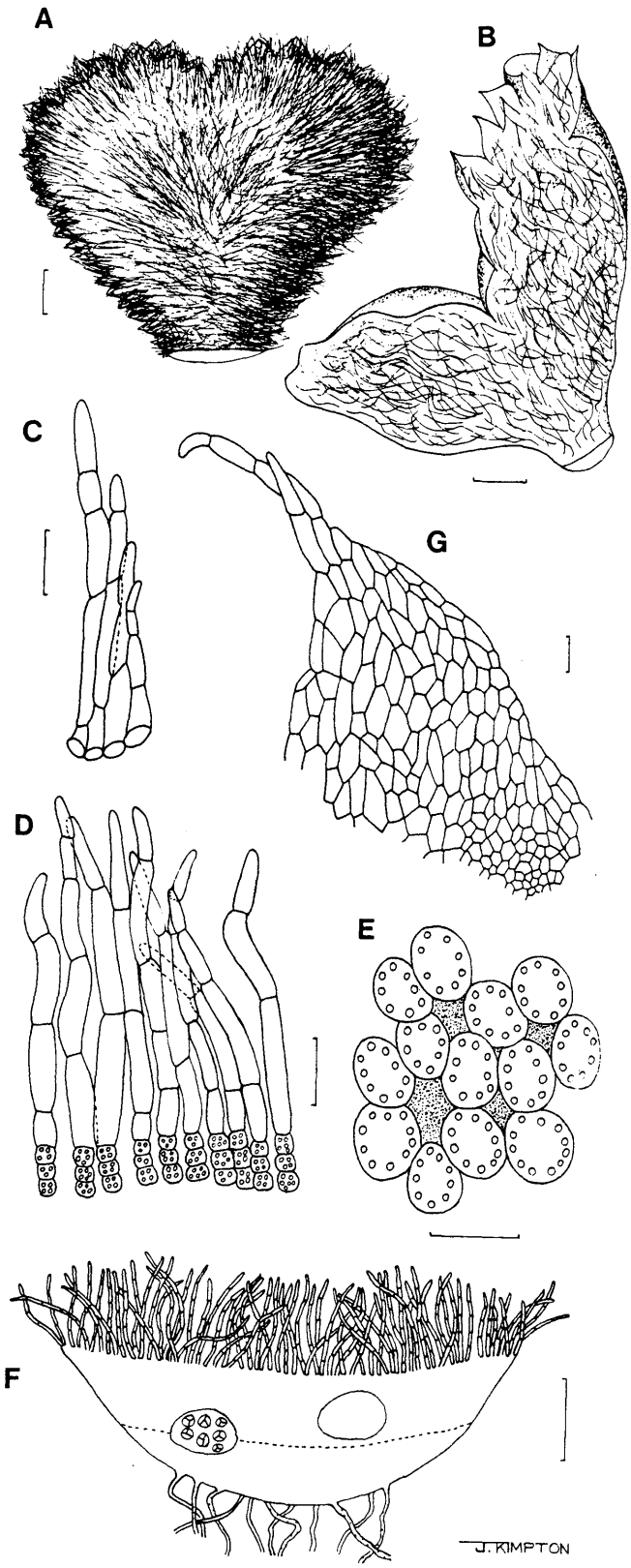


FIGURE 21.---*Riccia hirsuta* (A--G): A, thallus wet; B, thallus dry; C, filiform apex of scale; D, cross section of very long, slightly tapering epithelial cell pillars and assimilation tissue below; E, horizontal section through assimilation tissue, air canals stippled; F, cross section of branch; G, scale. (A, B, D, F, *S.M. Perold* 2182; C, E, G, *Oliver* 8040). Scale bars on A, B, F = 1 mm; C, D, G = 100 µm; E = 50 µm.

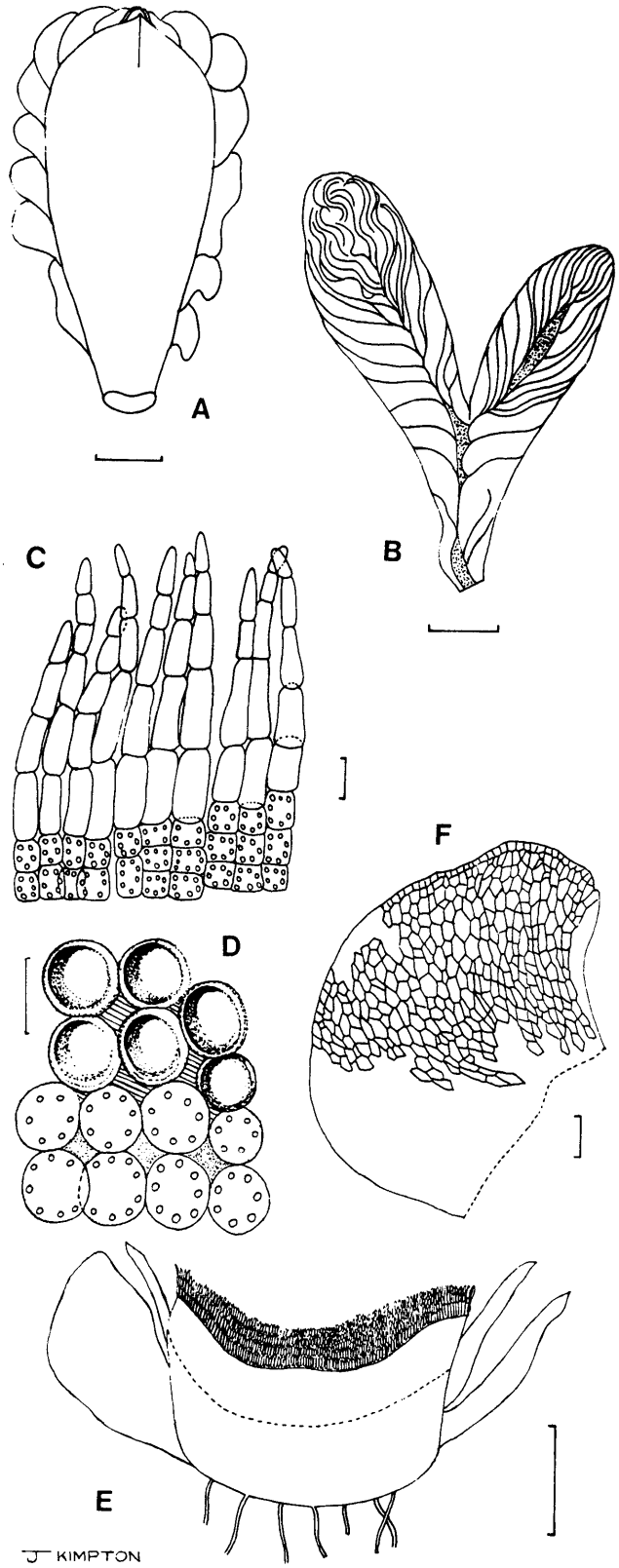


FIGURE 22.---*Riccia simii* (A--F): A, thallus wet; B, thallus dry; C, cross section of long tapering epithelial cell pillars and assimilation tissue below; D, horizontal section through basal cells of dorsal pillars with air pores hatched, and through assimilation tissue with air canals stippled; E, cross section of 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 on A, B, E = 1 mm; C, D = 50 µm; F = 100 µm.

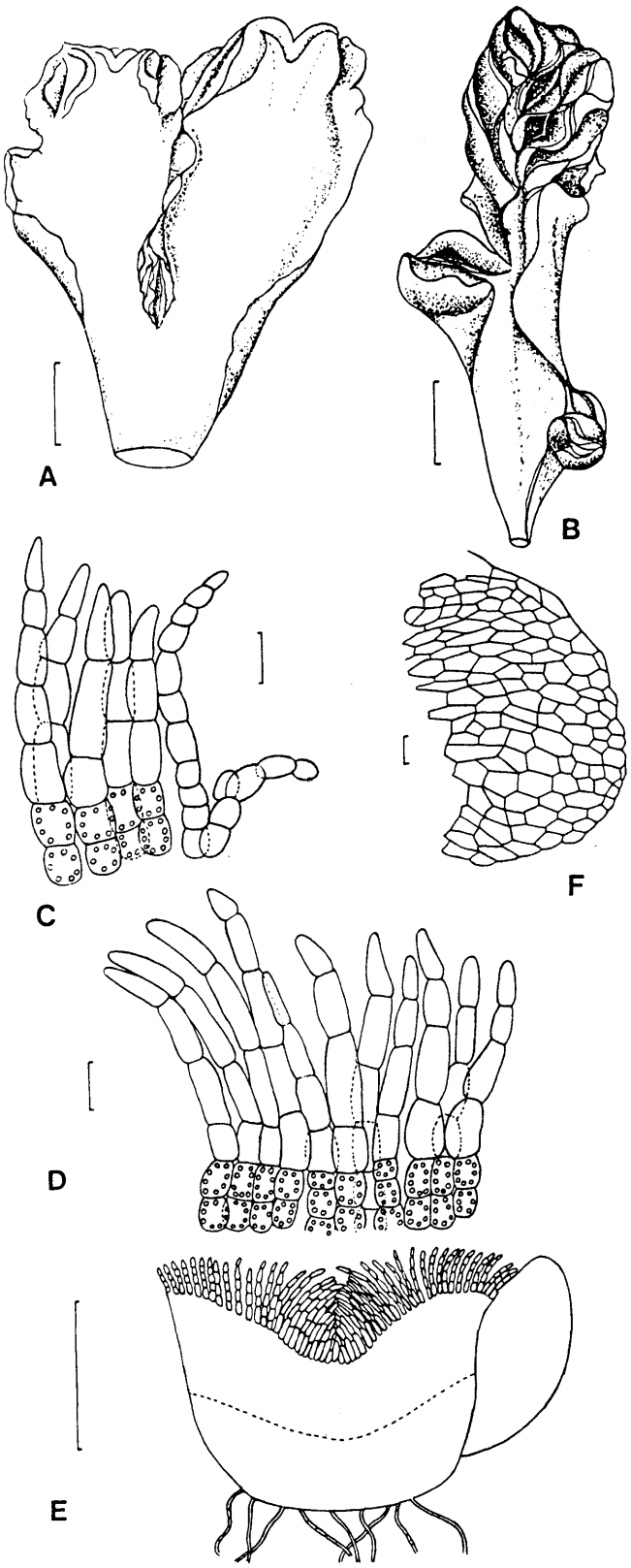


FIGURE 23.---*Riccia vitrea* (A--F): A, thallus wet; B, thallus dry; C, cross section toward margin, of erect epithelial cell pillars and scales; D, section of arched and erect epithelial cell pillars, assimilation tissue below; E, cross section of branch; F, scale. (A, D, F, *S.M. Perold* 2149; B, *S.M. Perold* 1475; C, E, *S.M. Perold* 1419). Scale bars A, B, E = 1 mm; C, D = 50 µm; F = 100 µm.

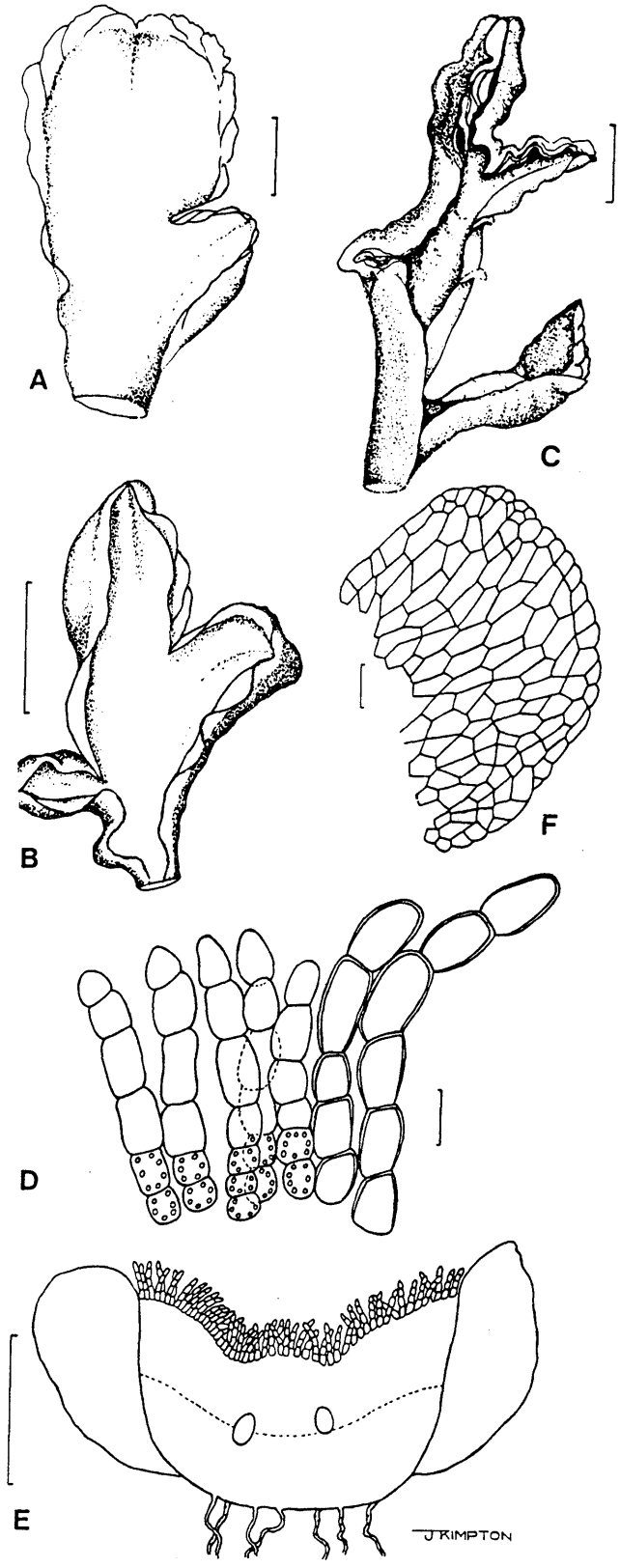


FIGURE 24.---*Riccia namaquensis* (A--F): A, thallus wet, from seepage area; B, thallus wet, from drier habitat; C, thallus dry; D, cross section toward margin of epithelial cell pillars and scales; E, cross section of branch; F, scale. (A, *S.M. Perold* 2136; B, *S.M. Perold* 2036; C, *S.M. Perold* 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.

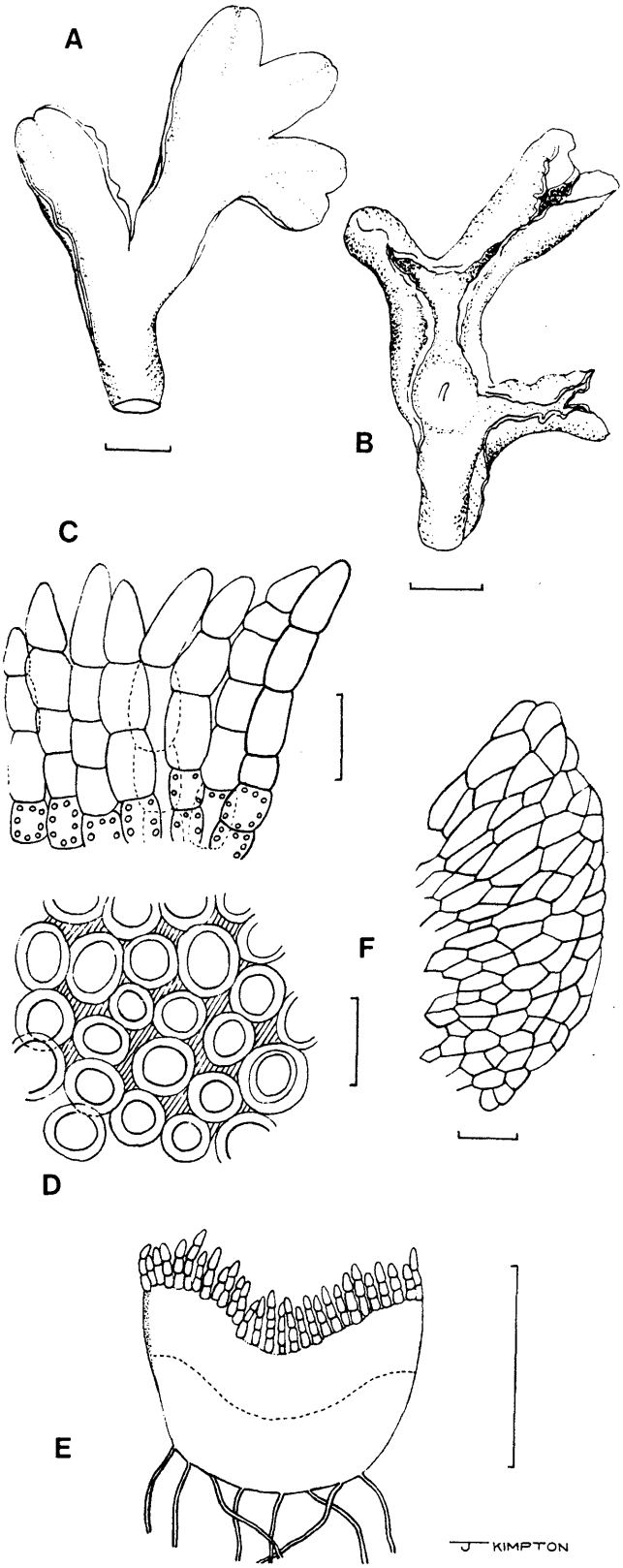


FIGURE 25.---*Riccia albomarginata* (A--F): A, thallus wet; B, thallus dry; C, cross section toward margin of epithelial cell pillars and scale; D, epithelial cell pillars and air pores from above; E, cross section of branch; F, scale. (A, C, E, *S.M. Perold* 1979; B, *S.M. Perold* 2118; D, *S.M. Perold* 538; F, *S.M. Perold* 2031 p.p.). Scale bars A, B, E = 1 mm; C, D = 50 µm; F = 100 µm.

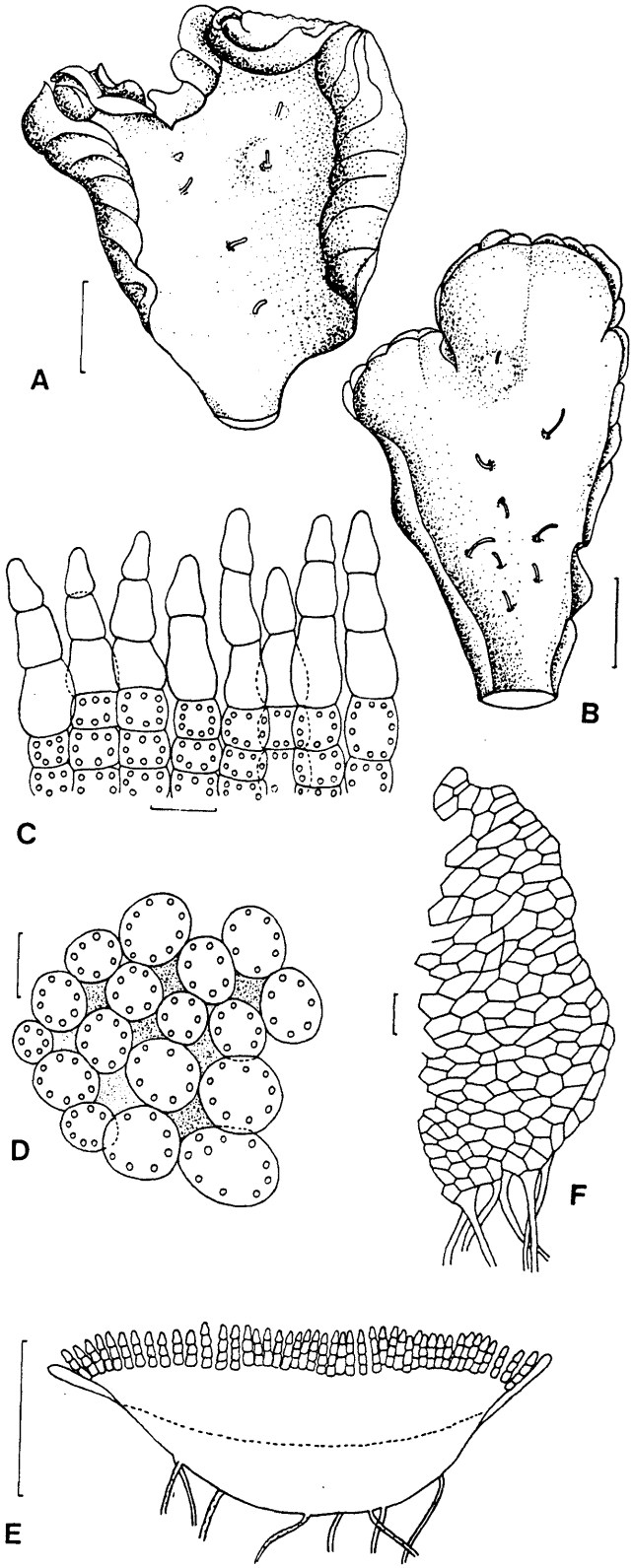


FIGURE 26.—*Riccia ampullacea* (A–F): A, thallus dry; B, thallus wet; C, cross section of epithelial cell pillars and assimilation tissue below; D, horizontal section through assimilation tissue, air canals stippled; E, cross section of branch; F, scale. (A–F, *Van Rooy* 3573). Scale bars A, B, E = 1 mm; C, D = 50 µm; F = 100 µm.

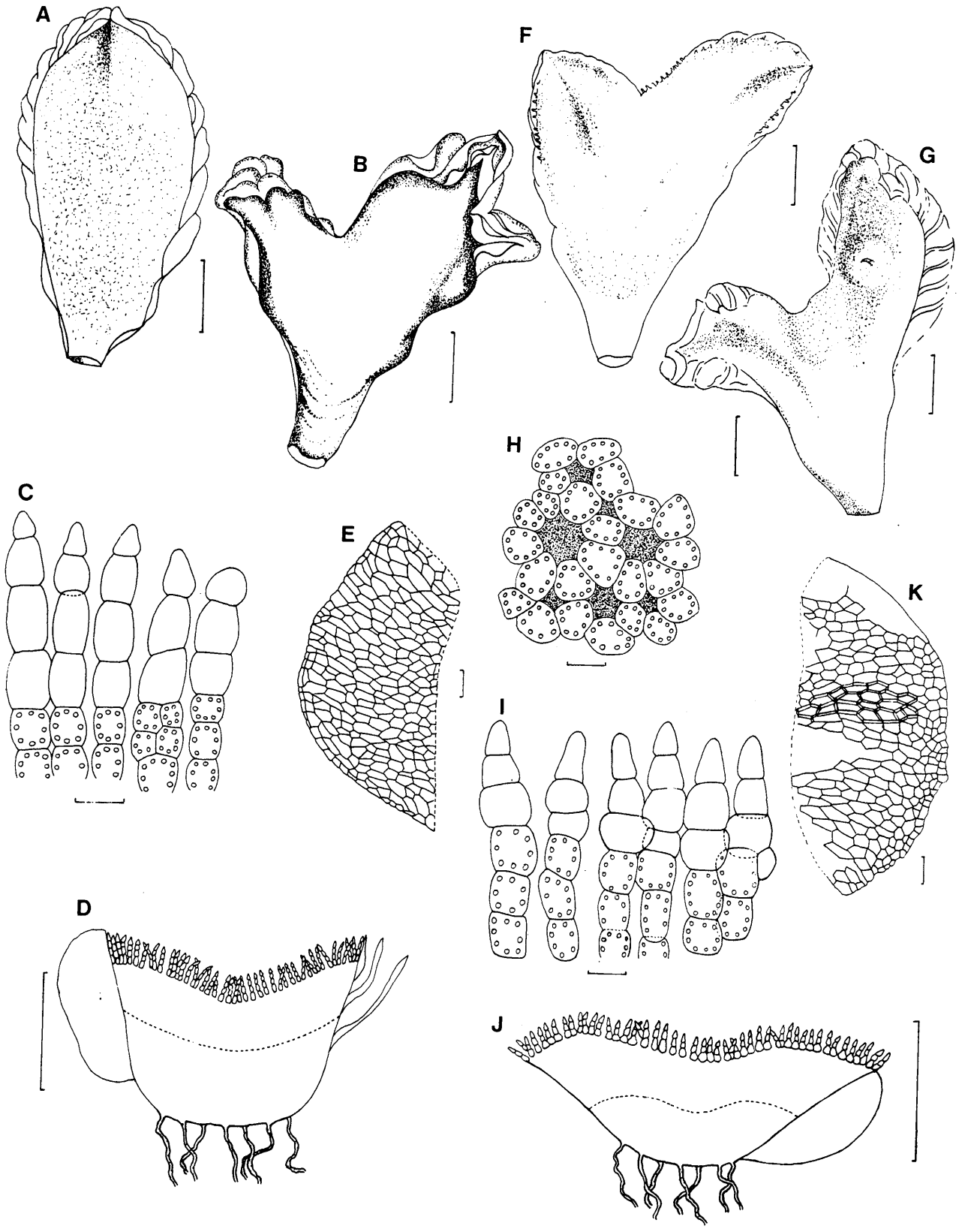


FIGURE 27.---*Riccia parvo-areolata* (A--E): A, thallus wet; B, thallus dry; C, cross section of epithelial cell pillars, assimilation tissue below; D, cross section of branch; E, scale. *R. albovestita* (F--K): F, thallus wet; G, thallus dry; H, horizontal section through assimilation tissue, air canals stippled; I, cross section of short tapering epithelial cell pillars, assimilation tissue below; J, cross section of branch; K, scale. (A, *S.M. Perold* 1727; B, C, D, *S.M. Perold* 1726; E, *J.M. Perold* 26; F, G, *Smook* 6583). Scale bars A, B, D, F, G, J = 1 mm; C, H, I = 50 µm; E, K = 100µm.

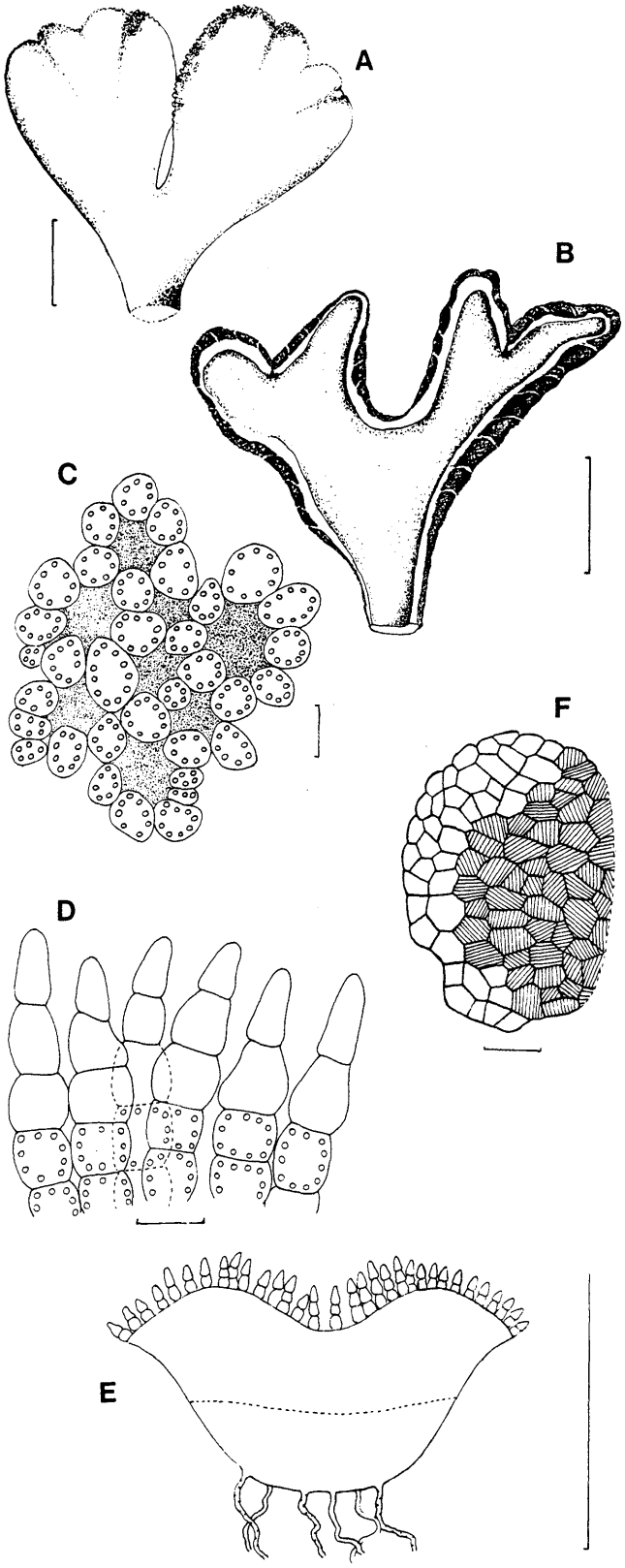


FIGURE 28.---*Riccia alatospora* (A--F): A, thallus wet; B, thallus dry; C, horizontal section through assimilation tissue, air canals stippled; D, cross section of epithelial cell pillars, assimilation tissue below; E, cross section of branch; F, scale. (A, C--E, *Oliver* 9025; B, F, *S.M. Perold* 468). Scale bars A, B, E = 1 mm; C, D = 50 µm; F = 100 µm.

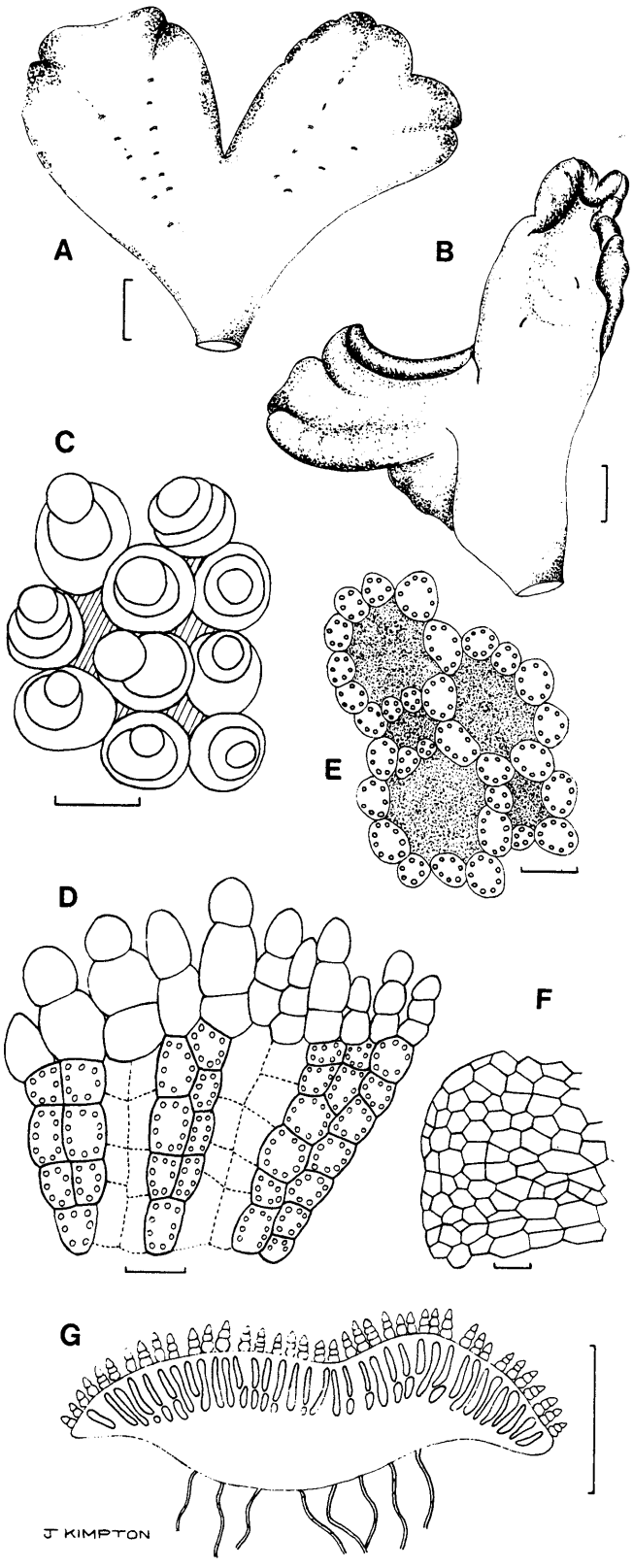


FIGURE 29.---*Riccia hantamensis* (A--G) = A, male thallus wet; B, female thallus dry; C, short tapering epithelial cell pillars and air pores (hatched) from above; D, cross section of epithelial cell pillars, assimilation tissue below, with wider air canals; E, horizontal section through assimilation tissue, air canals stippled; F, scale; G, cross section of 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.

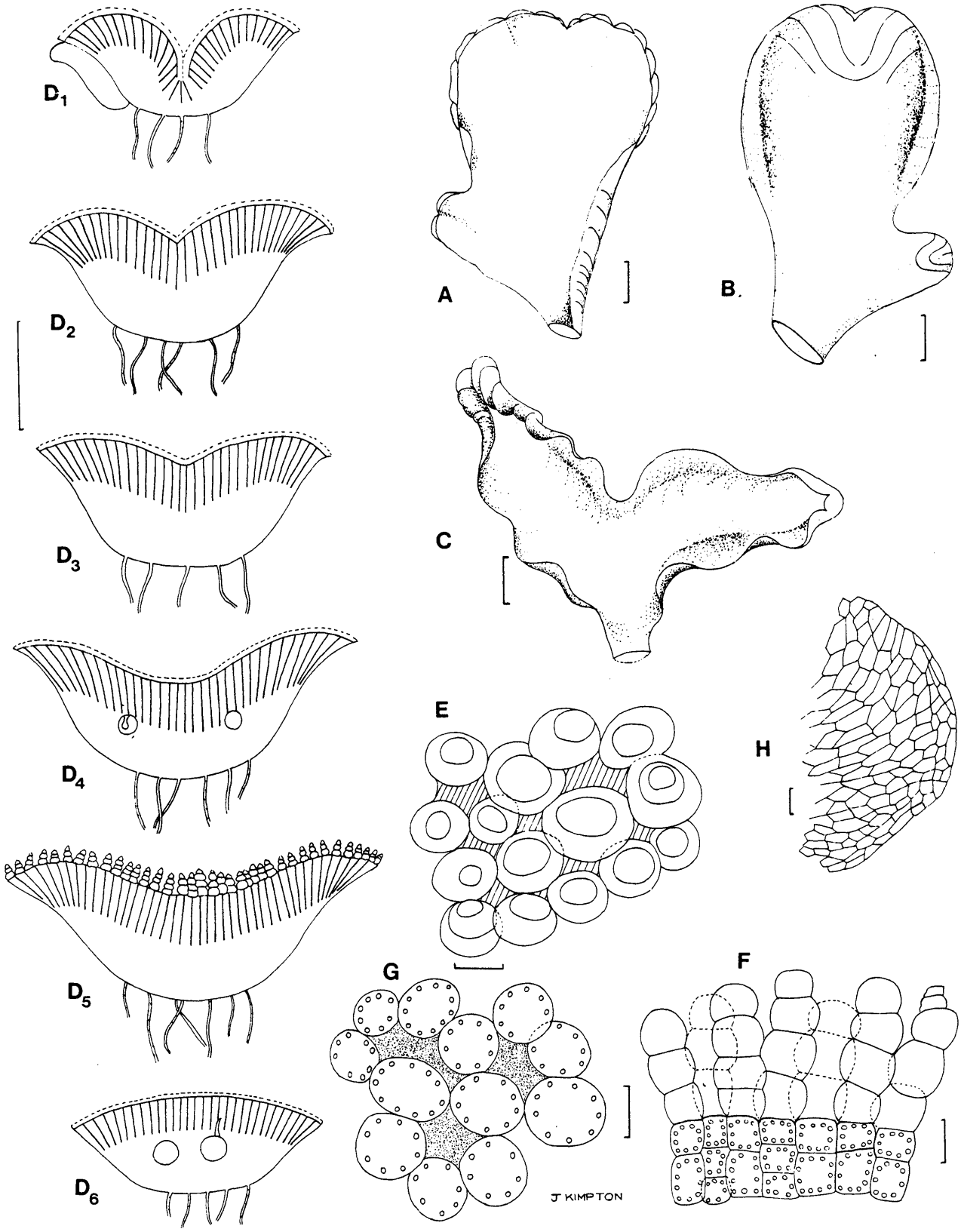


FIGURE 30.---*Riccia concava* (A--H): A, thallus wet; B, ventral face of thallus; C, thallus dry; D, cross sections of branch at different distances from apex to base; E, epithelial cells and air pores (hatched) from above; F, cross section of epithelial cell pillars and assimilation tissue below; G, horizontal section through 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.

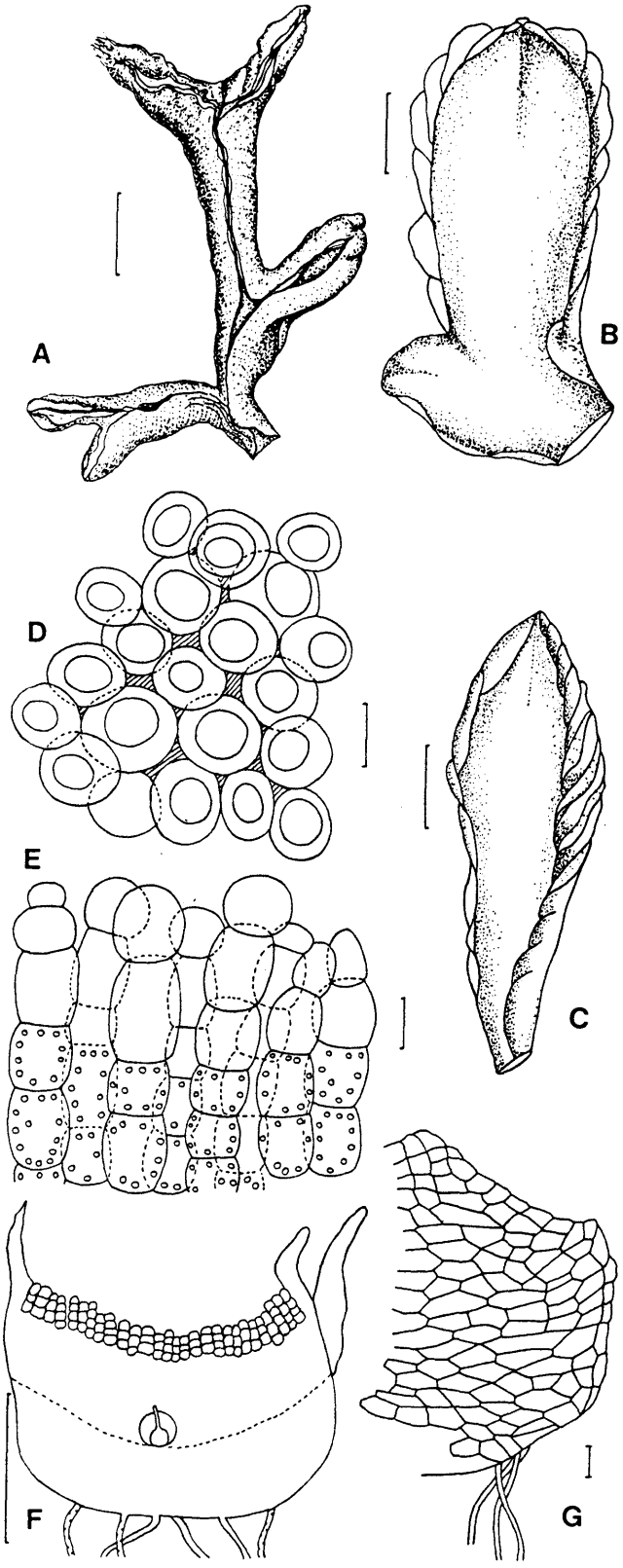


FIGURE 31.---*Riccia elongata* (A--G): A, thallus dry; B, thallus wet and fully expanded; C, thallus generally with partly inflexed sides; D, epithelial cells and air pores (hatched) from above; E, cross section of epithelial cell pillars and assimilation tissue below; F, cross section of branch, scales 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.

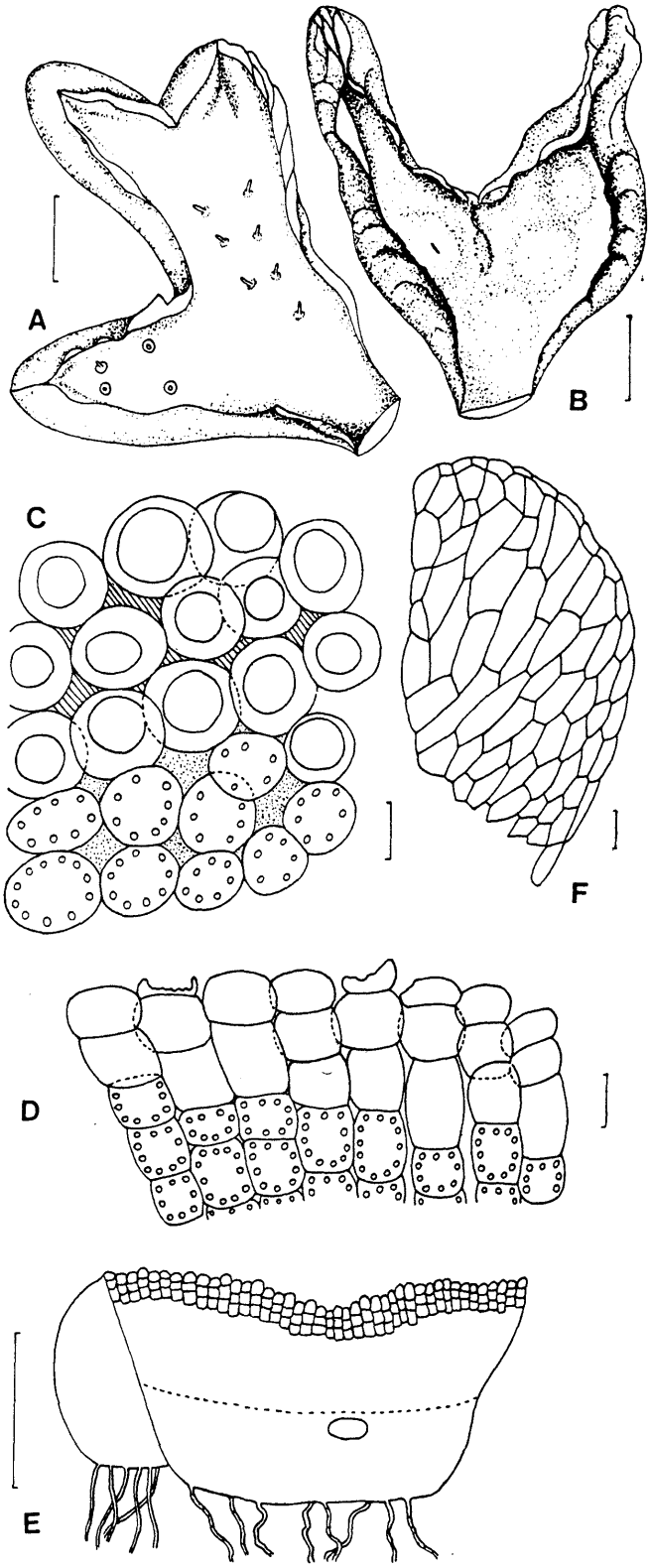


FIGURE 32.---*Riccia trachyglossum* (A--F): A, thallus wet; B, thallus dry; C, epithelial cell pillars and air pores (hatched) seen from above, assimilation tissue with air canals below; D, cross section of epithelial cell pillars and assimilation tissue; E, cross section of branch; F, scale. (A, C, D, F, *S.M. Perold* 2530; B, *Van Rooy* 3539; E, *J.M. Perold* 33). Scale bars on A, B, E = 1 mm; C, D = 50 µm; F = 100 µm.

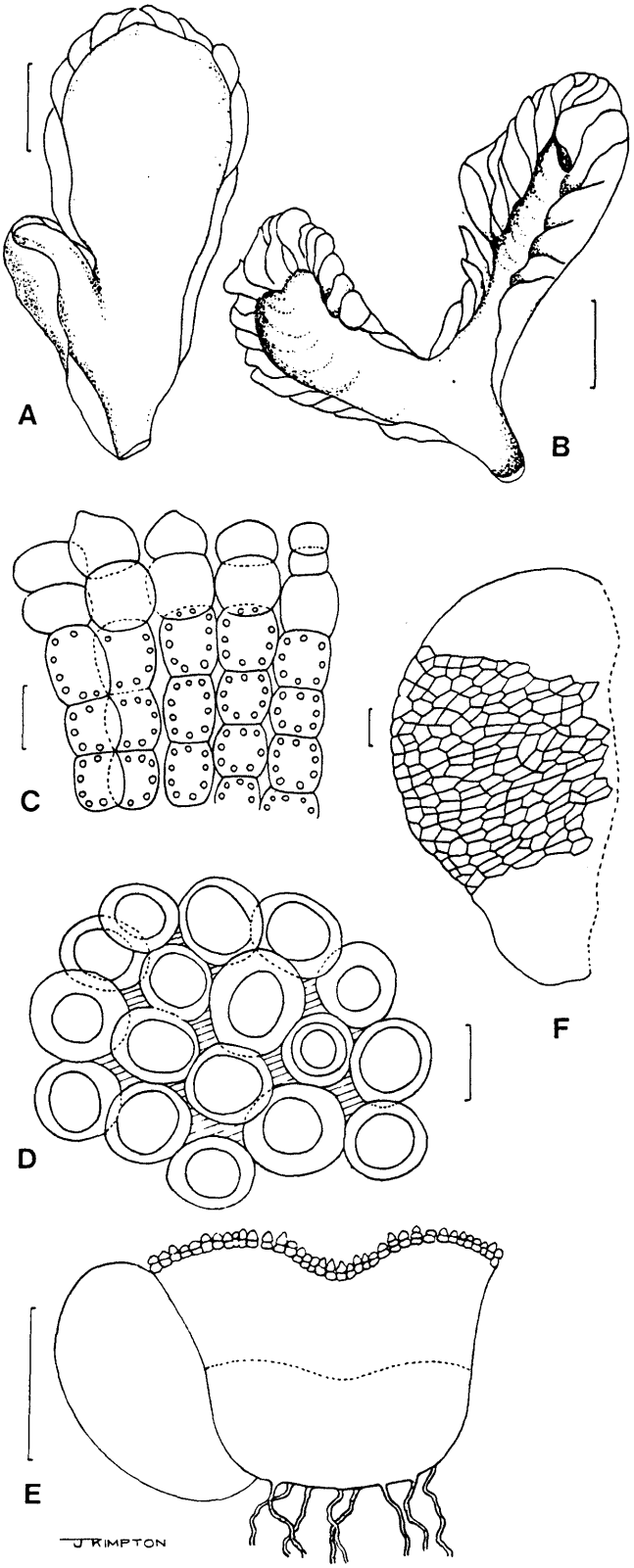


FIGURE 33.---*Riccia furfuracea* (A--F): A, thallus wet; B, thallus dry; C, cross section of epithelial cell pillars and assimilation tissue below; D, epithelial cells and air pores (hatched) from above; E, cross section of branch; F, scale. (A, *S.M. Perold* 2180; B, *Oliver* 8910; C, D, *S.M. Perold* 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.

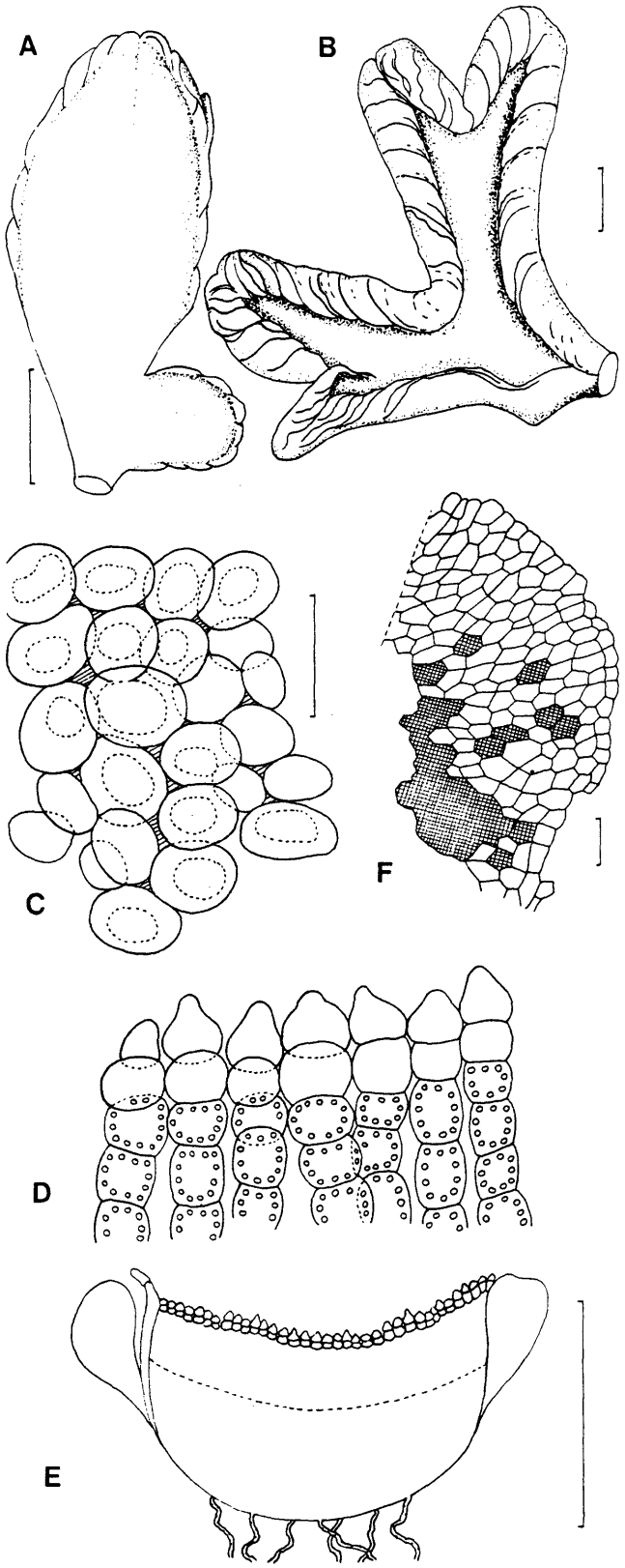


FIGURE 34.—*Riccia pulveracea* (A--F): A, thallus wet; B, thallus dry; C, epithelial cells and air pores (hatched) from above; D, cross section of epithelial cells and assimilation tissue below; E, cross section of branch; F, scale. (A--F, *Smook* 6962c). Scale bars A, B, E = 1 mm; C, D = 50 μm; F = 100 μm.

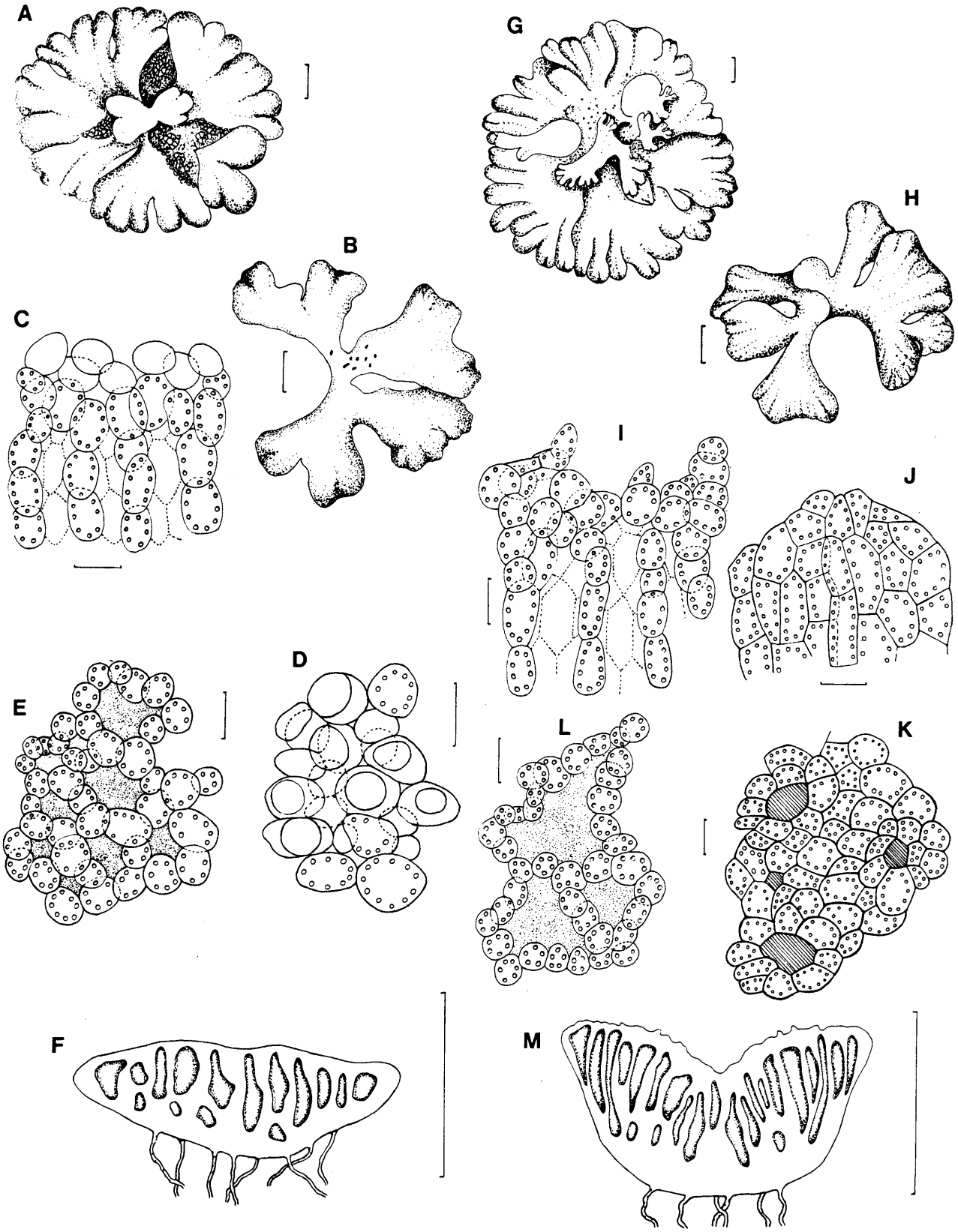


FIGURE 35.---*Riccia crystallina* (A--F): A, complete rosette; B, partial rosette; C, cross section of epidermal cells and assimilation tissue below; D, epidermal cells from above; E, horizontal section through assimilation tissue, air canals stippled; F, cross section of branch. *R. cavernosa* (G--M): G, complete rosette; H, partial rosette; I, cross section of epidermal cells and assimilation tissue below; J, dorsal epidermis forming a 'dome' over larger air chamber; K, several epidermal 'domes' and air pores (hatched) from above; L, horizontal section through air chambers (stippled); M, cross section of branch. (A, D, E, 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.

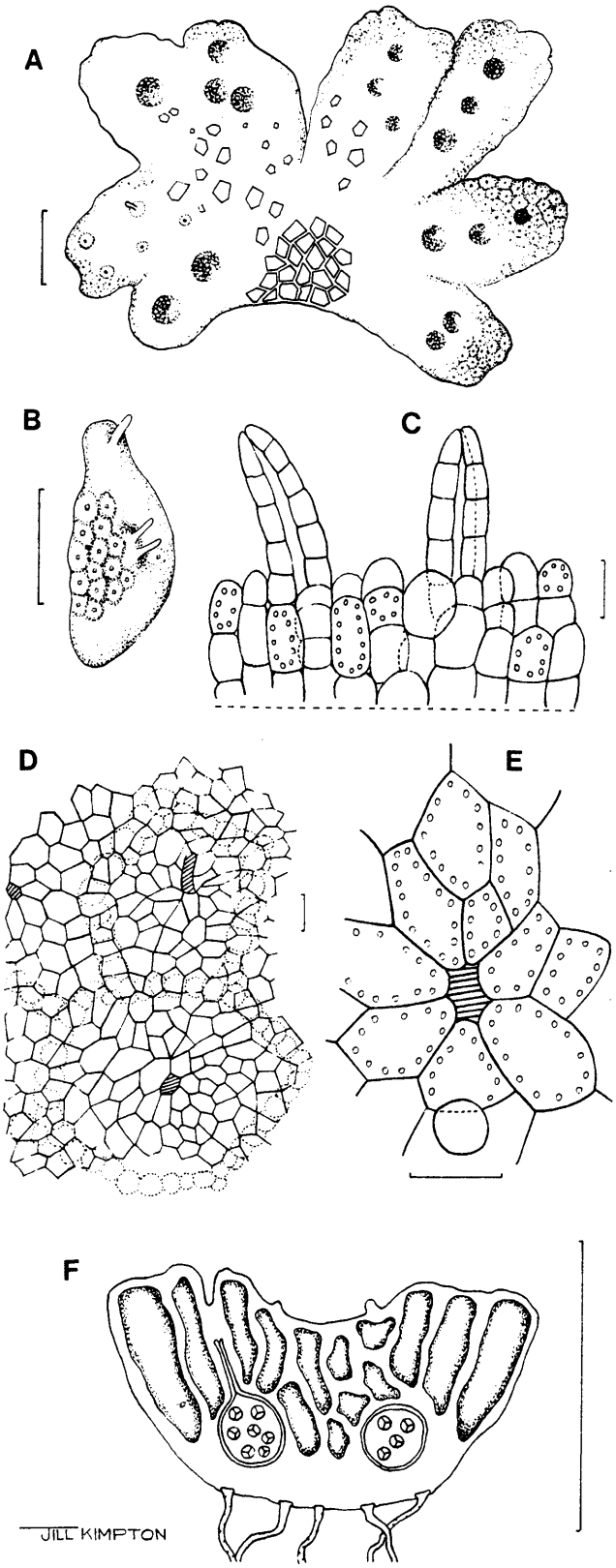


FIGURE 36.—*Riccia cupulifera* (A–F): A, female thallus in partial rosette; B, small male thallus; C, longitudinal section of same, with two antheridial necks; D, epidermal cells and air pores (hatched) overlying air chambers, as seen from above; E, air pore (hatched) with surrounding cells, only one of scattered rounded cells shown, seen from above; F, cross section of 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.

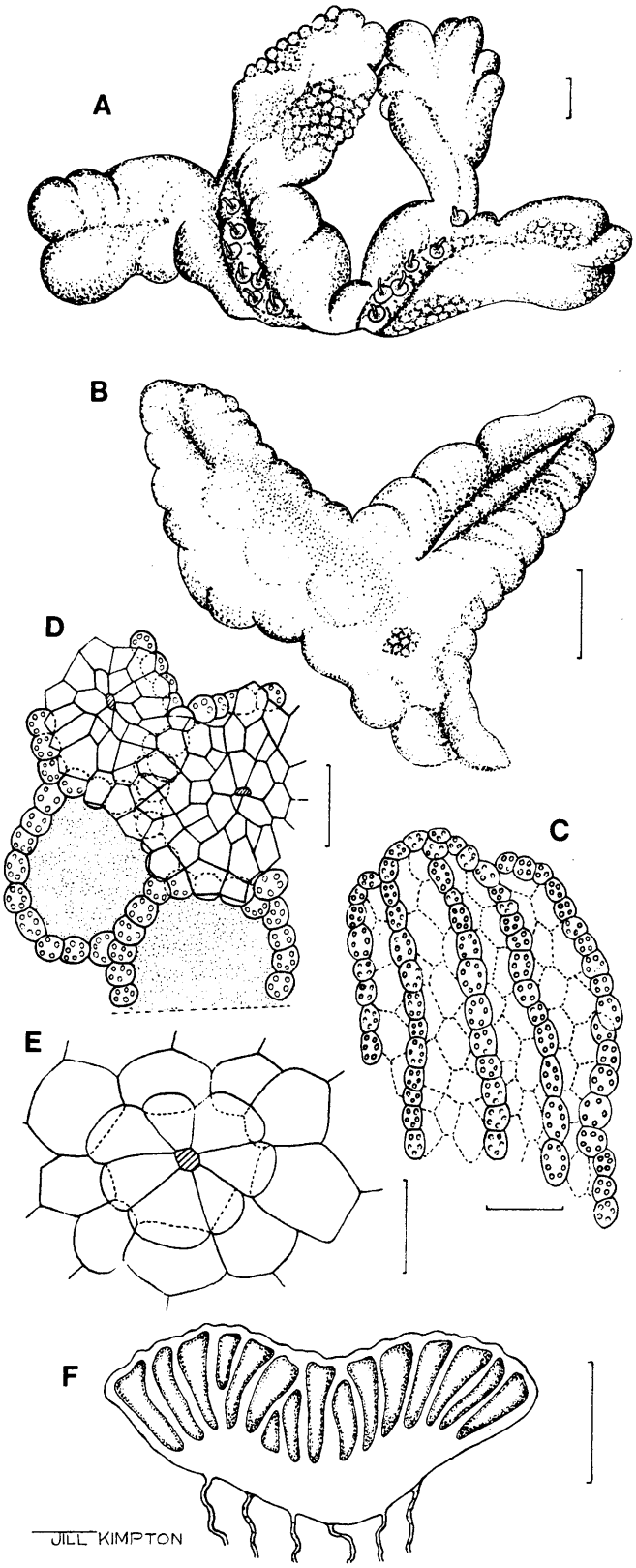


FIGURE 37.—*Riccia bullosa* (A–F): A, male thallus; B, female thallus; C, cross section of epidermis and assimilation tissue; D, epidermal cells and air pores (hatched) overlying air chambers, the latter exposed (and stippled) below; E, air pore (hatched) and surrounding cells as seen from above; F, cross section of 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.

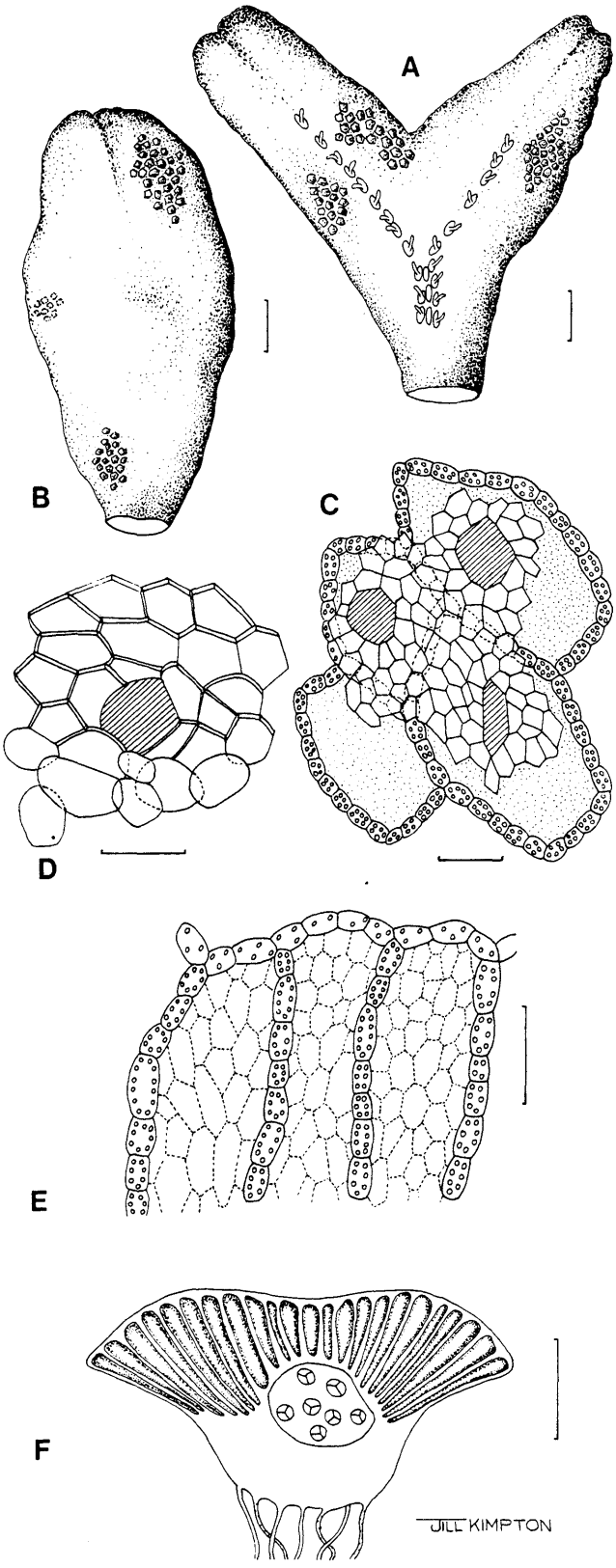


FIGURE 38.---*Riccia garsidei* (A--E): A, male thallus; B, female thallus; C, epidermal cells and air pores (hatched) overlying air chambers, as seen from above; D, air pore (hatched) with surrounding cells; E, cross section of part of thallus through air chambers; F, cross section of branch. (A--F, *Duthie* 15/11/1937). Scale bars A, B, F = 1 mm; C, E = 100 µm; D = 50 µm.

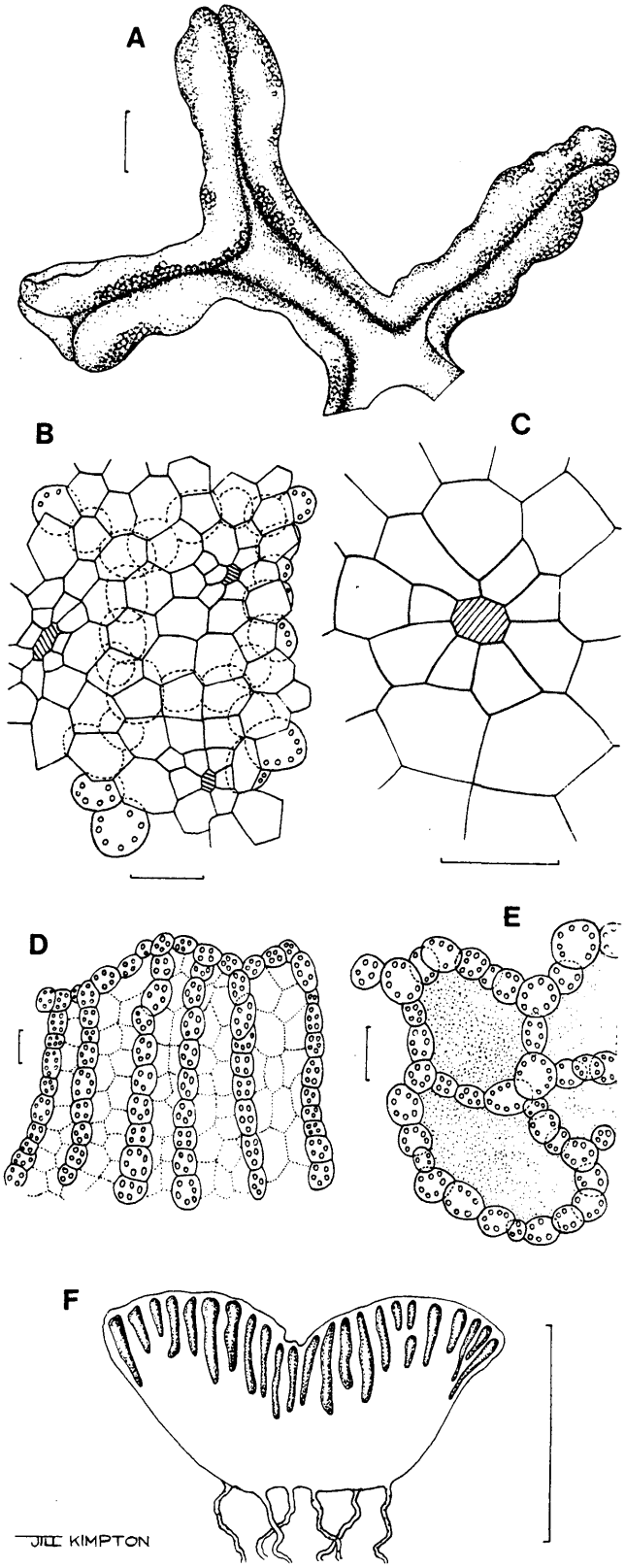


FIGURE 39.—*Riccia volkii* (A–F): A, thallus; B, epidermal cells and air pores (hatched), overlying air chambers, as seen from above; C, air pore (hatched) and surrounding cells from above; D, cross section of epidermis and assimilation tissue below; E, horizontal section through air chambers (stippled); F, cross section of 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.

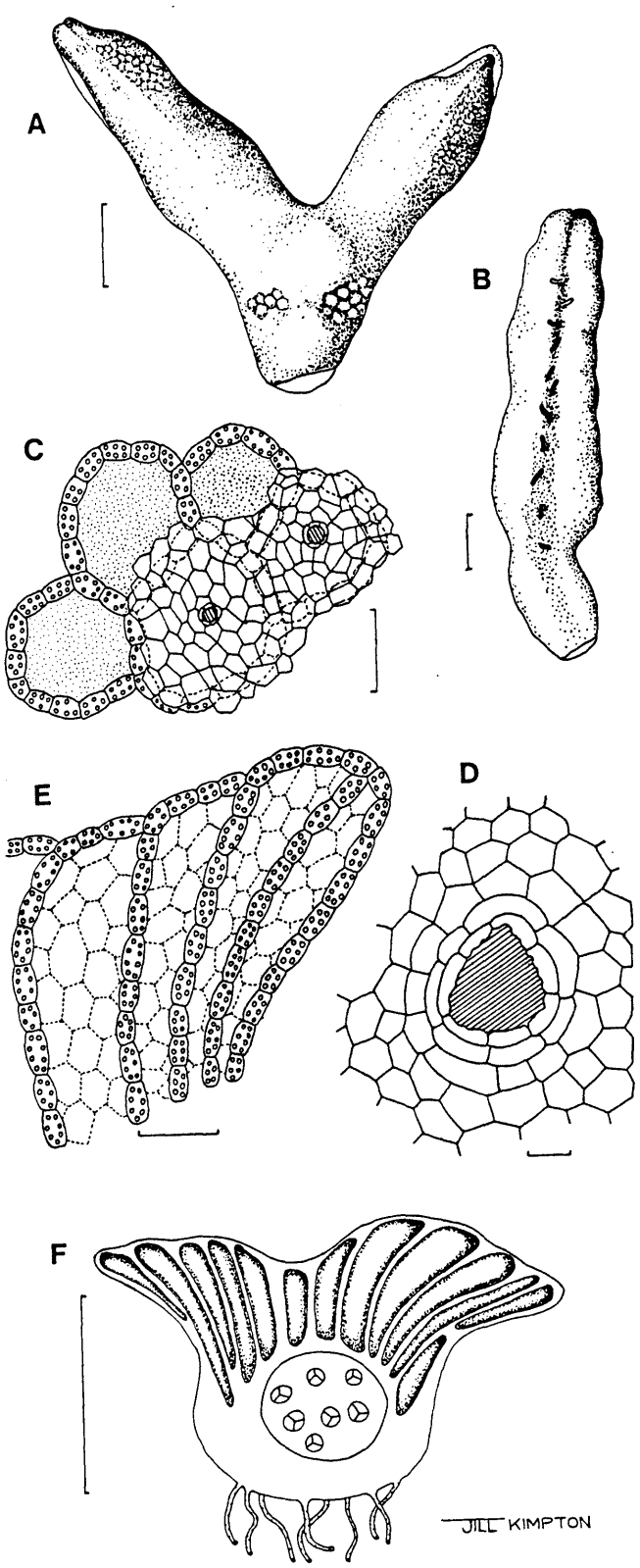


FIGURE 40.---*Riccia rubricollis* (A--F): A, female thallus; B, male thallus; C, epidermal cells and air pores (hatched), overlying air chambers, as seen from above; D, air pore (hatched) with surrounding cells; E, cross section of part of thallus showing air chambers; F, cross section of female thallus. (A--F, *Duthie* 5014). Scale bars A, B, F = 1 mm; C, E = 100 μm; D = 50 μm.

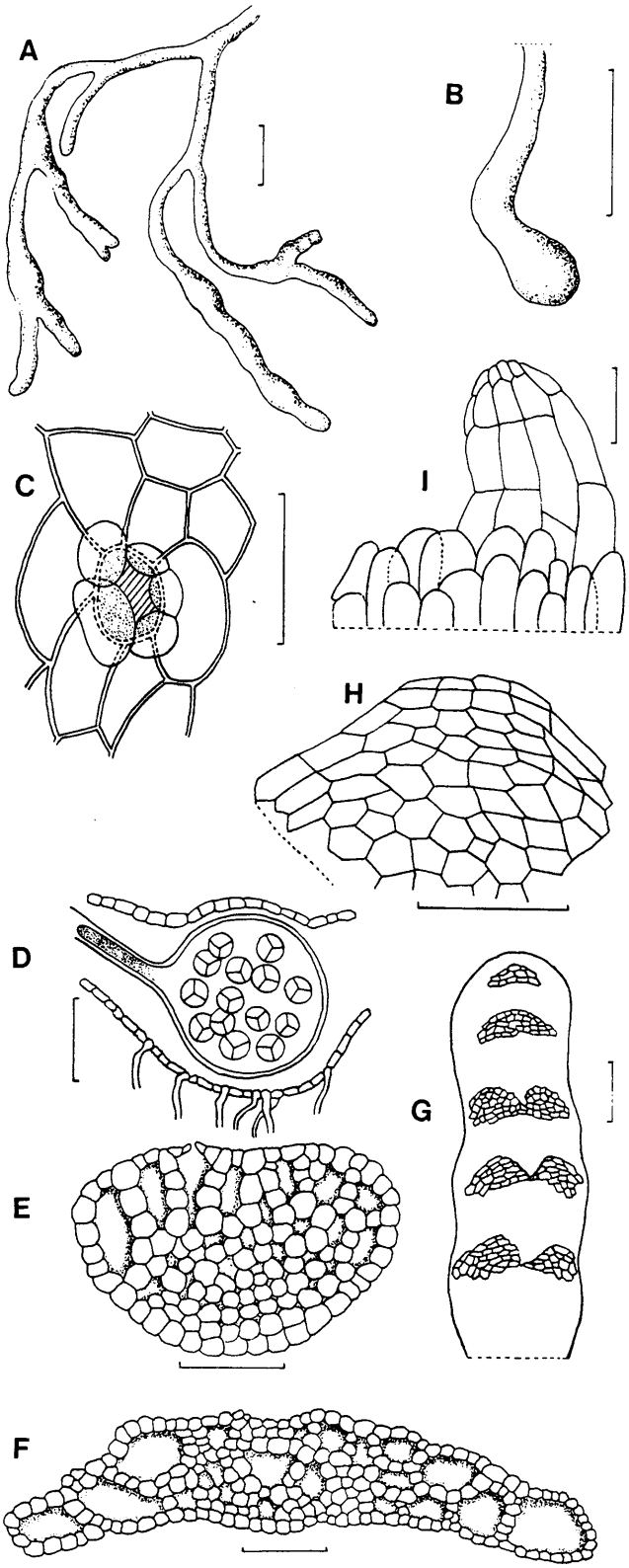


FIGURE 41.---*Riccia stricta* (A--G): A, thallus; B, ventral stolon; C, air pore (hatched) with thin-walled surrounding cells and thicker-walled epidermal cells, part of air chamber stippled; D, longitudinal section through sporangium; E, cross section of narrow branch from drier habitat; F, cross section of 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-CH 1119; I, *S.M. Perold* 842). Scale bars A, B = 1 mm; C, I = 50 µm; D, F, G = 200 µm; E, H = 100 µm.

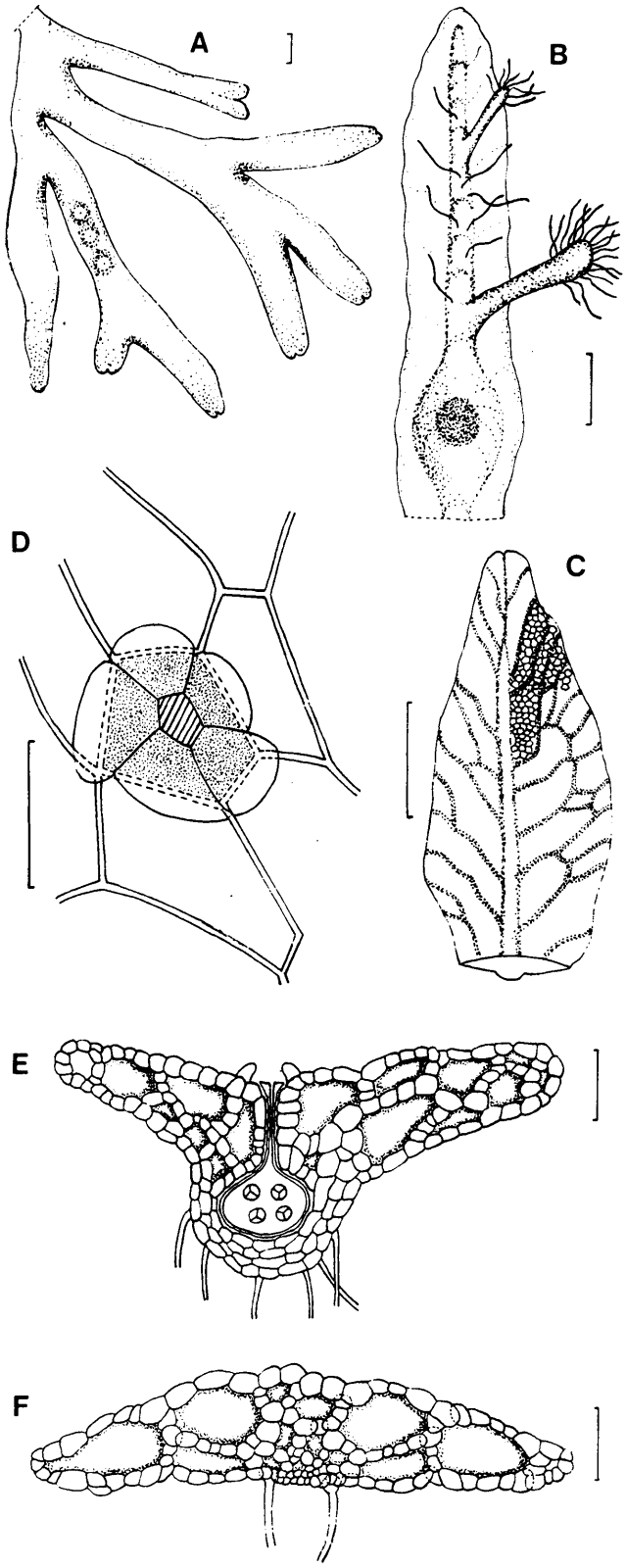


FIGURE 42.---*Riccia purpurascens* (A--F): A, thallus; B, ventral face with stolons and sporangium; C, dorsal face with air chambers and epidermal cells partly drawn in; D, air pore (hatched), with thin-walled surrounding cells and thicker-walled epidermal cells, part of air chamber stippled; E, cross section of branch at sporangium; F, cross section of 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.

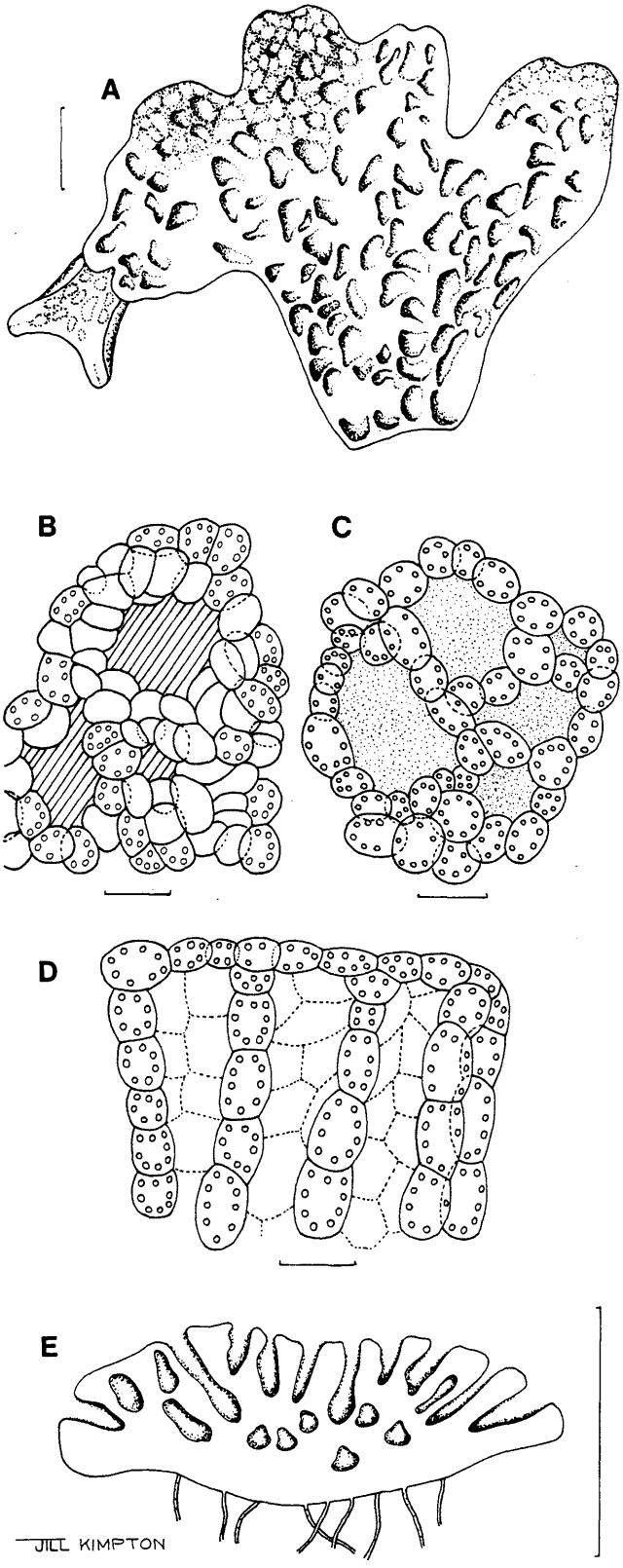


FIGURE 43.---*Riccia curtisii* (A--E): A, female thallus with small male thallus projecting from underneath, at the left side; B, epidermal cells and air pores (hatched) from above; C, horizontal section through assimilation tissue, air chambers stippled; D, cross section of epidermis and assimilation tissue; E, cross section of branch. (A, *S.M. Perold* 641; B--E, *S.M. Perold* 2395a). Scale bars A, E = 1 mm; B--D = 100 µm.

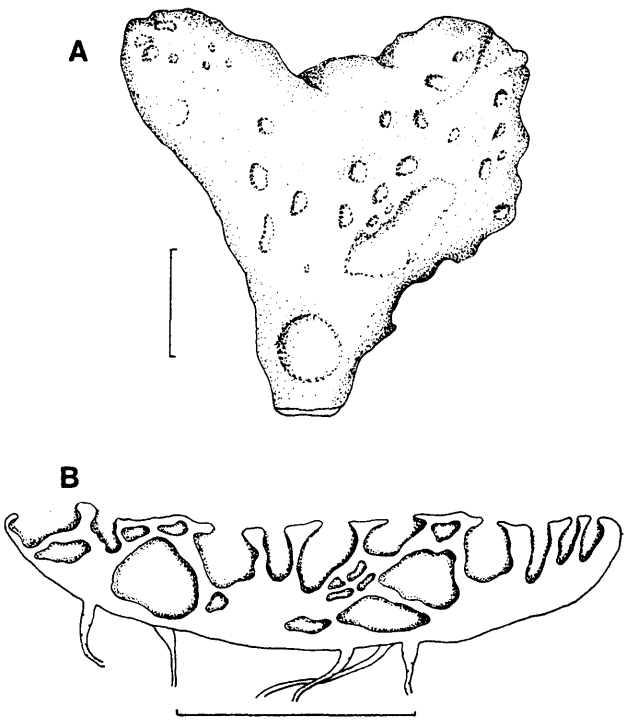


FIGURE 44.---*Riccia perssonii* (A, B): A, female thallus; B, cross section of branch. (A, B, *Volk* 2059). Scale bars A, B = 1 mm.

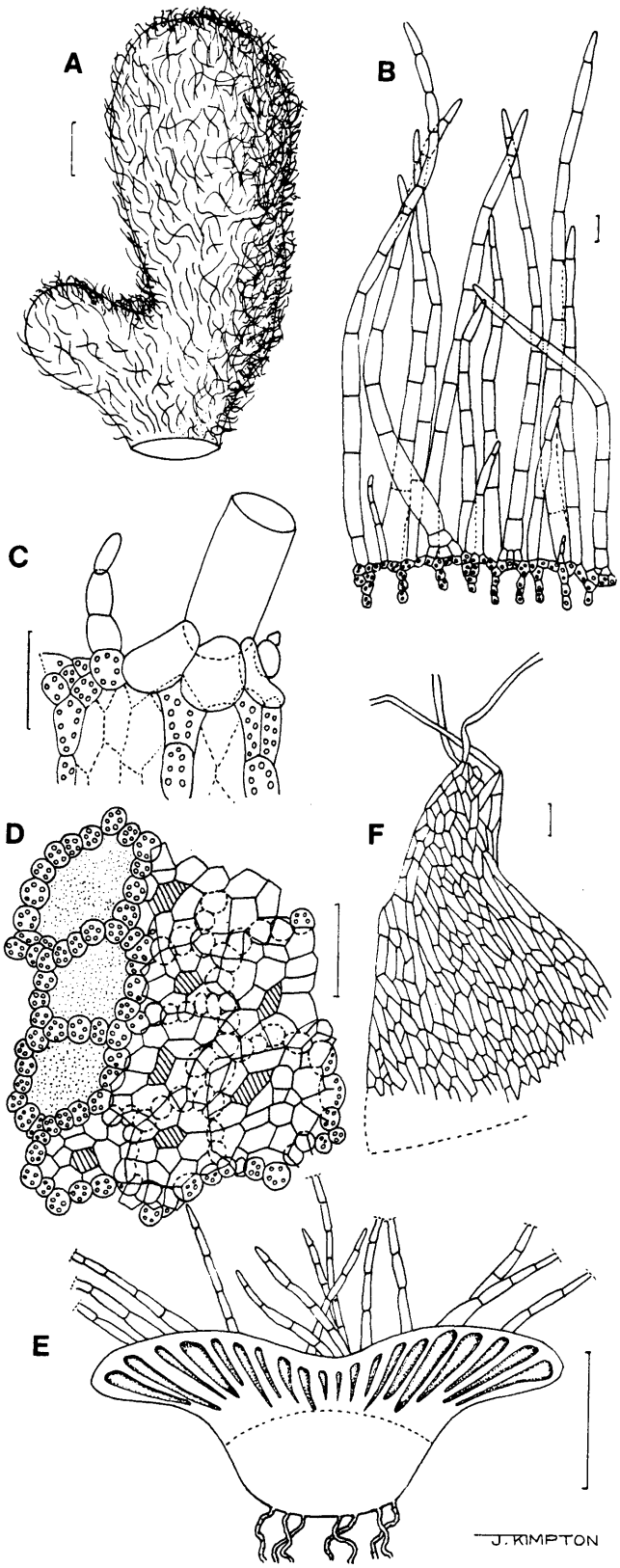


FIGURE 45.---*Riccia tomentosa* (A--F): A, thallus; B, cross section of dorsal hair pillars and top of assimilation tissue below; C, at right, cells supporting base of large hair; at left small hair; below assimilation tissue; D, as viewed from below, horizontal section near dorsal surface: on the left, air chambers (stippled) exposed; on the right, air pores (hatched) and epidermis; E, cross section of branch; F, scale. (A, *S.M. Perold* 1495; B--D, F, *S.M. Perold & M.J.A.W. Crosby* 2157; E, *S.M. Perold* 1556). Scale bars A, E = 1 mm; B--D, F = 100 μm.

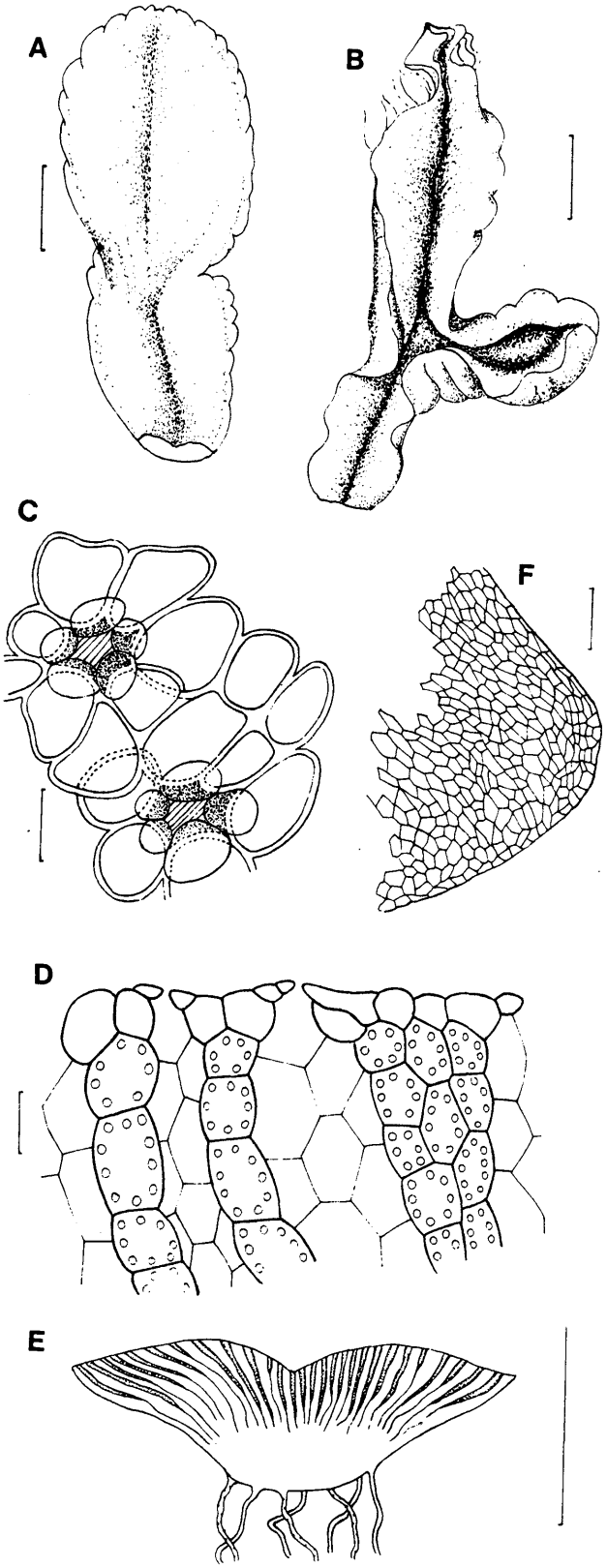


FIGURE 46.---*Riccia schelpei* (A--F): A, thallus wet; B, thallus dry; C, thick-walled epidermal cells with small, thin-walled cells surrounding the air pores (hatched), air chambers below, partly stippled, seen from above; D, cross section of epidermis and assimilation tissue; E, cross section of branch; 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.

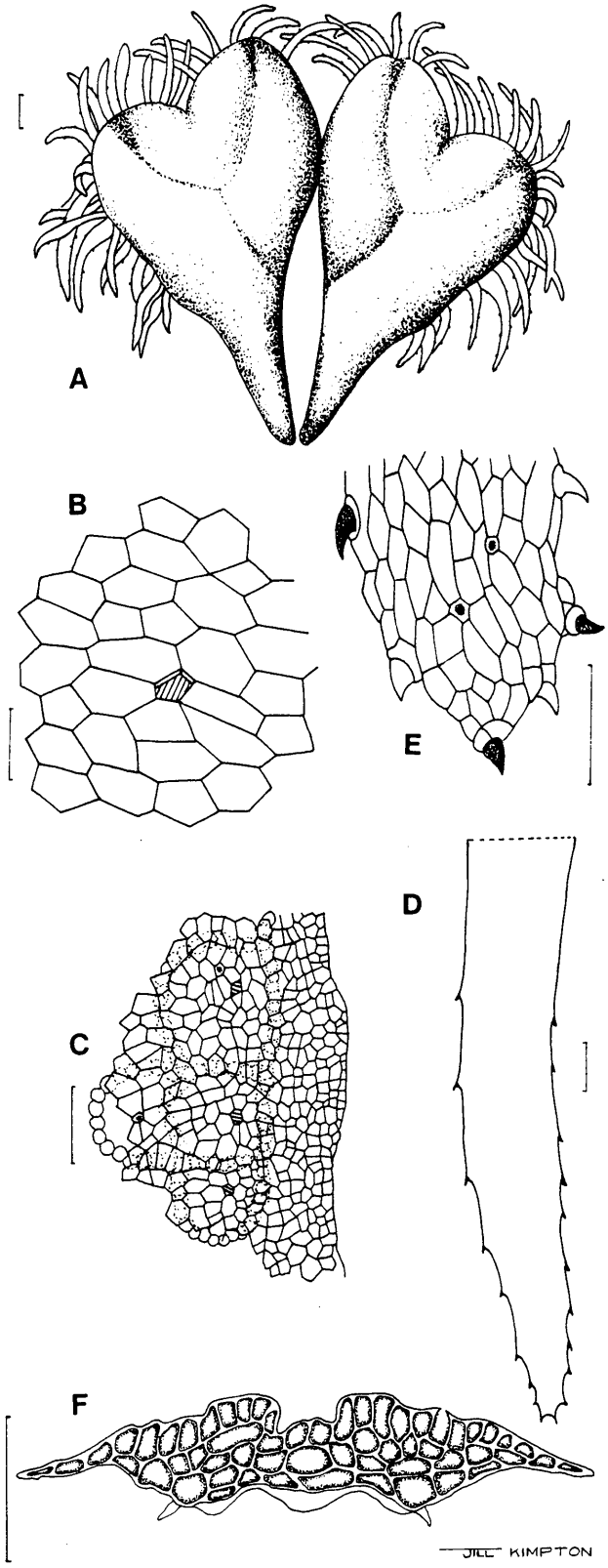


FIGURE 47.---*Ricciocarpos natans* (A--F): A, thallus of aquatic form; B, dorsal epidermis and air pore (hatched); C, dorsal epidermis with air pores (hatched) and occasional oil cells (with solid specks), overlying air chambers left, thin marginal area right; D, scale; E, more enlarged tip of scale, showing oil cells (solid speck) and toothed margin; F, cross section of branch. (A--F, *Ward* s.n.). Scale bars A, F = 1 mm; B, E = 50 μm; C, D = 100 μm.

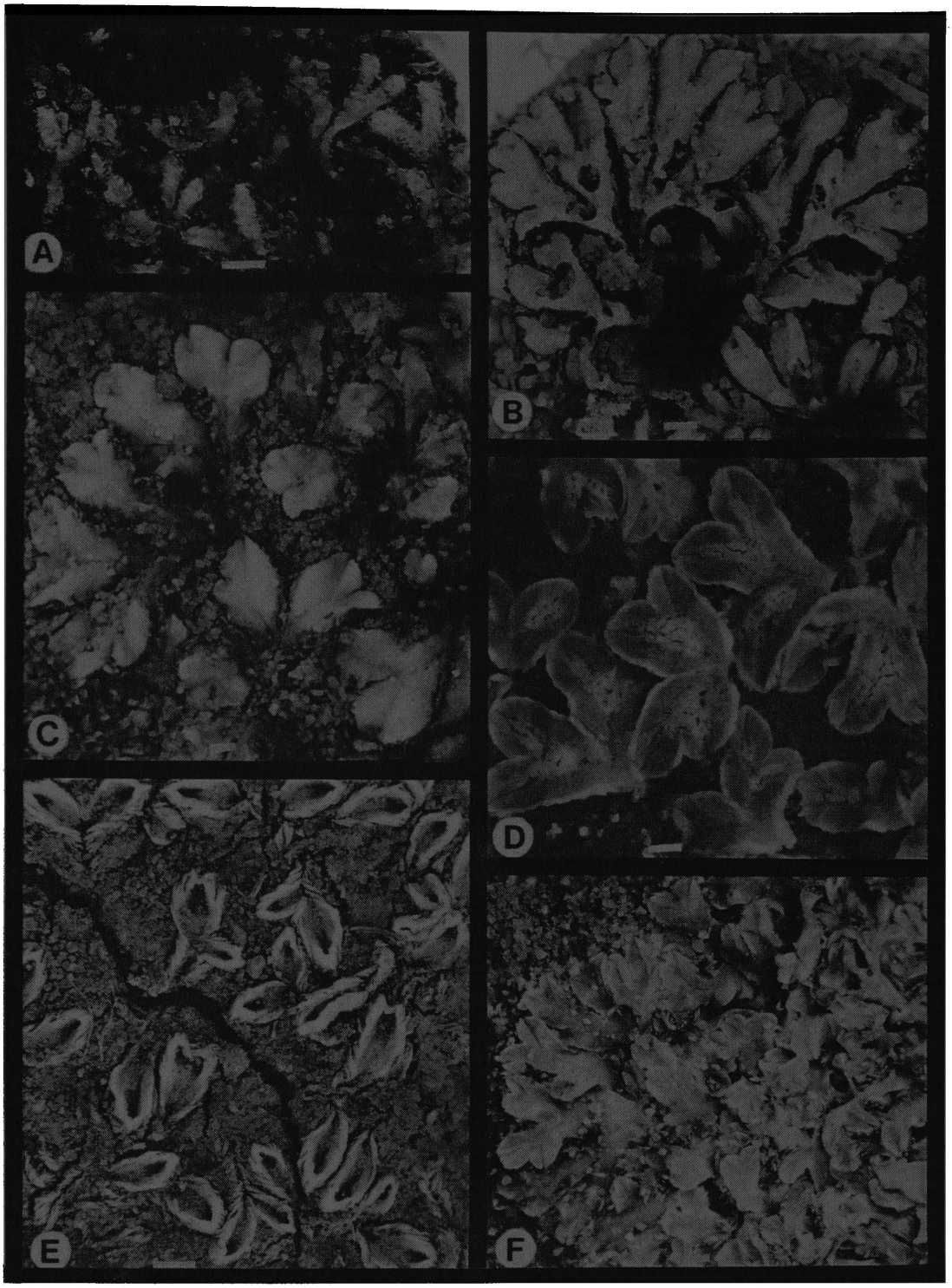


PLATE 1.---A, *Riccia microciliata*: branches; B, *R. okahandjana*: partial rosette; C, *R. congoana*: partial rosette; D, *R. albolimbata*: scattered branches; E, *R. argenteolimbata*: scattered branches; F, *R. montana*: crowded branches. (A, *S.M. Perold* 383; B, *Van Rooy* s.n.; C, *Smook* 5139; D, *Volk* 86/927; E, *Volk* 84/713; F, *Oliver* 8354). Scale bars A--F = 1 mm.

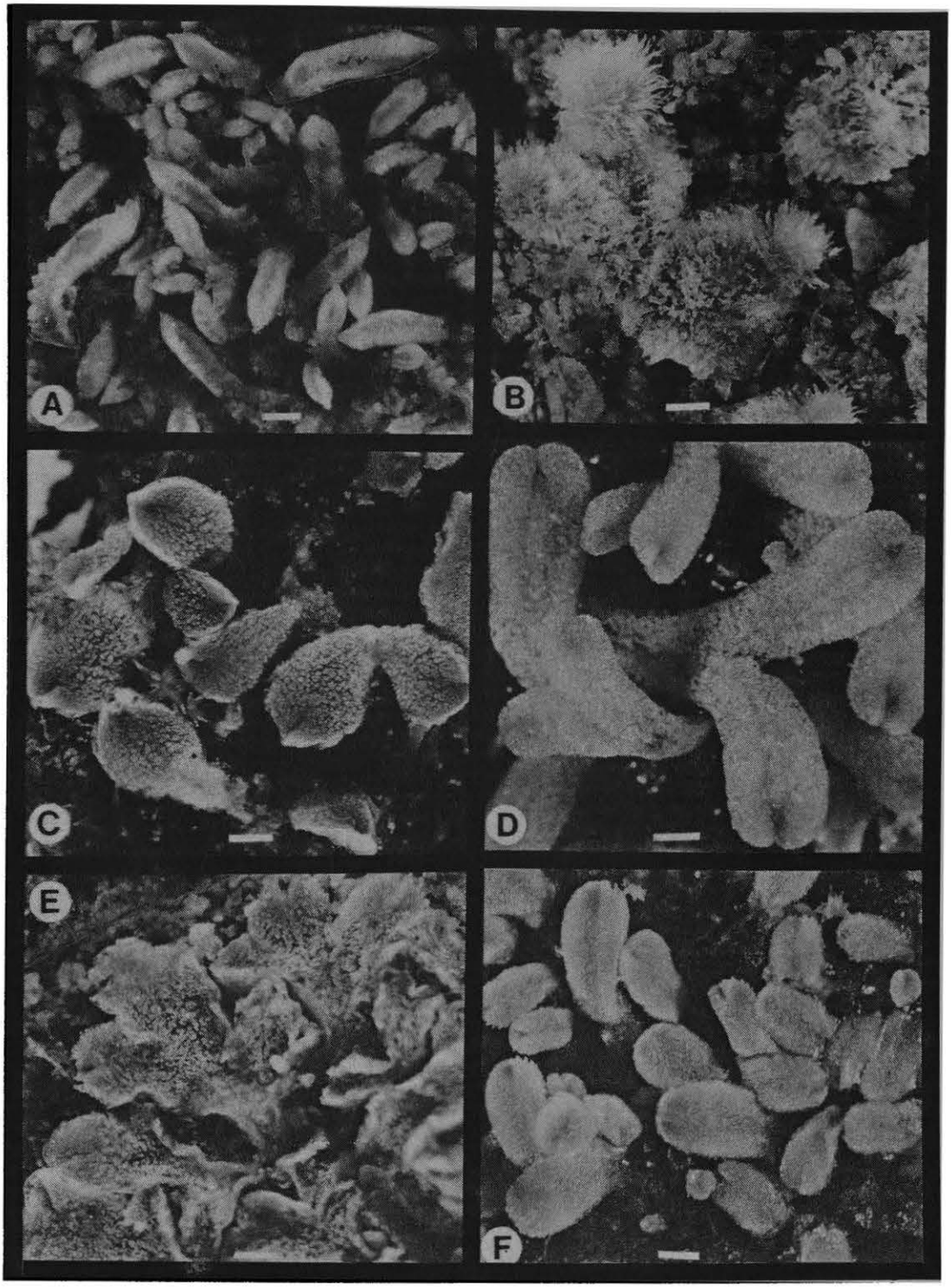


PLATE 2.---A, *Riccia villosa*: crowded thalli; B, *R. hirsuta*: scattered branches; C, *R. parvo-areolata*: scattered branches; D, *R. hantamensis*: overlapping branches; E, *R. namaquensis*: crowded thalli; F, *R. pulveracea*: crowded branches. (A, *Oliver* s.n.; B, *S.M. Perold* 2101; C, *S.M. Perold* 2136; D, *S.M. Perold* 1830; E, S.M. Perold 2136; F, *Smook* 6990). Scale bars A--F = 1 mm.

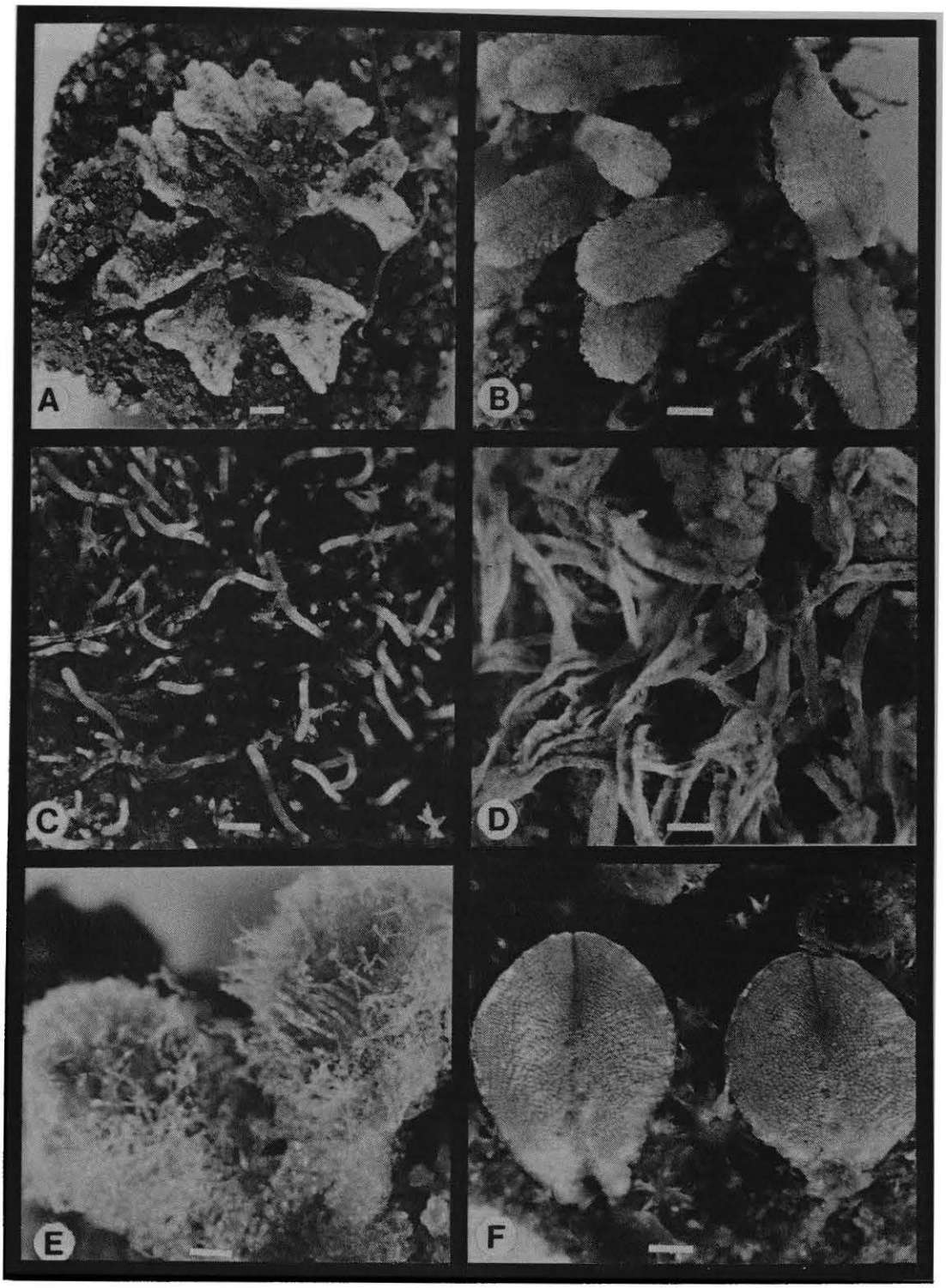


PLATE 3.---A, *Riccia cupulifera*: rosette; B, *R. volkii*: crowded branches; C, *R. stricta*: overlapping branches; D, *R. purpurascens*: overlapping branches; E, *R. tomentosa*: hairy branches; F, *R. schelpei*: deeply grooved branches. (A, *S.M. Perold* 2395; B, *S.M. Perold* 2472; C, *S.M. Perold* 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.

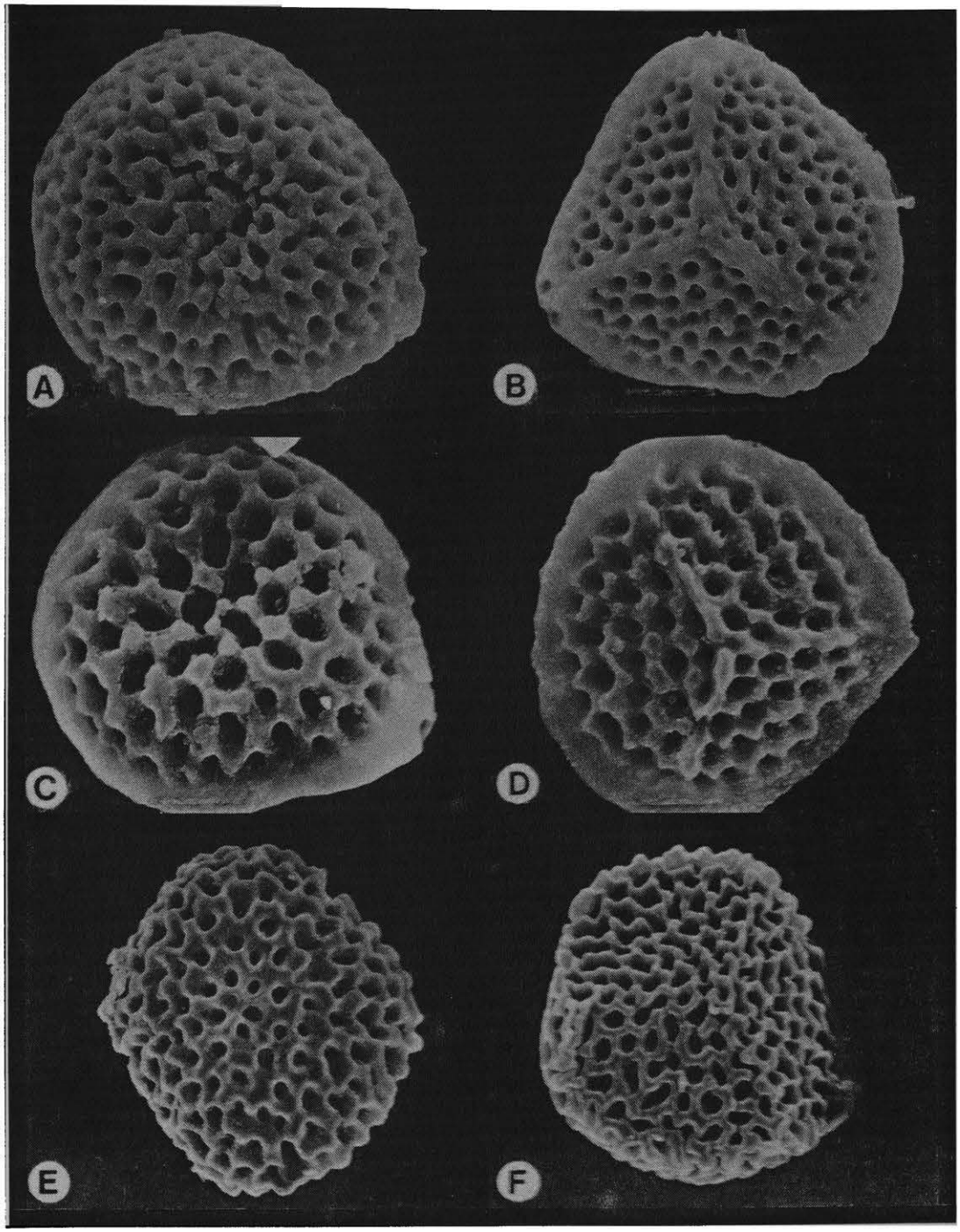


PLATE 4.---*Riccia trichocarpa* (A, B): A, distal spore face; B, proximal spore face. *R. crozalsii* (C, D): C, distal spore face; D, proximal spore face. *R. microciliata* (E, F): E, distal spore face; F, proximal spore face. (A, B, *S.M. Perold* 748; C, *Morley* 305; D, *S.M. Perold* 1149 p.p.; E, F, *S.M. Perold* 102). Magnification A, B, D = x 600; C, E, F, = x 700.

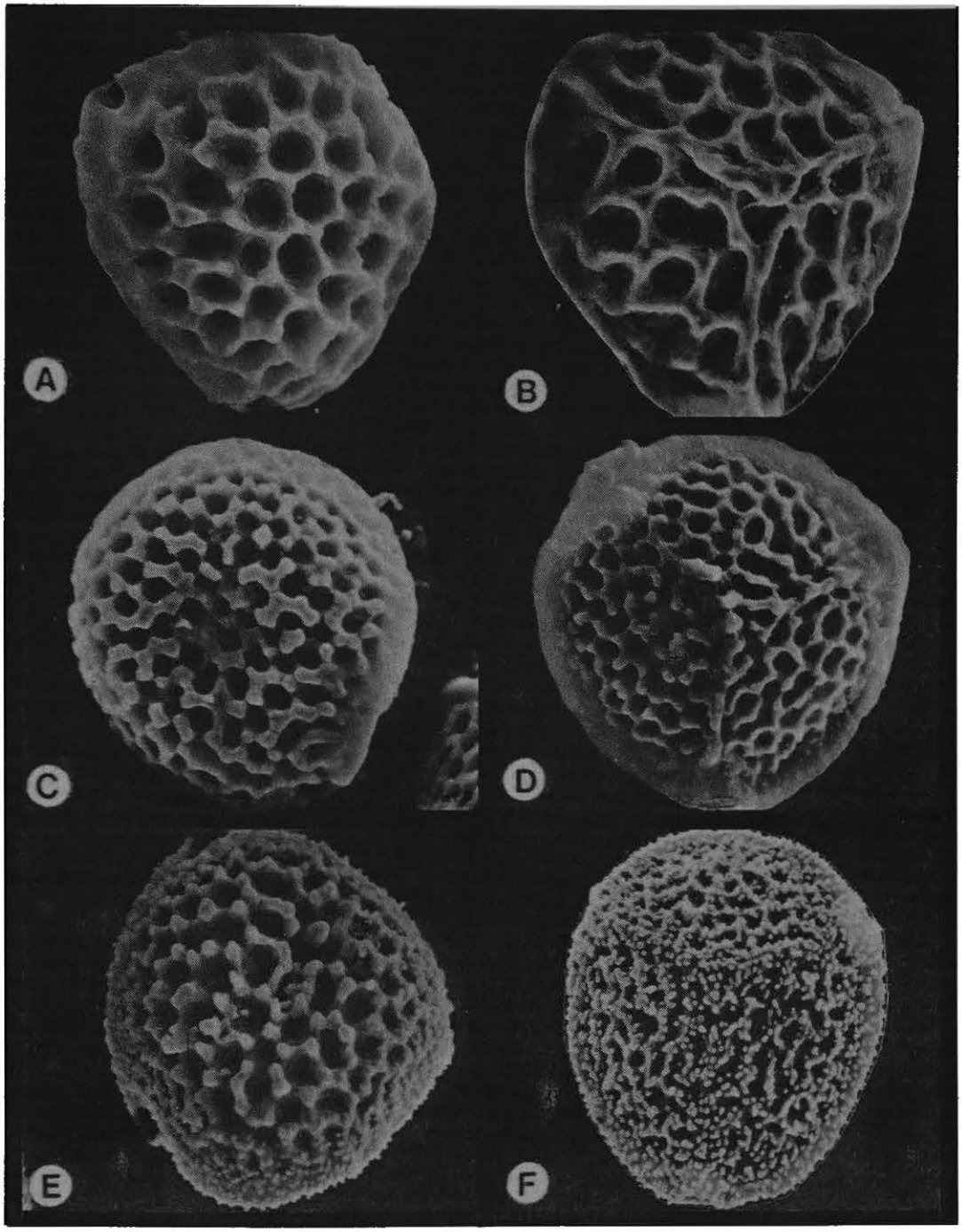


PLATE 5.---*Riccia natalensis* (A, B): A, distal spore face; B, proximal spore face. *R. mammifera* (C, D): C, distal spore face; D, proximal spore face. *R. sorocarpa* (E, F): E, distal spore face; F, proximal spore face. (A, *S.M. Perold* 679; B, *S.M. Perold* 430; C, D, *S.M. Perold* 447; E, *S. Arnell* 303; F, *S. Arnell* 7). Magnification A, C, D = x 600; B, E, F = x 700.

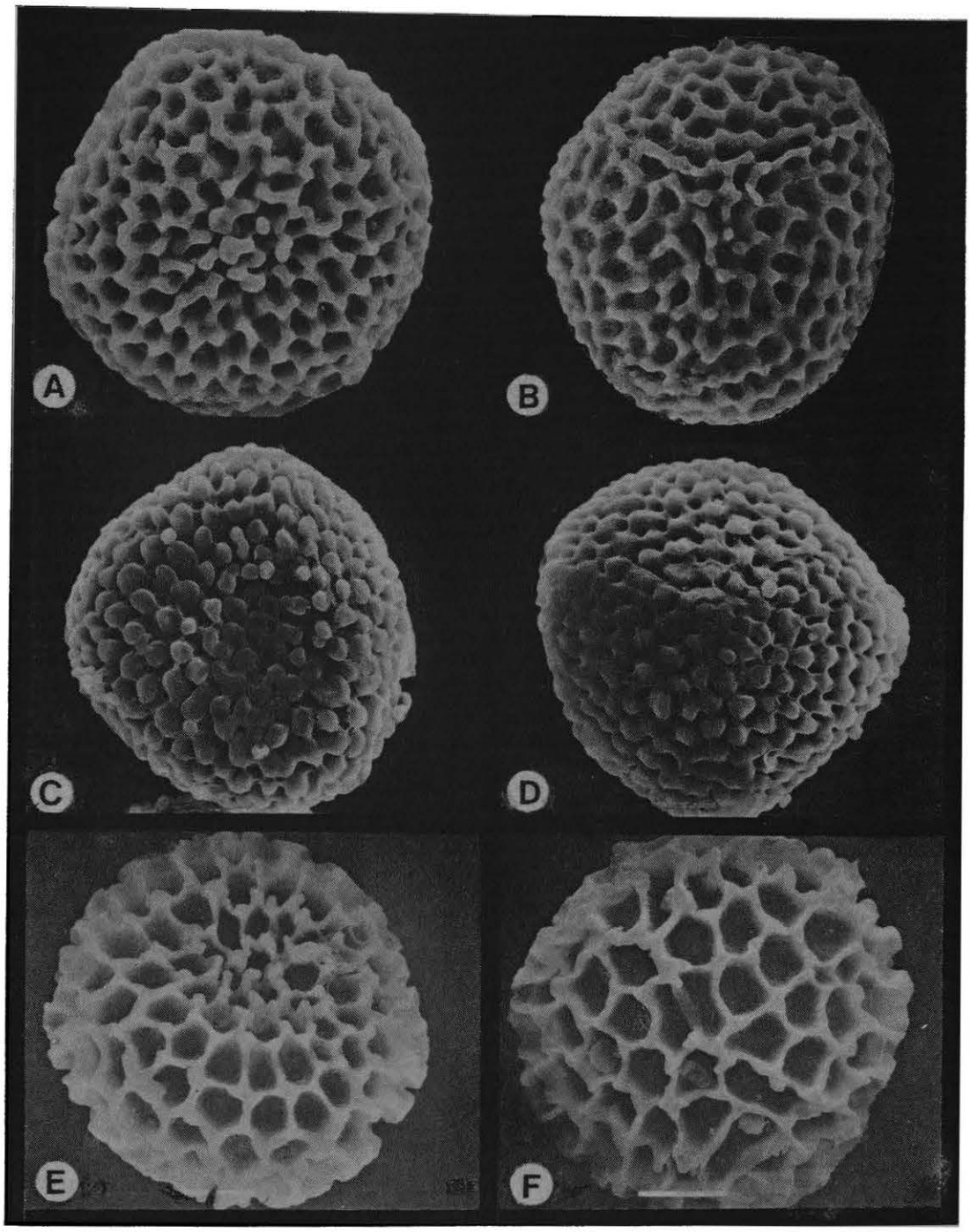


PLATE 6.---*Riccia atropurpurea* (A, B): A, distal spore face; B, proximal spore face. *R. okahandjana* (C, D): C, distal spore face; D, proximal spore face. *R. congoana* (E, F): E, distal spore face; F, proximal spore face. (A, *S.M. Perold* 782b; B, *Volk* 84/710; C, D, *Volk* 88/005; E, F, *S.M. Perold* 394). Magnification A--F = x 600.

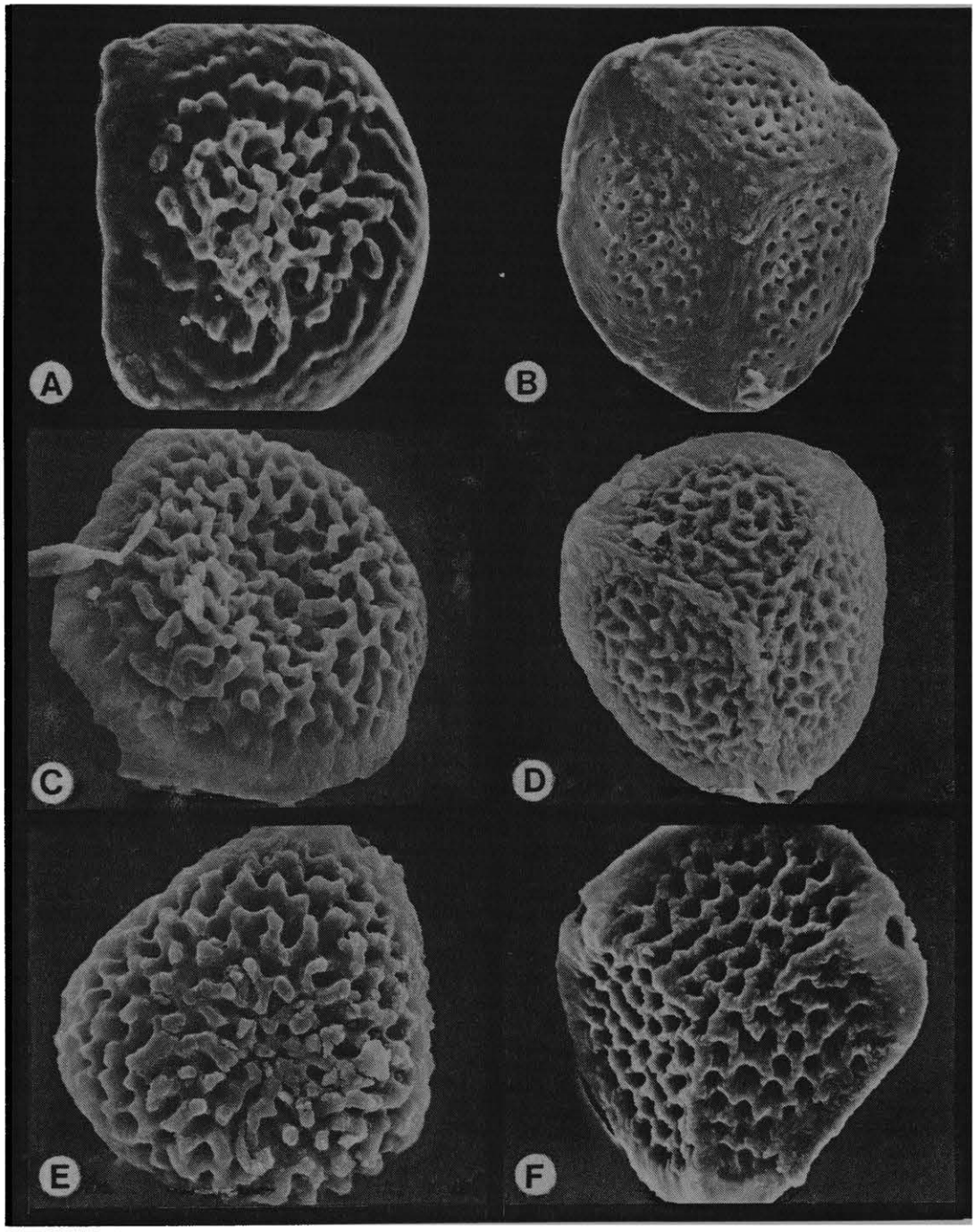


PLATE 7.---*Riccia limbata* (A, B): A, distal spore face; B, proximal spore face. *R. angolensis* (C, D): C, distal spore face; D, proximal spore face. *R. nigrella* (E, F): E, distal spore face; F, proximal spore face. (A, *S. Arnell* 67a; B, *Garside* 6276; C, *E. Retief* 1543a; D, *S.M. Perold* 1275; E, *Duthie* 5023a; F, *S.M. Perold* 1147). Magnification A, D = x 700; B = x 600; C, E, F = x 800).

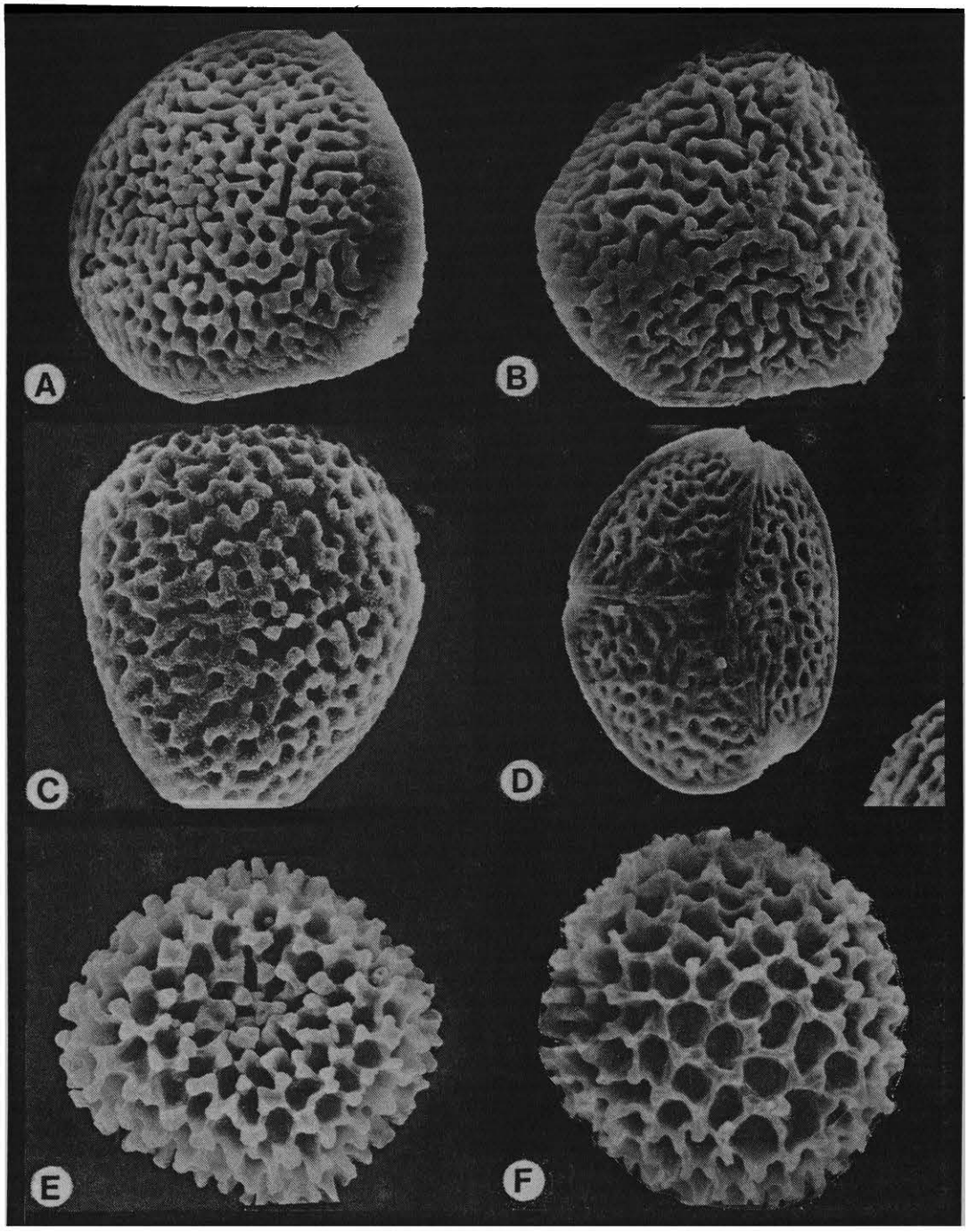


PLATE 8.—*Riccia macrocarpa* (A, B): A, distal spore face; B, proximal spore face. *R. pottsiana* (C, D): C, distal spore face; D, proximal spore face. *R. runssorensis* (E, F): E, distal spore face; F, proximal spore face. (A, B, *S.M. Perold* 888; C, D, *Duthie* 5463; E, F, *Volk* 81/125c). Magnification A, B, D = x 700; C = x 1000; E, F, = x 600.

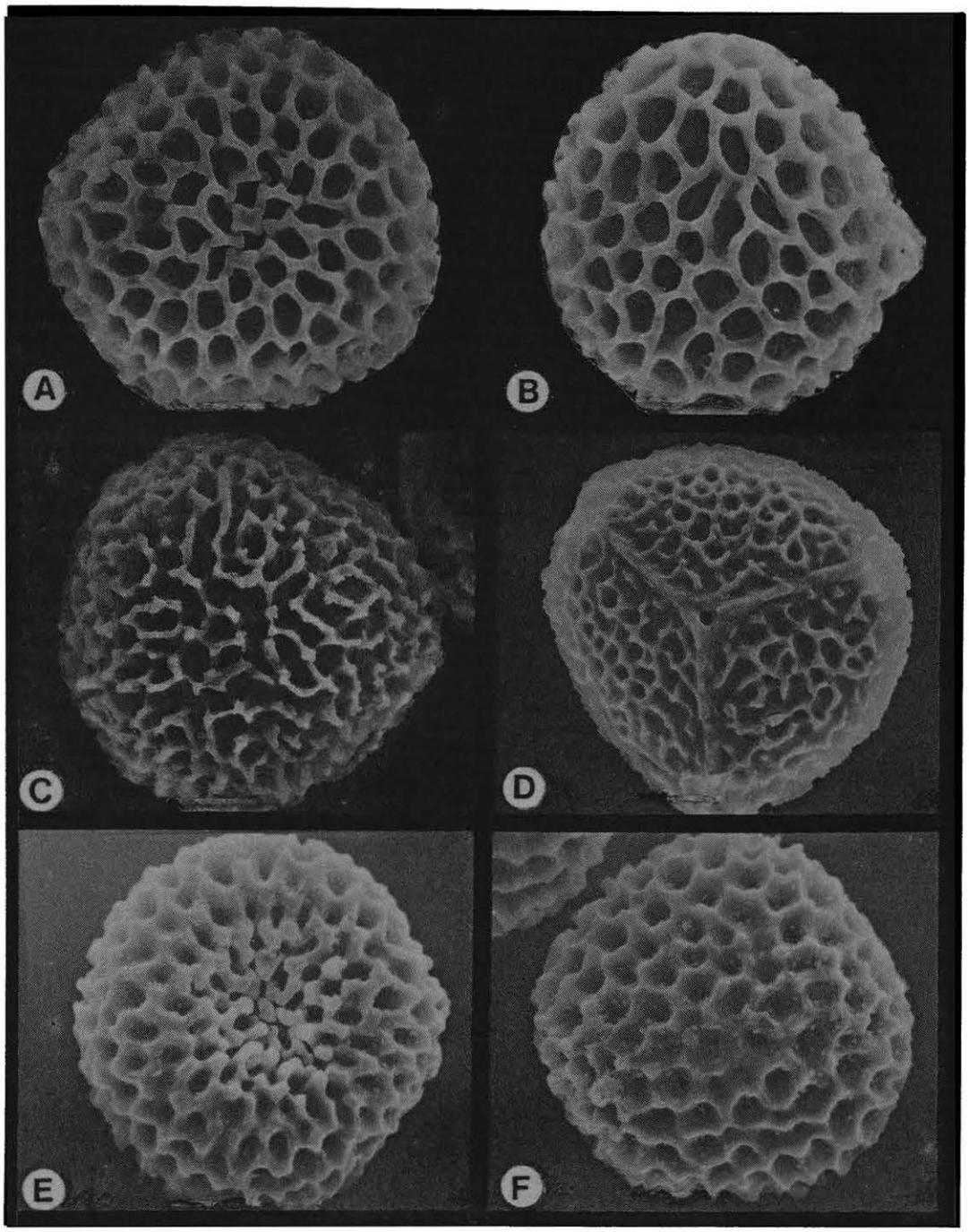


PLATE 9.—*Riccia rosea* (A, B): A, distal spore face; B, proximal spore face. *R. albolimbata* (C, D): C, distal spore face; D, proximal spore face. *R. argenteolimbata* (E, F): E, distal spore face; F, proximal spore face. (A, B, *S.M. Perold* 135a; C, *Volk* 81/921; D, *Stephansen* 5393; E, F, *Volk* 86/930a). Magnification A–F = x 700.

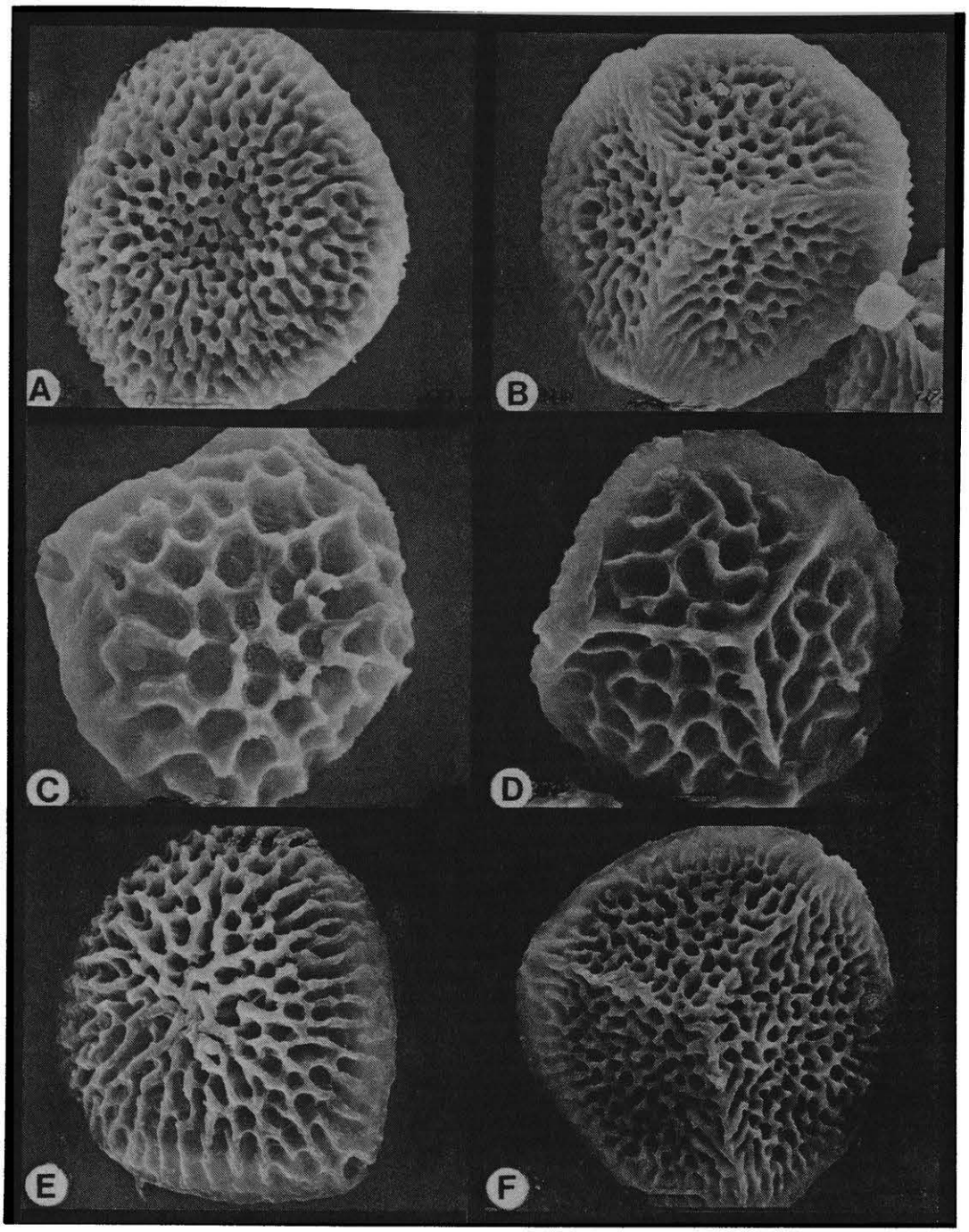


PLATE 10.---*Riccia albornata* (A, B): A, distal spore face; B, proximal spore face. *R. montana* (C, D): C, distal spore face; D, proximal spore face. *R. alboporosa* (E, F): E, distal spore face; F, proximal spore face. (A, B, *Smook* 6862a; C, D, *Van Rooy* 3549a; E, F, *Oliver* 8849). Magnification A, B, E, F = x 700; C, D = x 800.

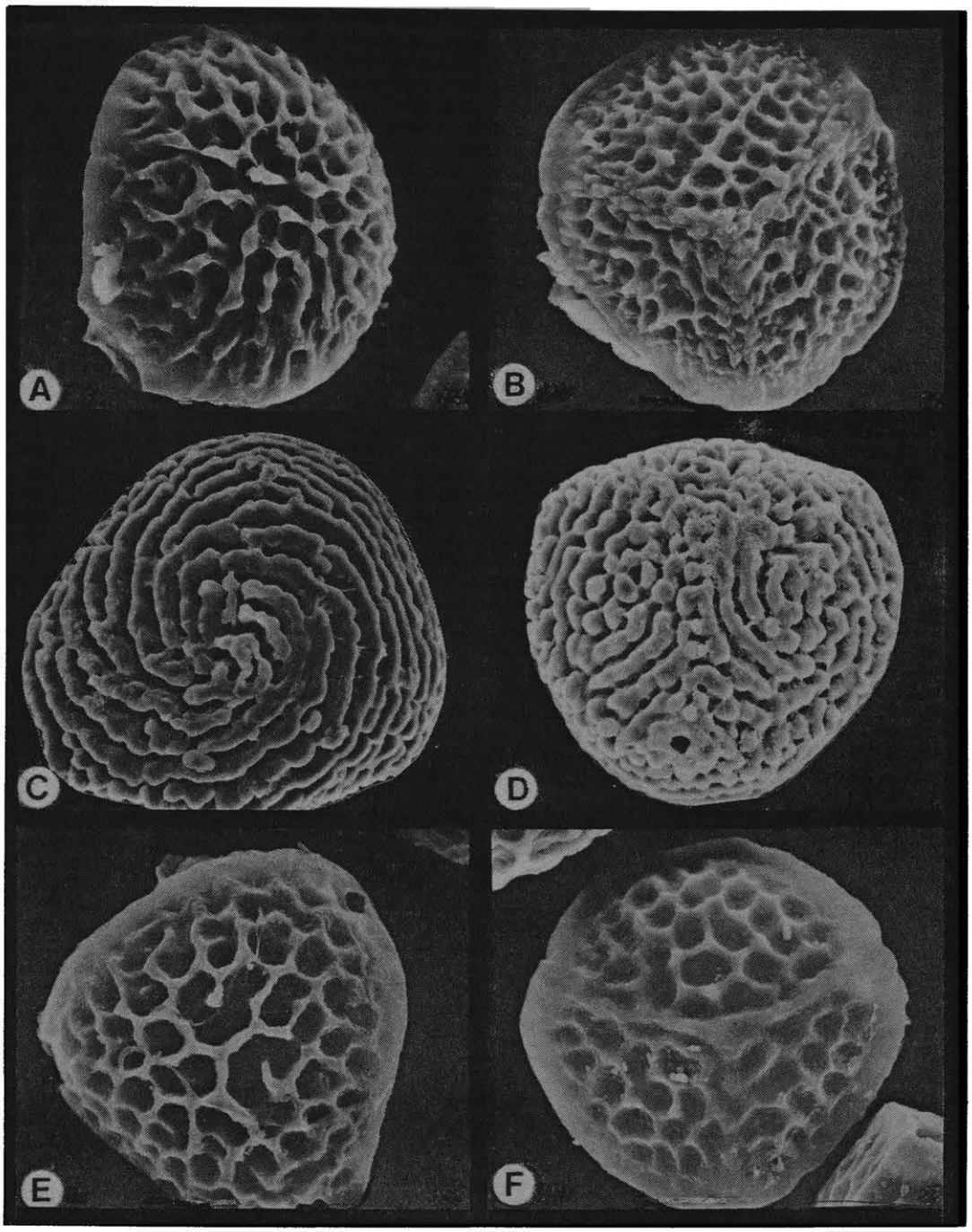


PLATE 11.—*Riccia bicolorata* (A, B): A, distal spore face; B, proximal spore face. *R. villosa* (C, D): C, distal spore face; D, proximal spore face. *R. hirsuta* (E, F): E, distal spore face; F, proximal spore face. (A, B, *Smook* 6990a; C, D, *Oliver* 8039; E, *Oliver* 8040; F, *S.M. Perold* 2100). Magnification A--D = x 700; E, F = x 500.

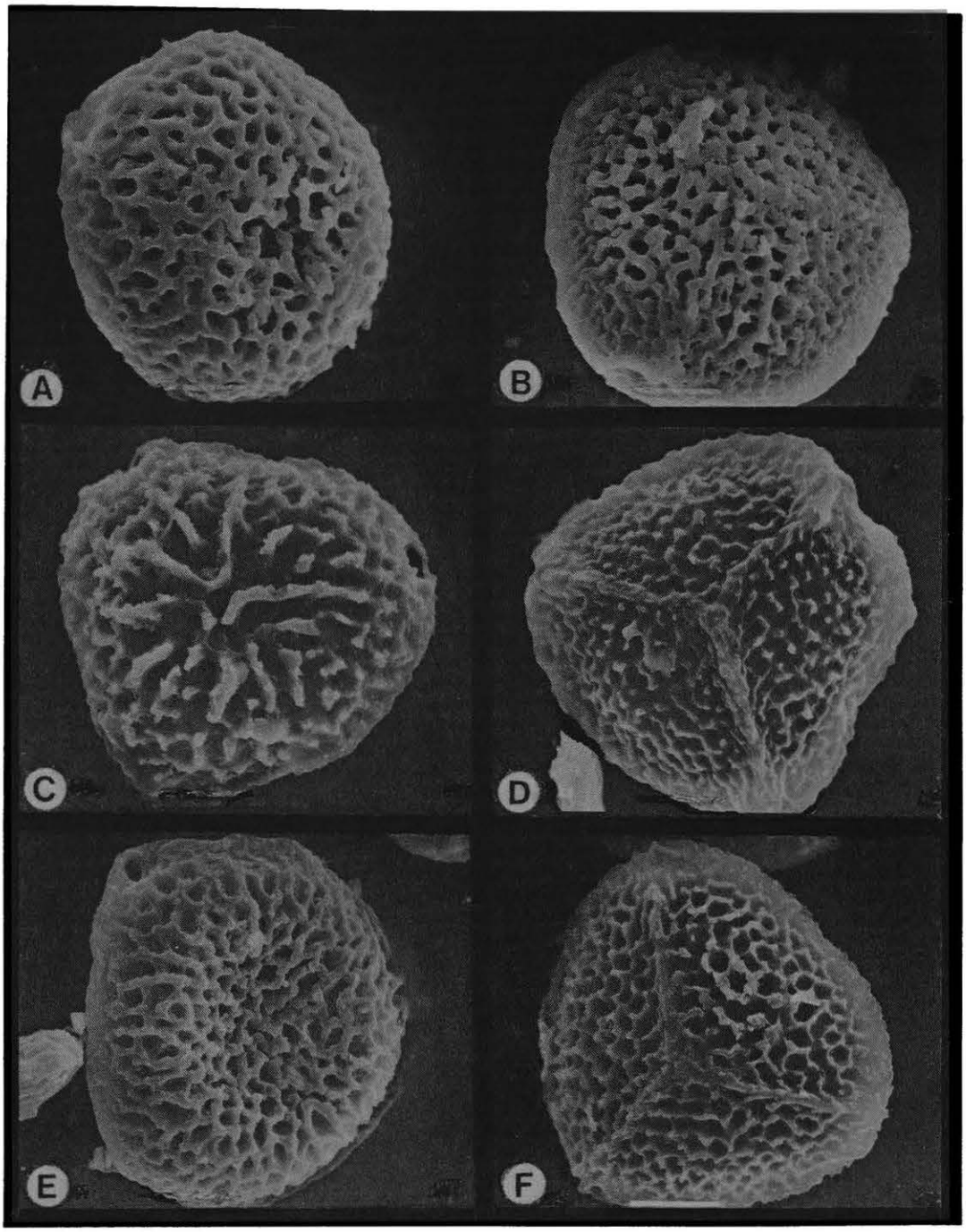


PLATE 12.---*Riccia simii* (A, B): A, distal spore face; B, proximal spore face. *R. vitrea* (C, D): C, distal spore face; D, proximal spore face. *R. namaquensis* (E, F): E, distal spore face; F, proximal spore face. (A, B, *J.M. Perold* 39a; C, D, *S.M. Perold* 1425; E, F, *S.M. Perold* 1420). Magnification A--D = x 700; E, F = x 800.

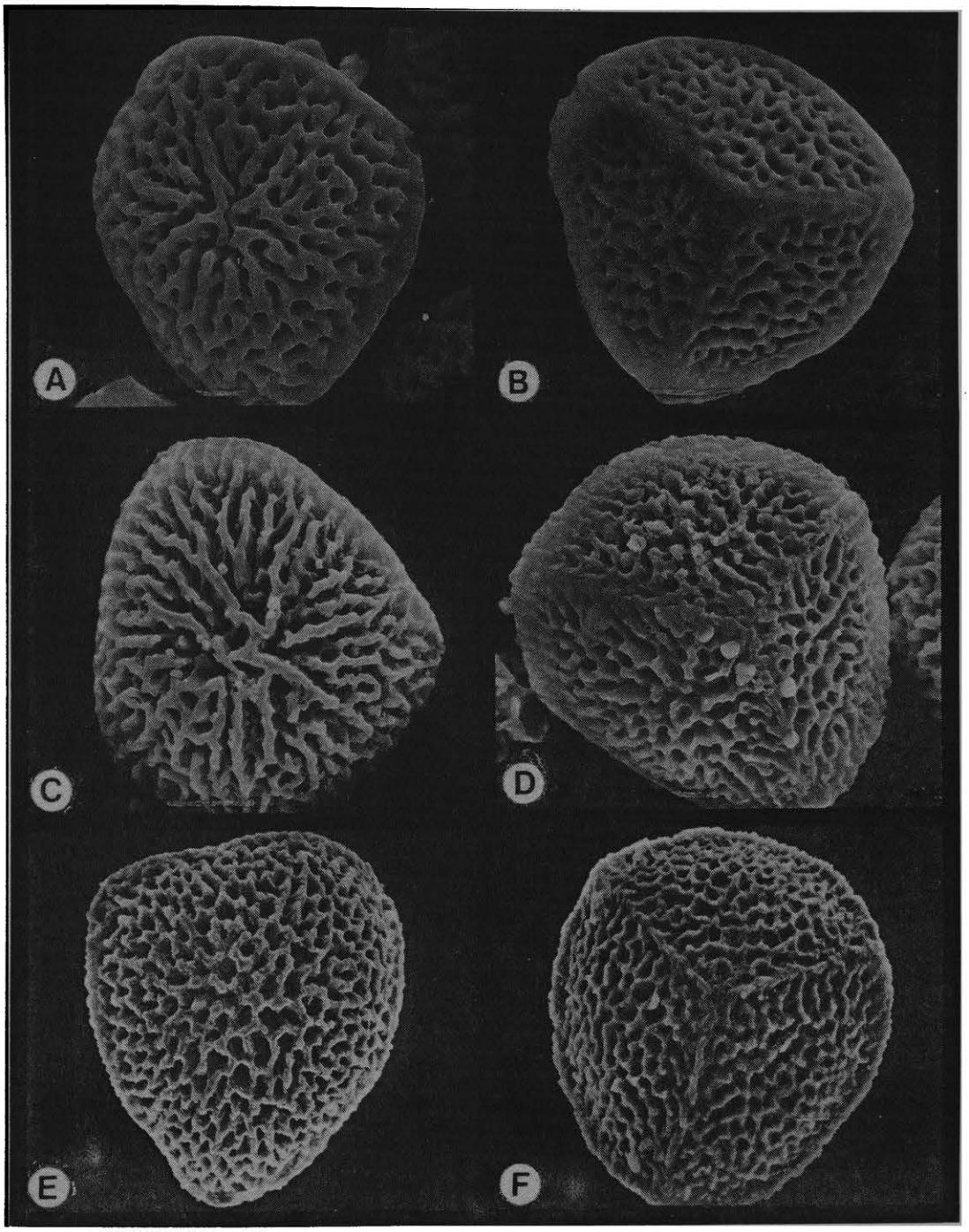


PLATE 13.---*Riccia albomarginata* (A, B): A, distal spore face; B, proximal spore face. *R. ampullacea* (C, D): C, distal spore face; D, proximal spore face. *R. parvo-areolata* (E, F): E, distal spore face; F, proximal spore face. (A, B, *S.M. Perold* 2383; C, D, *Van Rooy* 3164a; E, F, *J.M. Perold* 24). Magnification A, B = x 600; C--F = x 700.

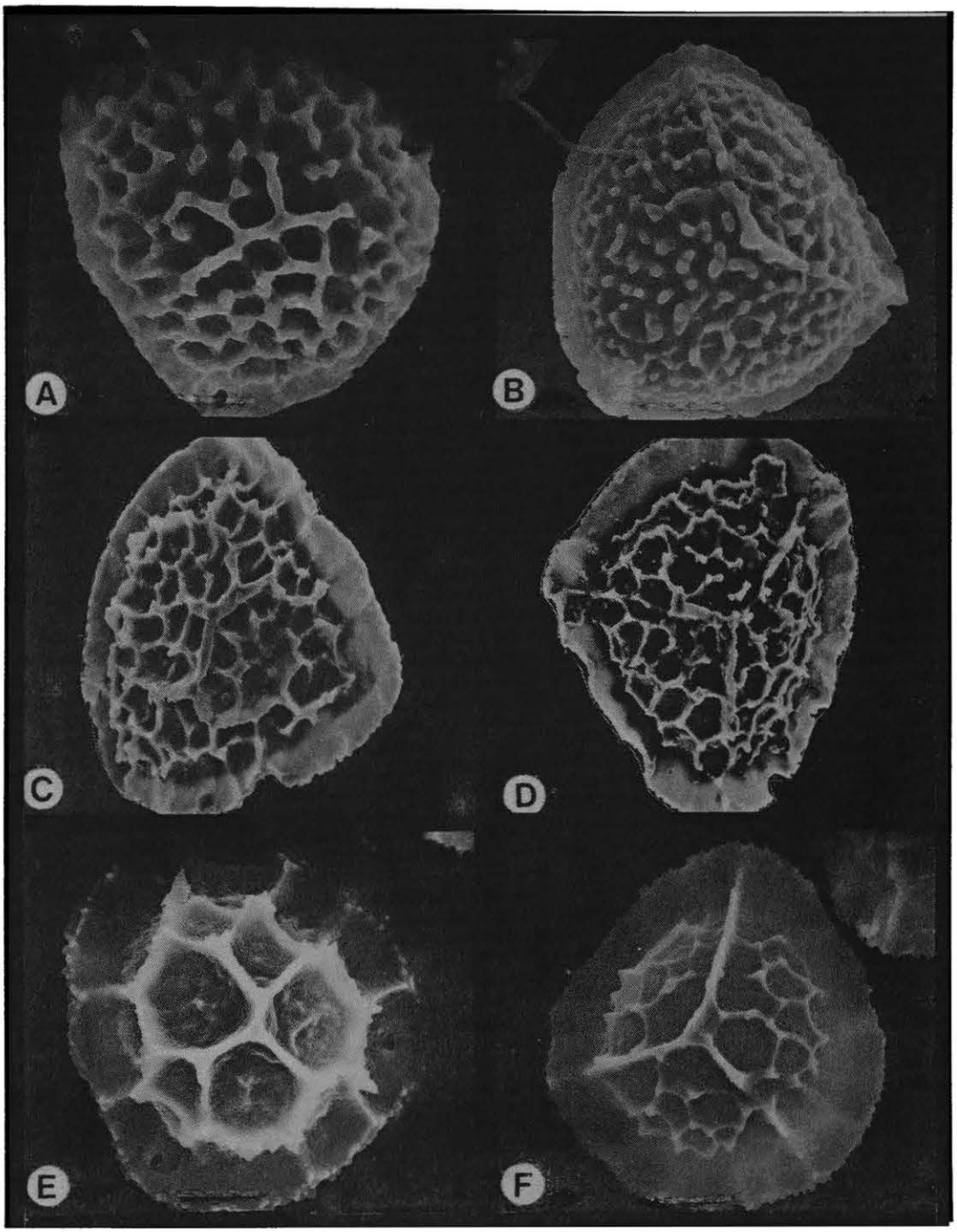


PLATE 14.---*Riccia albovestita* (A, B): A, distal spore face; B, proximal spore face. *R. alatospora* (C, D): C, distal spore face; D, proximal spore face. *R. hantamensis* (E, F): E, distal spore face; F, proximal spore face. (A, B, *J.M. Perold* 39; C, D, *Duthie* 5004b; E, F, *S.M. Perold* 1830). Magnification A, B = x 700; C, D = x 500; E, F = x 800.

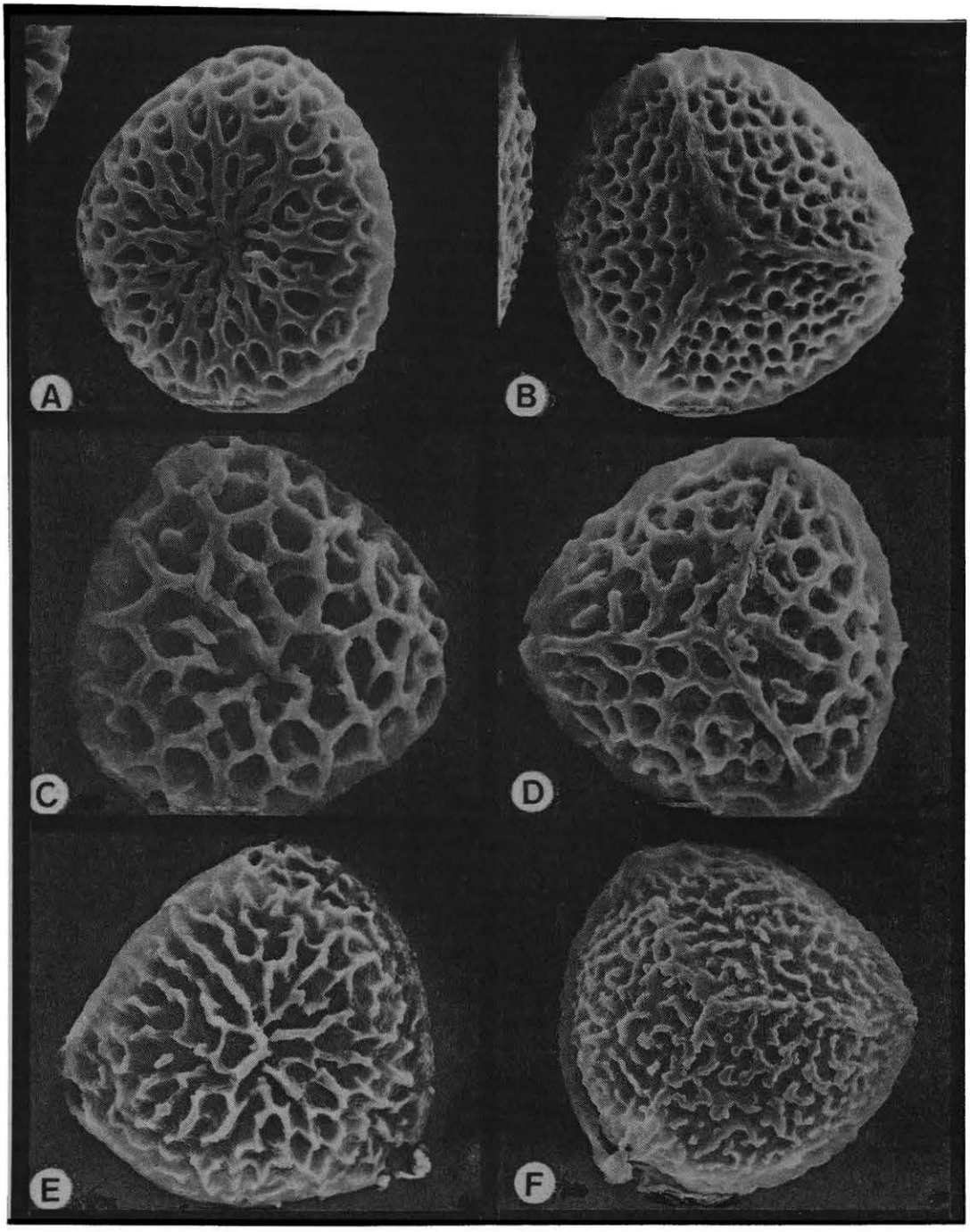


PLATE 15.---*Riccia concava* (A, B): A, distal spore face; B, proximal spore face. *R. elongata* (C, D): C, distal spore face; D, proximal spore face. *R. trachyglossum* (E, F): E, distal spore face; F, proximal spore face. (A, B, *Arnell* 30; C, D, *S.M. Perold* 2018; E, F, *J.M. Perold* 34). Magnification A, B, E, F = x 700; C, D = x 600.

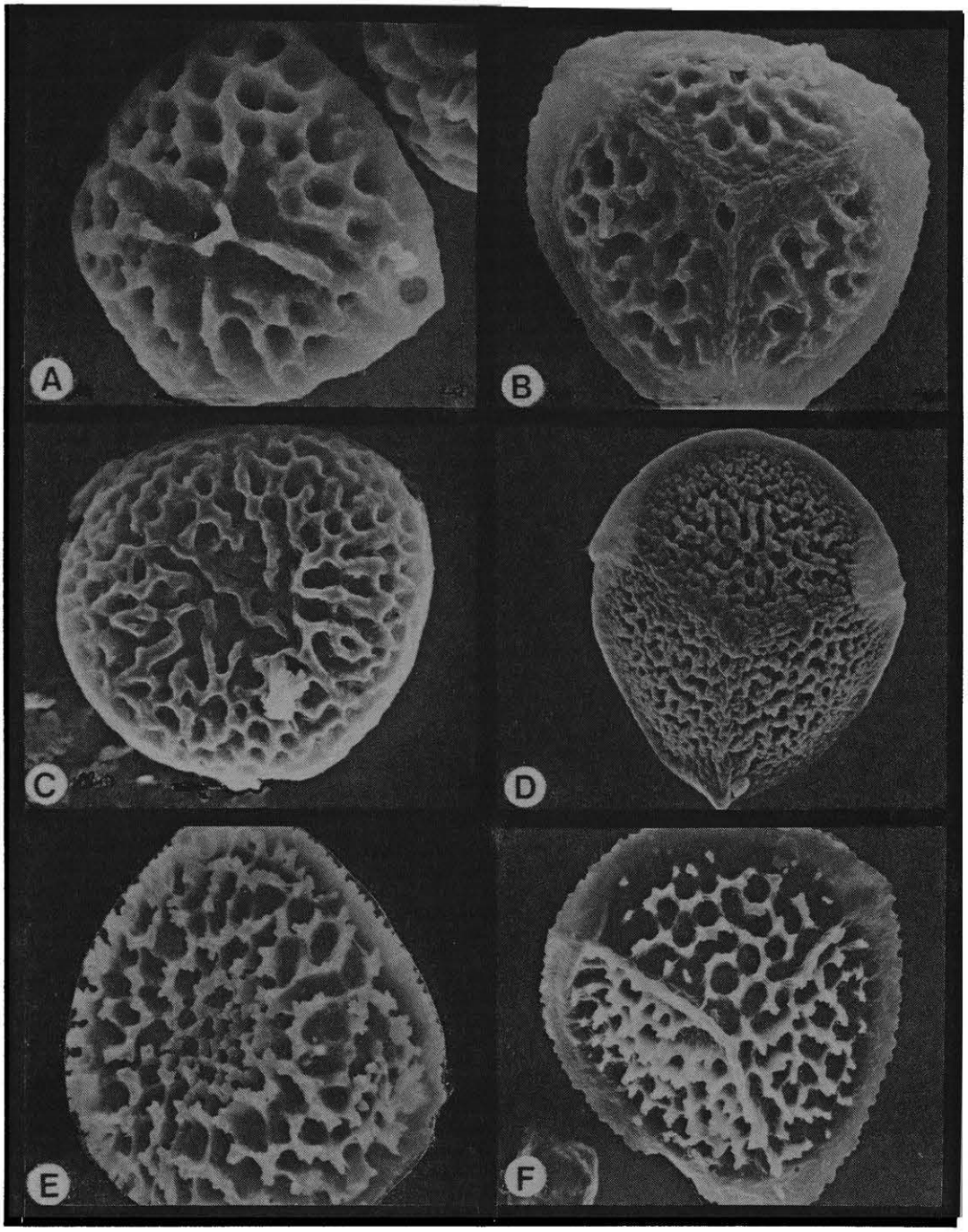


PLATE 16.---*Riccia furfuracea* (A, B): A, distal spore face; B, proximal spore face. *R. pulveracea* (C, D): C, distal spore face; D, proximal spore face. *R. crystallina* (E, F): E, distal spore face; F, proximal spore face. (A, *Oliver* 8957a; B, *Oliver* 8910a; C, *Duthie* 5484; D, *Duthie* 5455; E, F, *Duthie* 5529). Magnification A--D = x 700; E, F = x 1000.

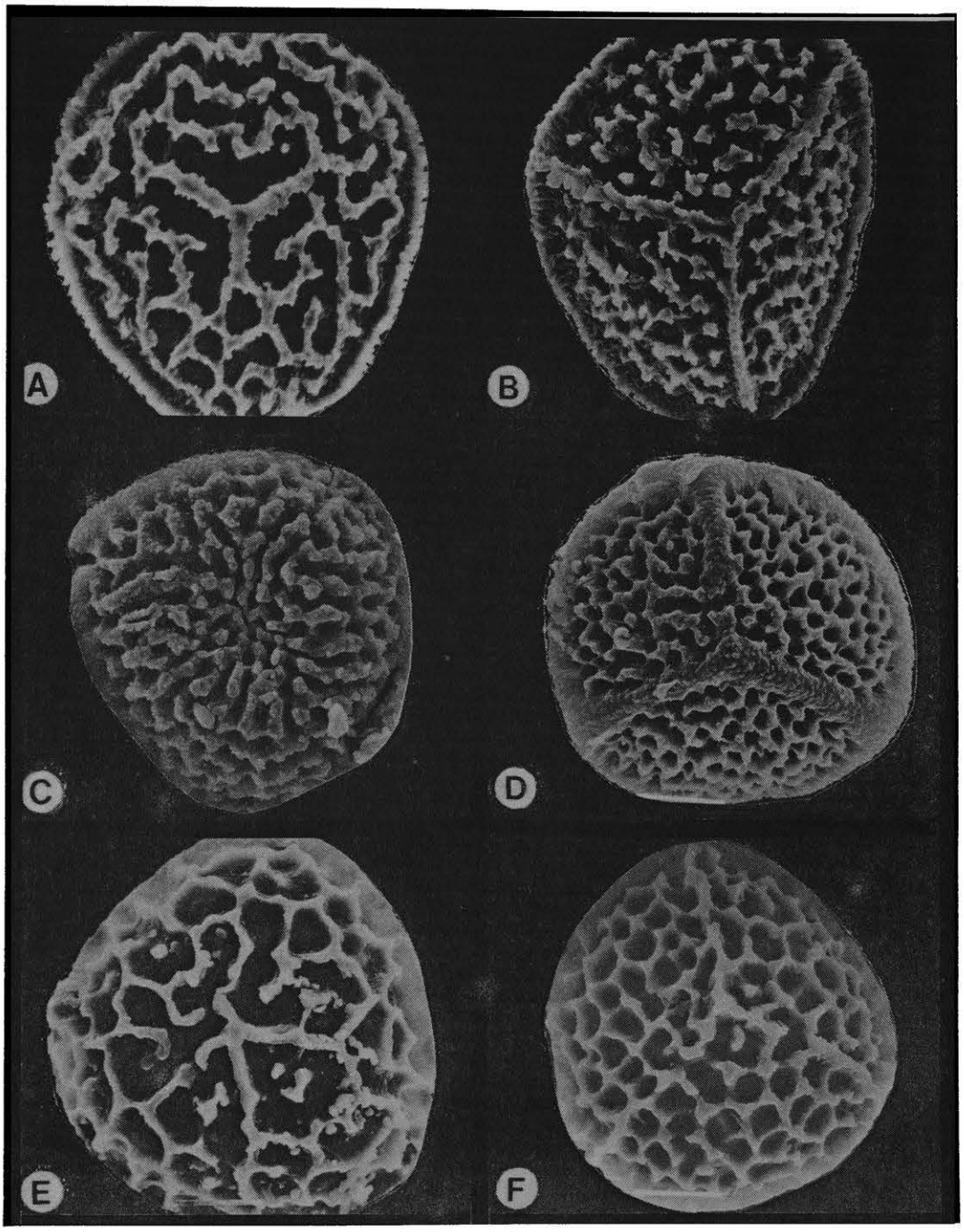


PLATE 17.---*Riccia cavernosa* (A, B): A, distal spore face; B, proximal spore face. *R. cupulifera* (C, D): C, distal spore face; D, proximal spore face. *R. bullosa* (A, B): A, distal spore face; B, proximal spore face. (A, B, *Koch* 14934; C, D, *S.M. Perold* 2371; E, F, *S.M. Perold* 467). Magnification A, B = x 700; C--E = x 600; F = x 500.

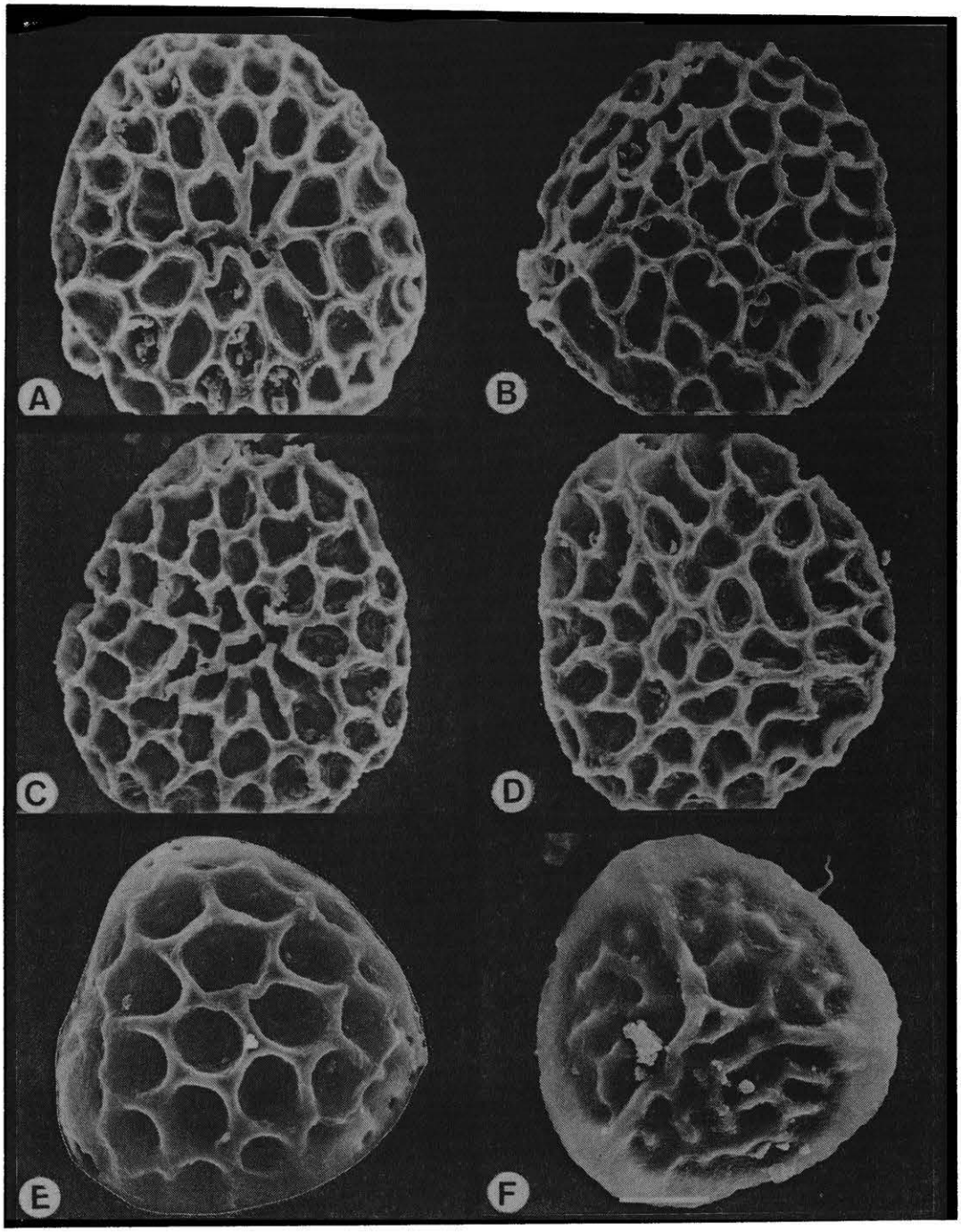


PLATE 18.---*Riccia garsidei* (A, B): A, distal spore face; B, proximal spore face. *R. volkii* (C, D): C, distal spore face; D, proximal spore face. *R. rubricollis* (E, F): E, distal spore face; F, proximal spore face. (A, B, *Garside* 2; C, D, *Volk* 81/230; E, F, *Duthie* 5014). Magnification A, B, E, F = x 600; C, D = x 700.

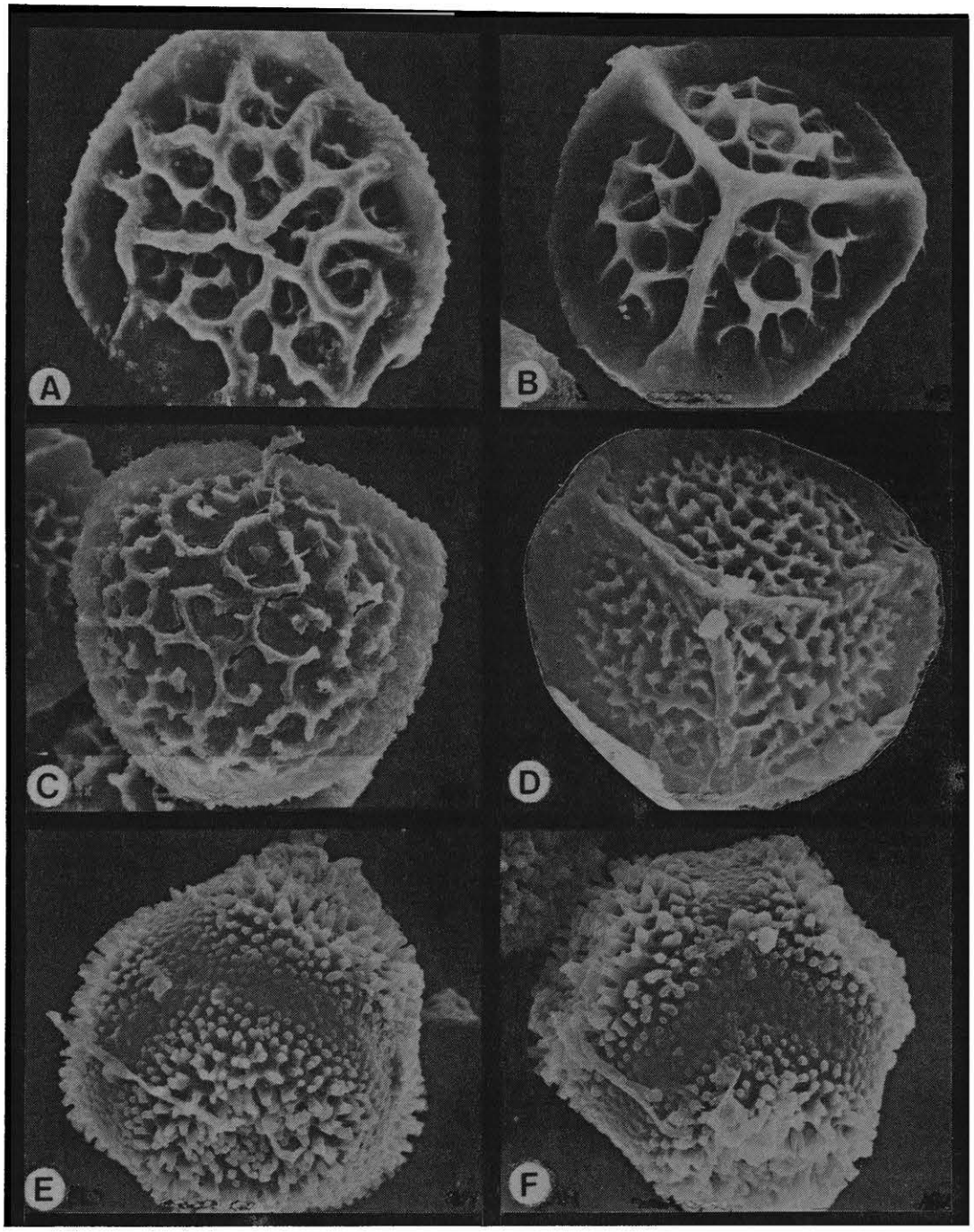


PLATE 19.---*Riccia stricta* (A, B): A, distal spore face; B, proximal spore face. *R. purpurascens* (C, D): C, distal spore face; D, proximal spore face. *R. curtisii* (E, F): E, F, spore tetrads. (A, *Eyles* 1405; B, *Wells* 57; C, D, *Garside* 7; E, F, *S.M. Perold* 2059). Magnification A--D = x 800; E, F, = x 600.

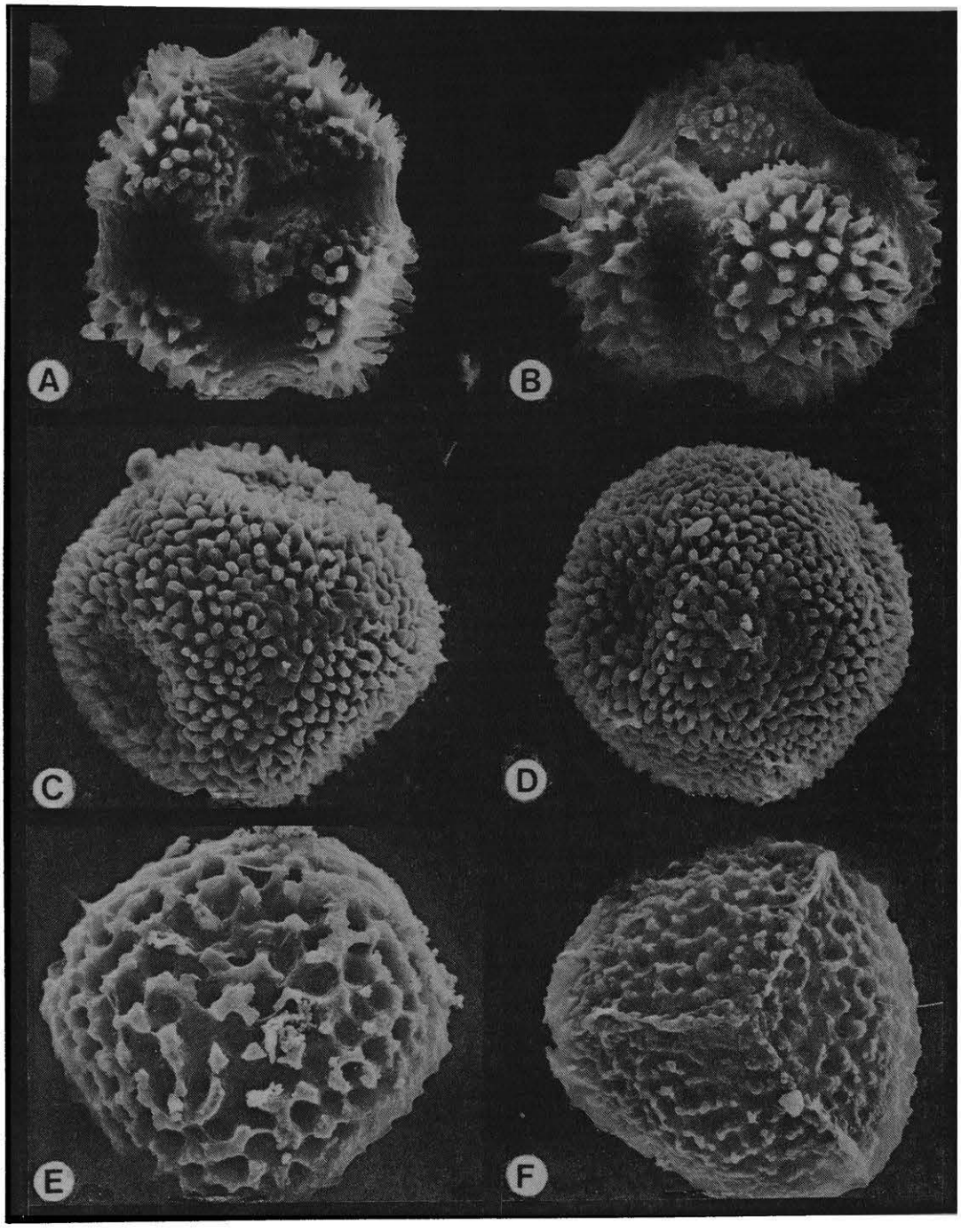


PLATE 20.---*Riccia perssonii* (A, B): A, B, spore tetrads. *R. tomentosa* (C, D): C, D, spore tetrads. *R. schelpei* (E, F): E, distal spore face; F, proximal spore face. (A, B, *Volk* 2059; C,CL D, *S.M. Perold* 1495; E, F, *S.M. Perold* 1426a). Magnification A--D = x 600; E, F = x 700.

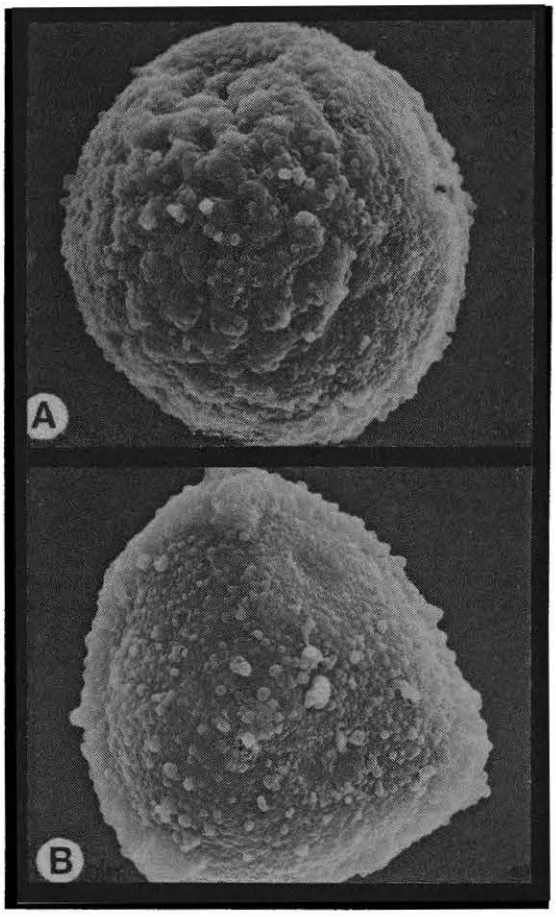
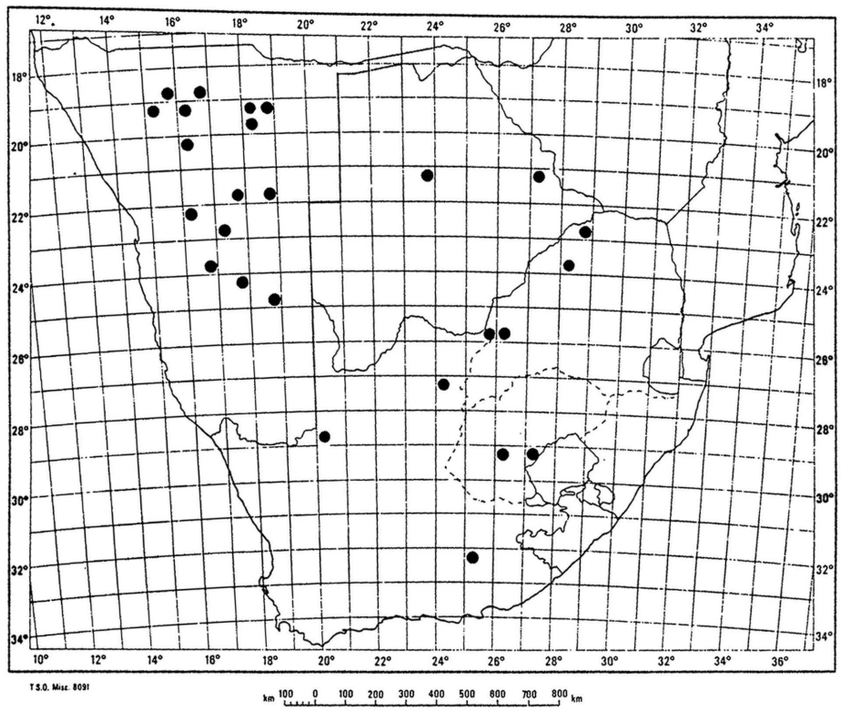
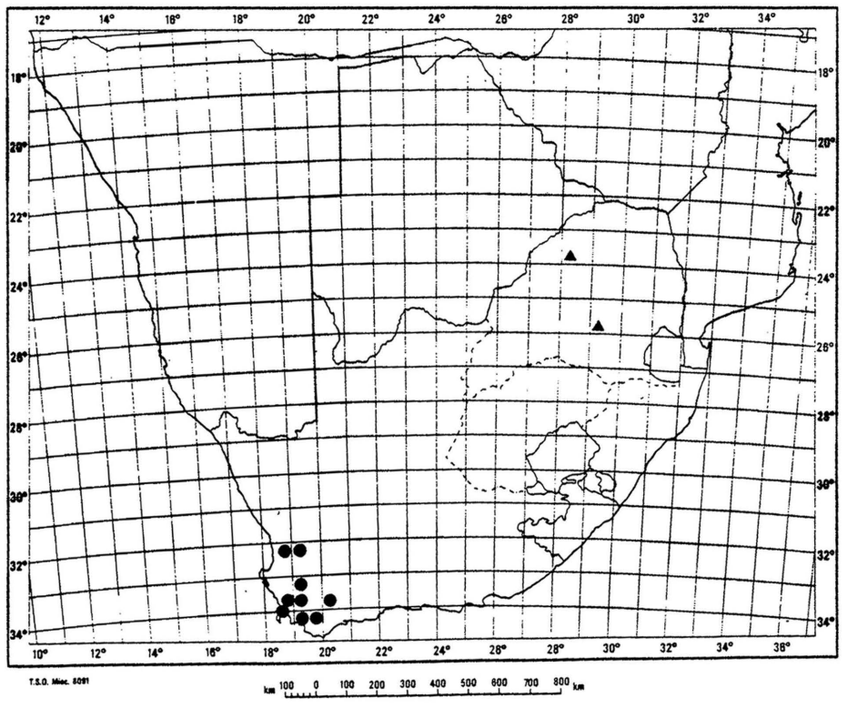


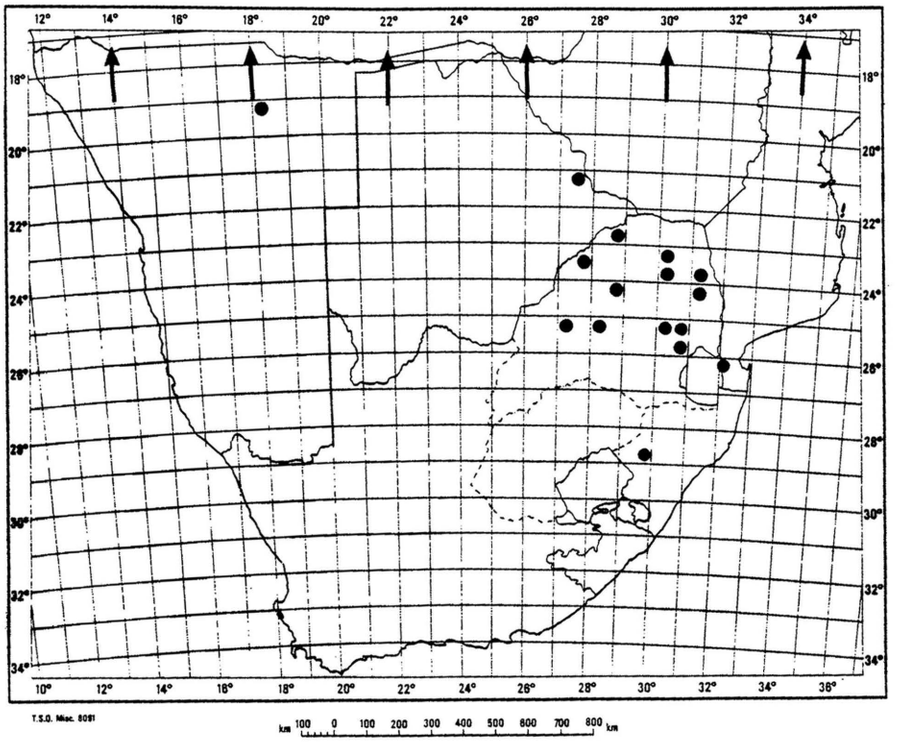
PLATE 21.—*Ricciocarpos natans* (A, B): A, distal spore face; B, proximal spore face. (A, B, *Ward* s.n.). Magnification A, B = x 800.



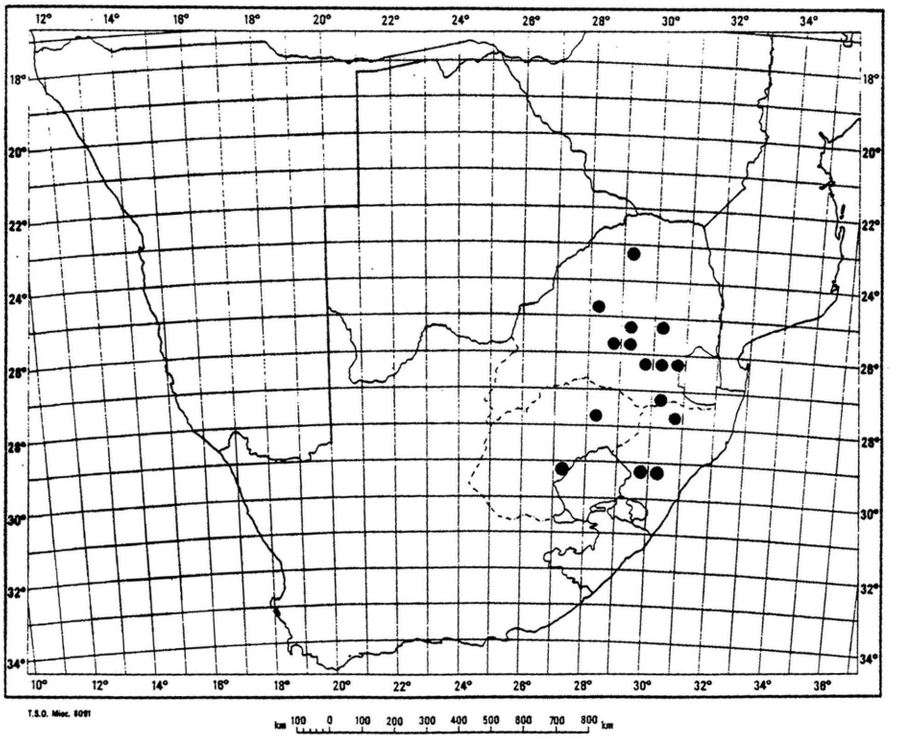
MAP 1.— Distribution of *Riccia trichocarpa* in southern Africa.



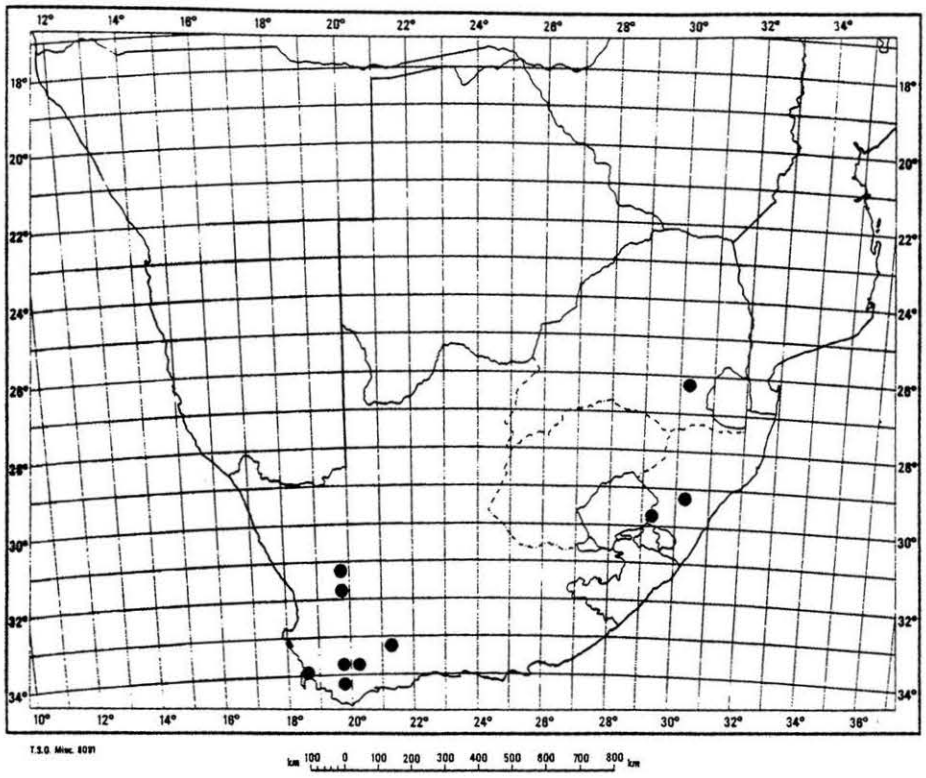
MAP 2.--- Distribution of *Riccia crozalsii* (dots) and *R. mammifera* (triangles) in southern Africa.



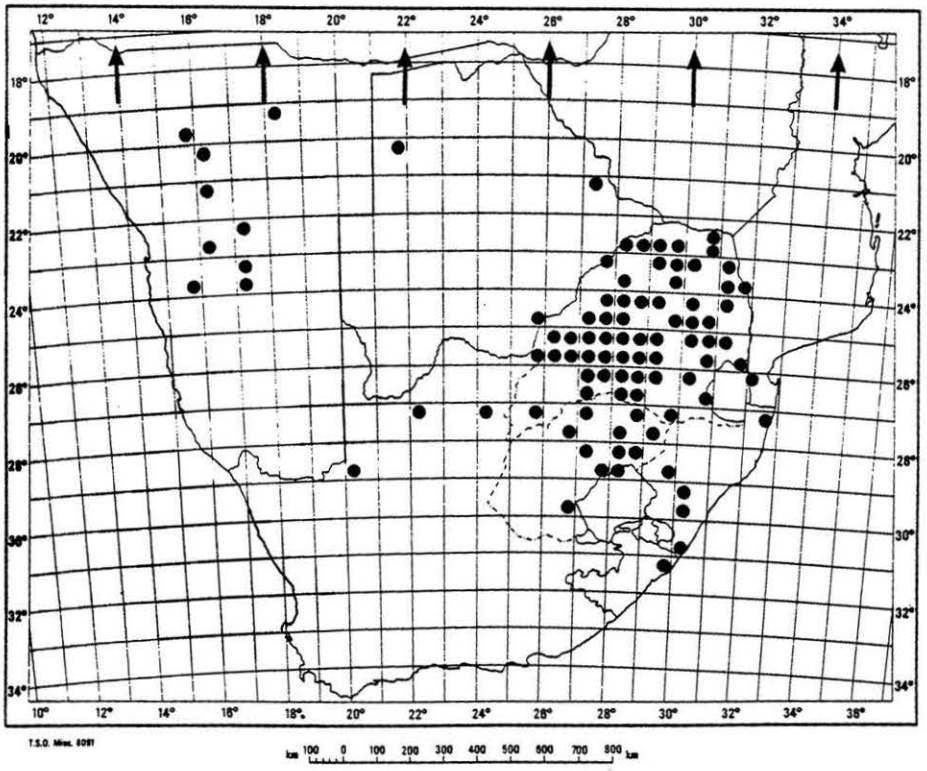
MAP 3.--- Distribution of *Riccia microciliata* in southern Africa.



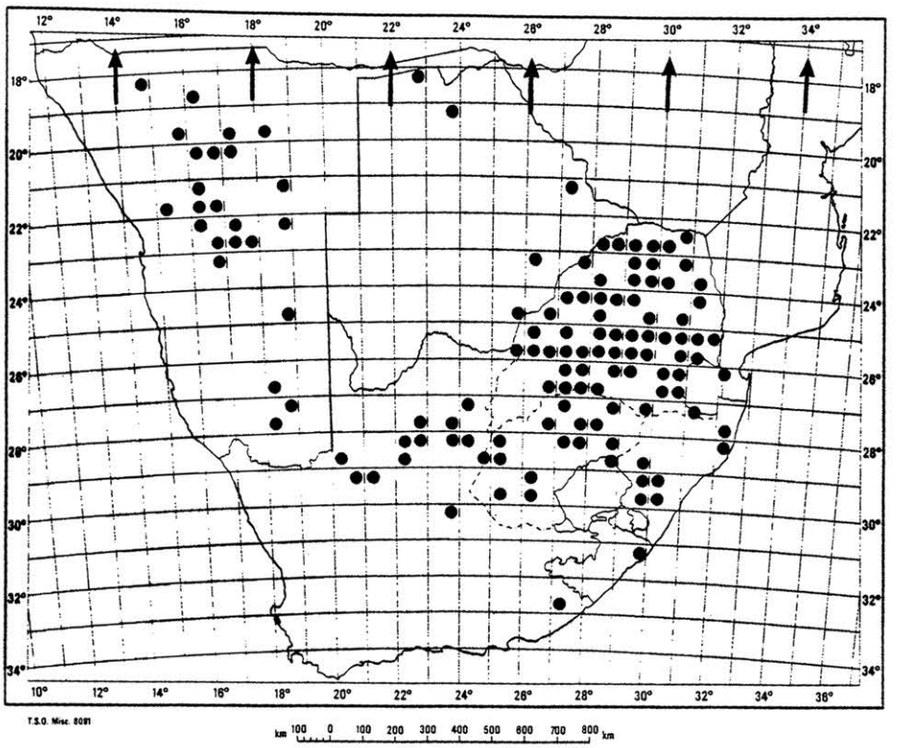
MAP 4.--- Distribution of *Riccia natalensis*.



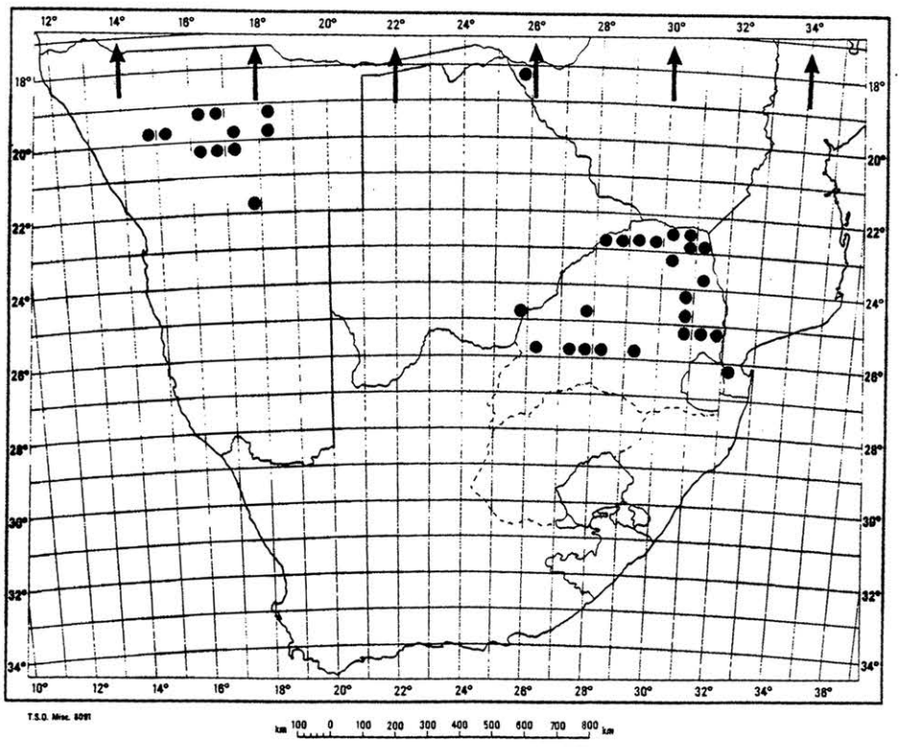
MAP 5.— Distribution of *Riccia sorocarpa* in southern Africa.



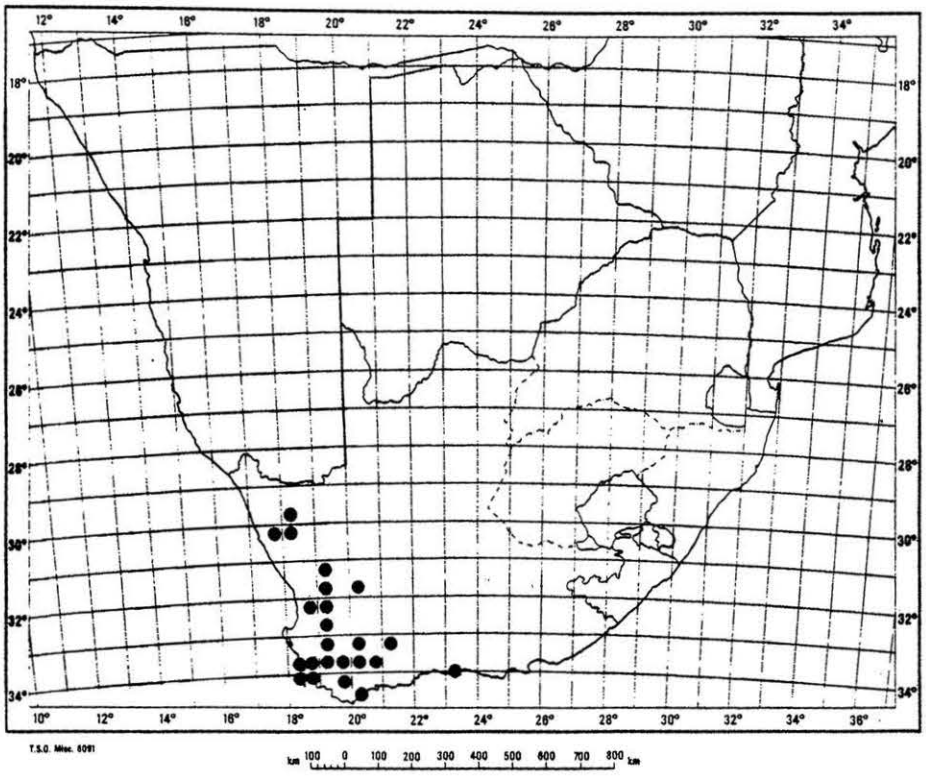
MAP 6.— Distribution of *Riccia atropurpurea* in southern Africa.



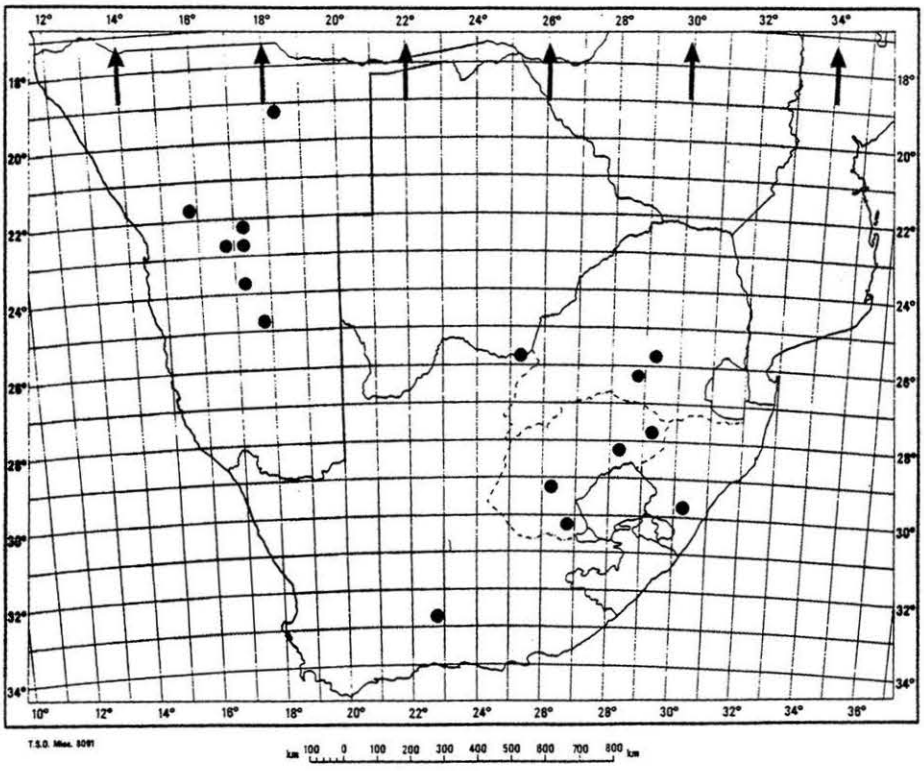
MAP 7.— Distribution of *Riccia okahandjana* in southern Africa.



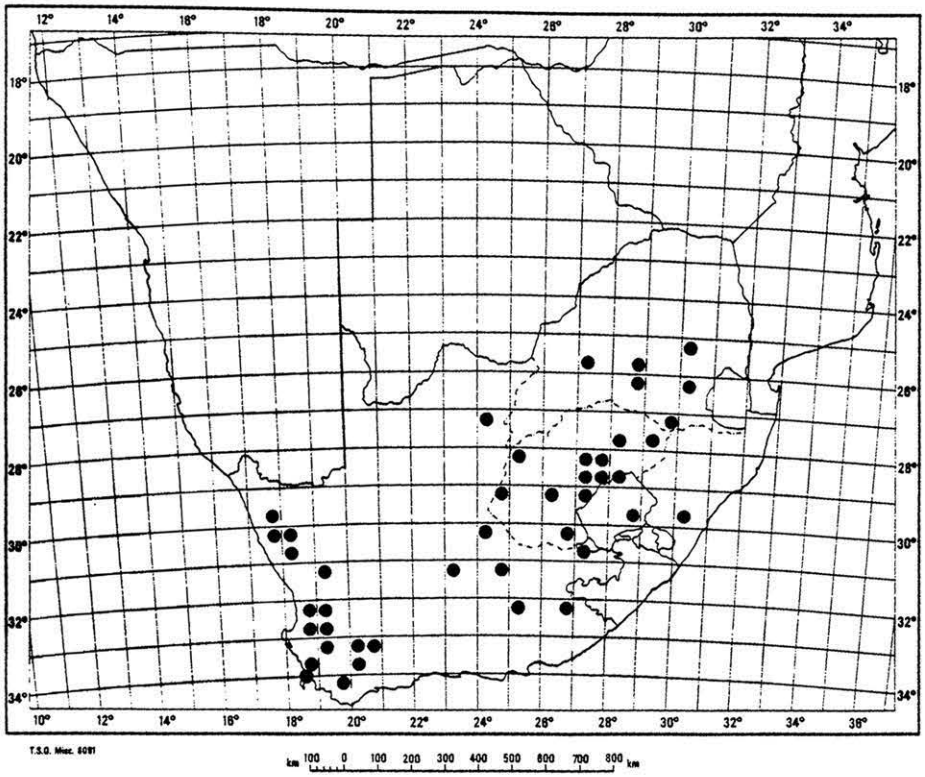
MAP 8.— Distribution of *Riccia congoana* in southern Africa.



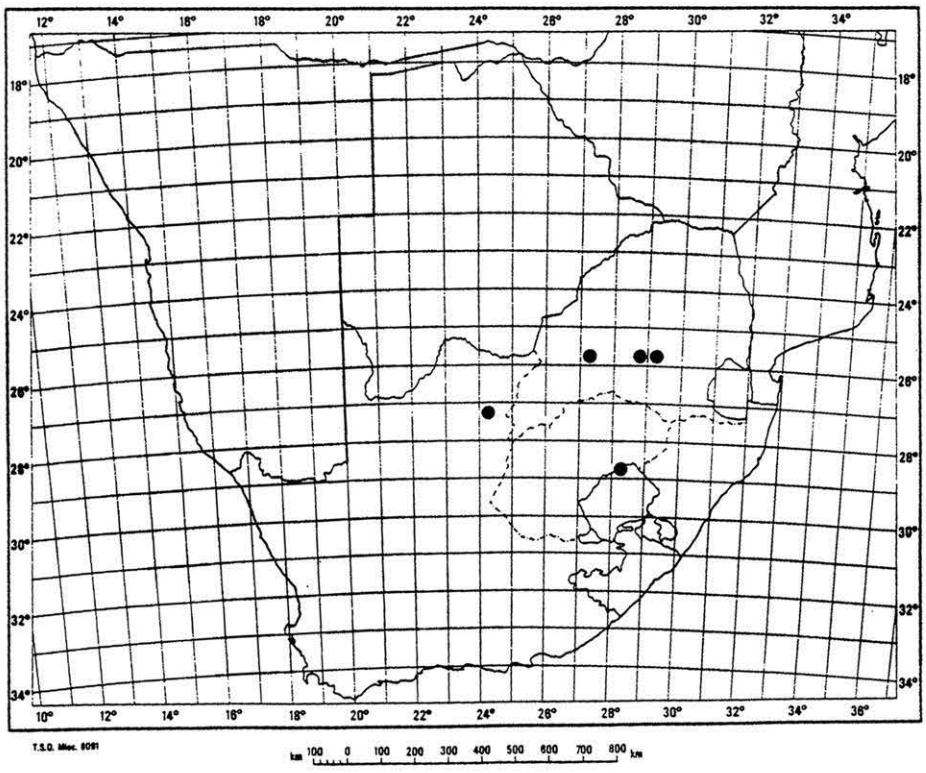
MAP 9.— Distribution of *Riccia limbata*.



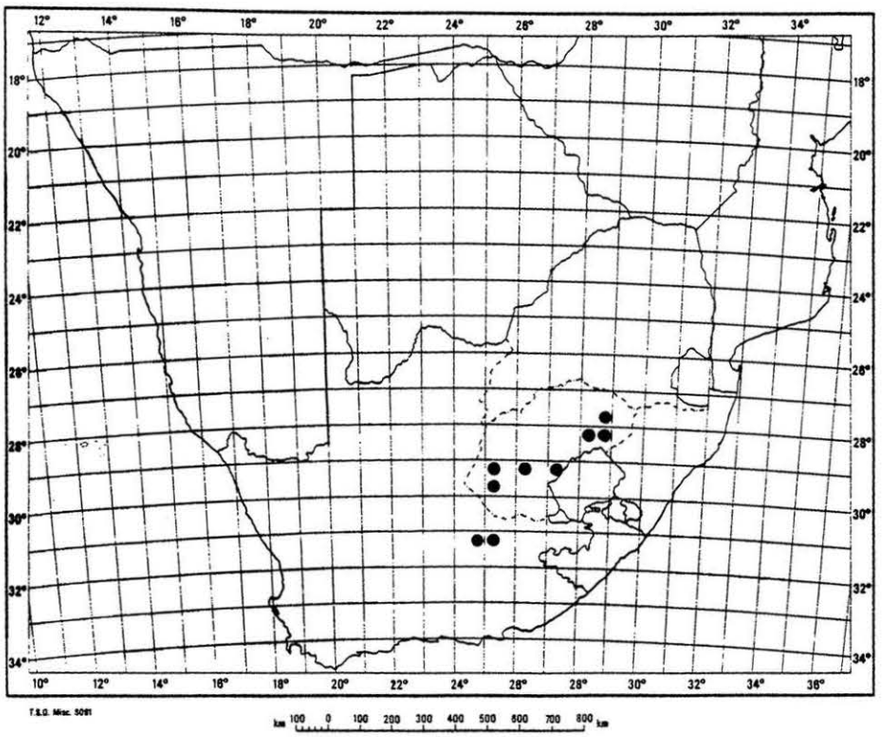
MAP 10.— Distribution of *Riccia angolensis* in southern Africa.



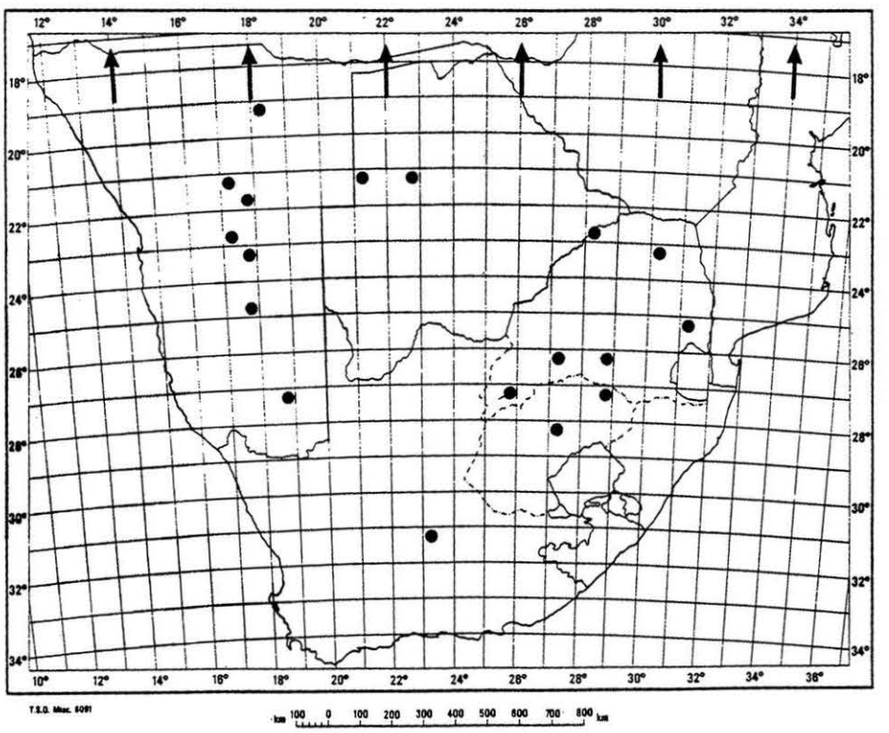
MAP 11.— Distribution of *Riccia nigrella* in southern Africa.



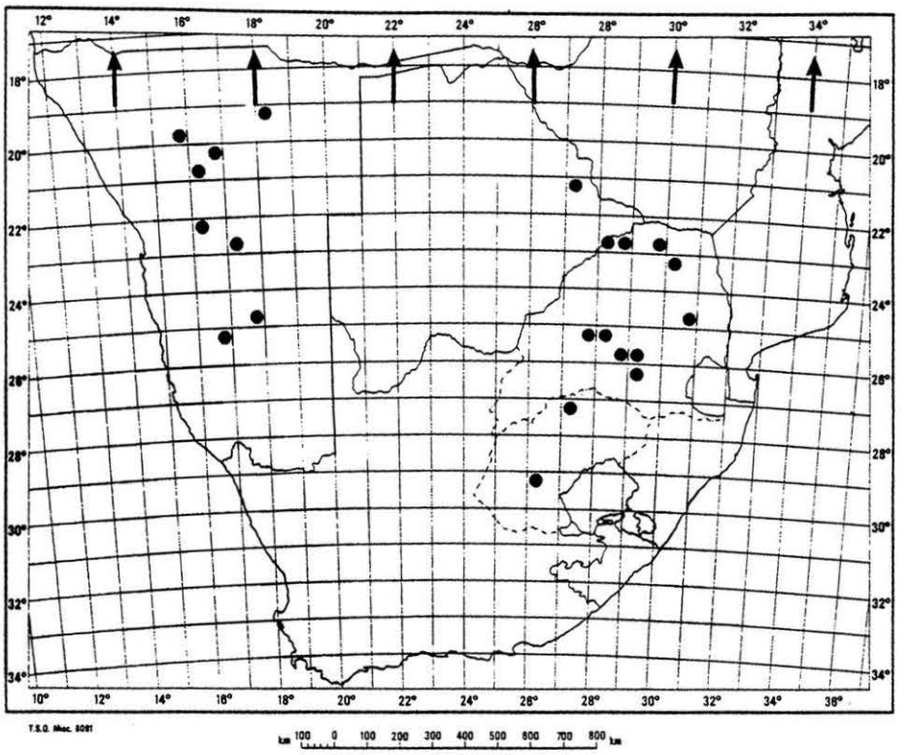
MAP 12.— Distribution of *Riccia macrocarpa* in southern Africa.



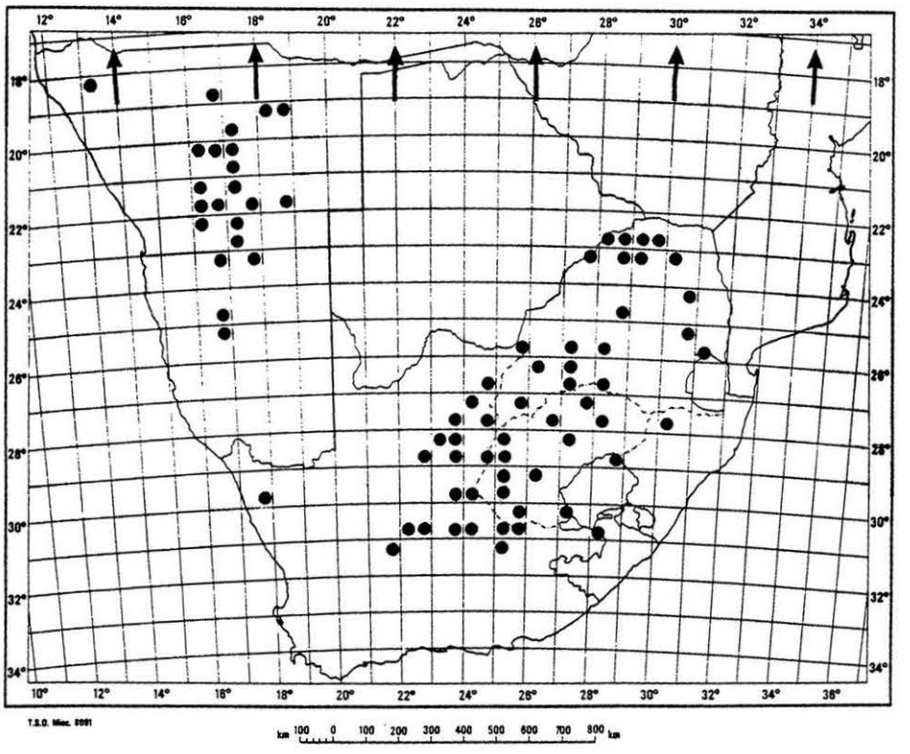
MAP 13.--- Distribution of *Riccia pottsiana*.



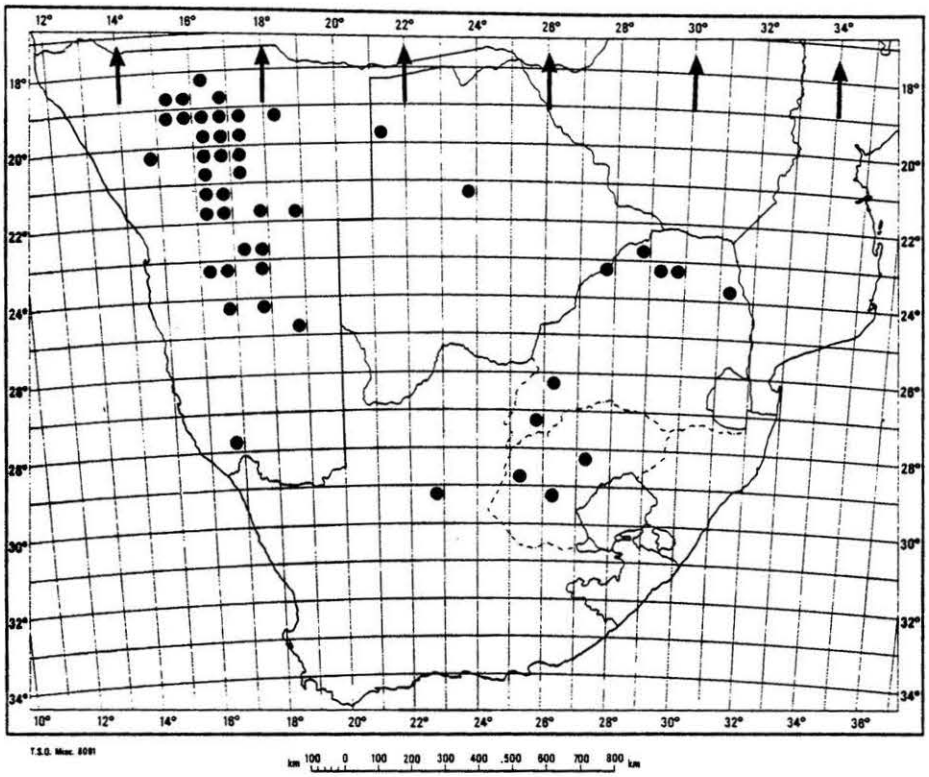
MAP 14.--- Distribution of *Riccia runssorensis* in southern Africa.



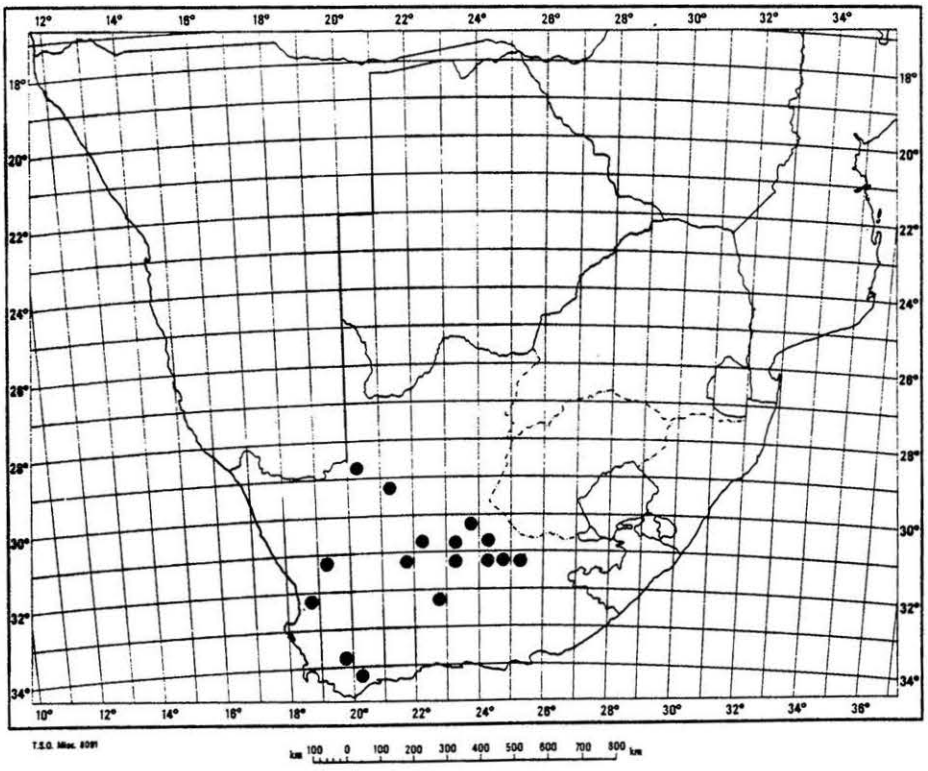
MAP 15.--- Distribution of *Riccia rosea* in southern Africa.



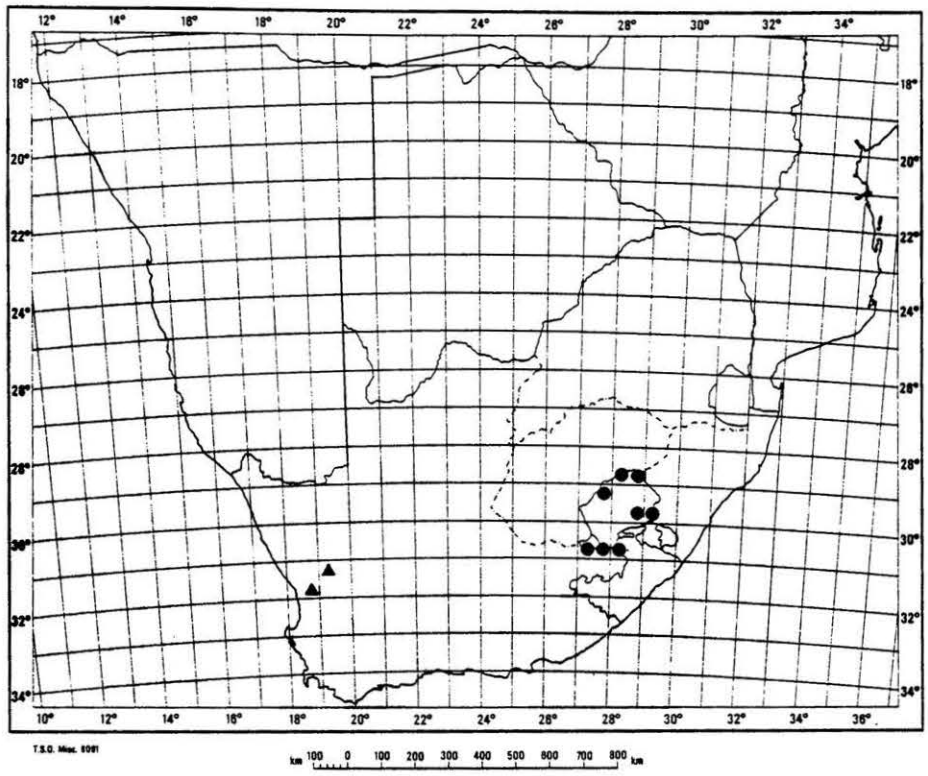
MAP 16.--- Distribution of *Riccia albolimbata* in southern Africa.



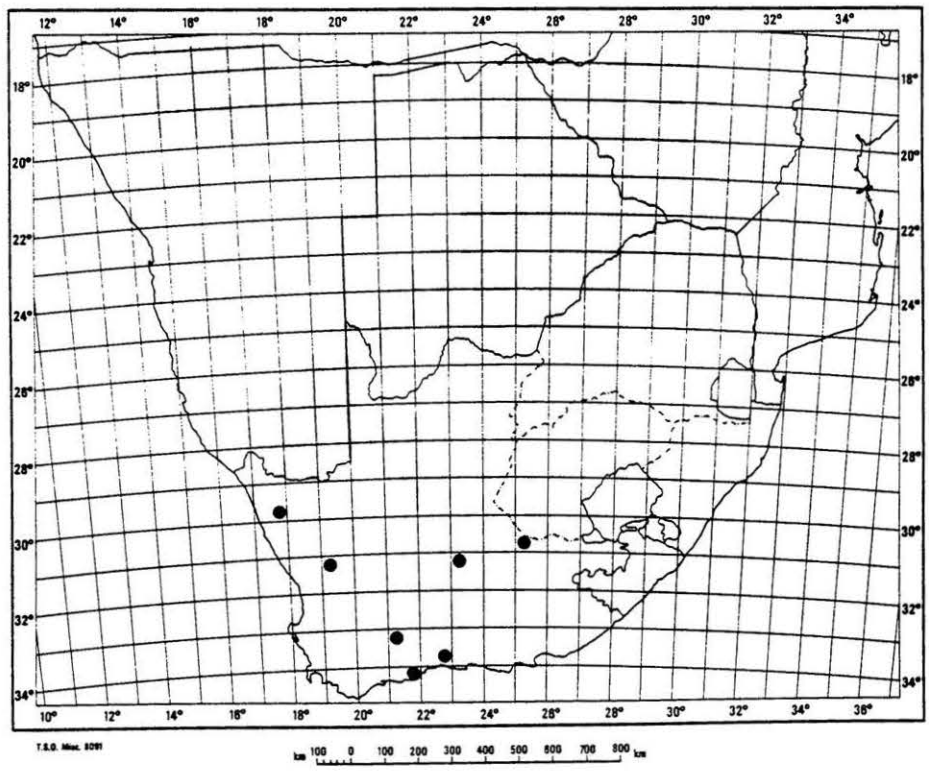
MAP 17.--- Distribution of *Riccia argenteolimbata* in southern Africa.



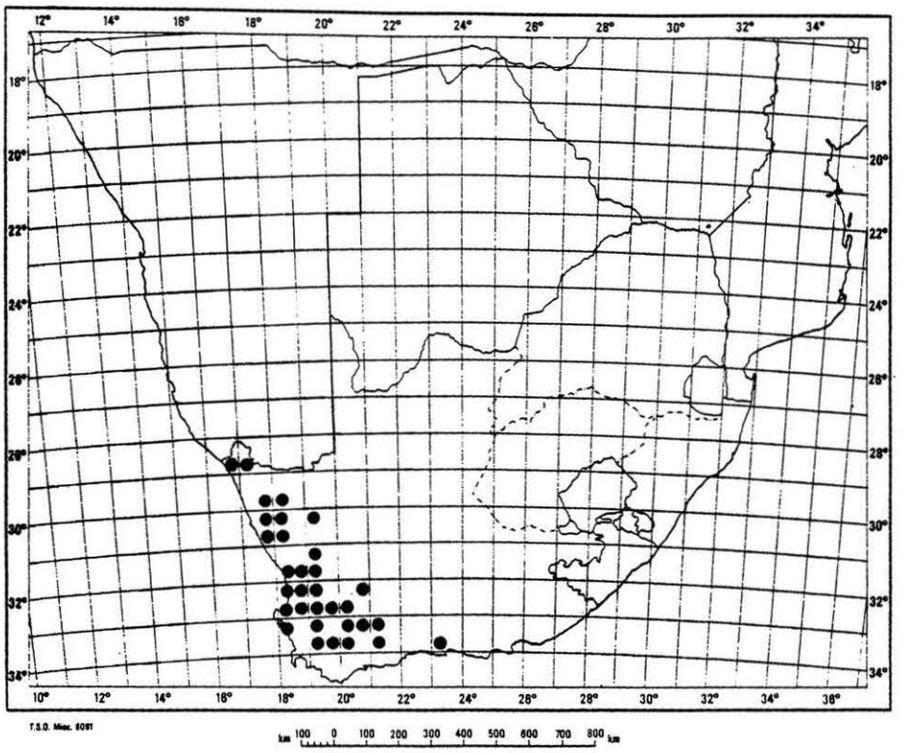
MAP 18.--- Distribution of *Riccia albornata*.



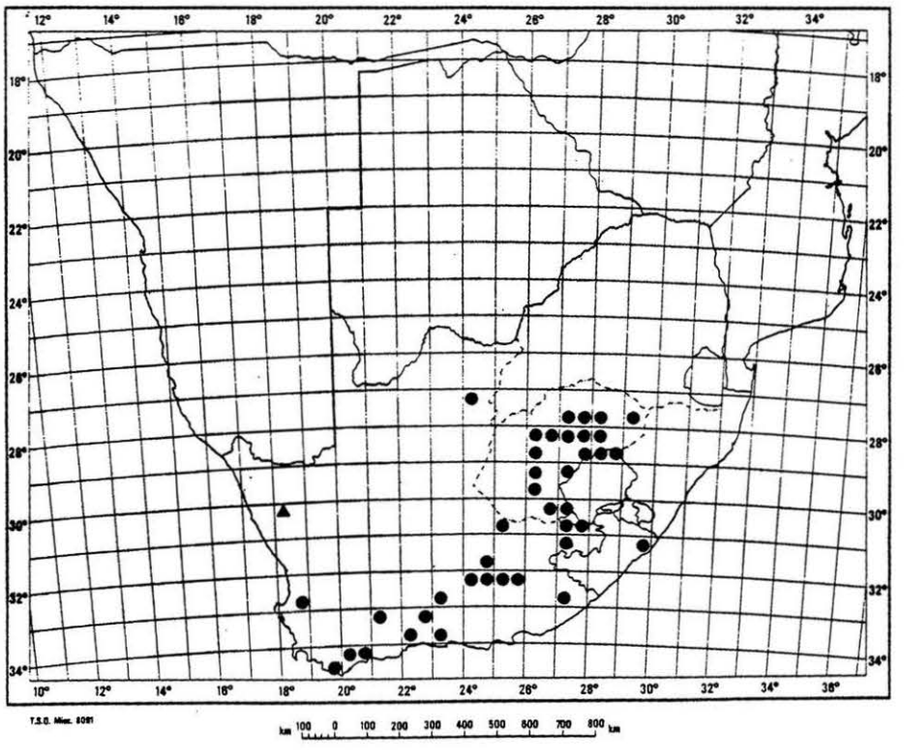
MAP 19.— Distribution of *Riccia montana* (dots) and *R. alboporosa* (triangles).



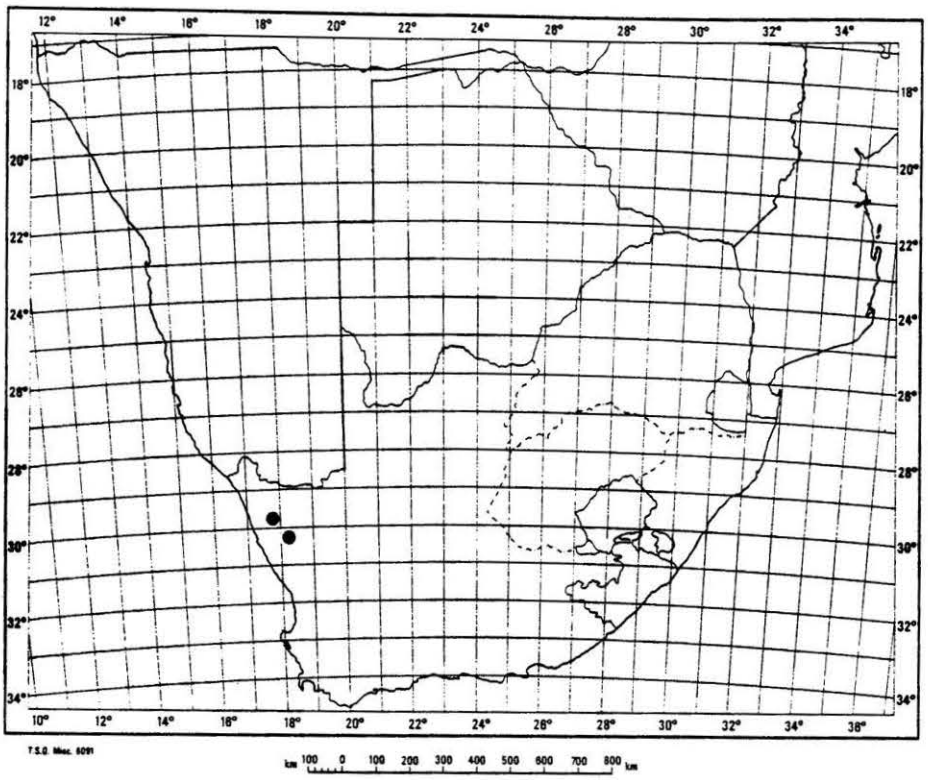
MAP 20.— Distribution of *Riccia bicolorata*.



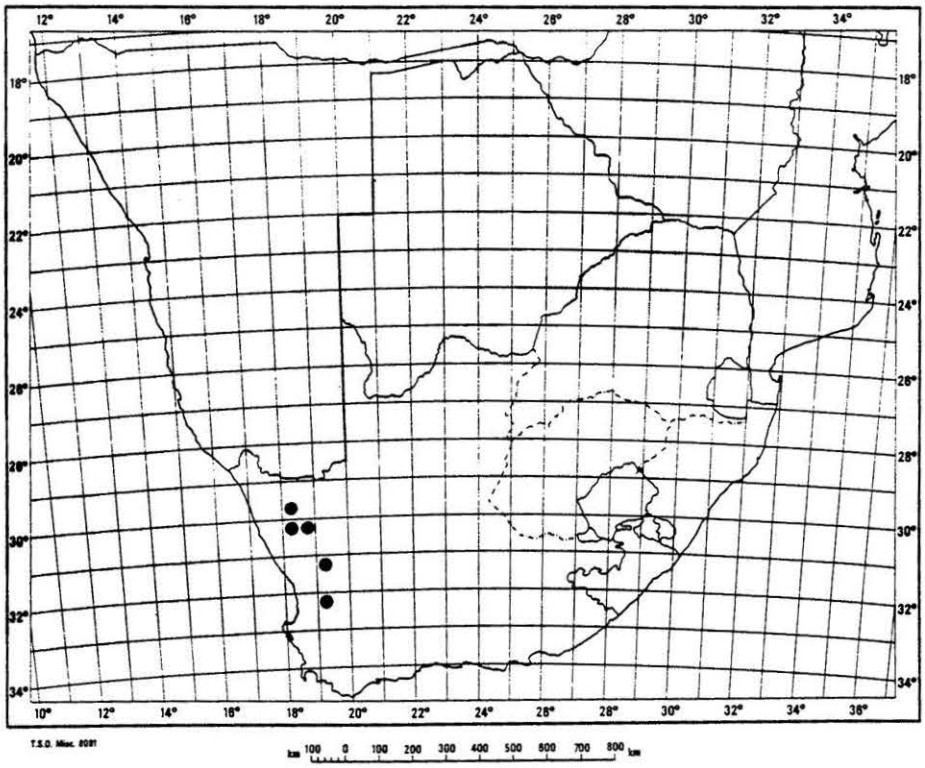
MAP 21.— Distribution of *Riccia villosa*.



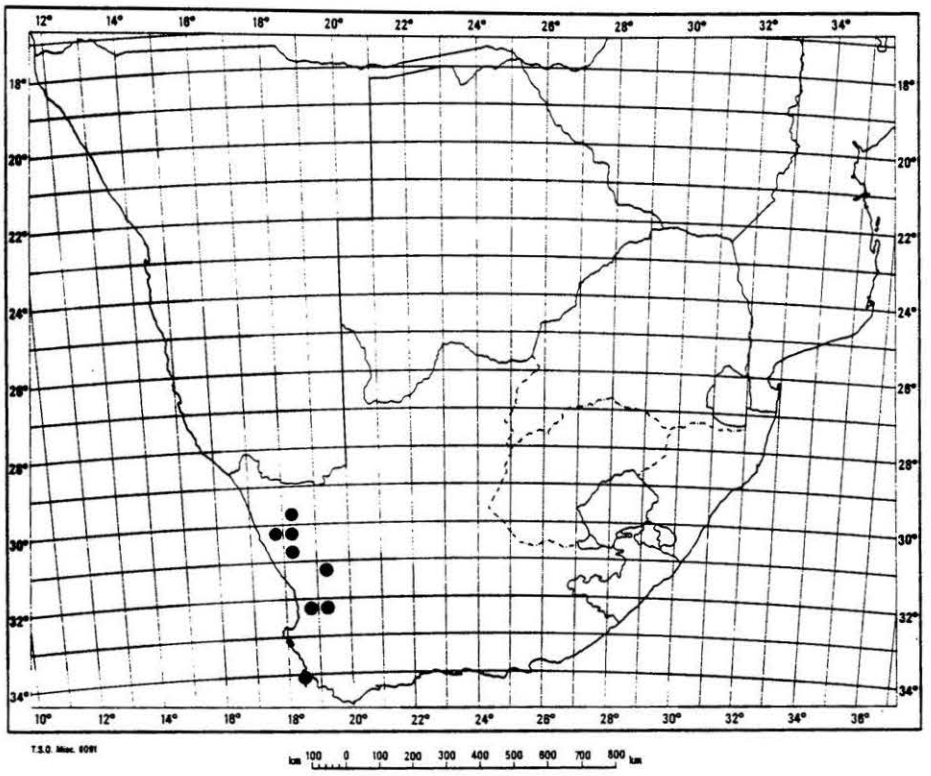
MAP 22.--- Distribution of *Riccia hirsuta* (triangles) and *R. simii* (dots).



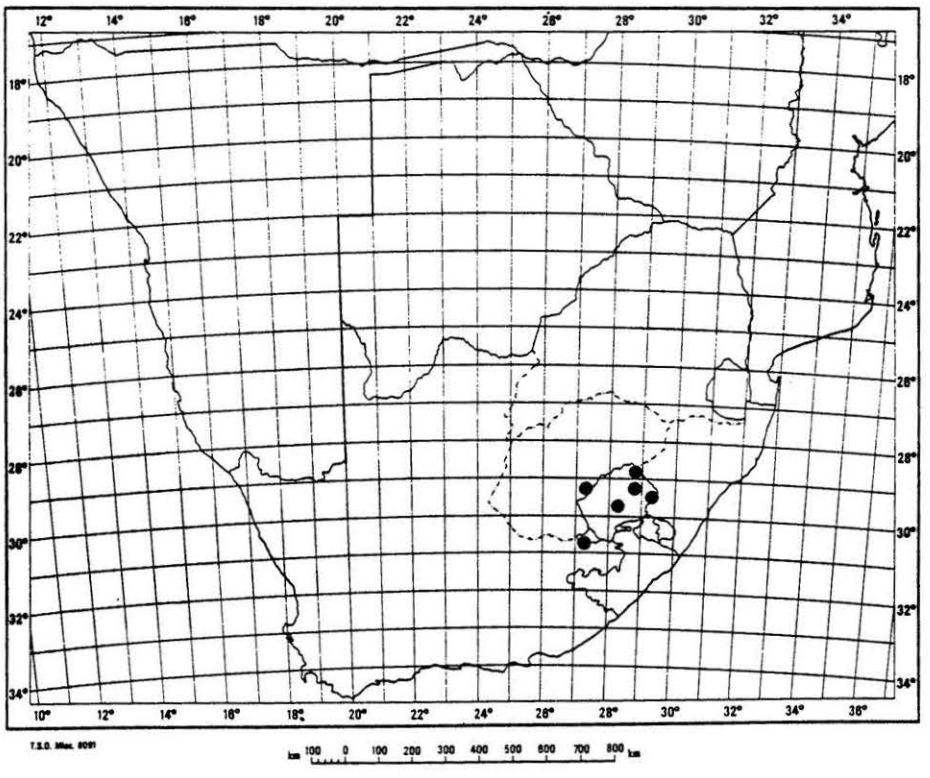
MAP 23.— Distribution of *Riccia vitrea*.



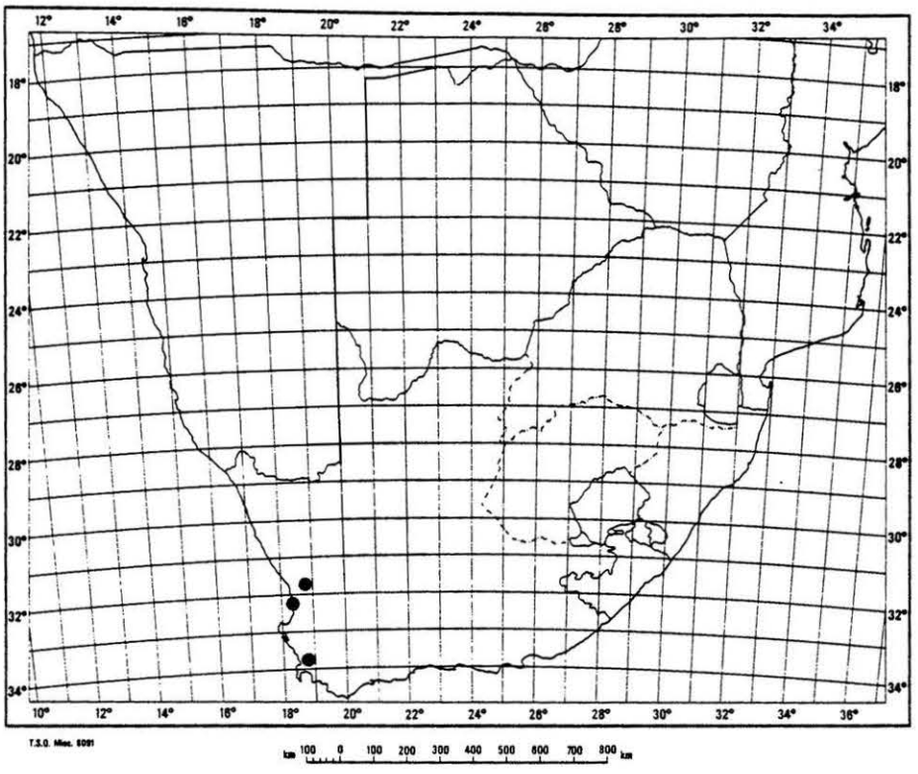
MAP 24.— Distribution of *Riccia namaquensis*.



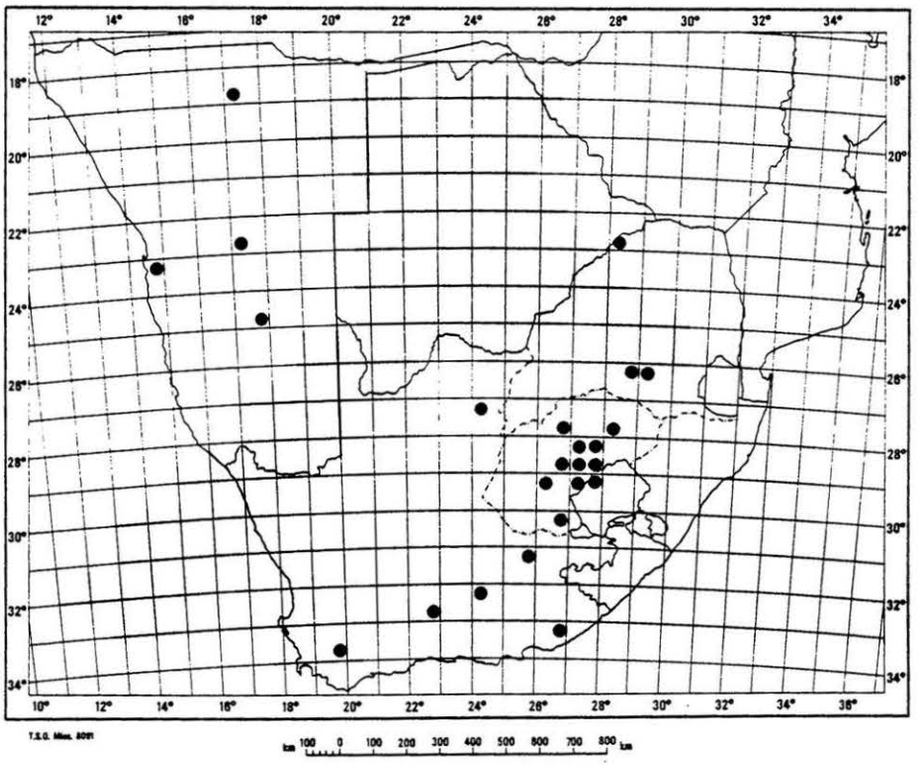
MAP 25.--- Distribution of *Riccia albomarginata*.



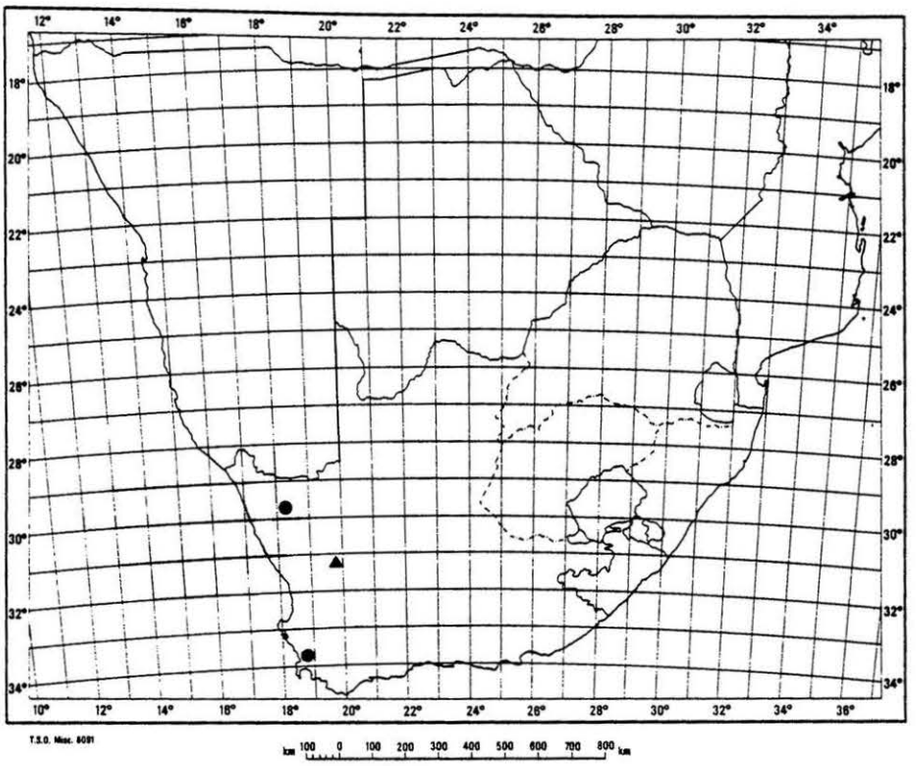
MAP 26.--- Distribution of *Riccia ampullacea*.



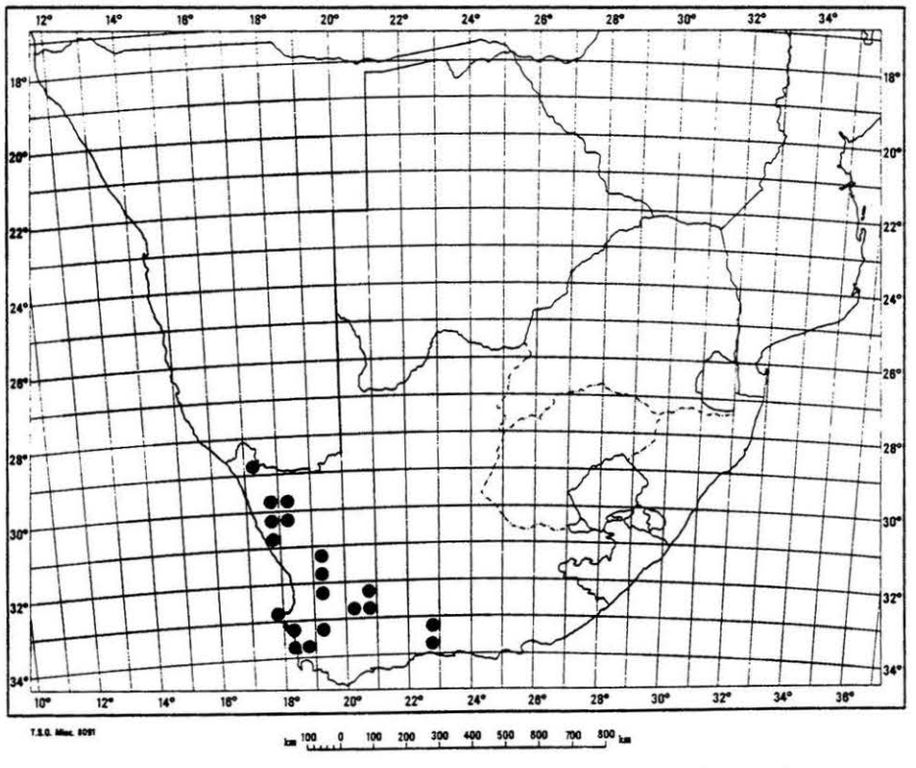
MAP 27.--- Distribution of *Riccia parvo-areolata*.



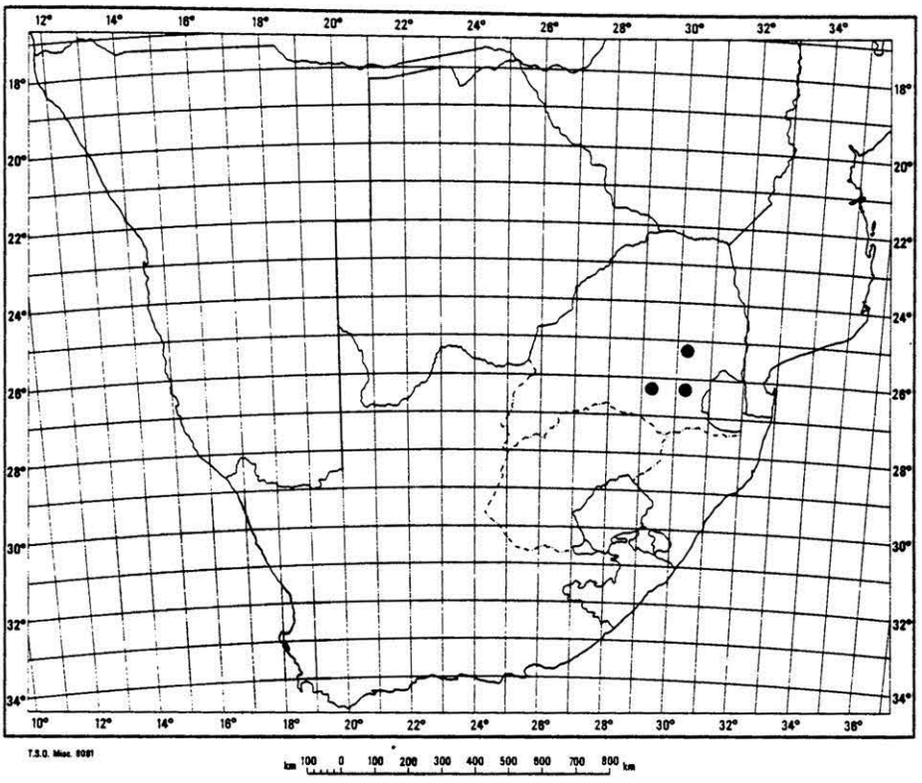
MAP 28.--- Distribution of *Riccia albovestita*.



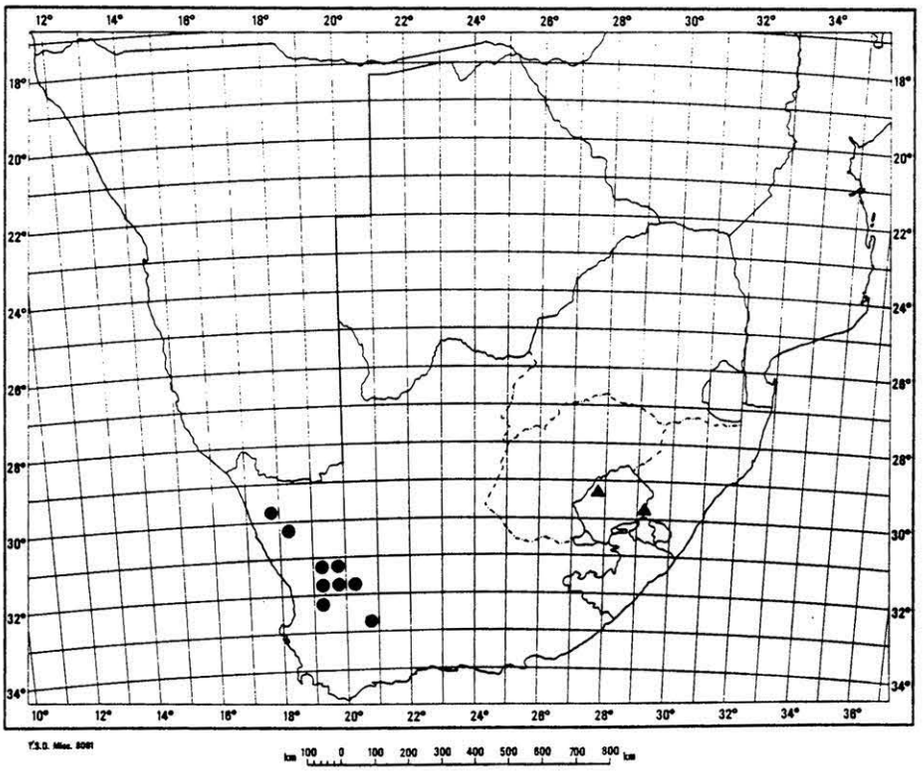
MAP 29.— Distribution of *Riccia alatospora* (dots) and *R. hantamensis* (triangles).



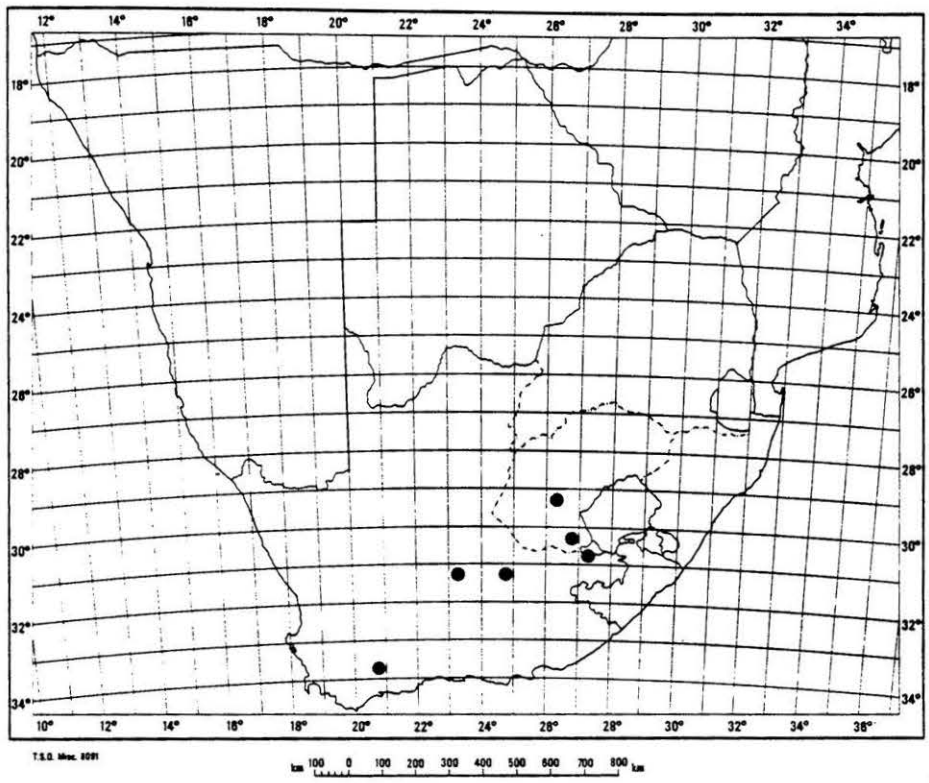
MAP 30.— Distribution of *Riccia concava*.



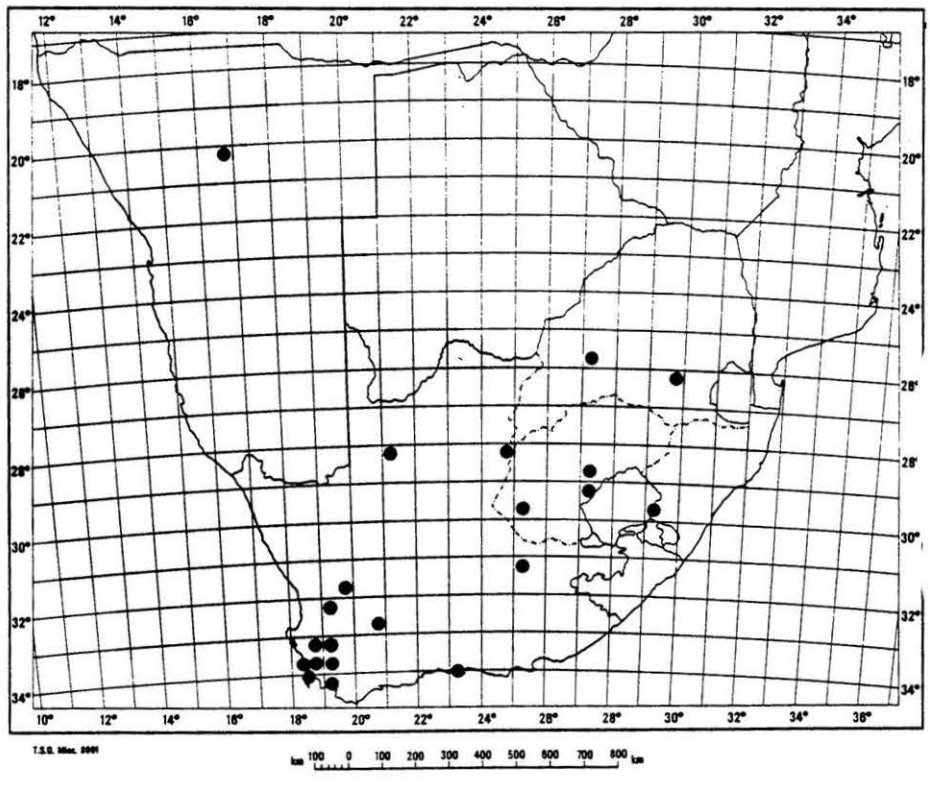
MAP 31.--- Distribution of *Riccia elongata*.



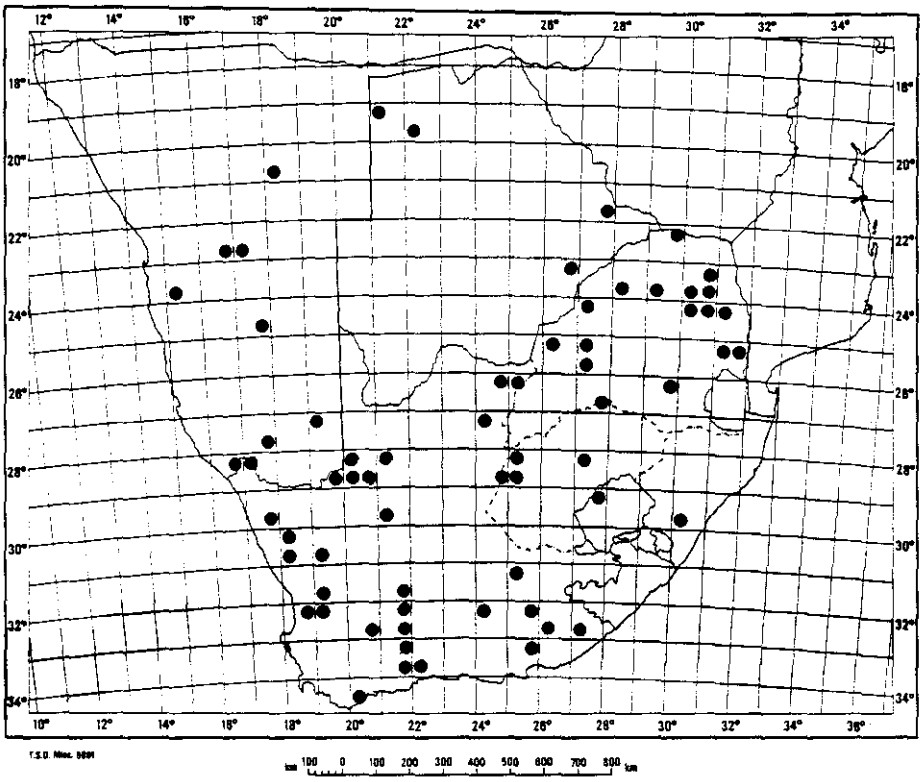
MAP 32.--- Distribution of *Riccia trachyglossum* (triangles) and *R. furfuracea* (dots).



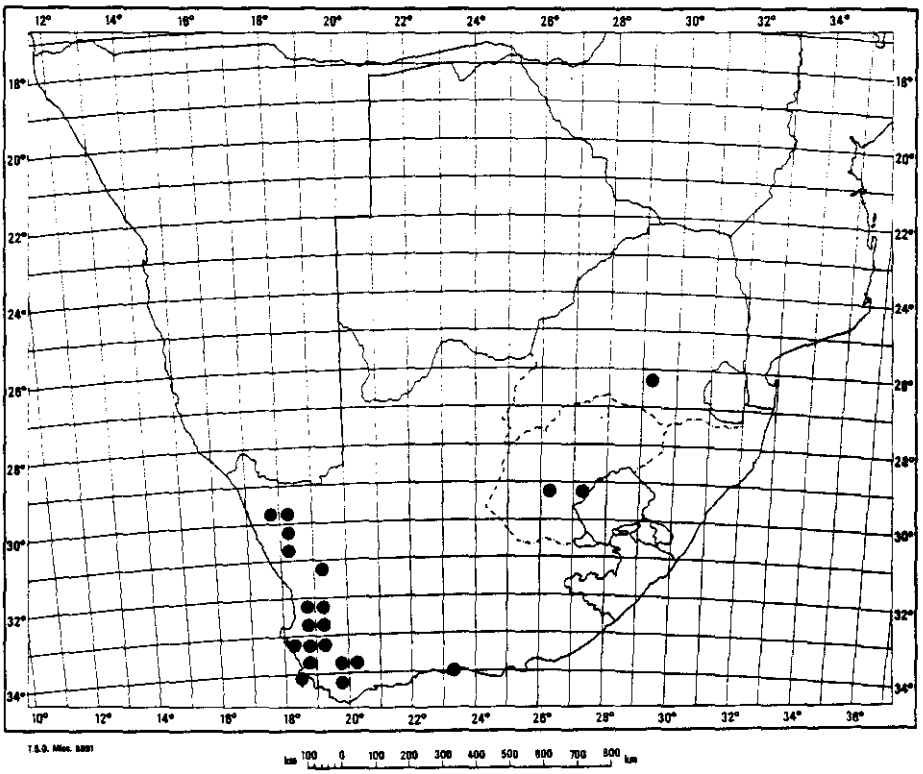
MAP 33.— Distribution of *Riccia pulveracea*.



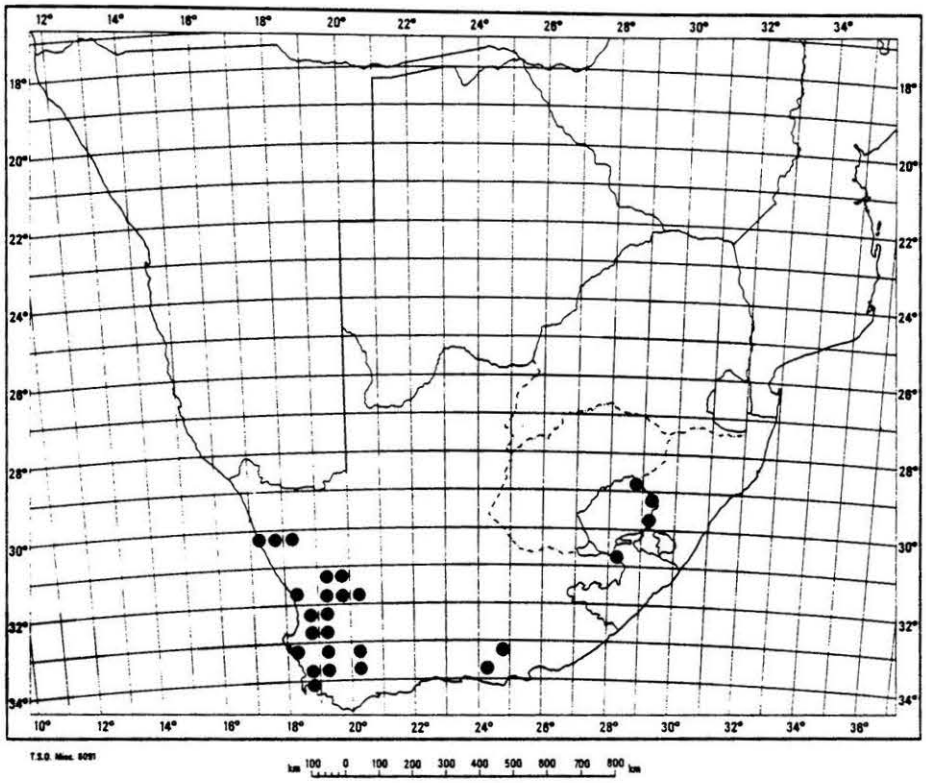
MAP 34.— Distribution of *Riccia crystallina* in southern Africa.



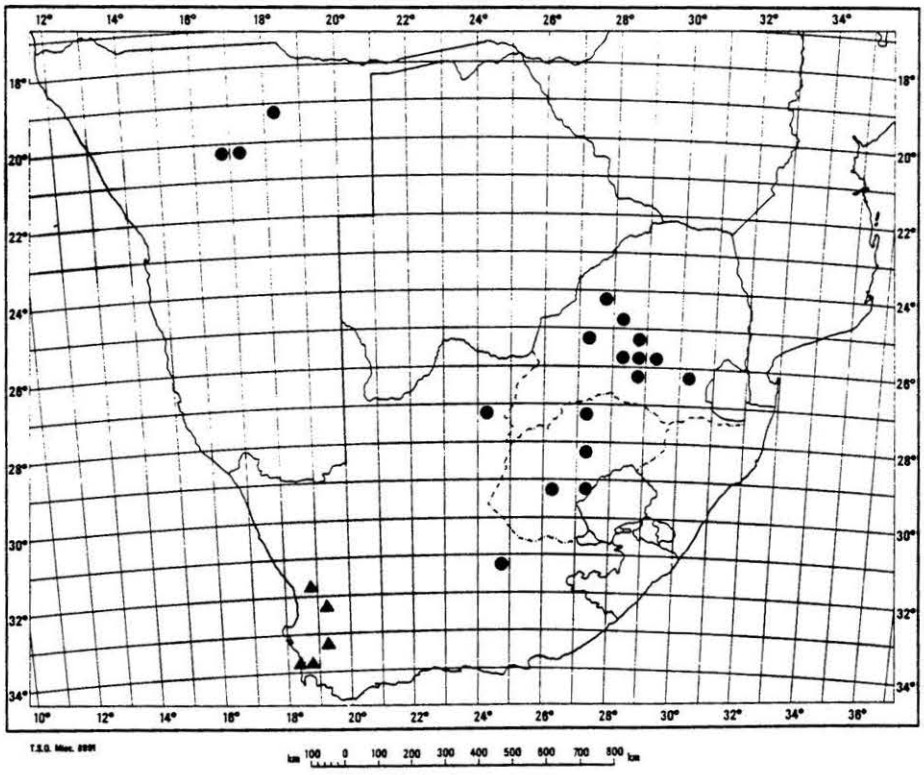
MAP 35.— Distribution of *Riccia cavernosa* in southern Africa.



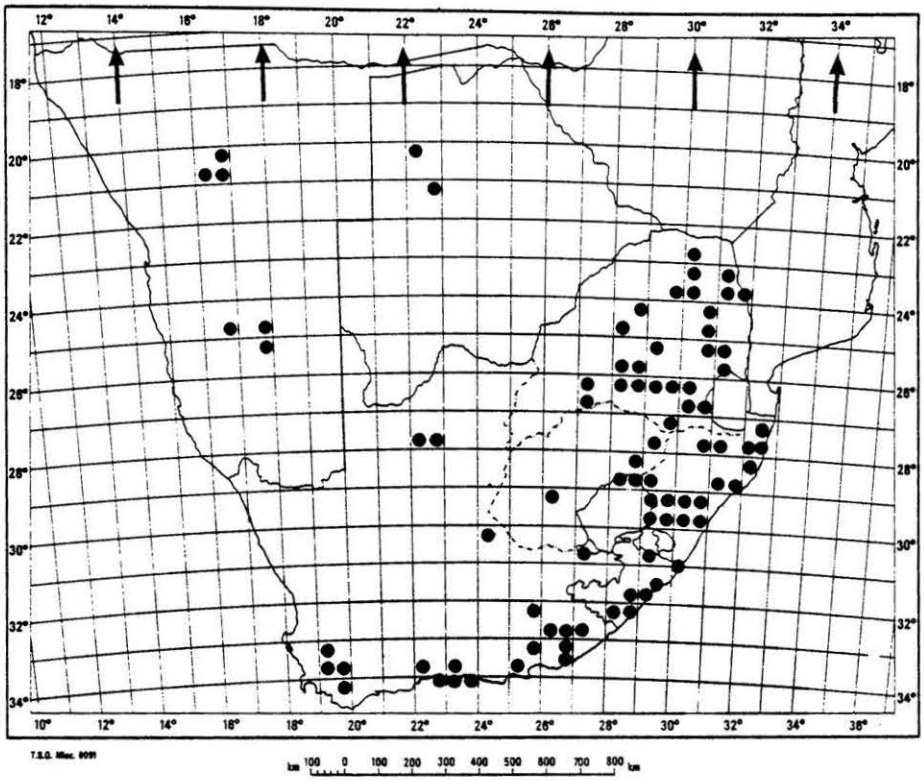
MAP 36.— Distribution of *Riccia cupulifera*.



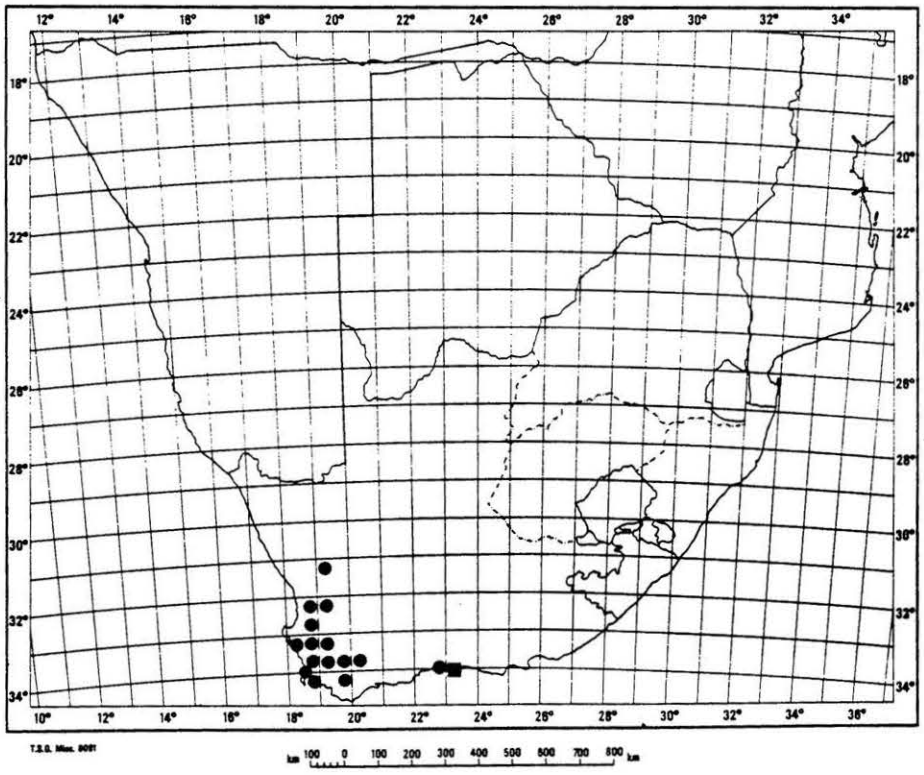
MAP 37.--- Distribution of *Riccia bullosa*.



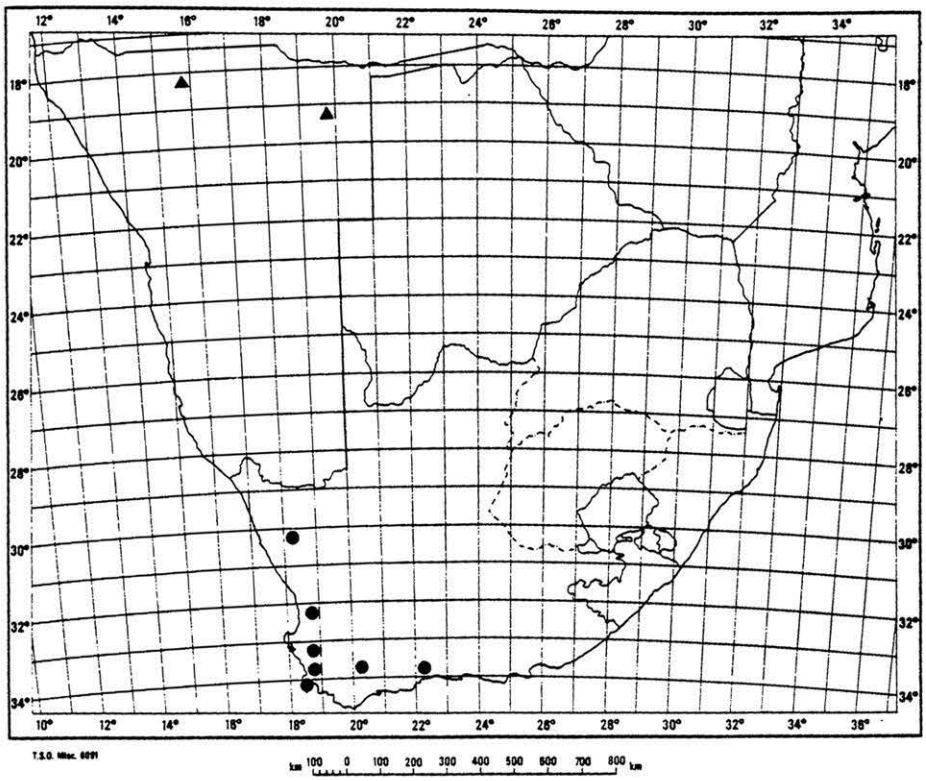
MAP 38.--- Distribution of *Riccia garsidei* (triangles) and *R. volkii* (dots).



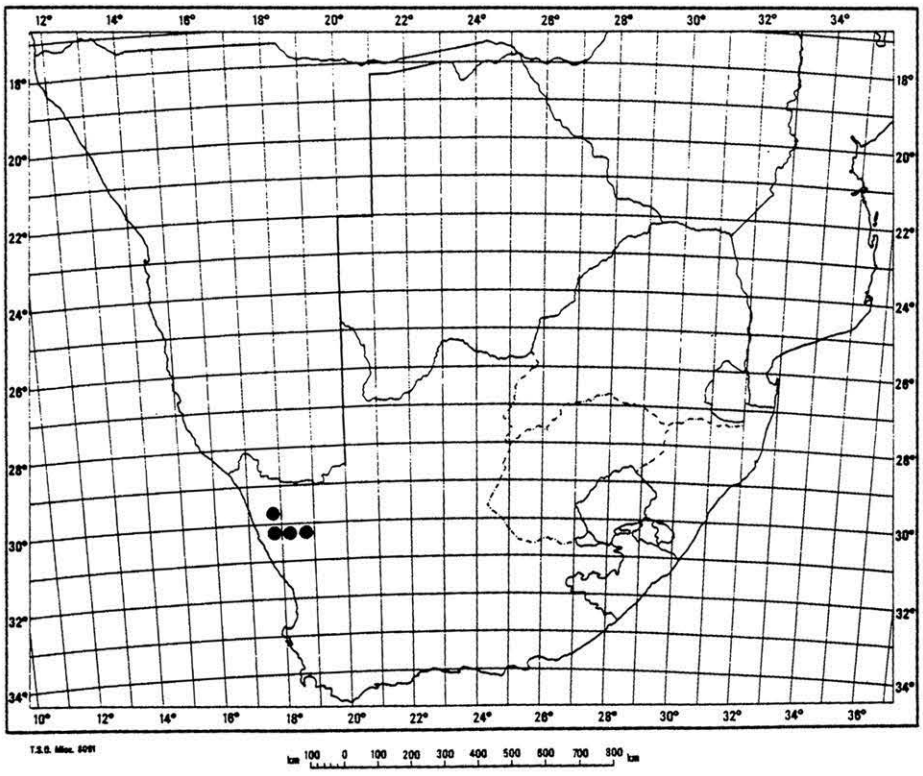
MAP 39.— Distribution of *Riccia stricta* in southern Africa.



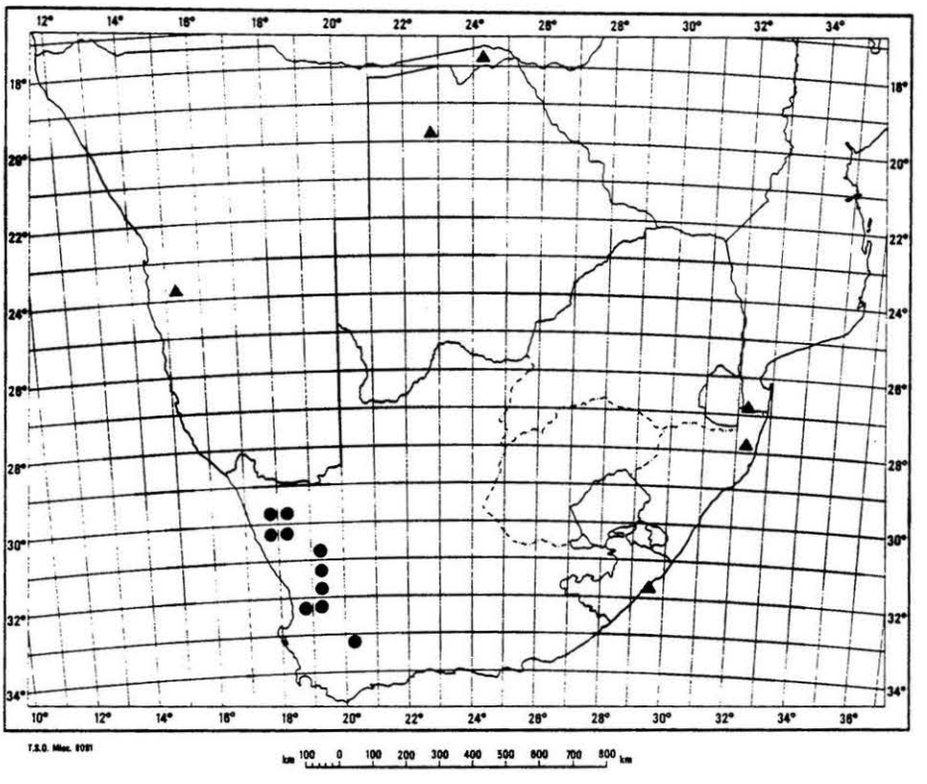
MAP 40.— Distribution of *Riccia rubricollis* (square) and *R. purpurascens* (dots).



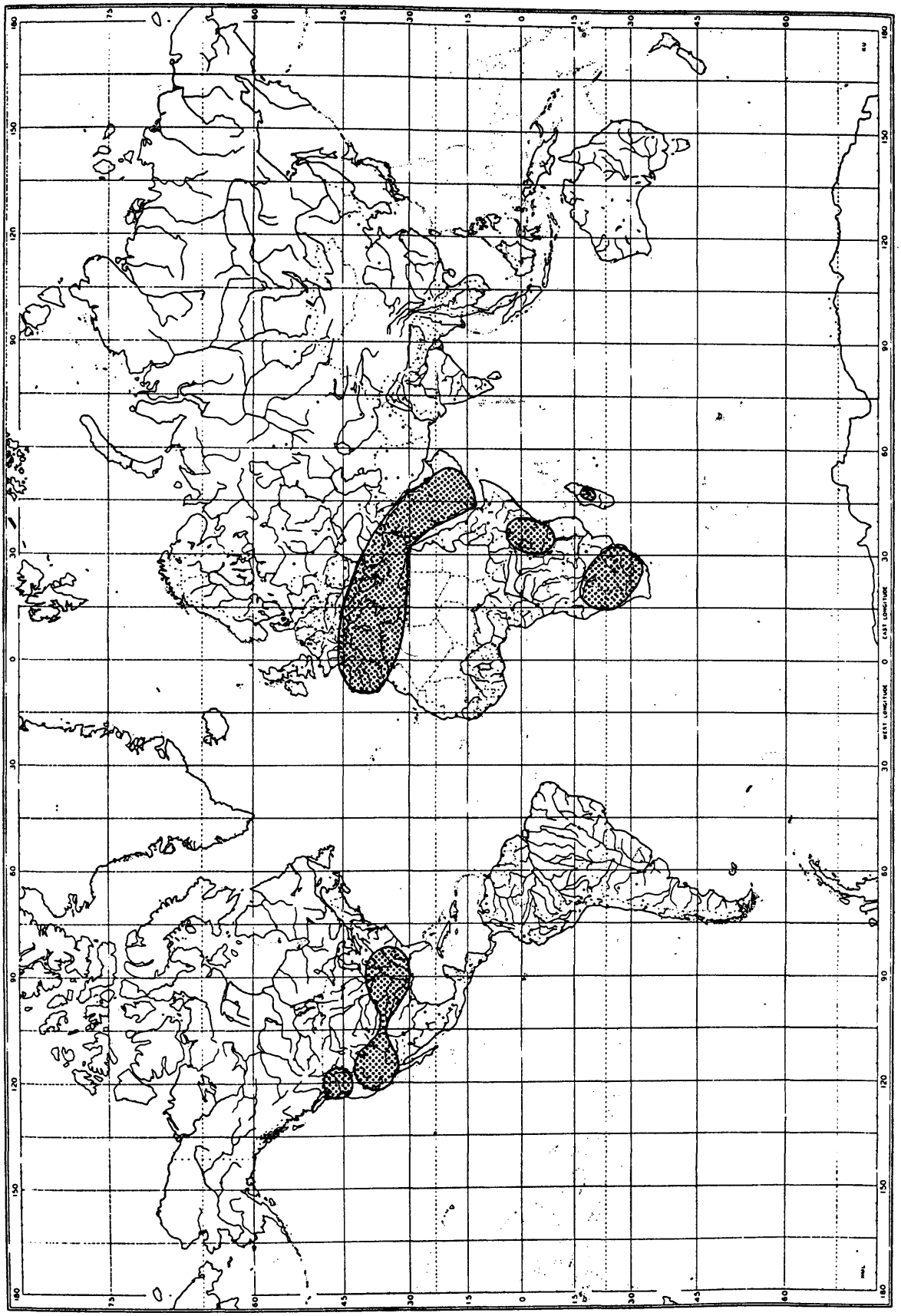
MAP 41.--- Distribution of *Riccia curtisii* (dots) and *R. perssonii* (triangles) in southern Africa.



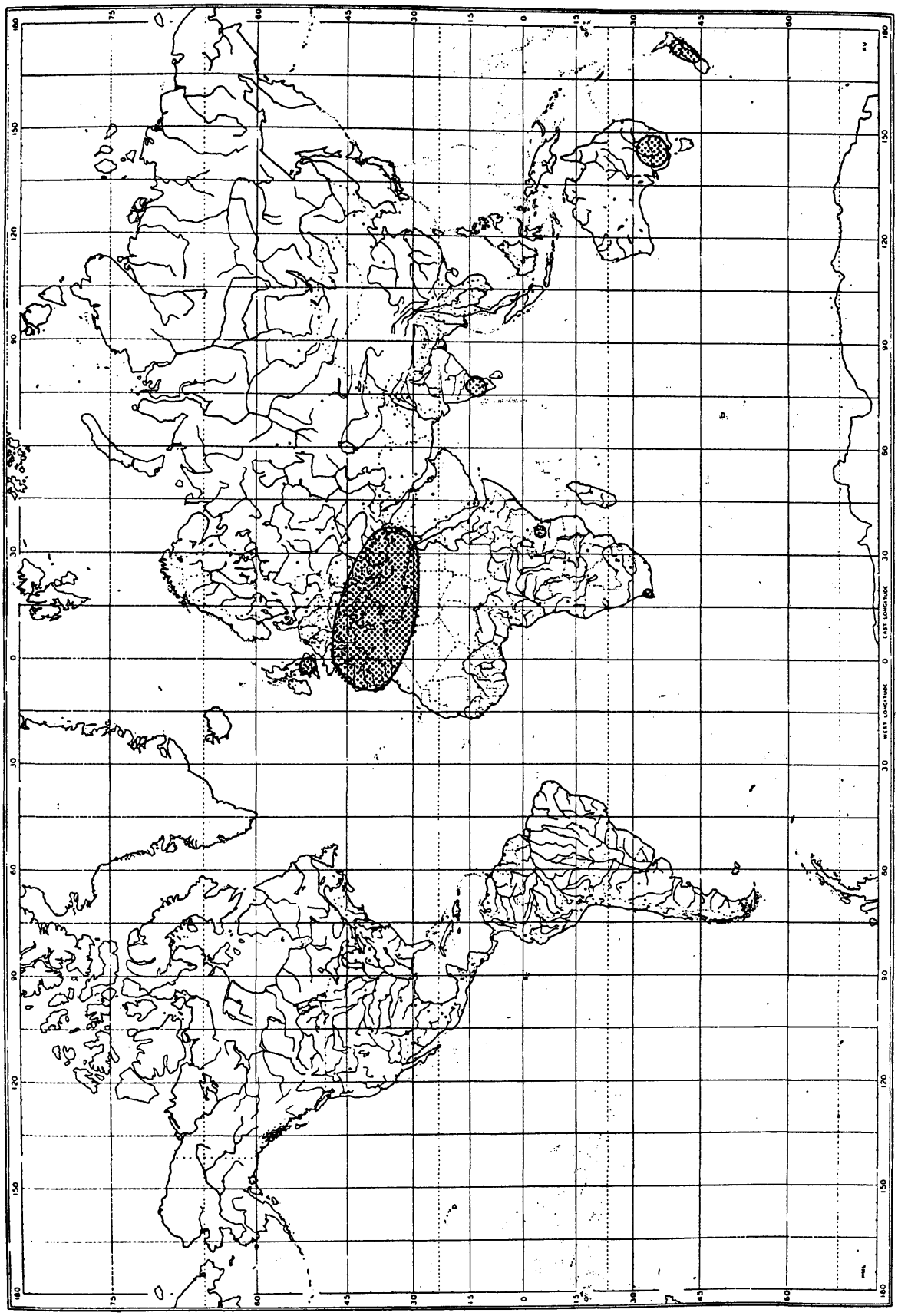
MAP 42.--- Distribution of *Riccia tomentosa*.



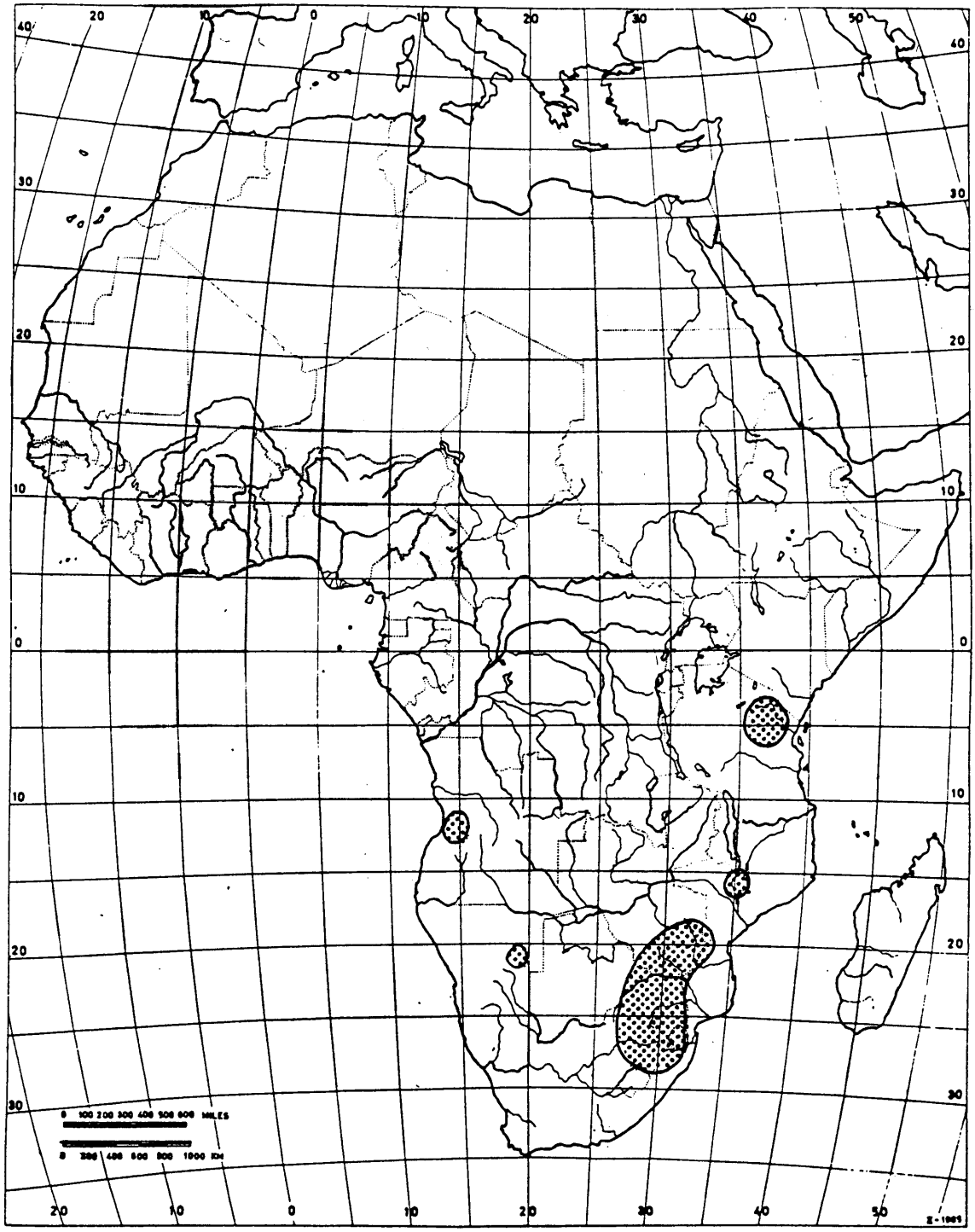
MAP 43.— Distribution of *Riccia schelpei* (dots) and *Ricciocarpos natans* (triangles) in southern Africa.



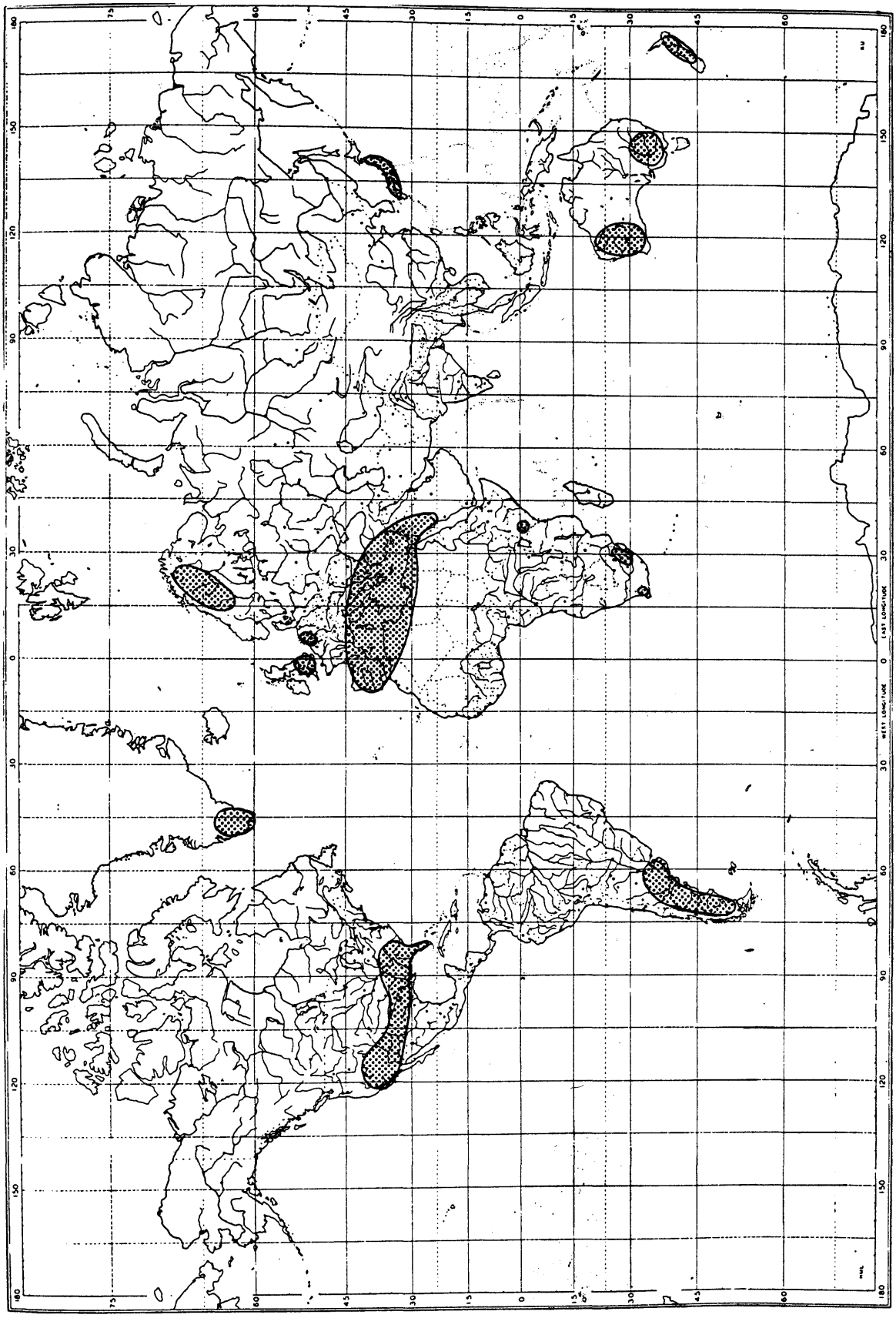
MAP 44.— Known distribution range of *Riccia trichocarpa*.



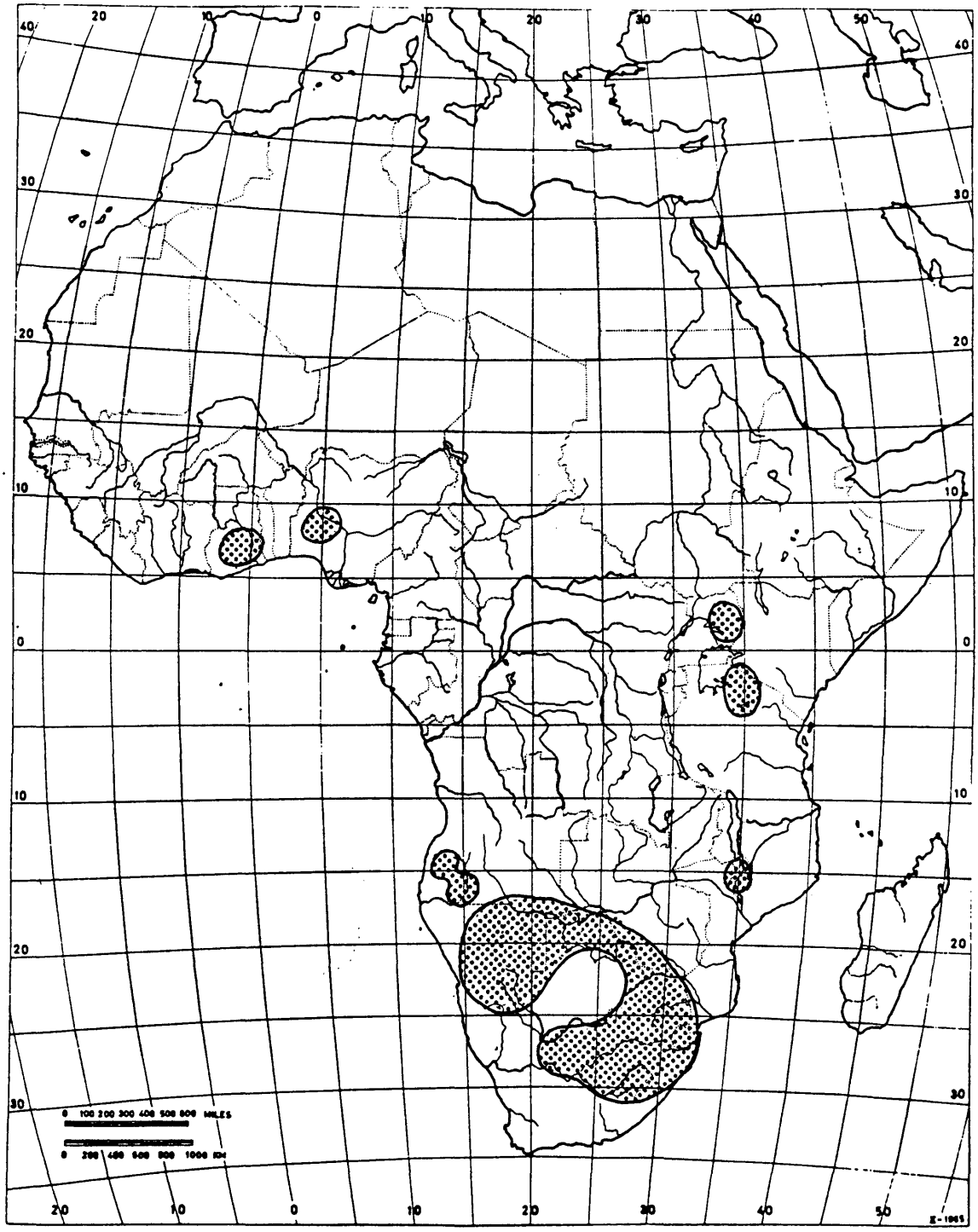
MAP 45.— Known distribution range of *Riccia crozalsii*.



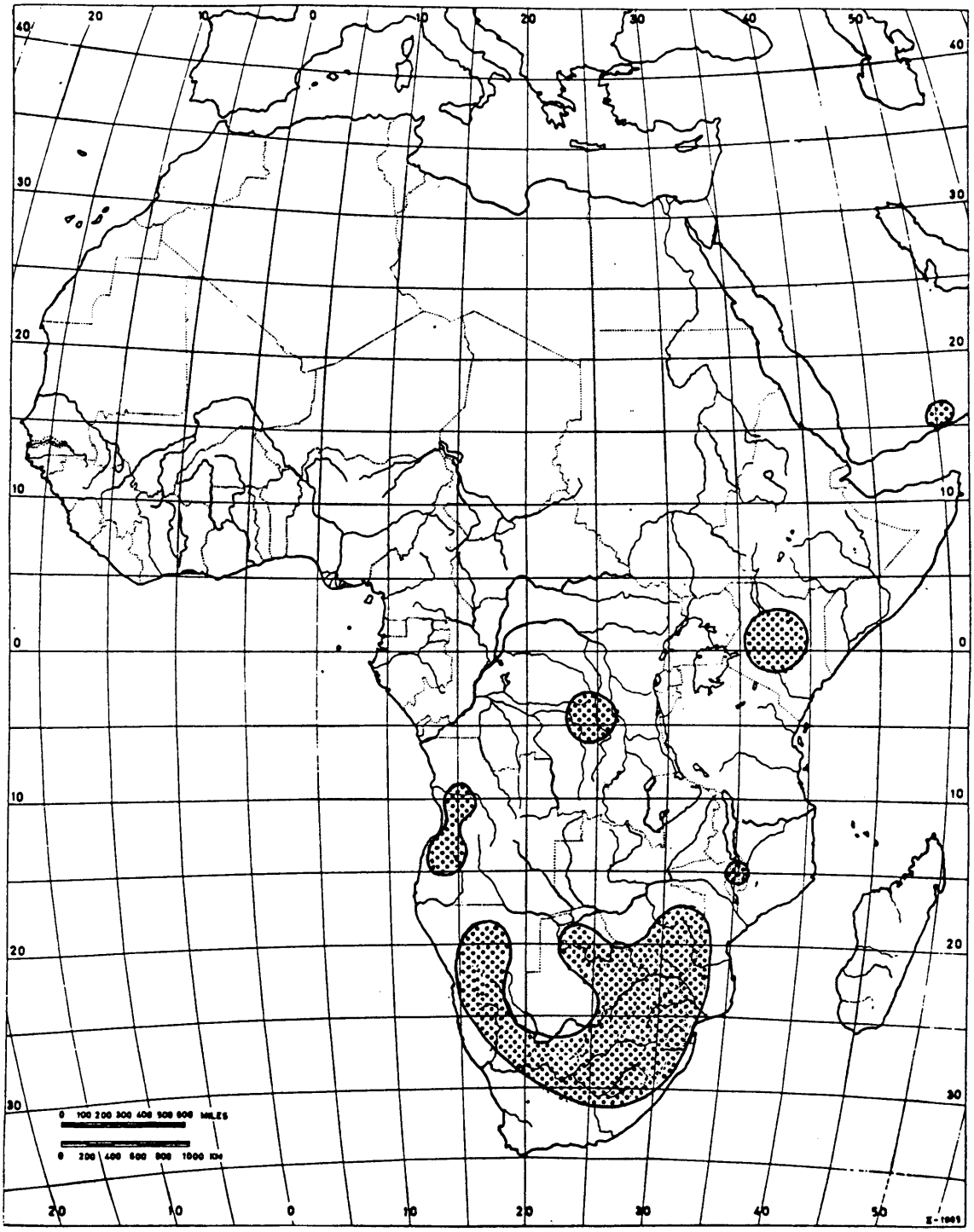
MAP 46.— Known distribution range of *Riccia microciliata*.



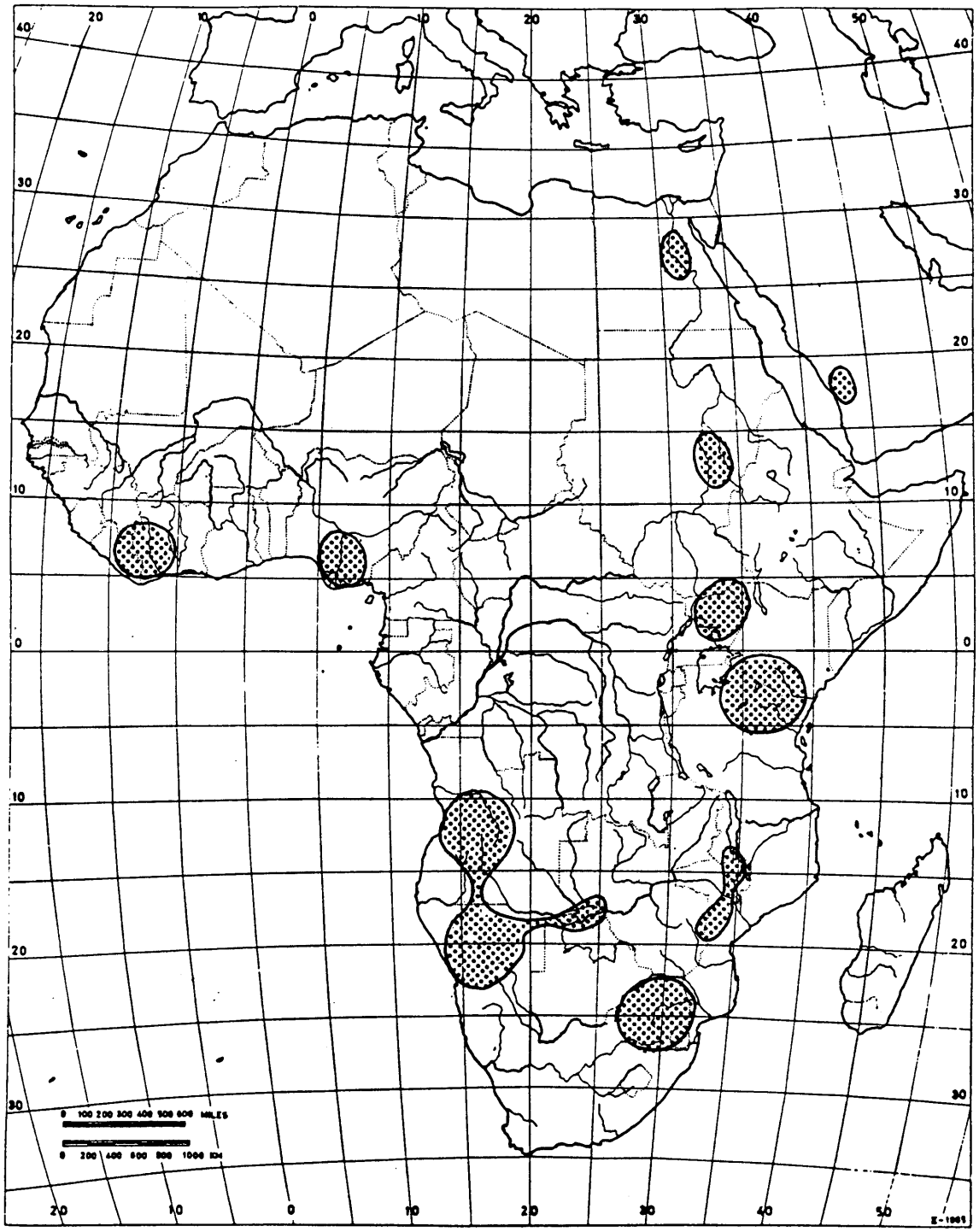
MAP 47.--- Known distribution range of *Riccia sorocarpa*.



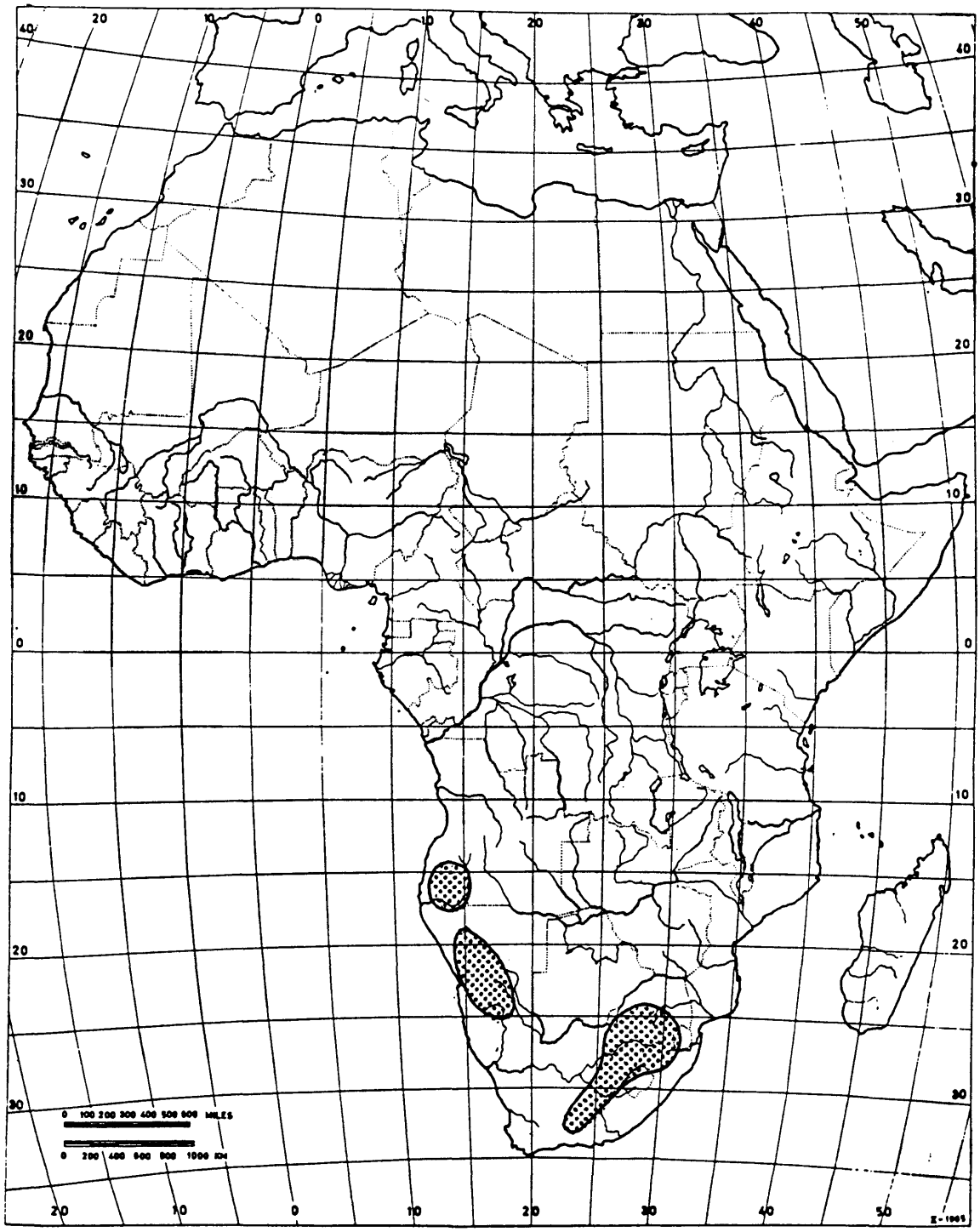
MAP 48.— Known distribution range of *Riccia atropurpurea*.



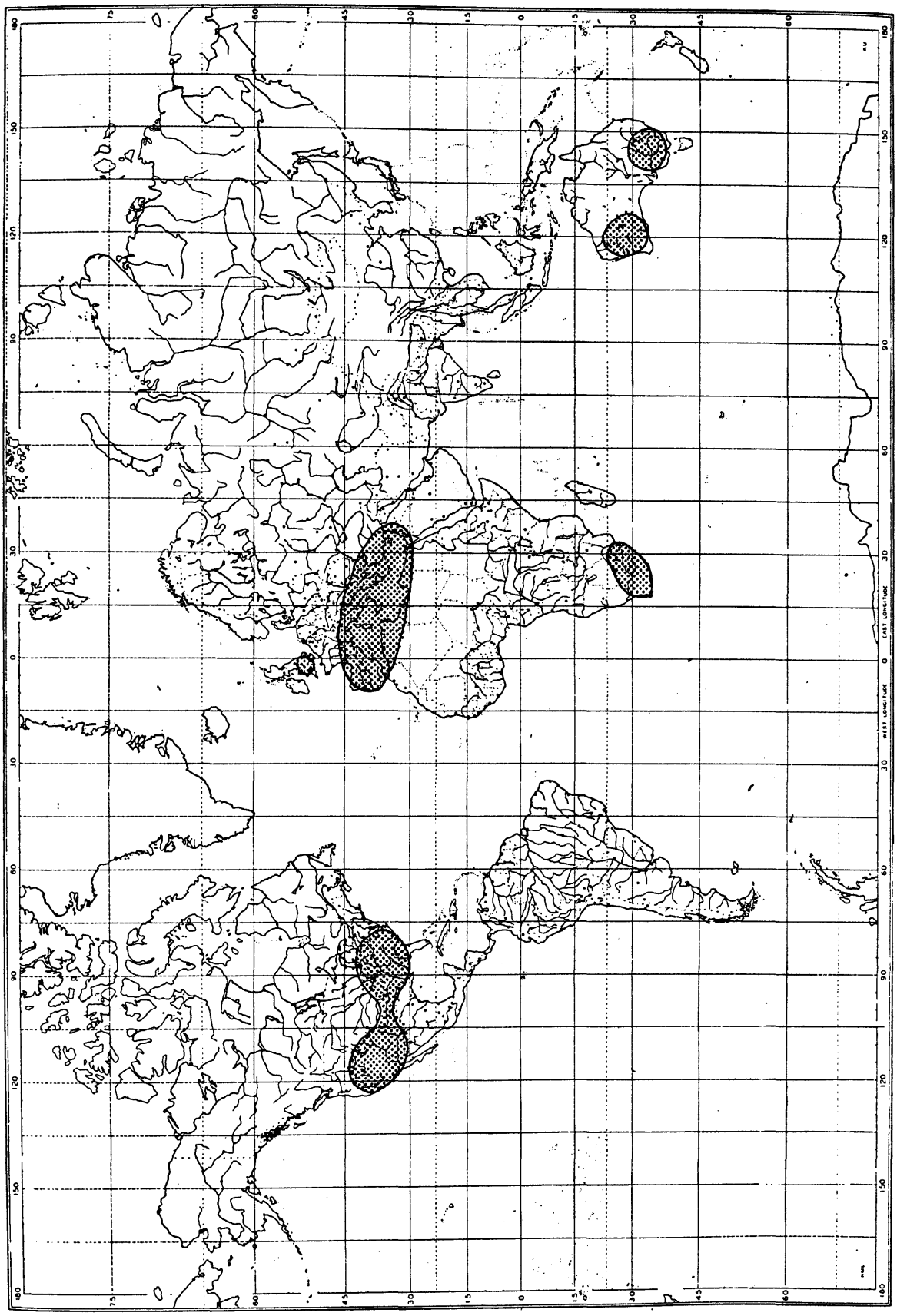
MAP 49.— Known distribution range of *Riccia okahandjana*.



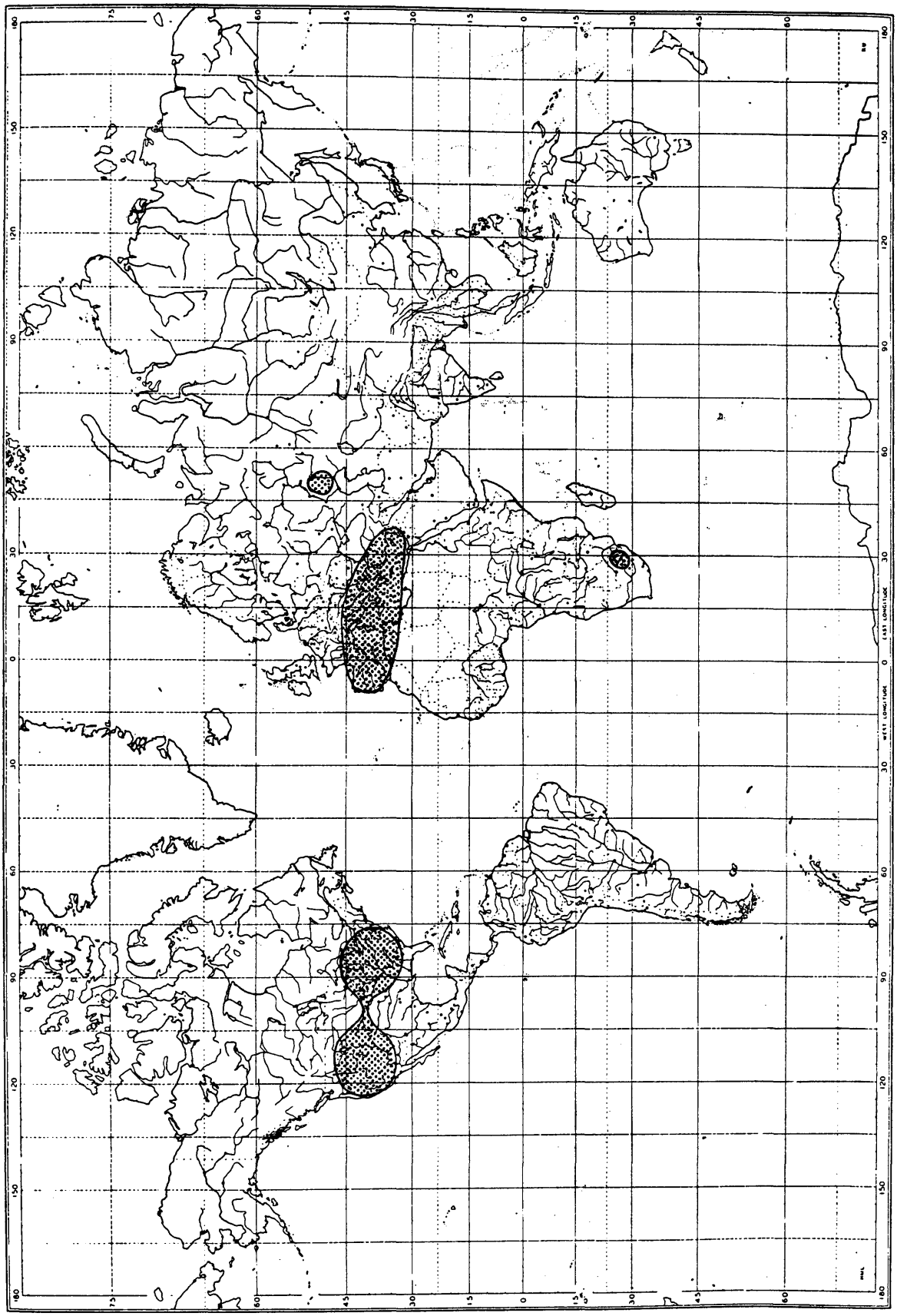
MAP 50.--- Known distribution range of *Riccia congoana*.



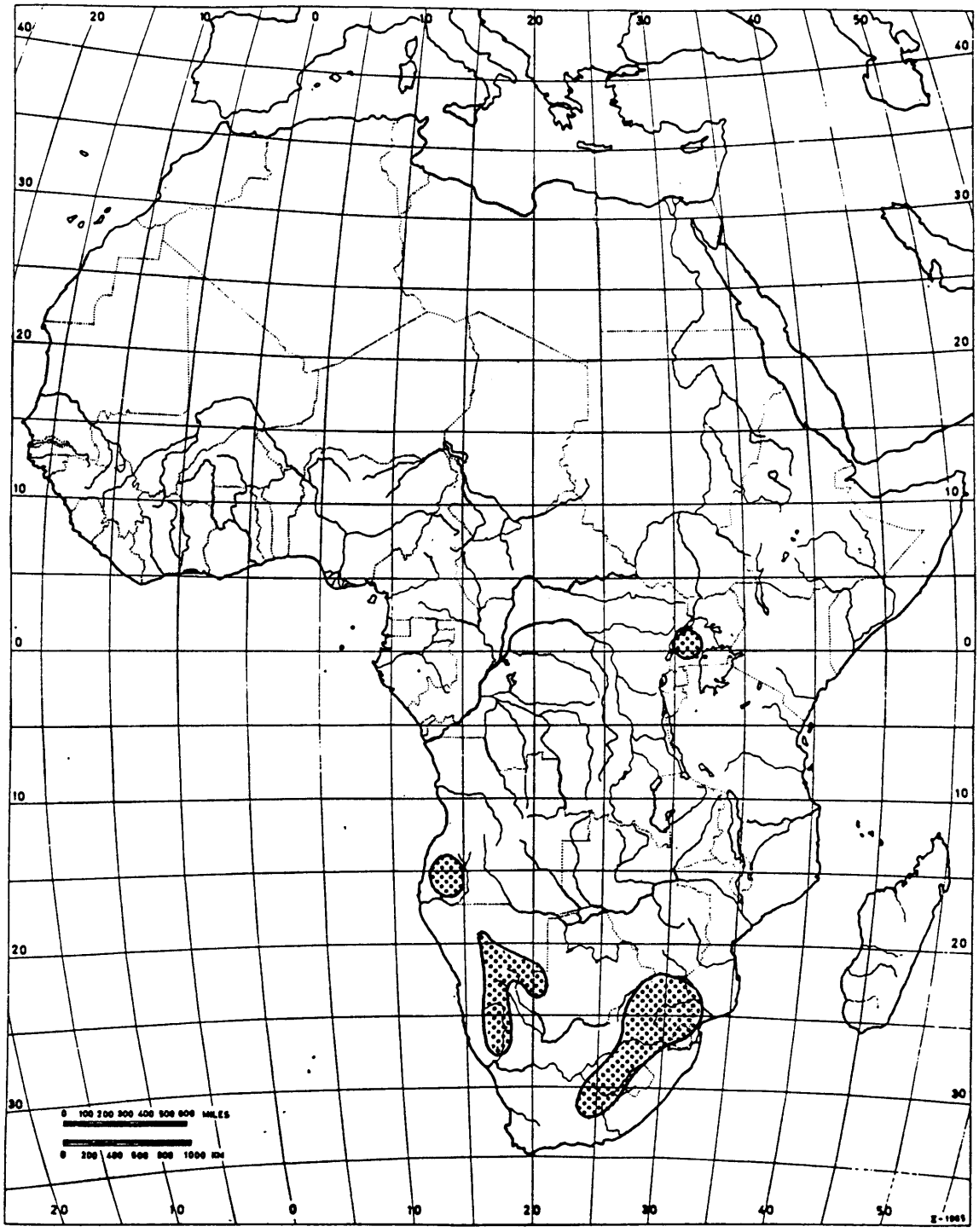
MAP 51.— Known distribution range of *Riccia angolensis*.



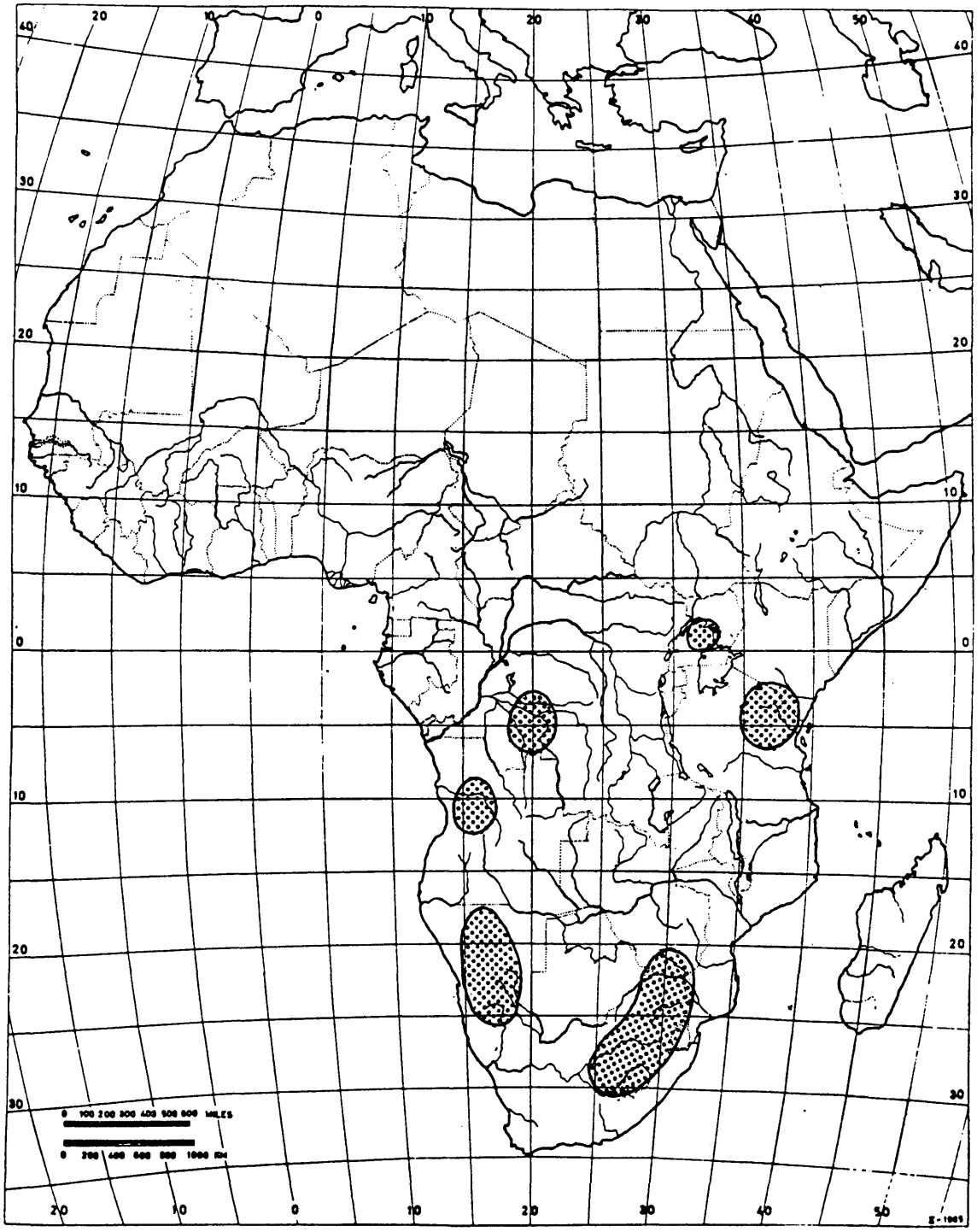
MAP 52.--- Known distribution range of *Riccia nigrella*.



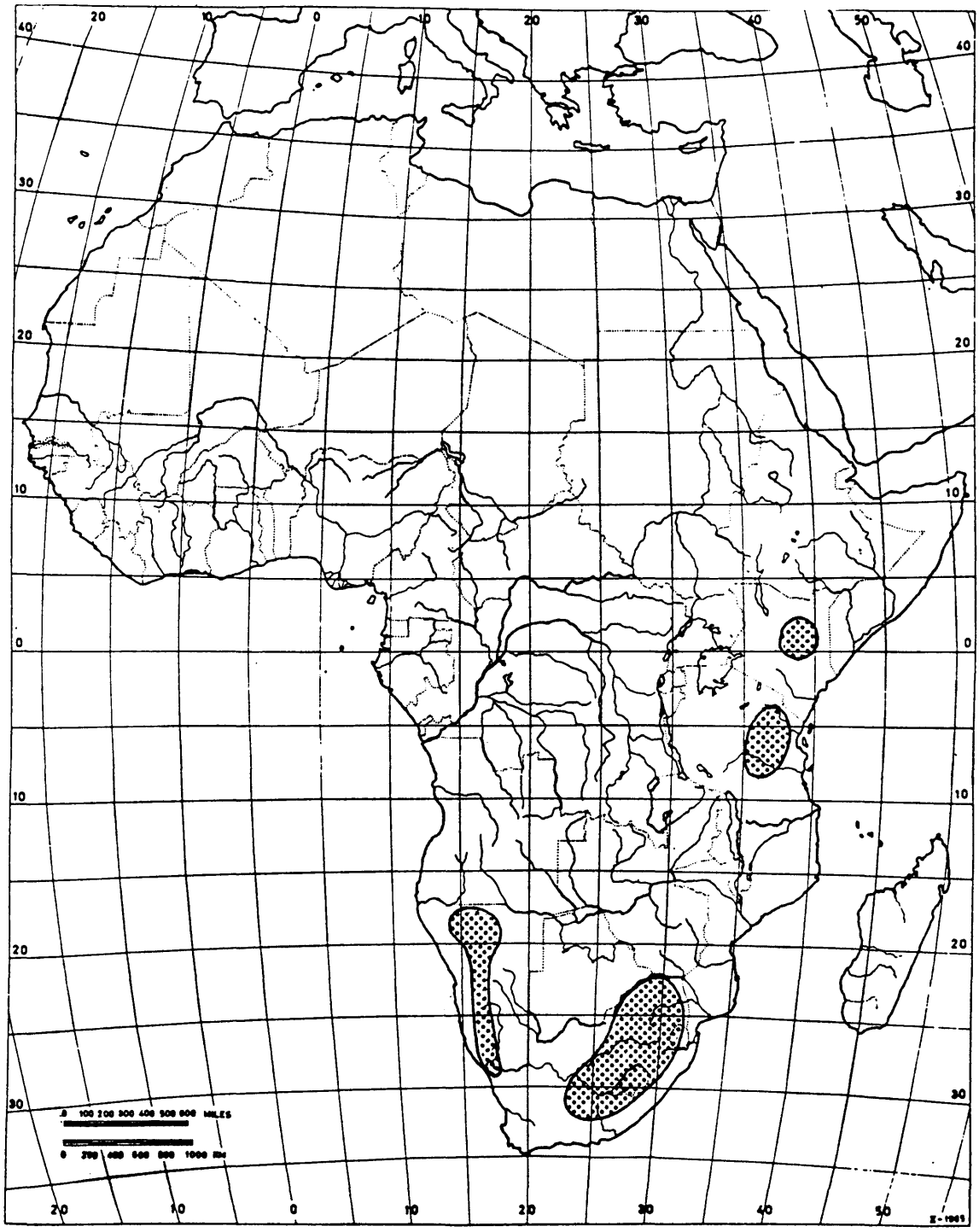
MAP 53.— Known distribution range of *Riccia macrocarpa*.



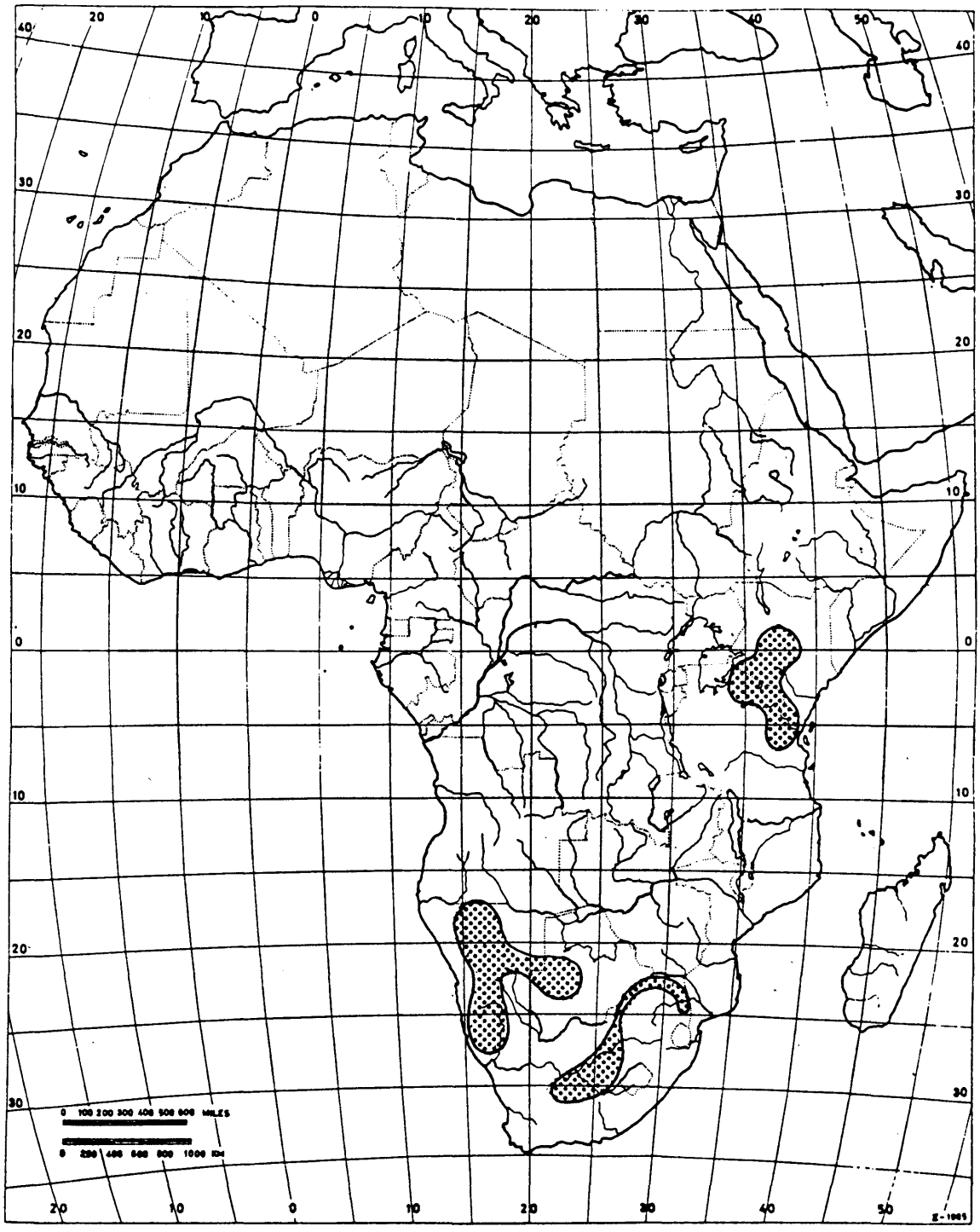
MAP 54.--- Known distribution range of *Riccia runssorensis*.



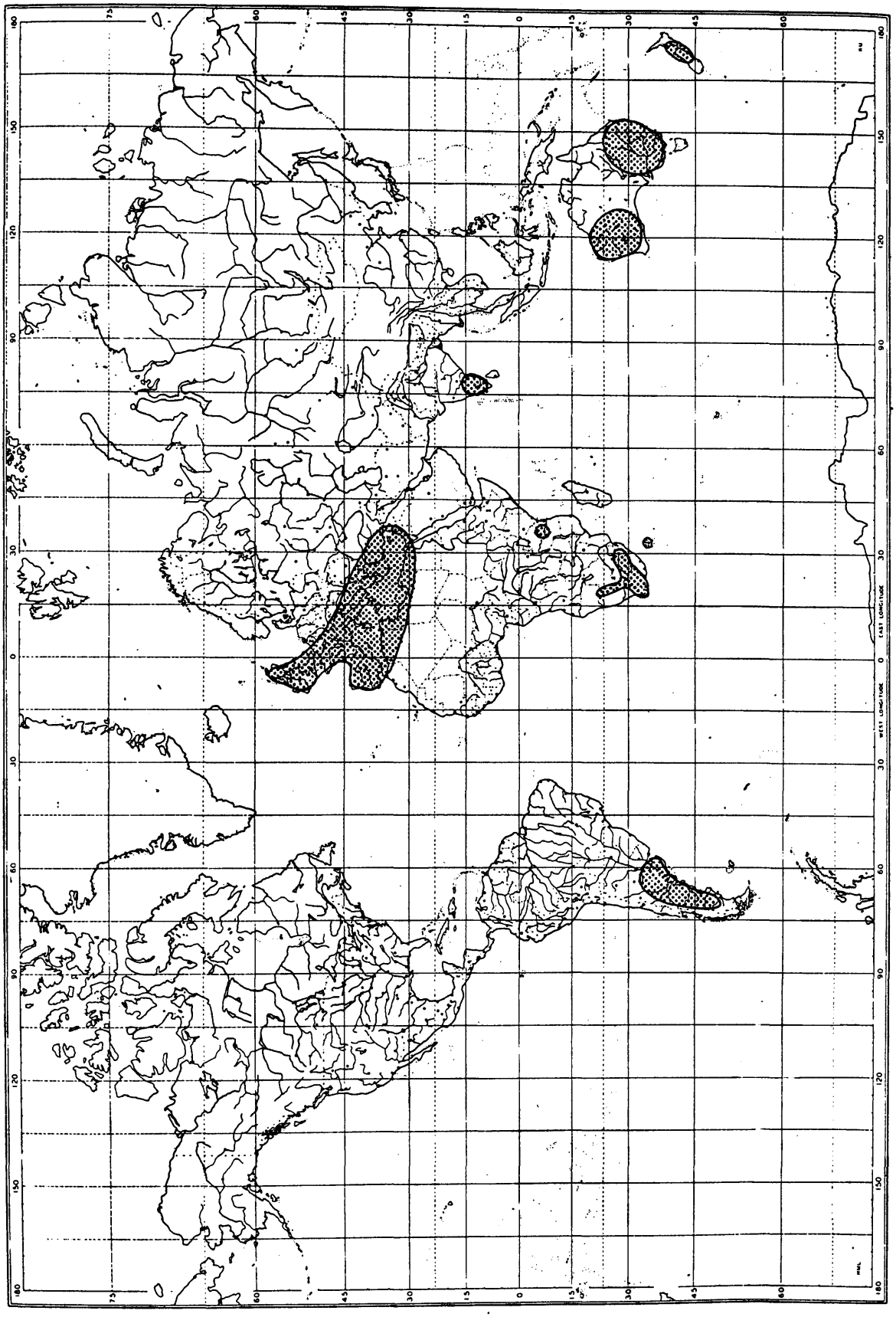
MAP 55.— Known distribution range of *Riccia rosea*.



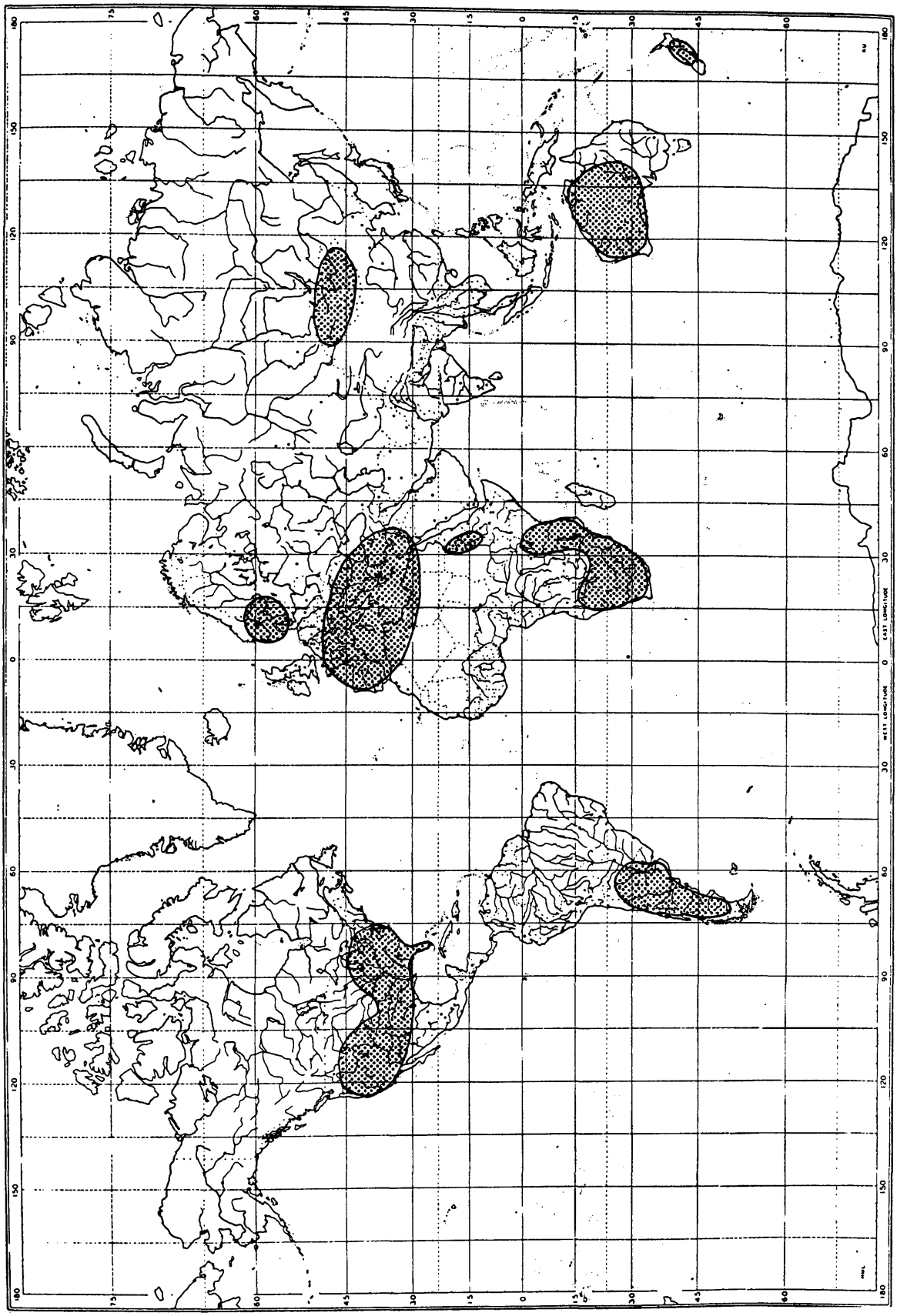
MAP 56.— Known distribution range of *Riccia albolimbata*.



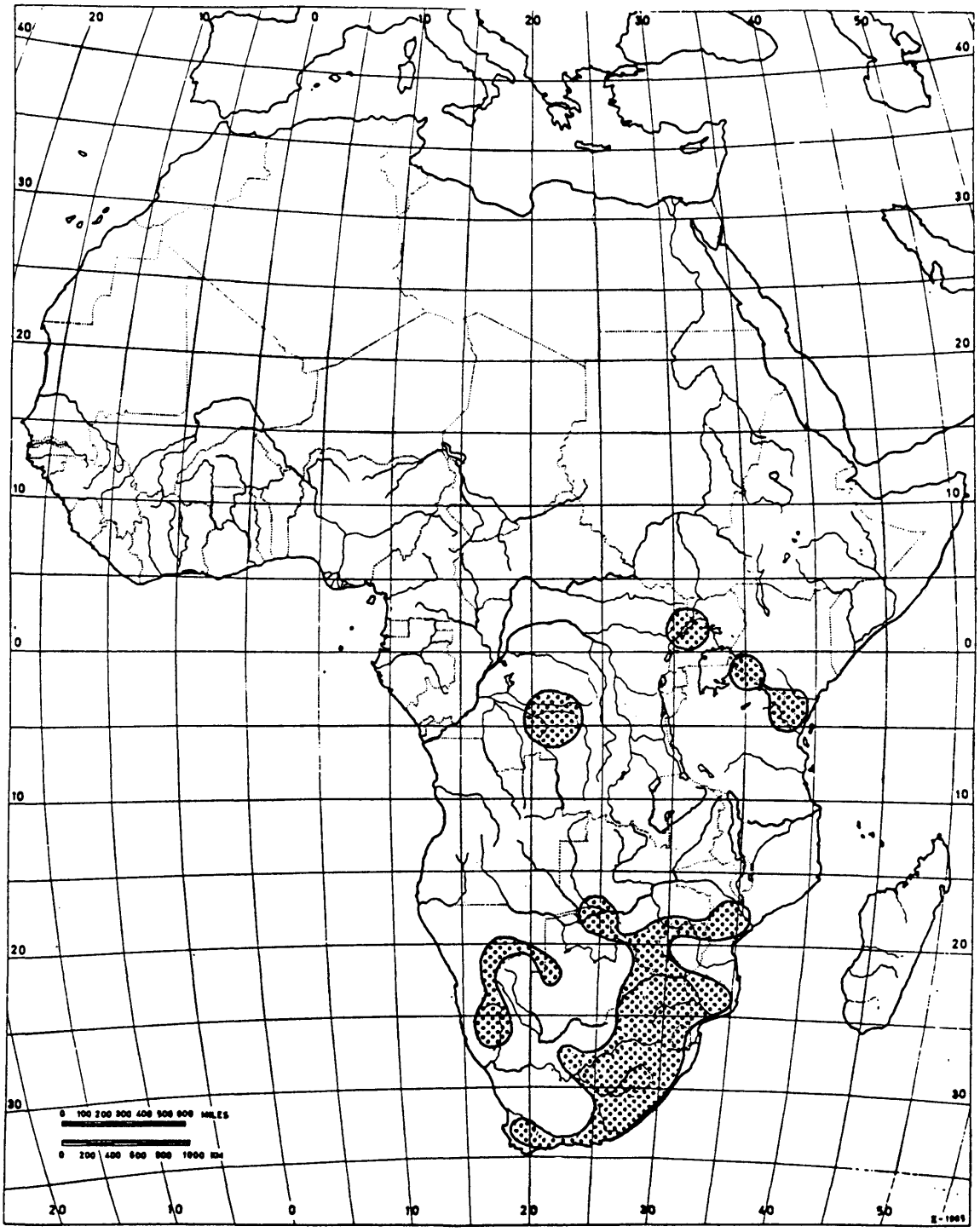
MAP 57.— Known distribution range of *Riccia argenteolimbata*.



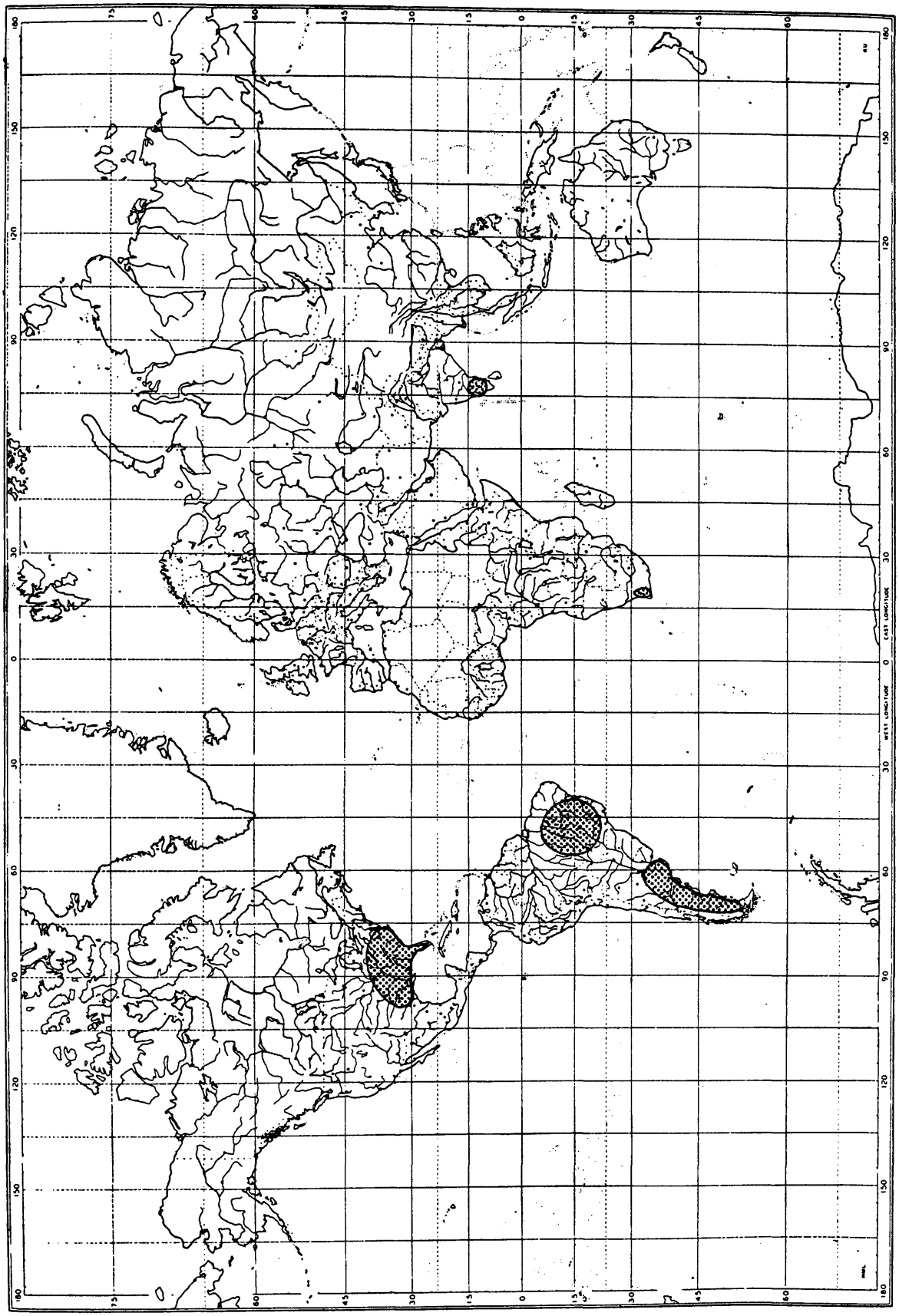
MAP 58.— Known distribution range of *Riccia crystallina*.



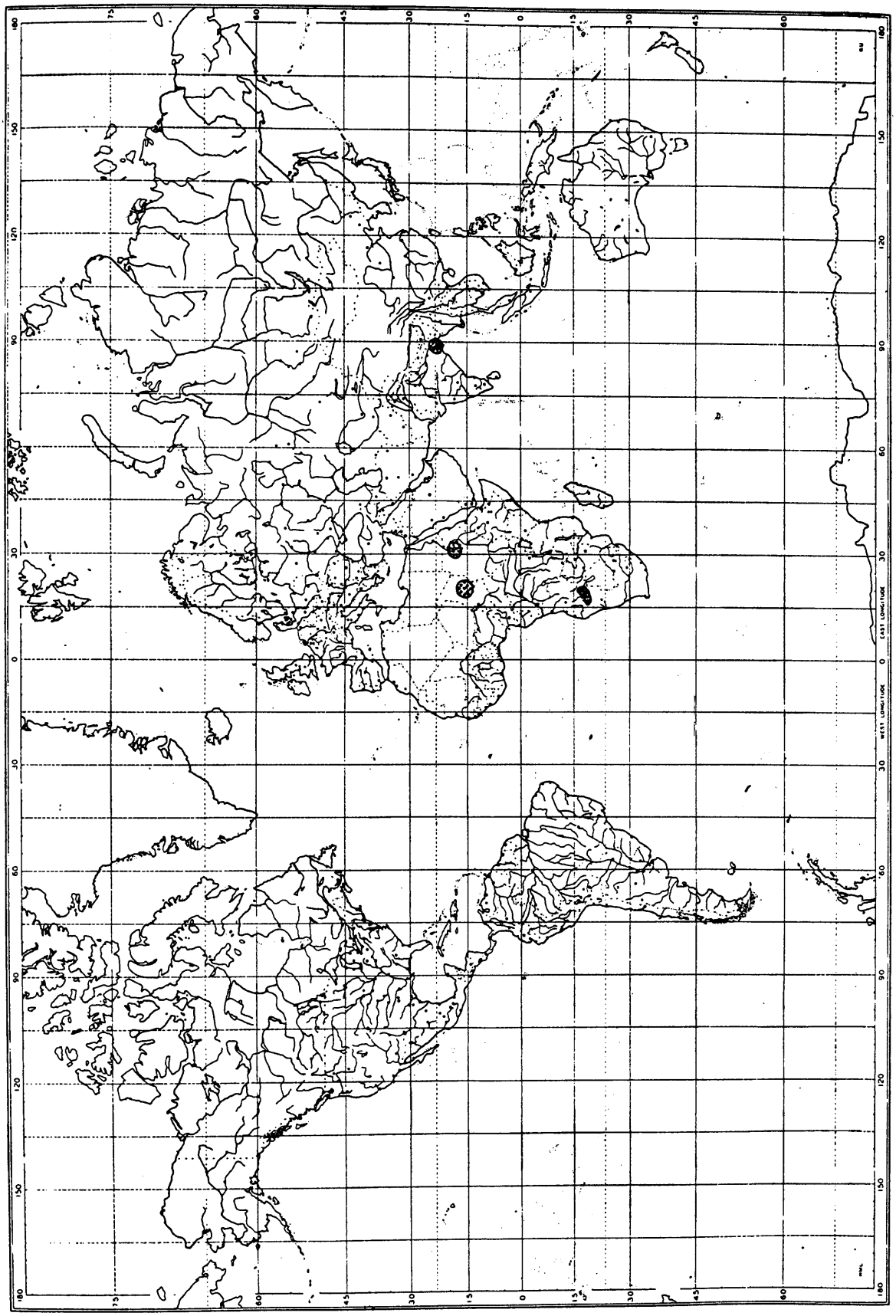
MAP 59.--- Known distribution range of *Riccia cavernosa*.



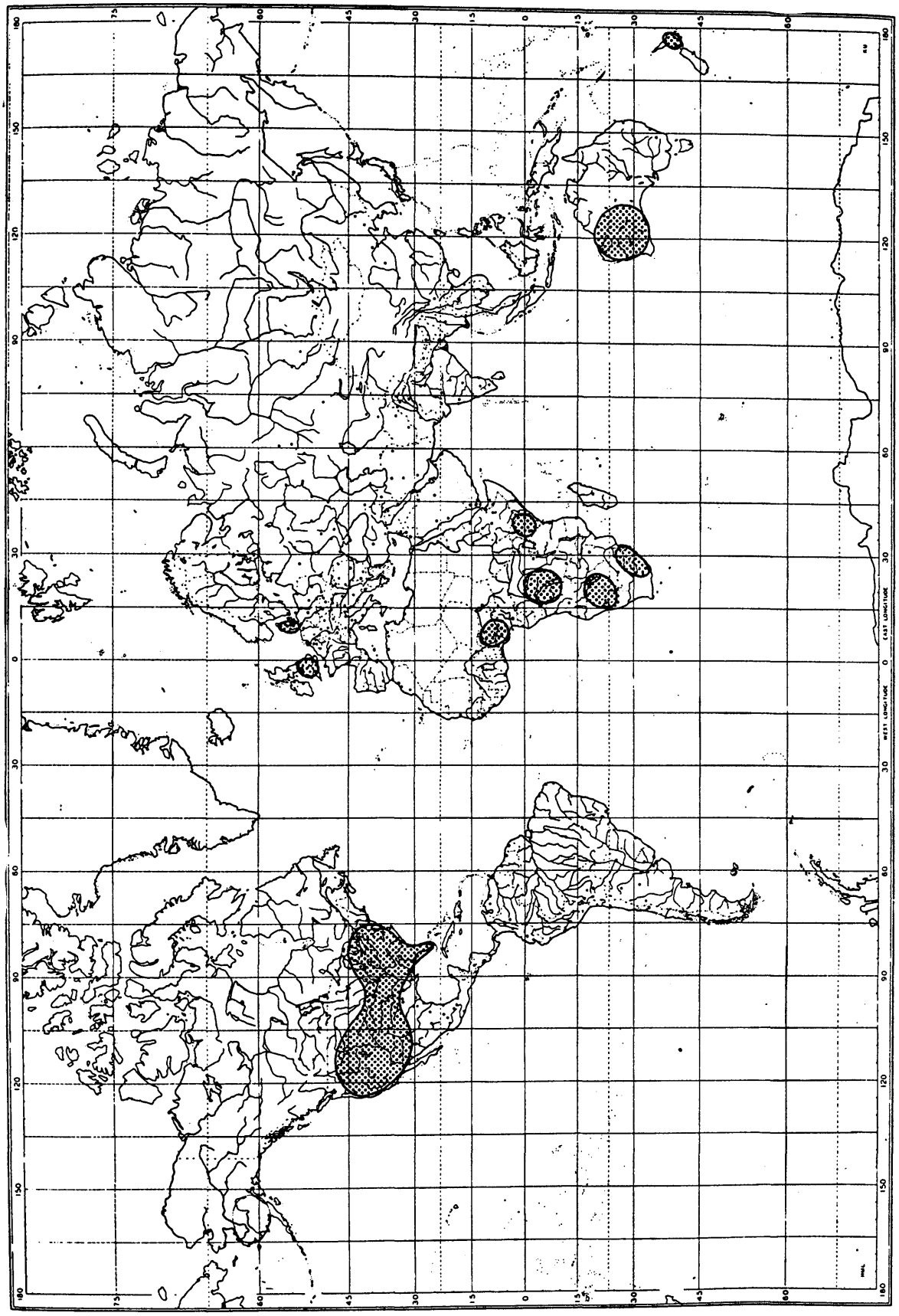
MAP 60.— Known distribution range of *Riccia stricta*.



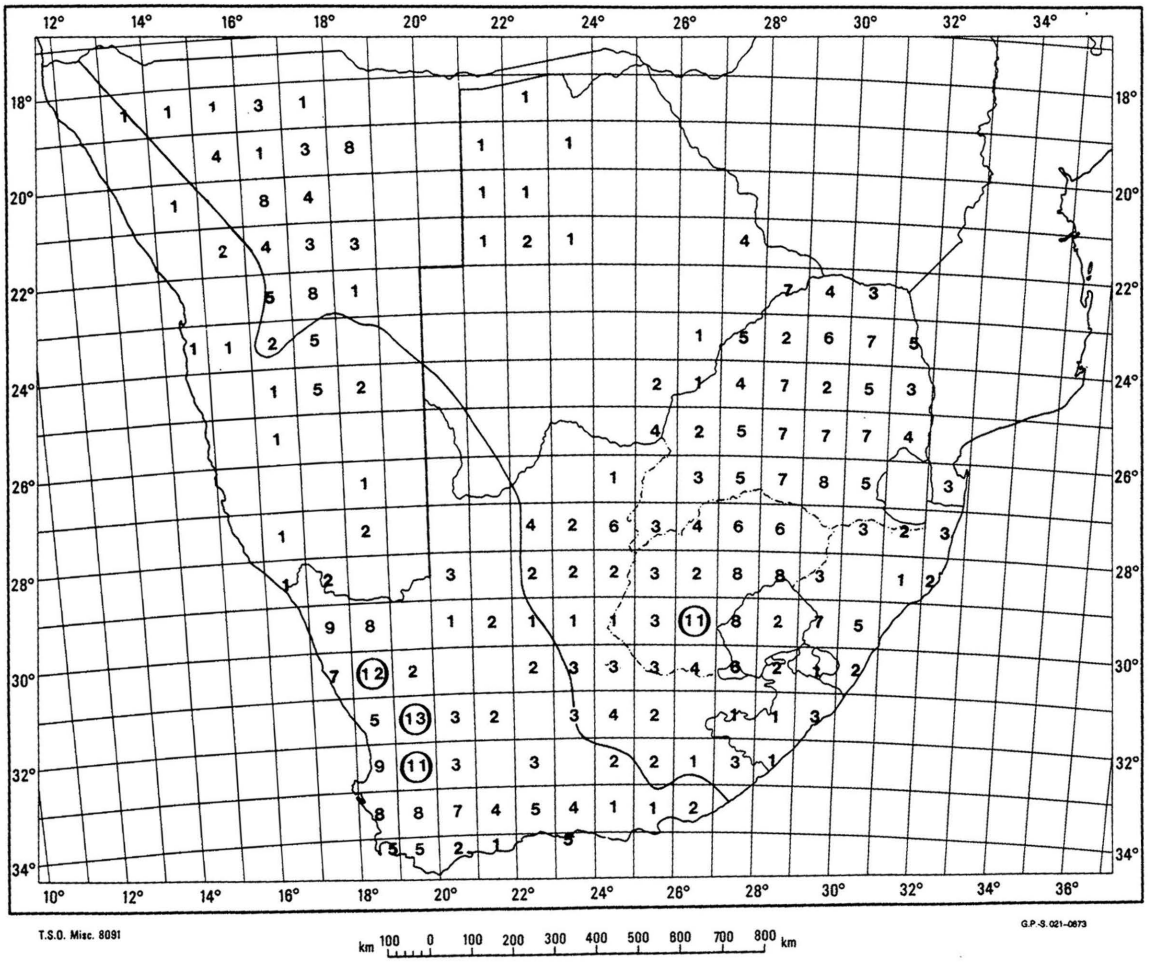
MAP 61.— Known distribution range of *Riccia curtisii*.



MAP 62.— Known distribution range of *Riccia perssonii*.



MAP 63.— Known distribution range of *Ricciocarpos natans*.



MAP 64.--- Number of species of *Riccia* endemic to southern Africa. Two centres of diversity are shown. The solid line separates winter and summer rainfall areas.