

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*.