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The taxonomic history of the Ricciaceae (1937–1995) and a classification of sub-Saharan Ricciae

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ABSTRACT

The taxonomic history of the Ricciaceae (1937–1995) is reviewed. Over the years many attempts have been made to subdivide and rearrange the taxa in this large and puzzling family, but consensus has still not been reached. Hepaticologists are therefore urged to undertake more revisions worldwide, using modern methods of investigation to aid them in, hopefully, coming to an eventual agreement in defining the limits of subgenera, sections, species and subspecies in the Ricciae. In addition, a classification of sub-Saharan Ricciaceae, partially based on informal groups, is herein proposed.

UITTREKSEL

'n Oorsig van die taksonomiese geskiedenis van die Ricciaceae (1937–1995) word gegee. Oor die jare heen is talle pogings aangewend om die taksons in hierdie groot en moeilike familie op te deel en te herrangskik, maar eenstemmigheid is nog nie bereik nie. Hepatikoloë word aldus aangemoedig om verdere hersienings wêreldwyd te onderneem en om moderne ondersoekmetodes aan te wend, wat hopelik sal help om uiteindelik eenstemmigheid te bereik oor die omskrywing van subgenusse, seksies, spesies en subspesies in die Ricciae. Verder word 'n klassifikasie van die Ricciaceae van Afrika, suid van die Sahara, wat gedeeltelik op informele groepe gebaseer is, hier voorgestel.

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INTRODUCTION

Upon recently re-reading Duthie & Garside's (1937) excellent account of the taxonomic history of the Ricciaceae, which begins with John Ray (1696) and spans the next ± 240 years, I was once more struck by the many attempts to subdivide and rearrange the taxa in this large and puzzling family during that time.

This publication aims to cover in chronological order the most important regional studies of the Ricciaceae, that span the period between the survey by Duthie & Garside and the present.

It has now become accepted practice to recognize only two genera in the family, the monotypic *Ricciocarpos* and the species-rich *Riccia*. Both genera are characterized by the simplicity of the sporophytes, which are immersed in the thallus, and by the lack of elaters. The assimilation

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tissue in *Ricciocarpos* (formerly section *Hemiseuma*) contains tiered air chambers, whereas in *Riccia* it has either narrow air canals or rather wide, uniseriate air chambers. Other major differences between *Ricciocarpos* and *Riccia* are the following: *Ricciocarpos* is terrestrial or aquatic; in the latter the ventral scales are much elongated and pendant, with the margins serrate; single oil bodies are scattered throughout the cells of the scales and thallus; the antheridia and archegonia are in groups confined to the median groove of the thallus. Except for the *Riccia fluitans* complex, which is often aquatic and has small ventral scales that are never pendant, *Riccia* species are terrestrial and the scales are sometimes evanescent, but mostly reach to the thallus margins or extend above them; oil bodies are absent and the gametangia are not strictly confined to the median groove of the thallus.

Although there are intermediate forms with regard to the width of the air spaces in *Riccia*, the two groups classified here are generally recognized respectively as subgenus (rarely as section) *Riccia* (formerly *Lichenoides* or *Euriccia*) and as subgenus *Ricciella* (formerly, occasionally, as genus or as section). In the latter, two formal subdivisions have been recognized for a long time by the position of the capsule in the thallus and by the direction of liberation of the spores, i.e. the spores can be liberated dorsally (section *Spongodes* Nees) or ventrally (section *Ricciella* (A. Br.) Rchb.). Only informal subdivisions of subgenus *Riccia* have, however, been recognized until recently, as it was thought that not enough was known about several aspects of many species in this subgenus, that occurs worldwide, to make formal subdivisions.

OVERVIEW OF REGIONAL STUDIES

In the following overview diagnostic features are not cited verbatim from each author's text, but information is extracted from the description and keys and then combined in an abbreviated form more or less retaining the author's choice of words.

1. DUTHIE & GARSIDE (1937, 1939): South Africa

In 1937 Duthie & Garside published their detailed history of the group. Although they were aware of at least 11 species in the genus *Riccia* from the Stellenbosch Flats alone, they dealt with only five species in the section, then referred to as *Ricciella*.

1.1 Genus *Riccia*: upper photosynthetic zone in majority of species consisting of pillar-like vertical rows of cells separated by narrow air spaces, terminal cells of vertical rows usually larger and devoid of chlorophyll.

1.1.1 Section '*Ricciella*': upper zone consisting of air chambers, apparently strictly uniseriate and separated by plates of chlorophyll-containing cells; chambers roofed over by epidermis perforated by simple air pores which enlarge and later on cause the dorsal surface to become pitted; spores liberated from dorsal surface of thallus, but deeply imbedded and clearly visible from below; common, annual species.

R. plana Taylor (synonym of *R. crystallina* L.); *R. rautanenii* Steph. (synonym of *R. cavernosa* Hoffm. emend. Raddi). Spores separate at maturity; monoicous.

R. cupulifera A.V. Duthie. Spores separate at maturity; dioicous; heterothallic.

R. curtisii (James ex Austin) Austin (corrected author citation); *R. compacta* Garside (air chamber layer rather more compact and firmer). Spores retained in permanent tetrads; dioicous; heterothallic.

Nowadays species that retain their spores in permanent tetrads are assigned to subgenus *Thallocarpus* (Lindb.) Ast (1975).

Duthie & Garside suggest that the Ricciaceae may be a polyphyletic group, derived along several lines of descent. Their work together was discontinued when Duthie retired in 1939.

2. FRYE & CLARK (1937–1947): North America

Frye & Clark recognized three genera in the Ricciaceae, namely *Riccia*, *Ricciocarpus* (orth. var.) and *Oxymitra*.

2.1 Genus *Riccia*: thalli growing on damp or wet soil or suspended in water but not floating; air spaces narrow or chambered; antheridia and archegonia scattered; sporophyte without involucre; air pores inconspicuous, not stellate, the walls radiating from them not greatly thickened; divided into sections *Euriccia* and *Ricciella*.

2.1.1 Section *Euriccia*: air chambers are spaces between vertical or subvertical columns of photosynthetic cells; species assigned here are grouped together by absence or presence of cilia and by size of scales.

R. dictyospora Howe, *R. macallisteri* Howe, *R. bifurca* Hoffm.; *R. glauca* L., *R. sorocarpa* Bisch., *R. campbelliana* Howe, *R. nigrella* DC., *R. albida* Sull., *R. austinii* Steph. Margins of thallus without cilia; scales conspicuous or inconspicuous.

R. californica Austin, *R. hirta* (Austin) Underw., *R. beyrichiana* Hampe ex Lehm., *R. trichocarpa* Howe, *R. donnellii* Austin. Margins of thallus with cilia.

2.1.2 Section *Ricciella*: air chambers polyhedral hollows bounded by unistratose walls; margins of thallus lack cilia; ventral scales lacking or rudimentary.

R. membranacea Gottsche & Lindenb., *R. frostii* Austin, *R. crystallina* L. (misidentified and is *R. cavernosa*), *R. sullivantii* Austin. Mature spores not grouped in tetrads.

R. curtisii. Mature spores remaining attached in tetrads.

R. fluitans L. Thalli free-floating or stranded; segments narrowly linear.

In all modern treatments, two of the species they included in section *Ricciella*, *R. curtisii* and *R. membranacea*, are assigned to different subgenera, namely *Thallocarpus* (as mentioned before) and *Leptoriccia* (Schuster 1984) respectively.

2.2 Genus *Ricciocarpus* Corda: *R. natans* (L.) Corda. Thalli floating to stranded or rarely growing on very wet

soil; antheridia and archegonia located in median groove; dorsal surface distinctly reticulate on account of air chambers visible through it; monotypic.

2.3 Genus *Oxymitra* Bisch.: *O. androgyna* Howe. Thalli growing on soil, air chambers large, subvertical, prismatic or pyramidal; sporophyte with conspicuous conic or triangular-pyramidal involucre; pores stellate due to greatly thickened walls radiating from them.

Müller (1940) segregated the family Oxymitraceae from the family Ricciaceae, to accommodate the genus *Oxymitra* in the suborder Ricciineae. Although its sporophytes are similar to those of the Ricciaceae, its thalli and chromosome number are different, for which reasons it is best treated in a separate family. Garside (1958), however, described a new species of *Oxymitra*, *O. cristata*, from South Africa, but referred it to the family Ricciaceae and not to Müller's (1940) family Oxymitraceae, although he mentioned Müller's publication. This was presumably done because Garside was unsure whether the name *Oxymitra* would be upheld.

3. SCHUSTER (1949): central and western New York

In an early study on the Hepaticae of this region, Schuster treated *Ricciocarpus* and *Riccia* (with 6 local species) in the Ricciaceae.

3.1 Genus *Ricciocarpus* Corda: *R. natans*. Aquatic; occurring in circumneutral or somewhat calcareous waters, shallow and still or occasionally stranded on shore; thallus broad; ventral scales purple, dense, stiff, sword-like.

3.2 Genus *Riccia*: no subgenera or sections are mentioned, but the key distinguishes between the following two groups:

3.2a Group 1. *R. fluitans* (a mostly aquatic species), *R. crystallina*, *R. sullivantii* (the latter bracketed, because it only presumably occurs in the above area), *R. frostii*. 'Photosynthetic tissue loose, separated by more or less widely polyhedral air chambers, walls between chambers only one cell thick; ventral scales absent or obsolete.'

3.2b Group 2. *R. sorocarpa*, *R. arvensis* Austin (a synonym of *R. bifurca* Hoffm.). 'Photosynthetic tissue compact, with narrow vertical or subvertical, canal-like air chambers (at times becoming polyhedral near margins); spores areolate to alveolate, over 65 µm in longer diameter.'

4. SCHUSTER (1953): Minnesota and adjacent regions

Subsequently in reporting on the family Ricciaceae (Suborder Ricciineae) from Minnesota and adjacent regions, Schuster (1953) followed the conventional treatment of placing in it the genera *Ricciocarpus* and *Riccia*. In the latter he now recognized two subgenera, *Ricciella* and *Euriccia* (with two sections).

4.1 Genus *Ricciocarpus*: *R. natans*. Aquatic or subaquatic, floating on water surface or stranded; in imperfect, partial rosettes, with long, linear ventral scales; thallus with narrow, sharp, median groove, air pores and scattered oil cells.

4.2 Genus *Riccia*: thallose forms with sporophyte reduced and surrounded by thallus tissue; air pores vestigial and very inconspicuous, surrounded by hardly modified cells; terrestrial forms in rosettes, but some species normally aquatic; very variable.

4.2.1 Subgenus *Ricciella*: internal photosynthetic tissue loose, forming large, polyhedral chambers (i.e. not compact in structure in cross section); ventral scales rudimentary; marginal cilia of thallus lacking; dorsal surface of terrestrial forms often lacunose and spongiose with age.

R. fluitans (with related European taxa, *R. rhenana* Lorb., *R. duplex* Lorb. and R. *canaliculata* Hoffm. not yet found in North America). Thallus segments narrowly linear, less than 0.7 mm wide; free-floating under water; sterile.

R. frostii, *R. crystallina* (misidentified and is *R. cavernosa*), *R. sullivantii* (the latter with sporangia bulging and rupturing ventrally). Thallus segments relatively broad, always terrestrial; spores various.

4.2.2 Subgenus *Euriccia:* photosynthetic tissue compact; spores always regularly areolate on external faces, with or without wing margin.

R. austini (sic).*R. dictyospora*, *R. macallisteri*, *R. sorocarpa*, *R. arvensis*. Thallus margins acute, sharp or rarely obtuse, without obvious cilia; scales large, hyaline or purple, protruding beyond thallus margins or not.

R. hirta, *R. beyrichiana*, *R. trichocarpa*. Thallus margins obtuse, never sharp, with distinct cilia.

4.2.2.1 Section *Hirtae*: *R. hirta*, *R. beyrichiana*, *R. arvensis*, and *R. eldeeniae* Jacobs (a synonym of *R. warnstorfii* Limpr. ex Warnst.). Defined as 'extreme xeric forms which may show cilia and development of purplish pigmentation of lateral thallus margins under extreme insolation'.

4.2.2.2 Section Papillosae: *R. atromarginata* Levier. Defined as 'extreme xeric forms abundantly hirsute'. No mention is made of the author(s) of the two sections, nor are there Latin descriptions or references that I could trace, so I must infer that possibly, Schuster himself was the author of these two sections which were, of course, then not validly published.

5. MEIJER (1951): The Netherlands

5.1 Genus *Riccia* is defined by Meijer as including land and water form species, frequently with ventral scales; the compact rosette-shaped thalli are less strongly forked in the land forms than in the water forms, which have thin, narrow lobes that branch regularly and frequently; chlorophyll-containing cells have smaller or larger air spaces between; in isolated species reduced air pores are present; two subgenera are recognized.

5.1.1 Subgenus *Euriccia*: chlorophyll-containing top portion of thallus with narrow air canals bounded by 4 cell pillars:

R. glauca. Thallus 4–5 times wider than thick in transverse section.

R. subbifurca Warnst. ex Crozals (with large scales), *R. bifurca*, *R. beyrichiana* (the latter two species with small scales), *R. sorocarpa* (distinguished by the secon-

dary epidermis having thickened walls). Thallus 1–3½ times wider than thick in tranverse section; thallus margins with few or no cilia.

5.1.2 Subgenus *Ricciella*: top portion of thallus contains large superimposed air chambers separated on all sides by unicellular walls; (they are said to have the ability to adopt an amphibian life style).

R. canaliculata (land form). Thallus ± twice wider than thick, not or seldom branching.

R. crystallina, *R. huebeneriana* Lindenb. Thallus in a rosette, spongy in older parts or with pitted appearance dorsally.

R. rhenana, *R. fluitans*. Thallus not in a rosette, dorsally not pitted.

Meijer remarked on the problems encountered in studying dried *Riccia* material and the desirability of examining living examples.

6. MÜLLER (1951–1958): Europe

Müller also recognized two genera, *Ricciocarpus* and *Riccia* in the family Ricciaceae.

6.1 Genus *Ricciocarpus*: *R. natans*. Thalli floating on water; with long, band-shaped ventral scales hanging down; can also manifest as a land form, when ventral scales are small; assimilation tissue with large, tiered air chambers, air pores present; oil bodies scattered in thallus and ventral scales; gametangia sunken along centre of thallus.

6.2 Genus *Riccia*: land forms or submerged in water; ventral scales small, rarely projecting above thallus margins; assimilation tissue in parallel cell rows or chambered; air pores sometimes present in subgenus *Ricciella*; oil cells lacking and gametangia scattered over whole surface of thallus.

6.2.1 Subgenus *Ricciella*: assimilation tissue consists of chambers; simple air pores are now and then present in roof over chambers.

R. frostii, *R. crystallina*, *R. crystallina* var. *angustior* Nees (= *R. cavernosa*), *R. huebeneriana*. Thalli in small or large rosettes; spores various.

R. fluitans, *R. canaliculata*, *R. rhenana*, *R. duplex*. Thalli linear, rarely forked; dorsally often clearly marked into areas; some mostly aquatic.

Müller attempted (rather like Stephani (1898) and others before him) to arrange the large number of species in the subgenus *Euriccia* into informal groups, the members of which are related by one or more shared characters, e.g. the presence of cilia along the thallus margins or by papillae on the dorsal surface or by thickened walls in the (sub)dorsal cells.

6.2.2 Subgenus *Euriccia*: assimilation tissue consists of cell rows, ending in a larger cell on top.

6.2.2a Group Ciliifera

R. ciliifera Link, *R. gougetiana* Mont., *R. gougetiana* var. *erinacea* Schiffn., *R. zachariae* Lorb., *R. sommieri* Levier, *R. melitensis* C. Massal., *R. macrocarpa* Levier. Some thalli with single cilia, but not a very constant character.

6.2.2b Group Ciliata

R. ciliata Hoffm., var. *epilosa* Warnst. var. *intumescens* Bisch., var. *violacea* Kny, *R. canescens* Steph., *R. crozalsii* Levier, *R. michelii* Raddi, *R. bicarinata* Lindb. Thallus margins mostly with numerous long cilia.

6.2.2c Group Bifurca

R. bifurca, *R. beyrichiana*. Terminal branches with margins raised and swollen; median groove wide and shallow.

6.2.2d Group Sorocarpa

R. ligula Steph., *R. warnstorfii*, *R. sorocarpa* (subdorsal cells with thickened walls), var. *heegii* Schiffn., *R. breidleri* Jur., *R. oelandica* C.E.O. Jensen. Small plants, mostly linear or lingulate, rarely with a few cilia.

6.2.2e Group Papillosa

R. papillosa Moris. Dorsal surface and along margins with large papillae.

6.2.2f Group Nigrella

R. subbifurca, *R. nigrella*, *R. atromarginata* var. *glabra* Levier, *R. trabutiana* Steph. Thalli mostly in small rosettes; sometimes with deep median groove; occasionally with blunt papillae dorsally.

6.2.2g Group Lamellosa

R. lamellosa Raddi. Ventral scales large, hyaline and extending above thallus margins.

6.2.2h Group Glauca

R. glauca var. *subinermis* (Lindb.) Warnst. Thalli thin; at margins occasionally with short hairs; in rosettes; scales colourless.

7. ARNELL (1956): Scandinavia

In his treatment of the 'Hepaticae of the Moss Flora of Fennoscandia', Arnell placed the family Ricciaceae in the suborder Ricciineae H. Buch and also recognized two genera, *Ricciocarpus* and *Riccia*.

7.1 Genus *Ricciocarpus*: *R. natans*. Floating form with long ventral scales hanging down, land form with smaller scales; cordate; leathery; greyish green to dark green; dorsally with pores surrounded by 5 or 6 thin-walled guard cells; assimilative tissue containing several large air chambers, one lying above the other; ventral tissue thin; oil cells present; antheridia in small groups sunken in the middle.

7.2 Genus *Riccia*: dorsal surface of thallus not leathery; yellowish to dark green; assimilative tissue consisting of vertical cell rows with interposed vertical, air-filled canals, or consisting of the walls of the air chambers, the upper of which each has a little pore in the middle of its roof; antheridia scattered or in groups, not crowded in special organs.

7.2.1 Subgenus *Euriccia*: assimilative tissue consists of vertical cell rows surrounding narrow vertical air canals.

R. cilifera (sic), *R. glauca*, *R. dalslandica* S.W. Arnell, *R. beyrichiana*, *R. bifurca*, *R. ciliata*, *R. warnstorfii*, *R. subbifurca*, *R. sorocarpa*. Thalli in rosettes or not; small or large; branches thick or thin; narrow or wide; margins winged or not, round or acute, naked or with cilia; epidermal cells rarely thick-walled.

7.2.2 Subgenus *Ricciella*: assimilative tissue consists of irregular chambers, separated by walls one cell thick.

R. canaliculata, *R. crystallina* var. *angustior* (= *R. cavernosa*), *R. rhenana*, *R. fluitans*, *R. duplex*, *R. frostii*, *R. huebeneriana*. Thalli linear, little-branched or repeatedly furcate, thick or thin, reticulate, occasionally aquatic, mostly terrestrial, sometimes in rosettes, large or small, dorsally pitted.

8. JONES (1957): tropical Africa

The usual two genera were recognized by Jones in The 'Ricciaceae in Tropical Africa'.

8.1 Genus *Ricciocarpus*: *R. natans*. Very widely distributed; floating in still water; with long pendant ventral scales.

8.2 Genus *Riccia*: subdivided into the subgenera *Ricciella* and *Euriccia*.

8.2.1 Subgenus *Ricciella* (A. Braun) Boulay *sensu lato*: assimilation tissue with air chambers (aquatic or terrestrial).

R. fluitans. Floating on water or growing on wet soil; branches elongated, parallel-sided, 0.5–1.0 mm wide; air chambers occupying most of thallus; spores rare.

R. membranacea. Branches many times broader than thick, tapering into thin wings; dorsally areolate, older parts becoming cavernous; air chambers large, occupying most of thallus, except for 2 or 3 layers of basal tissue in median part.

R. moenkemeyeri Steph. Branches tapering, apically sharply channelled; becoming pitted dorsally; scales distant, not reaching edge of thallus.

R. rautanenii (synonym of *R. cavernosa*). Large, spongy rosettes; margins of thallus thick.

R. intermedia E.W. Jones. Branches parallel-sided, apically sharply grooved; air chambers medianly narrow and inconspicuous, like in *Euriccia*, but wider toward the margins. *Riccia intermedia* was regarded by Jones as intermediate between *Ricciella* and *Euriccia* with respect to the width of the air chambers or air canals; it was later placed in synonymy under *R. discolor* Lehm. & Lindenb. by Pandé & Udar (1958) and classified in *Euriccia*.

Jones refers to Duthie & Garside's publications (1937; 1939) and stresses that *Ricciella sensu lato* contains several well-marked groups of species which are worthy of sectional, if not of subgeneric rank.

8.2.2 Subgenus *Euriccia*: assimilation tissue with closely packed filaments.

R. trichocarpa. Margins of thallus with long, hyaline cilia.

R. nigrosquamata E.W. Jones (= *R. berriei* E.W. Jones), *R. nigerica* E.W. Jones, *R. lanceolata* Steph., *R. radicosa* Pearson, *R. rhodesiae* S.W. Arnell, *R. runssorensis* Steph., *R. congoana* Steph., *R. angolensis* Steph., *R. papillispora* Steph. (*R. albomarginata* Bisch. and *R. limbata* Bisch. are confined to the southwestern Cape). Margins of thallus without cilia, ventral scales extend to, or greatly exceed margins of thallus, distant or approximate or imbricate; hyaline or with hyaline margins or dark violet; thallus winged or not, when flanks steeply ascending; spores subglobose or tetrahedral.

The type specimen of *R. rhodesiae*, *S.W. Arnell 1291* (S), is a mixed collection of *R. rhodesiae* and *R. atropurpurea* Sim, and Jones mistakenly identified the *R. atropurpurea* portion of the specimen as *R. rhodesiae*; *R. rhodesiae* and *R. nigrosquamata* were placed in synonymy under *R. congoana* by Perold (1986b).

9. PANDÉ & UDAR (1958): India

9.1 Genus *Riccia*: divided into subgenera *Euriccia* and *Ricciella*.

9.1.1 Subgenus *Euriccia*: thalli with compact assimilatory zone and narrow air spaces.

R. melanospora Kashyap. Thallus bluish green; segments small; anteriorly sulcate, rest nearly flat; cilia both on margins and on surface, small and broad.

R. warnstorfii. Thallus yellow-green; segments narrow, linear, apex rounded; deeply sulcate anteriorly and sulcus broader behind; cilia large.

R. crozalsii. Thallus bluish green; segments lanceolate; anteriorly deeply sulcate, rest very broadly channelled.

R. tuberculata Pandé & Udar. Thallus small, about 3 times broader than high; tubercular thickenings on cells of assimilatory filaments; spores irregularly reticulate or papillate, winged.

R. discolor. Male plants comparatively smaller than female; spore reticulate, unwinged.

R. billardieri Mont. & Nees. Thallus large, 4–6 times broader than high; spores reticulate, with prominent projections.

R. gangetica S. Ahmad. Thallus small, about three times broader than high; spores black, with 8–16 small reticulations across distal face.

9.1.2 Subgenus *Ricciella*: thalli with loosely arranged assimilatory zone and wider air spaces.

R. huebeneriana. Thalli narrow, repeatedly branched; spores small.

R. plana (synonym of *R. crystallina*). Thalli narrow, repeatedly branched; spores much larger.

R. frostii. Thalli forming well-defined rosettes, female rosette normally larger than male; spores incompletely reticulate.

Riccia cruciata is mentioned in the key, but there is no description of it.

10. HÄSSEL DE MENÉNDEZ (1963): Argentina

Hässel de Menéndez treated the Argentinian Ricciaceae.

10.1 Genus *Ricciocarpus: R. natans*. Plants floating or terrestrial; photosynthetic layer formed by several superimposed air chambers; ventral layer almost absent; scales in 3–5 series on both sides of midline.

10.2 Genus *Riccia*: plants terrestrial; photosynthetic layer formed by one layer of air spaces surrounded by walls of adjoining cells or by columns of chlorophyllose cells; ventral layer developed; scales in 1 or 2 series.

10.2.1 Subgenus *Ricciella*: photosynthetic tissue consisting of air chambers separated by walls one cell thick; pores surrounded by complete rings or not, cells similar to the others in dorsal walls of air chambers.

R. paranaensis Hässel, *R. stenophylla* Spruce. Thalli linear, capsules ventrally prominent as described by A. Braun.

R. membranacea, R. crystallina (misidentified and is *R. cavernosa*), *R. plana, R. frostii, R. paraguayensis* Spruce, *R. curtisii*. Thalli frequently in rosettes; capsules slightly or ventrally not prominent; spores separating at maturity except in *R. curtisii*, where they are united in tetrads.

10.2.2 Subgenus *Riccia*: photosynthetic tissue formed by chlorophyllose columns separated by narrow canals.

R. lindmanii Steph. Thallus margins without cilia.

R. bialbistrata Hässel. Thallus margins with cilia.

R. iodocheila Howe. Apex of thallus with some purple papillae.

R. austinii, R. andina Müll.Frib., *R. plano-biconvexa* Steph., *R. campbelliana, R. squamata* Nees, *R. fruchartii* Steph. Walls of dorsal cells not thickened.

R. sorocarpa, R. dorsiverrucosa Hässel. Walls of dorsal cells thickened.

No formal or informal groupings were made in either subgenus. *Riccia crystallina*, as treated by Hässel, is actually *R. cavernosa*, as the two species were frequently confused until Jovet-Ast (1964, 1966) cleared up the matter. Hässel selected *R. glauca* as the lectotype of the genus *Riccia*, because Howe's lectotype, *R. crystallina*, belongs in subgenus *Ricciella* and it is therefore contrary to previous practice.

The specimen, leg. *Sleumer 1755*, identified as *R. campbelliana* by Hässel, has large dark red scales, in contrast to those from other specimens of this species, in which they are inconspicuous, fragile and hyaline, splashed with brown and purple patches (Perold & Volk 1988a). Schuster (1992a) has assigned it to a new subspecies, *R. campbelliana* subsp. *austrigena*. *Riccia dorsiverrucosa* (as well as *R. andina* Müll.Frib.) were recently placed in synonymy under *R. mauryana* Steph. by Jovet-Ast (1991).

11. ARNELL (1963): southern Africa

In his book *Hepaticae of South Africa*, Arnell (1963) recognized Müller's Oxymitraceae and the family Ricciaceae in the suborder Ricciineae. For the rest he followed the same classification here as in his earlier work (Arnell 1956) on Scandinavian Ricciaceae. He made no attempt to arrange the species in the genus *Riccia* into sections or groups.

11.1 Genus *Ricciocarpus*: *R. natans*. Floating on water (with long, serrate scales) or growing on mud; dorsal surface leathery, reticulate, greyish green to dark green; air chambers large; pores present, surrounded by 5 or 6 thin-walled guard cells; ventral tissue thin; ventral face with several rows of purplish ventral scales, numerous and long in aquatic form; oil bodies in scales and thallus; antheridia in small groups, sunken in the midline of thallus; sporogonia rare, immersed in thallus.

11.2 Genus *Riccia*: most species only have land forms, but some species in subgenus *Ricciella* have both terrestrial and aquatic forms; dorsal surface of thallus not leathery; pores lacking except in some species of subgenus *Ricciella*; ventral scales generally small; green layer of assimilative tissue consists either of vertical cell pillars with interposed air-filled spaces or (consists) of walls of air chambers; oil bodies lacking; antheridia scattered or in groups, not crowded in special organs.

11.2.1 Subgenus *Euriccia*: assimilative tissue composed of cell pillars surrounded by air spaces.

R. canescens (synonym of *R. trichocarpa*), *R. crozalsii*. Margin of thallus with long cilia.

R. villosa Steph., *R. albomarginata* Bisch., *R. concava* Bisch. Margin of thallus usually without cilia; dorsally velvet-like by the presence of free cell pillars.

R. sorocarpa. Epidermal cells in 2 layers, second layer with thick walls.

R. coronata Sim, *R. natalensis* Sim. Epidermal cells with thin walls, some of them elongated and free.

R. atropurpurea, R. limbata, R. angolensis, R. albolimbata S.W. Arnell, *R. albosquamata* S.W. Arnell, *R. capensis* Steph., *R. rhodesiae, R. pottsiana* Sim, *R. warnstorfii* (an introduced species), *R. runssorensis, R. okahandjana* S.W. Arnell. Epidermal cells in one layer, not forming free pillars, but an adherent dorsal layer; scales absent or present, large or small, hyaline or purple to black.

11.2.2 Subgenus *Ricciella*: assimilative tissue composed of large air chambers with walls one cell thick.

R. fluitans, R. stricta A.V. Duthie ined. Thalli with long, linear segments, usually aquatic plants or rarely to frequently terrestrial.

R. purpurascens Lehm. Usually terrestrial, large plants; tuber formation on ventral stolons.

R. perssonii S.A. Kahn, *R. curtisii, R. spongosa* S.W. Arnell, *R. compacta*. Tetrads of spores permanently adherent, male plants much smaller than female ones.

R. cupulifera, R. rautanenii, R. plana, R. crystallina. Monoicous, except for *R. cupulifera* which is dioicous; spores separating when mature; plants in rosettes; male and female plants the same size or male plants slightly smaller.

R. bullosa Steph. (Link ex Lindenb. is actually the author), *R. garsidei* Sim, *R. montaguensis* S.W. Arnell, *R. volkii* S.W. Arnell, *R. rubricollis* Garside & A.V. Duthie ined. Plants not forming complete rosettes, simple or dichotomously branched, very thick.

Arnell (1957) had previously described several new *Riccia* species based on collections made by Volk in Namibia, but had failed to recognize that the species with velvet-like dorsal surfaces (Arnell 1963) form a distinct group (later named section *Pilifer* O.H. Volk); *R. villosa*, *R. albomarginata* and *R. concava* belong together in this group and are quite distinct from ciliate species; no *R. coronata* Sim specimens could be traced; *R. capensis*, as interpreted by Arnell, was *R. nigrella*, whereas *R. capensis* Steph. is a synonym of *R. limbata* Bisch. (Perold & Volk 1988b); *R. albosquamata* was placed in synonymy under *R. albolimbata* (Perold 1989); *R. rhodesiae* is a synonym of *R. congoana* (Perold 1986b); *R. pseudolimbata* S.W. Arnell is a synonym of *R. angolensis*; *R. chrystallina* (sic) is *R. cavernosa* and *R. plana* is a synonym of *R. crystallina*; *R. montaguensis* is a synonym of *R. bullosa* (Perold 1991c); *R. spongosa* is a synonym of *R. curtisii* (Perold 1991a).

12. VANDEN BERGHEN (1972): Zaïre, Zambia

Vanden Berghen reported on the Ricciaceae of Zaïre's province Shaba and of Zambia. *Ricciocarpus natans* specimens were listed, as well as several *Riccia* species, but the latter were not assigned to any particular subgenus.

12.1 Genus *Ricciocarpus*: *R. natans*. Thallus with wide air cavities and small pores surrounded by 6–8 cells on the dorsal face; floating in water, with long violet scales, or when at water's edge, without long scales; oil bodies isolated in specialized cells; antheridia and archegonia surrounded by a rudimentary involucre in the median groove.

12.2 Genus *Riccia*: plants annual or perennial; terrestrial or aquatic; thallus dichotomously branched, frequently forming small rosettes; thalli with air cavities generally narrow; ventral scales mostly present, sometimes evanescent; without oil cells; antheridia and archegonia not surrounded by an involucre.

R. membranacea. Thalli very thin, 6–10(–15) times wider than thick; lobes 2.8–4.0 mm wide.

R. fluitans. Plants freely floating in water or stranded on mud; capsules strongly protruding on ventral face of thallus; lobes up to 1 mm wide; ventral scales absent or very reduced and evanescent.

R. cavernosa, *R. moenkemeyeri*, *R. intermedia*, *R. symoensii* Vanden Berghen. Terrestrial plants; capsules not strongly protruding on ventral face of thallus; lobes generally 1–2 mm wide; ventral scales absent or very reduced, or large and violet.

As mentioned before, *R. intermedia* has been synonymised under *R. discolor*. It also appears, from Vanden Berghen's description and illustration of the spores of his so-called *R. fluitans*, that he was actually dealing with *R. stricta*.

13. JOVET-AST (1975): diverse areas

Twenty years ago Jovet-Ast studied the species *R. perssonii* and *R. curtisii*, which retain their spores in permanent tetrads. Previously, on account of the tetrad spores, Austin (1869) had placed *R. curtisii* in his new genus, *Cryptocarpus*, but Lindberg (1874) called attention to the fact that the generic name, *Cryptocarpus*, was already in use and proposed the name *Thallocarpus*, instead. Subsequently, however, these plants were treated under subgenus *Ricciella*, until *Thallocarpus* was reinstated as an independent subgenus by Jovet-Ast (1975).

14. CAMPBELL (1975, 1977): New Zealand

14.1 Genus *Ricciocarpos*: *R. natans*. Plants in spongy, partial rosettes, up to 20 mm in diameter; when floating in ponds, little-branched and green or yellow-green in colour; dorsally firm and convex, with deep median furrow; upper epidermis interrupted by simple air pores; composed below of several series of large air chambers bounded by unistratose walls; ventrally with few rhizoids but with numerous conspicuous and characteristic pendant scales, toothed, ribbon-shaped and reddish violet or brownish green in colour; when temporarily stranded on shore, freely branched; with numerous smooth and tuberculate rhizoids; scales only rudimentary; rarely fertile in either aquatic or land form.

14.2 Genus *Riccia*: divided into two subgenera.

14.2.1 Subgenus *Riccia*: with a rather compact photosynthetic layer consisting of more or less vertical filaments separating narrow air chambers.

R. crozalsii. Margin of thallus with cilia, mainly near apex, 200–500 µm long.

R. ciliata. Cilia abundant along margin, 600–900 µm long.

R. sorocarpa. Dorsal groove deep and narrow.

R. bifurca, *R. glauca*. Dorsal groove shallow and wide.

14.2.2 Subgenus *Ricciella*: photosynthetic layer spongy and consisting of unistratose walls enclosing polyhedral air chambers.

R. fluitans. Thallus free-floating or stranded, not attached; segments narrowly linear.

R. crystallina. In glassy green or grey-green spongy rosettes; air chambers large and in several layers.

R. vesiculosa (Carrington & Pearson) Steph., formerly thought to be *R. bullosa* (pers. comm.), green or olive-green, strap-shaped and large; median air chambers narrow, those of the wings larger and in layers.

15. GROLLE (1976, 1983): Europe and adjacent regions

Grolle in his 'Lebermoose Europas' divided *Riccia*, as usual, into the subgenera *Riccia* and *Ricciella* (A. Br.) Boulay. In 1983 he stated the authors of the latter subgenus to be (A. Br.) Rchb., with *R. fluitans* as the newly selected lectotype. Two sections were recognized, namely *Ricciella* and *Spongodes* (the latter with the newly selected lectotype, *R. crystallina*). No attempt was made to arrange the species into groups, nor are diagnostic characters given.

16. NA-THALANG (1980): Australia

In her study of Australian Ricciae, Na-Thalang thought it incorrect for the two subgenera, *Riccia* and *Ricciella*,

to be separated on the size of the air chambers, because the characteristics of air chambers, pores and epidermal cells ought to be considered more important than the size of the air chambers.

16.1 Genus *Riccia*: monoicous or dioicous; complete or incomplete rosettes or in gregarious patches; mostly land forms; annual or perennial; upper surface normally sulcate; margins sometimes with cilia or scales of various sizes; dorsal part with compact tissue in vertical columns or with loosely arranged tissue forming polyhedral air chambers; capsules with neither seta nor foot, normally embedded in thallus.

16.1.1 Subgenus *Riccia*: upper part of thallus composed of compact tissue arranged in almost vertical columns; air chambers narrow, without specialized air pores; epidermal cells hyaline.

16.1.1.1 Section *Viridisquamata* Na-Thalang: *R. caroliniana* Na-Thalang. Dorsal part of thallus consists of compact, hyaline tissue; chlorophyll-bearing layer at ventral side of thallus, but almost whole thallus pellucid, destitute of chloroplasts except a few towards apex, margins and ventral layer next to scales; scales narrowly oblong, green, cells containing chloroplasts, imbricate and persistent, 1 or 2 layers of cells in thickness; branches furcate or bifurcate.

16.1.1.2 Section *Riccia*: chlorophyll-bearing layer at dorsal part of thallus; consists of compact vertical columns of green cells terminated by hyaline epidermal cells, each air space normally enclosed by 4 vertical columns; in some species, air chambers close to the margin may be enlarged, when surrounded by 5 or 6 columns.

Three groups are recognised.

16.1.1.2a Group Ciliatae: thalli bear cilia at margins and sometimes on dorsal surface.

16.1.1.2aa Subgroup Longiciliata: plants with long cilia on thallus and on capsule.

R. longiciliata Na-Thalang, *R. crinita* Taylor, *R. areolata* Na-Thalang. Closely related species, but with different spore characters.

Seppelt (1983) subsequently reduced Na-Thalang's *R. longiciliata* and *R. areolata* to synonyms of *R. crinita*. *Riccia longiciliata*, with n = 16, is regarded by him as only a polyploid of *R. crinita*, with n = 8, and it was concluded that the three species cannot be satisfactorily delimited by spore characteristics, neither can they be differentiated by morphological gametophyte characteristics.

16.1.1.2ab Subgroup Crozalsii: plants with short cilia on thallus, none borne on capsule.

R. crozalsii, *R. blackii* Na-Thalang, *R. asprella* Carrington & Pearson. Thalli small to larger; margins tumid and raised; channel broad.

16.1.1.2b Group Squamatae: thalli with scales reaching to or extending beyond margins.

16.1.1.2ba Subgroup Macrospora: thalli with variable purple scales; spores globose.

R. macrospora Steph., *R. gangetica*, *R. billardieri*, *R. discolor*. Colour of scales and thalli sensitive to environmental change.

16.1.1.2bb Subgroup Limbata: scales dark purple; spores triangular-globular, proximal face with triradiate mark.

R. limbata, *R. nigrella*. Colour of scales not easily changed.

16.1.1.2bc Subgroup Sorocarpa: scales hyaline; mostly annuals.

R. sorocarpa, *R. lamellosa*. Introduced species.
R. marginata Carrington & Pearson, *R. olgensis* Na-Thalang, *R. rorida* Na-Thalang. Australian species, probably endemic.

16.1.1.2c Group Laevigatae: scales small, only present under apex of thallus.

R. bifurca, *R. albida*. Introduced species; thallus margins rounded, the latter species being the only *Riccia* with smooth and rounded spores.

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

Two groups are recognized.

16.1.2a Group Terrestriae: land forms, sometimes growing on mud.

16.1.2aa Subgroup Crystallina: annual plants; in round and compact rosettes.

R. crystallina, *R. cavernosa*. Thalli not strap-like, broader than 1.5 mm; capsules not bulging markedly on ventral surface.

16.1.2ab Subgroup Papulosa: large thalli, 3–6 mm wide.

R. papulosa Steph., *R. spongiosula* Na-Thalang. Plants not strictly annual; forming rosettes only in young stages.

16.1.2ac Subgroup Vesiculosa: thalli smaller, 2–3(4) mm wide; hygrophilous plants.

R. vesiculosa (Carrington & Pearson) Steph., *R. muscicola* Steph., *R. deserticola* Steph., *R. crassa* Steph., *R. junghuhniana* Nees & Lindb., *R. collata* Na-Thalang. Scales mostly small and hyaline.

16.1.2b Group Aquaticae-Terrestriae: thalli narrow-linear or strap-like; multifurcate; capsules bulging on ventral surface.

R. luticola Na-Thalang, *R. duplex*, *R. multifida* Steph. Plants growing in water or on land; upper surface marked out by air chamber areas or not.

Na-Thalang's groups were not given formal taxonomic status, because she considered a worldwide appraisal of the genus a necessity before formalizing taxa below the

level of subgenus. Schuster (1992a), however, correctly points out that these informal groupings are 'nomenclaturally irrelevant'.

17. JOVET-AST (1984): Australia

Jovet-Ast raised Na-Thalang's (1980) section *Viridisquamata* (containing *R. caroliniana*) to subgeneric rank, because of the very unusual structure of its lobes, which could represent either a primitive stage, i.e. a relictual endemic of Australia, or else a parallel lineage to the genus *Riccia*. Its spores are, however, comparable to those of many other species of *Riccia*. Jovet-Ast, therefore, thought it preferable to maintain it in the genus *Riccia*.

17.1 Genus *Riccia*

17.1.1 Subgenus *Viridisquamata* (Na-Thalang) Ast: *R. caroliniana*. Dorsal part of thallus hyaline and compact; ventral part of thallus chlorophyll-bearing, i.e. layers inverted compared with other species of *Riccia*; ventral side of lobes with rows of chlorophyllose lamellae which are not scales; distal face of spores reticulate, forming 9 or 10 rounded areolae across diameter; proximal face similarly ornamented.

18. VOLK (1983): Namibia and southern Africa (and elsewhere)

In 1981 Volk described a new *Riccia* species, *R. albovestita*, from Namibia. It, and others like it, are characterized by a dorsal epithelium of loose, erect cell pillars, which Arnell (1963) had referred to as 'velvet-like', but had not segregated into a distinct group. This was subsequently done by Volk (1983), when he created his new section *Pilifer*. He also proposed a new classification for the genus *Riccia*, in an attempt to avoid the problems caused by intermediate forms with regard to the width of the air canals/air chambers. This classification was no longer to be based on the width of the air chambers, but rather on the number and size of the air pores in the dorsal epithelium/epidermis of the thallus.

18.1 Genus: *Riccia*

18.1.1 Subgenus A. *Riccia* (*Euriccia* auct.): outer dorsal layer consisting of an epithelium of hyaline cells; without sharply delimited air pores.

18.1.1.1 Section *Viridisquamata*: *R. caroliniana*. Chlorophyllose tissue limited to ventral side of thallus and scales.

18.1.1.2 Section *Riccia* [Lichenoides (Bisch.) Nees]: *R. glauca*, *R. sorocarpa*, *R. limbata*, *R. angolensis* etc. Chlorophyll mostly in dorsal tissues; ventral scales not green; top cells of epithelium close together.

18.1.1.3 Section *Pilifer* O.H. Volk: *R. villosa* Steph., *R. albovestita* O.H. Volk, *R. concava* Bisch. etc. Upper cells of epithelium free, hair-like pillars.

18.1.2 Subgenus B. *Spongodes* (Nees) O.H. Volk: outer dorsal layer consisting of an epidermis with chlorophyll and sharply delimited air pores.

18.1.2.1 Section *Thallocarpus*: *R. perssonii*, *R. curtisii*. Spores in permanent tetrads.

18.1.2.2 Section *Spongodes* Nees: *R. crystallina*, *R. cavernosa*, *R. volkii*. Ripe spores free; sporangia opening dorsally.

18.1.2.3 Section *Ricciella* (A. Braun, pro gen.) Bisch.: *R. fluitans*, *R. canaliculata*, *R. stricta* etc. Sporangia bulging and opening ventrally.

19. SCHUSTER (1984, 1985): diverse areas

Schuster proposed a new subgenus, *Leptoriccia*, for *R. membranacea*, as well as a third genus in the Ricciaceae, namely his monotypic *Pteroriccia* R.M. Schust. to accommodate *R. villosa* Steph.

19.1 Genus *Riccia*

19.1.1 Subgenus *Leptoriccia* R.M. Schust.: *R. membranacea*. Thallus very thin with vestigial ventral tissue; spores with numerous papillae, not arising from a reticulum.

19.2 Genus *Pteroriccia* R.M. Schust.: *R. villosa* Steph. Thallus with tall dorsal cell pillars and large erect, imbricate ventral scales, margins serrate.

On account of the above characters Schuster thought that *Pteroriccia* was at least as distinct from *Riccia* as the water form of the separate, unrelated genus, *Ricciocarpus*, which has long, trailing, ventral scales also with serrate margins.

20. PEROLD (1986): southern Africa

In response to Schuster's publication on *Pteroriccia* Perold (1986a) attempted to draw attention to O.H. Volk's section *Pilifer*, which was instituted for the reception of all the then (and later) known *Riccia* species with tall, loose dorsal cell pillars. She also pointed out that scale margins vary considerably in some species of *Riccia*, from crenate to serrate to having long, multicellular appendages in a then, as yet, undescribed species. The new genus instituted by Schuster was accordingly regarded as synonymous with *Riccia*.

21. SCHUSTER (1985): worldwide

Schuster (1985), however, had already reduced the status of his genus *Pteroriccia* (here regarded as a synonym of section *Pilifer* O.H. Volk) to that of subgenus *Pteroriccia* (R.M. Schust.) R.M. Schust. after restudying the *Pteroriccia* complex and finding that the ventral scale criterion, which had strikingly isolated his type species, did not hold for several other taxa in the same taxonomic unit. He also thought that *Pilifer* O.H. Volk was illegitimate, as he had assumed (incorrectly, however) that no type species had been designated, whereas Volk (1983) had indeed selected *R. albomarginata* as the type species of his section *Pilifer*. Schuster (1985) recognized six subgenera in the Ricciaceae.

21.1 Genus: *Riccia*

21.1.1 Subgenus *Spongodes* (Nees) O.H. Volk: dorsal epidermis distinct, complete, becoming lacunose, chlorophyllose, with pores; air chamers large, polyhedral; ventral tissue several cell layers thick.

21.1.2 Subgenus *Leptoriccia* R.M. Schust.: dorsal epidermis distinct, complete, becoming lacunose, chlorophyllose with pores; air chambers large, polyhedral; ventral tissue vestigial.

21.1.3 Subgenus *Thallocarpus* [Austin (sic)] Ast: spores coherent in permanent tetrads; plants unisexual, strikingly heterothallic with dwarf males.

21.1.4 Subgenus *Riccia*: epithelial tissues in mutually connate cell rows between which vertical air canals are distinct.

21.1.5 Subgenus *Pteroriccia* (R.M. Schust.) R.M. Schust.: epithelial tissues free-standing, independent multicellular uniseriate hairs, formed of elongated cells; ventral scales typically large, projecting beyond thallus margins.

21.1.6 Subgenus *Viridisquamata* (Na-Thalang) Ast: chloroplasts limited to ventral strata of thallus; ventral lamellae bistratose and chlorophyllose.

22. SCOTT (1985): southern Australia

22.1 Genus *Riccia*: thallus often distinctly coloured; wedge-shaped, usually wider than thick; bifurcating frequently and forming rosettes; ventral scales conspicuous or not; antheridia and archegonia sunken in pits along mid-line of thallus; sporophyte merely a 'bag of spores' also sunken in thallus; spores with elaborate sculpturing on surface which seems to be diagnostic of each species; divided into two subgenera which are ± distinct.

22.1.1 Subgenus *Riccia* (*sensu stricto*): upper layer of thallus firm, consisting of compact vertical pillars of cells, closely packed together and joined at the top, forming a firm, close tissue with narrow, vertical air slots and an even, homogeneous upper surface.

R. asprella, R. crozalsii, R. crinita. Thallus margins with hairs, fine or coarse, few or abundant, confined to apex or not.

R. limbata, R. nigrella. Medium-sized or small; bordered by black ventral scales.

R. sorocarpa, R. cartilaginosa Steph. Smallish or large; ventral scales hyaline and just reaching thallus margin.

R. bifurca. Upper surface broadly channelled.

R. lamellosa, R. rorida. Thalli rimmed by white scales, extending beyond margins.

R. albida. Upper surface narrowly grooved; chalky white with calcareous incrustation.

22.1.2 Subgenus *Ricciella*: upper layer of thallus spongy; loosely arranged chlorophyllous tissue, forming polyhedral or large and irregular air chambers, usually with definite air pores; epidermal cells with chloroplasts except around air pores.

R. crystallina, R. cavernosa. Plants in circular rosettes; upper epidermis granular or rough or cavernous even near apex.

R. vesiculosa, R. spongiosula, R. papulosa. Plants dorsally sometimes becoming cavernous in older parts or honeycombed, except at apex or only at base.

R. multifida, R. duplex. Thalli narrow, strap-like, less than 1.5 mm broad; thick or thin; with or without reticulation; grooved along midline or only at apex.

23. VOLK & PEROLD (1986a): South Africa

In 1986 Volk & Perold described a new species, *R. schelpei*, which is a very distinctive plant; it was assigned by them to the new monotypic subgenus *Chartacea* Perold, which is restricted to the winter rainfall region of the Western Cape.

23.1 Genus: *Riccia*

23.1.1 Subgenus *Chartacea: R. schelpei.* Thallus when dry, with papery texture, epidermis parchment-like with thick-walled hyaline cells; air pores surrounded by a ring of thin-walled, superimposed cells; spores reticulate-faveolate on distal face; proximal face with small shallow areolae, sprinkled with granules.

Later in the same year Volk & Perold (1986b) described another new species, *R. hirsuta*, which was placed in the new section *Micantes* O.H. Volk & Perold, subgenus *Spongodes* (Nees) O.H. Volk.

23.1.2 Subgenus: *Spongodes*

23.1.2.1 Section *Micantes*: *R. hirsuta.* Thallus dorsally densely covered with crowded multicellular, hairlike, hyaline shiny pillars; assimilation tissue with polyhedral air chambers; ventral scales triangular and apically split into cellular strands; spores single, ornamentation reticulate; spores with 3–5(6) large central areolae completely or incompletely subdivided, proximal face incompletely reticulate.

Unfortunately the description of *R. hirsuta* was based on two distinct, but rather similar species; fresh collections of *R. hirsuta* showed the assimilation tissue to have air canals and not polyhedral air chambers and hence to belong to section *Pilifer*, subgenus *Riccia*; section *Micantes* was accordingly rejected by Volk & Perold (1990).

24. JOVET-AST (1986): Mediterranean countries

Jovet-Ast's study of Mediterranean Ricciae was the culmination of the examination of several thousand specimens collected during 22 surveys around the Mediterranean Sea. Although only subgenus *Riccia* (with section *Riccia*) and subgenus *Ricciella* (with sections *Ricciella* and *Spongodes*) grow in the area treated, she listed five subgenera in her classification: *Riccia* (with sections *Riccia* and *Pilifer*), *Ricciella*, *Thallocarpus*, *Viridisquamata* and *Leptoriccia*. In her keys, of which there are several

to subgenus *Ricciella*, she referred to Grolle's lectotypification of section *Spongodes* Nees and of section *Ricciella*. No formal or informal groups or subgroups were recognized in section *Riccia*, and varieties based on small differences in size and colour were rejected.

24.1 Genus *Riccia*: thallus in the form of simple, linear lobes or ramified 1–4 times or in complete or partial rosettes; compact or spongiose; dorsal surface flat or with longitudinal median furrow; margins glabrous or bearing papillae or cilia; lateral surfaces with scales, small or large, colourless, or flecked with violet, orange, or dark violet or entirely dark violet.

24.1.1 Subgenus *Riccia*: thalli not spongiose, without air chambers; chlorophyllose tissue consisting of cells arranged in vertical rows, between them filiform aeration canals that open dorsally by minute openings; terrestrial species.

R. crustata Trab., *R. lamellosa*, *R. melitensis*, *R. sorocarpa*, *R. glauca*, *R. macrocarpa*, *R. sommieri*, *R. bifurca*, *R. subbifurca*, *R. warnstorfii*, *R. nigrella*, *R. trabutiana*. Thallus glabrous; upper surface white or not; scales various.

R. atromarginata, *R. papillosa*, *R. gougetiana*, *R. cilifera*, *R. bicarinata*, *R. trichocarpa*, *R. ciliata*, *R. michelii*, *R. beyrichiana*, *R. crozalsii*, *R. ligula*. Thallus bearing cilia or papillae.

24.1.2 Subgenus *Ricciella*: thalli spongiose and with numerous large lacunae opening to exterior; or thallus not spongiose, air chambers opening dorsally via pores; surrounding cells arranged stoma-like; air chambers separated by mostly unicellular walls.

24.1.2.1 Section *Spongodes*: thallus spongiose; dorsal surface bearing large lacunae or both lacunae and pores; capsules not very prominent on upper surface of lobes, enclosed in thallus; terrestrial species.

R. crystallina, *R. cavernosa*. Monoicous; thallus in rosettes.

R. frostii. Dioicous; pronouncedly heterothallic with male thallus much smaller than female thallus.

24.1.2.2 Section *Ricciella*: thallus mostly not spongiose, generally with dorsal epidermis bearing pores surrounded by regularly arranged cells; capsules protuberant on ventral surface of thallus; terrestrial or aquatic species.

R. perennis Steph., *R. huebeneriana*, *R. fluitans*, *R. duplex*, *R. canaliculata*. Thallus with or without clear areolation on dorsal surface; in *R. canaliculata* ventral apex of lobes covered by white scale, in other species not.

25. DAMSHOLT & HALLINGBÄCK (1986): Fennoscandia

Also published in 1986 was Damsholt & Hallingbäck's report on the Ricciae of Fennoscandia, which contained beautiful coloured photoprints to illustrate the different colours of the thalli as well as outstanding drawings by the Danish artist, Annette Pagh. Since they were dealing with local species, only two subgenera were recognized, neither were any sections separated in either of the subgenera.

25.1 Genus: *Riccia*

25.1.1 Subgenus *Ricciella*: thallus with air chambers in assimilation tissue; secondarily adapted to damp or fresh water environments since air pores are here used as a floating mechanism.

R. cavernosa, *R. huebeneriana*. Land plants; in partial or complete rosettes.

R. canaliculata, *R. fluitans*. The former species is terrestrial, whereas the latter is a land or a water plant; neither grows in rosettes.

25.1.2 Subgenus *Riccia*: thallus compact; assimilation tissue with closely spaced vertical cell rows; adapted to dry areas; upper surface of thallus closes up as the sides meet and so dehydration is prevented.

R. bifurca, *R. beyrichiana*, *R. sorocarpa*, *R. warnstorfii*, *R. subbifurca*, *R. gothica* Damsh. & Hallingb., *R. glauca*. Thallus margins often glabrous.

R. ciliata, *R. ciliifera*. Thallus margins mostly ciliate.

R. dalslandica is placed in synonymy under *R. ciliata* var. *epilosa*; *R. glauca* forma *colorata* S.W. Arnell is treated as a separate species, *R. gothica*, by the authors. Jovet-Ast (1994) expresses some doubt that Damsholt & Hallingbäck had indeed examined the true type specimen of *R. ciliata* and argues that they may have confounded *R. ciliata* and *R. trichocarpa*, since she had examined the types of both and found them to be different.

26. VOLK & PEROLD (1990): South Africa

Volk & Perold in correcting their initial error (Volk & Perold 1986b) now referred *R. hirsuta* to section *Pilifer*; *R. tomentosa*, the other element on which the original description of *R. hirsuta* had been partly based, was referred to subgenus *Thallocarpus*, section *Pannosae* (*sect. nov.*), since its spores (absent in the original collection) are retained in permanent tetrads. *Riccia tomentosa* and *R. hirsuta* share triangular ventral scales with apical filamentous strands and elongated dorsal cell pillars.

27. SMITH (1990): Britain and Ireland

Smith treated the liverworts of Britain and Ireland. He commented that there seemed to be no general agreement about the arrangement of species within the subgenus *Riccia*, since Grolle (1983) had arranged them in alphabetical order and the arrangements of Müller (1951–1958), Jovet-Ast (1986) and others differed. He chose to follow Jovet-Ast as hers was, at the time, the most recent authoritative account.

27.1 Genus *Ricciocarpus*: *R. natans*. Plants floating in base-rich or neutral ponds, ditches and canals or on mud of dried-out ponds; with conspicuous linear-lanceolate ventral scales (terrestrial forms with small scales); dorsal epidermis with small distinct pores and scattered oil cells.

27.2 Genus *Riccia*: plants terrestrial or, if aquatic, submerged; often winter ephemerals or annuals; ventral scales small to larger; pores lacking or, if present, vestigial and not surrounded by specialised cells; oil cells lacking.

27.2.1 Subgenus *Ricciella:* thallus with chambers; epidermis breaking down to form lacunae in older parts of thallus or not; margins without cilia.

27.2.1.1 Section *Spongodes*: plants terrestrial; dorsal epidermal cells in older parts of thallus breaking down to form lacunae, rendering thallus spongy in appearance; capsules embedded in thallus, not protruding strongly on ventral side.

R. cavernosa, R. crystallina, R. huebeneriana. Plants terrestrial; not strap-like; older parts spongy in appearance; capsules not protruding strongly on ventral side of thallus [except in *R. huebeneriana* (parenthesis mine)].

27.2.1.2 Section *Ricciella*: plants aquatic or terrestrial; epidermal cells on dorsal side of thallus not breaking down, older parts of thallus not spongy in appearance; capsules protruding very strongly on ventral side.

R. canaliculata, R. fluitans, R. rhenana. Thallus not channelled, except sometimes in older parts; not reticulate or often reticulate; capsules common or rare.

27.2.2 Subgenus *Riccia*: thalli never spongy in appearance; margins ciliate or not; dorsal epidermal cells frequently soon lost; chlorophyllose tissue composed of vertical columns with narrow air spaces, forming a compact layer of green cells.

R. crozalsii. Thallus lobes with ciliate margins, cilia curved over thallus when dry.

R. subbifurca, R. glauca, R. bifurca, R. beyrichiana. Thallus lobes with marginal cilia if growing under moist conditions; not inflexed over thallus when dry.

R. nigrella, R. sorocarpa. Thallus margins naked; subepidermal cells of thallus lobes thick-walled in *R. sorocarpa.*

28. VAN MELICK (1991): The Netherlands

Van Melick undertook a revision of 1 259 Dutch herbarium collections of *Riccia.* Earlier bryologists in the Netherlands evidently did not have a clear concept of many *Riccia* species as many specimens had been misidentified. Eleven species were retained by him and his classification also follows that of Jovet-Ast (1986), but he comments that there was no 'eenduidige opvatting over de taxonomische indeling van het genus *Riccia*'.

28.1 Genus *Riccia*: plants once to several times dichotomously furcate or in rosettes; dorsal surface of lobes smooth or with stomata-like pores or else with raised epidermal cells, otherwise with crater-like openings; ventral surface of lobes with rhizoids and scales, these laterally displaced with growth of thallus; on t.s. dorsally with wide air chambers enclosed by green walls or with compact, pallisade-like assimilation tissue; ventral tissue parenchyma-like, lacking oil cells; monoicous or dioicous; capsules sunken in thallus.

28.1.1 Subgenus *Riccia*: dorsal side of thallus not spongy, lacking network of small areas, but epidermis with hyaline, round or pear-shaped, generally ephemeral cells; margins without or with cilia; assimilation tissue dorsal, with compact, vertical cell rows, separated by narrow air canals; ventral $^1/_2$–$^2/_3$ of thallus compact storage tissue.

R. crozalsiii. Thallus lobes at margins with more than 20 cilia that arch over thallus when dry.

R. glauca, R. beyrichiana, R. bifurca, R. warnstorfii. Thallus lobes without or with fewer than 20 cilia at margins and not arched over thallus when dry.

R. subbifurca. Thalli scattered, rarely in rosettes.

R. sorocarpa. Thallus lobes with deep, sharp groove; upper epidermis 2-layered, subepidermis with thick-walled cells.

28.1.2 Subgenus *Ricciella*: dorsal side of thallus with obscure or clear network of small areas; epidermis unistratose, sometimes with stoma-like pores, sometimes lacunose; margins of thallus without cilia; assimilation layer composed of loose tissue with two or more irregular layers of large or small air chambers; storage tissue ventral ± $^1/_3$ of thallus.

28.1.2.1 Section *Spongodes*: plants growing on soil; dorsal side of thallus, especially in the older parts, spongy, caused by openings in epidermis; capsules ventrally bulging or not.

R. cavernosa. Thalli light green to yellow-green, turning brown with age; lobes 1.0–2.5 mm wide; groove absent; capsules sunken into thallus or dorsally slightly bulging.

R. huebeneriana. Thalli bright green, mostly with rose to wine-red flecks; lobes 0.3–1.0 mm wide; grooved; capsules bulging ventrally.

28.1.2.2 Section *Ricciella*: plants growing on soil or floating in water; dorsal side of thallus not spongy; epidermis without openings; capsules bulging ventrally.

R. canaliculata. Thallus lobes narrower at tips; ventral scales 1.5–2.0 times wider than high, apical scale reflexed cap-like over dorsal side.

R. *fluitans.* Thallus lobes widening at tips; ventral scales 2–5 times wider than high, apical scale not reflexed cap-like over dorsal side; land form or water form.

Riccia duplex and *R. rhenana* were not accepted as good species, because of the lack of constant diagnostic characters to differentiate them from *R. canaliculata* and *R. fluitans* respectively.

29. VOLK & PEROLD; PEROLD & VOLK; PEROLD (1984–1991): southern Africa

The Ricciaceae of southern Africa continued to be studied by Volk (1979–1984), then by Volk & Perold or by Perold & Volk (1984–1990) and lately by Perold (1991). Several new species were described between them.

In her Ph.D. thesis, Perold (1991a) recognized the following taxa in the Ricciae: subgenus *Riccia*, with two sections, *Riccia* (which was divided into the informal groups, 'Ciliatae' and 'Squamatae') and *Pilifer*, for which Schuster's subgenus *Pteroriccia* had not been adopted, as the composition of the air canals is no different from those in *Riccia*; subgenus *Ricciella* which was also divided into two sections, *Spongodes* (with two groups, 'Crystallina' and 'Vesiculosa'), and *Ricciella*; to subgenus *Chartacea*, *R. schelpei* was assigned and to subgenus *Thallocarpus*, *R. curtisii*, *R. compacta* and *R. perssonii*; section *Pannosae* was elevated to subgenus *Pannosae* (Perold) Perold. (See Perold's proposed classification of sub-Saharan Ricciae on p. 227.)

30. JOVET-AST (1991, 1993): Latin America

Jovet-Ast, in the study of the Ricciae of Latin America, listed the five subgenera previously recognized by her (Jovet-Ast 1986): *Riccia*, *Viridisquamata*, *Ricciella*, *Thallocarpus*, *Leptoriccia* and added a sixth one, *Chartacea*. Only four of these are from the area treated in these works, namely *Riccia*, *Thallocarpus*, *Ricciella* and *Leptoriccia*. In the subgenus *Riccia*, section *Riccia*, she used Stephani's (1898) two units, the Ciliatae and the Inermes, but introduced a refinement by distinguishing a third one, the Papillatae, for species with papillose lobes. Her groups were not given a specified rank and are informal.

30.1 Genus *Riccia*: thalli compact or spongiose; dorsal surface flat or with longitudinal median furrow; margins glabrous, or bearing papillae or cilia; lateral surfaces with scales.

30.1.1 Subgenus *Riccia*: chlorophyllose tissue compact, consisting of cells arranged in vertical rows with narrow air spaces between; epidermal pores simple.

30.1.1.1 Papillatae: margins of thallus lobes with papillae.

R. atromarginata var. *atromarginata*. Margins of lobes obtuse, papillae on the margins and lateral surfaces, 60–210 µm long, smooth.

R. violacea Howe var. *violacea*, *R. violacea* var. *laevis* Ast. Papillae on margins and lateral surfaces of lobes 25–130 µm long, granular or smooth.

R. iodocheila. Margins of lobes acute; papillae rare.

30.1.1.2 Ciliatae: margins of lobes with cilia.

R. horrida Ast, *R. trichocarpa*, *R. subdepilata* Ast, *R. enyae* Ast, *R. cubensis* S.W. Arnell. Lobes mostly abundantly and densely ciliate to base.

R. brasiliensis Schiffn., *R. lindmanii*. Lobes with few, sparse cilia.

30.1.1.3 Inermes: thallus margins glabrous, lacking papillae or cilia.

30.1.1.3a Group 1: *R. albida*. Lobes calcified; spores almost smooth.

30.1.1.3b Group 2: *R. albopunctata* Ast, *R. campbelliana*. Lobes not calcified; with idioblasts.

30.1.1.3c Group 3: *R. nigrella*, *R. boliviensis* Ast, *R. squamata*. Lobes not calcified; lacking idioblasts; scales brilliantly black.

30.1.1.3d Group 4: *R. vitalii* Ast, *R. ridleyi* A.Gepp, *R. wainionis* Steph., *R. ekmanii* S.W. Arnell. Lobes not calcified; lacking idioblasts; scales hyaline or violet; cells with 2 thickened bands.

30.1.1.3e Group 5: lobes not calcified; lacking idioblasts; scales hyaline; cells without thickened bands.

30.1.1.3ea Subgroup 1: *R. mauryana*. Inferior walls of epidermal cells granulose.

30.1.1.3eb Subgroup 2: *R. sanguineisporis* Ast. Inferior walls of epidermal cells smooth; cells of dorsal tissue all with thick walls.

30.1.1.3ec Subgroup 3: *R. sorocarpa*, *R. erythrocarpa* Ast. Inferior walls of epidermal cells smooth; cells of dorsal tissue not all with thick walls.

30.1.1.3ed Subgroup 4: *R. lamellosa*, *R. viannae* Ast. Inferior walls of epidermal cells smooth; cells of dorsal tissue with thin walls; scales white, extending beyond margins of lobes.

30.1.13ee Subgroup 5: *R. ianthina* Ast, *R. subplana* Steph., *R. plano-biconvexa*, *R. grandis* Nees, *R. australis* Steph., *R. taeniaeformis* Ast, *R. fruchartii*, *R. elliottii* Steph., *R. breutelii* Hampe ex Steph., *R. brittonii* Howe, *R. howellii* Howe. Inferior walls of epidermal cells smooth; cells of dorsal tissue with thin walls; scales hyaline or tinted with violet, not extending beyond margins of lobes.

30.1.2 Subgenus *Thallocarpus*: *R. curtisii*. Dorsal tissue with air chambers; dorsal epidermis with pores enclosed by cells, sometimes with lacunae; scales absent; spores fused in tetrad, surrounded by external layer of exine.

30.1.3 Subgenus *Leptoriccia*: *R. membranacea*. Thallus thin, one layer of lacunae and 2 or 3 layers of cells; scales present or reduced or absent; spores free at maturity, spherical, 40–67 µm in diameter, external layer of exine surrounding each spore; sporoderm ornamented with fine spinules.

30.1.4 Subgenus *Ricciella*: thallus thick, up to 15 layers of cells, spongy; spores tetrahedral, diameter greater than 65 µm; sporoderm ornamented with alveoli or tubercles.

30.1.4.1 Section *Spongodes*: thalli spongy, divided into wide lobes; capsules hardly projecting on the two surfaces of lobes; scales small or very reduced or absent.

R. crystallina, *R. cavernosa*. Thalli in rosettes, spongy, 10–35 mm in diameter.

30.1.4.2 Section *Ricciella*: thalli wide and deeply divided or in narrow strips; capsules projecting on ventral surface of lobes; scales small or rarely reaching edge of lobes.

R. frostii, *R. paraguayensis* Spruce. Dioicous; heterothallic; female plants in rosettes.

R. chiapasensis Ast, *R. dussiana* Steph.; *R. geissleriana* Ast, *R. hegewaldiana* Ast. Monoicous; lobes 1.5–4.0 mm wide; grouped together.

R. jovet-astiae Vianna emend. Vianna, *R. crassifrons* Spruce, *R. bahiensis* Steph., *R. stenophylla*, *R. limicola* Ast, *R. paranaensis*. Lobes 0.3–1.5 mm wide.

31. SCHUSTER (1992): North America (and elsewhere)

Schuster (1992a) maintained that infrageneric classifications in the genus *Riccia* were still unresolved. He now adopted a multiple system with eight recognizable subgenera, although he conceded that his attempts at dividing them up into a series of complexes and sections were largely provisional, since he collected chiefly in North America and Europe. He thought that it was up to students residing in the other areas to test the validity of his proposed new sections, and that other sections from Australia and Africa would without doubt have to be recognized. He nevertheless instituted 10 new sections and formally provided them with Latin descriptions and designated type species.

31.1 Genus *Riccia*: plants usually small; closely prostrate, normally on soil, rarely aquatic; annual to perennial; in rosettes or hemirosettes, occasionally gregarious; segments generally with a longitudinal dorsal groove which disappears proximally; thallus structure either with distinct, persistent, rarely disintegrating epidermis with pores, overlying polyhedral air chambers or without a continuous, defined epidermis and aerenchyma with vertical canal-like air chambers; thallus margins naked or with papillae, cilia or setae; ventral scales often inconspicuous; oil bodies absent; antheridia and archegonia sunken into thallus; sporophyte consisting of spherical capsule containing spores.

31.1.1 Subgenus *Riccia*: thalli with photosynthetic tissue compact, arranged in closely contiguous vertical cell rows separated by slender vertical air canals; dorsal epithelial cells breaking down, the hypodermal layer persistent, regularly arranged; scales small to large; cilia or papillae often present; spore release dorsal; spores single.

31.1.1.1 Section *Riccia*: thallus margins blunt or rounded, naked or with short cilia (under 300 µm); lacking specialized oil cells; scales relatively small, usually colourless or vestigial, failing to reach thallus margins; sulcus weakly impressed, soon widening and disappearing posteriorly.

31.1.1.1a Subsection *Riccia*: thalli never calcified and chalk-white dorsally; nearly always forming rosettes; sporangia tending to bulge more on ventral side of thallus than on dorsal; spores polar, with clearly defined wing margins.

R. glauca, *R. hirta*, *R. tenella* Jacobs, *R. bifurca*, *R. warnstorfii*, *R. beyrichiana*, *R. californica*, *R. setigera* R.M. Schust. Monoicous; thalli ciliate or not.

R. ozarkiana McGregor. Dioicous; dorsal sulcus wide.

31.1.1.1b Subsection *Albidae* R.M. Schust.: dorsal surface of thallus calcified, chalk-white; pores open into canals bounded by 5–7 cell rows; deep dorsal groove not widening posteriorly.

R. albida (= ?*R. crustata*). Epithelial cells persistent, tumid or sometimes conoidally inflated, rough with secreted calcium carbonate. This subsection was previously a section in Schuster (1992a).

31.1.1.2 Section *Lamellosae* R.M. Schust.: plants always naked on dorsal surface and margins; epidermal cells usually ephemeral and collapsing to irregular remnants, not thick-walled; dorsal groove sharp and usually ± persistent; scales two-ranked, usually well developed.

R. lamellosa Raddi subsp. *lamellosa*, *R. lamellosa* subsp. *austini* R.M. Schust., *R. andina* Müll.Frib. subsp. *andina*, *R. andina* subsp. *chionophora* R.M. Schust., *R. albolimbata*. Ventral scales hyaline, whitish, projecting beyond thallus margins.

R. albolimbata is a southern African taxon which Schuster now also reports from North America.

Jovet-Ast (1994) found spores in the type specimen of *R. andina* and has concluded that it is synonymous with *R. mauryana*, which Schuster has placed in another section, namely *Sorocarpae*.

R. macallisteri, *R. dictyospora*, *R. nigrella*, *R. campbelliana* Howe subsp. *campbelliana*, *R. campbelliana* subsp. *austrigena* R.M. Schust. Ventral scales not conspicuously projecting beyond moist thallus margins, usually pigmented.

31.1.1.3 Section *Sorocarpae* R.M. Schust.: monoicous; thalli light green; less compact than in section *Sommieri*; epithelial cells with thick bases; hypodermal cells firm; thallus margins lacking cilia; scales two-ranked and small; dorsal groove deep.

R. sorocarpa subsp. *sorocarpa*, *R. sorocarpa* subsp. *arctica* R.M. Schust., *R. sorocarpa* subsp. *erythrophora* R.M. Schust., *R. dorsiverrucosa*, *R. mauryana*. Ventral scales small, obscure, not or hardly imbricate, colourless or castaneous.

In her experience, Jovet-Ast (1994) finds *R. sorocarpa* to be a stable species, although there are certain modifications in the colour of the lobes and scales, in the thickness of the epidermal cell walls and in the diameter of the spores and size of the wing. She states that she is inclined to reject Schuster's subspecies of *R. sorocarpa* as they are based on a very small number of specimens seen by him and that the rank of subspecies is too important to designate to such weak variations.

31.1.1.4 Section *Sommieri* R.M. Schust.: dioicous; thalli deep green, with vertical purple flanks; very compact and

thick; epidermal cells delicate and hypodermal ones strikingly thickened.

R. sommieri. Ventral scales large, imbricate, blackish purple.

31.1.1.5 Section *Atromarginatae* R.M. Schust.: thalli dull, bluish green and deep purple or purple-black laterally; with a tendency to develop both blunt papillae and hyaline sharp, rigid cilia mostly under 80 µm long; spores opaque, nonpolar.

R. atromarginata forma *atromarginata*, *R. atromarginata* forma *glabra* Levier ex Müll.Frib., *R. violacea* var. *violacea* Howe, *R. violacea* var. *iodocheila* (Howe) R.M. Schust., *R. violacea* var. *laevis* R.M. Schust. Ventral scale small, often rudimentary, black-purple; margins sometimes with papilliform cells.

This section evidently consists of highly problematical species, subspecies, varieties and formae that need to be clarified.

31.1.1.6 Section *Ciliiferae* R.M. Schust.: thalli robust; ventrally with large keel and at apices often forming tubers; margins winged, often ciliate; sulcus deep, soon disappearing; scales hyaline, whitish, semicircular.

R. ciliifera, *R. gougetiana*, *R. erinacea* Schiffn., *R. melitensis* (from Malta). Thallus surfaces and margins mostly eciliate or with cilia 100–325 µm long.

Jovet-Ast (1994) doubts whether *R. melitensis* is placed correctly in this section, since it lacks marginal cilia; she also prefers to treat *R. erinacea* as a variety of *R. gougetiana* namely var. *armatissima* Levier ex Müll.Frib., because all its characteristics resemble those of *R. gougetiana*, except for the abundance of bristles.

31.1.1.7 Section *Ciliatae* R.M. Schust.: plants copiously ciliate with tapered, sharp cilia, 300–1000 µm long; median sulcus sharp near apices, soon broadened and shallow; flanks swollen; scales small, hyaline to purplish.

R. ciliata subsp. *ciliata*, *R. ciliata* subsp. *canescens* (Steph.) R.M. Schust., *R. ciliata* subsp. *grisea* R.M. Schust., *R. ciliata* subsp. *trichocarpa* (Howe) R.M. Schust., *R. crinita*. Cilia very thick-walled along at least one side, up to 1150 µm long; flanks usually purplish to purplish black.

Jovet-Ast (1983) has shown that *R. canescens* Steph. is a synonym of *R. trichocarpa* and she finds it unacceptable (Jovet-Ast 1994) that *R. trichocarpa* can be considered a subspecies of *R. ciliata*.

31.1.1.8 Section *Bicarinatae* R.M. Schust.: *R. bicarinata*. Thalli at margins with groups of 2–3 basally connate, thick-walled, sharp, roughened cilia; flanks ascending, blunt at margins; dorsally with sulcus soon widening.

31.1.1.9 Section *Albosquamatae* R.M. Schust.: *R. albosquamata* S.W. Arnell. Thalli without cilia or papillae; ventral scales with regularly oriented, almost quadrate, very firm-walled cells.

Arnell (1957, 1963) had based his description of *R. albosquamata* on two white-scaled species (Perold 1989), *R. albolimbata* and another which was later named *R. argenteolimbata*, using characters from both. *R. albosquamata* is regarded as a synonym of R. *albolimbata*; Schuster did not include this new section *Albosquamatae* in his later treatment (Schuster 1992b).

31.1.2 Subgenus *Ricciella*: most species terricolous or sometimes aquatic; dorsal epidermis chlorophyllose, smooth or with age lacunose; pores present although sometimes vestigial; thallus margins always lacking cilia; air chambers large; ventral scales in a single median row, semilunate, or (if 2-ranked) much reduced; sporophytes releasing spores ventrally or dorsally.

31.1.2.1 Section *Ricciella*: segments narrow and lingulate to linear, under 0.8 mm wide; dorsal epidermis normally persistent, usually perceptibly areolate; pores not enlarging.

R. fluitans, *R. stenophylla*, *R. rhenana*, *R. canaliculata*, *R. duplex*, *R. huebeneriana* subsp. *huebeneriana*, *R. huebeneriana* subsp. *sullivantii* (Austin) R.M. Schust., *R. paranaensis*. Scales remaining in a single median row or soon splitting into 2 rows; capsules protruding ventrally; some species aquatic or land plants.

Schuster (1992b) places *R. perennis* in synonymy under *R. canaliculata*, as Müller (1953–1958) had done before him, but this is emphatically rejected by Jovet-Ast (1994) who states that they are so different in appearance that one can recognize them even with the naked eye.

31.1.2.2 Section *Cavernosae* R.M. Schust.: thalli in rosettes, fleshy and succulent; photosynthetic tissue loose, air chambers large, polyhedral; dorsal epidermis delicate; pores enlarging with age and thallus becoming lacunose.

R. cavernosa, *R. crystallina*. Ventral scales apparently lacking or small and ephemeral.

Schuster (1992a) remarks that his section *Cavernosae* is perhaps identical with Nees's *Spongodes* but he finds the latter ambiguous because it includes both *R. bullosa* and *R. crystallina*. Whether *R. bullosa* remains in section *Spongodes* is not mentioned. Perold (1991a) referred *R. bullosa* to section *Spongodes*, group 'Vesiculosa'.

Schuster (1992b) notes that the prior usage of *R. crystallina* (for *R. cavernosa* sensu Jovet-Ast 1964; 1966) and *R. plana* (for *R. crystallina* sensu Jovet-Ast) was adopted by all workers and should have been preserved by pertinent lectotypification. *Riccia crystallina* has been lectotypified by Perold (1992) with the typotype held at FI and shows that Jovet-Ast was correct after all.

31.1.2.3 Section *Frostii* R.M. Schust.: *R. frostii*. Growing in rosettes; heterothallic with small male plants; photosynthetic tissue relatively compact with air chambers narrow and tall; scales lacking or vestigial; spores dorsally released.

31.1.3 Subgenus *Leptoriccia*: *R. membranacea*. Thalli delicate, exceedingly flat and thin, chiefly consisting of

epidermis and air chambers; ventral tissue vestigial; scales seemingly absent; sporangia ventrally protruding, spores single, spherical, apolar, covered in spines.

31.1.4 Subgenus *Thallocarpus*: dorsal epidermis chlorophyllose, with pores, becoming lacunose; thalli spongy, soft-textured; strongly heterothallic with much smaller male plants; assimilation tissue with large and high air chambers in 1–3 layers; spore release dorsal; spores in tetrads; rhizoids mostly smooth or in part conspicuously tuberculate.

31.1.4.1 Section *Thallocarpus*: thalli with dorsal surface smooth; ventral scales lacking or vestigial; spores of tetrad separated by distinct, ± smooth connecting band; spore surface with spine-like tubercles.

R. curtisii, *R. leptothallus* R.M. Schust., *R. howei* R.M. Schust. Plants forming rosettes or irregularly gregarious, with or without colour dimorphism in the sexes.

31.1.4.2 Section *Chaetoriccia* R.M. Schust.: *R. tomentosa*. Distinct from sect. *Thallocarpus* in (a) thalli dorsally shaggy-haired, with long free-standing filaments formed of elongated cells; (b) ventral scales conspicuous, hyaline, triangular, apices bearing filaments formed of several cells; (c) spore tetrads only obscurely tetrahedral, very closely armed with papillae.

Riccia tomentosa was placed in subgenus *Thallocarpus*, section *Pannosae* by Volk & Perold (1990) and *Pannosae* was later elevated to the rank of subgenus (Perold 1991), but these must have escaped Schuster's notice, when he created the new section *Chaetoriccia* for *R. tomentosa*.

31.1.5 Subgenus *Chartacea*: *R. schelpei*. Dorsal epidermis firm, thick-walled, echlorophyllose; pores conspicuous, surrounded by 5 or 6 small, thin-walled cells elevated above epidermal cells; thallus grooved, margins acute; gametangia limited to groove; spores single.

31.1.6 Subgenus *Micantes*: *R. hirsuta*. Dorsal epidermis densely invested with tapered ciliform (1)2–7-celled 'hairs'; pores obscure; ventral scales large, 2-ranked, shaggy; spores (95)115–125(130) µm in diameter.

As pointed out above, the original description of *R. hirsuta* was based on two distinct, but superficially rather similar species, *R. hirsuta* (section *Pilifer)* and *R. tomentosa* (subgenus *Thallocarpus*, section *Pannosae*, (Volk & Perold 1990)). It is regrettable that the initial mistake by Volk & Perold was perpetuated by Schuster (1992a, b).

31.1.7 Subgenus *Pteroriccia*: epithelial cells in the form of free-standing, independent multicellular uniseriate and often tapered hairs, mostly formed of elongated cells; distal cells of epithelial filaments persistent, typically smaller, often conoidal and/or conspicuously elongated.

R. villosa, *R. parvo-areolata* O.H. Volk & Perold. Mostly with large ventral scales projecting beyond thallus margins.

31.1.8 Subgenus *Viridisquamata*: *R. caroliniana*. Dorsal tissues devoid of chlorophyll, which is almost wholly limited to ventral strata of thallus; ventral surface with bistratose chlorophyllose transverse lamellae in V-shaped configurations, these giving rise to reduced unistratose ventral scales.

31.2 Genus *Ricciocarpus*: *R. natans*. Plants floating, occasionally terrestrial; dorsal surface with distinct pores surrounded by 5 or 6 cells; air chambers large and conspicuous; ventral scales linear, numerous, sword-like; oil bodies present; antheridia sunken in thallus or along median groove.

DISCUSSION

The above treatment has resulted in numerous species being assigned to different sections and groups in the works by Jovet-Ast (1991, 1993), and Schuster (1992a, b). One is also faced with the anomalous situation, that in two articles in the same publication, following directly on one another (Perold 1993; Fischer 1993), the same taxon, *R. vulcanicola* Eb. Fisch., is placed in two different sections, since Perold followed the time-honoured tradition of placing *R. crystallina* (and its allies, in this case *R. vulcanicola*) in section *Spongodes* Nees, whereas Fischer chose to follow Schuster (1992a, b), and placed it in section *Cavernosae*.

Anyone is, of course, free to follow the treatment of their choice, but for later students, it could be very confusing. However laudable the motive for arranging the large number of *Riccia* species into a series of more or less natural complexes or sections, so that they can be more easily 'digested', six of the 11 new sections proposed by Schuster (1992a) in the genus *Riccia* have only one species and four of the subgenera also only have one representative each. So, are we really making progress or are we just proliferating the number of higher ranking taxa, some of which may not stand the test of time? It calls to mind a remark attributed to the late Prof. Tom Harris of Reading University, 'You can always make any genus (or subgenus for that matter) uniform merely by making it monospecific, and thereby defeating the object of classification'.

It is as well to bear in mind Hässel de Menéndez's (1976) cautionary advice, 'since the nomenclatural system does not allow us to abandon completely names which are no longer required, continuing in this way will only result in the accumulation of too many names, each of which will be protected by the Code'.

Until more revisions worldwide have been completed, using methods such as biochemical and DNA analysis, enzyme electrophoresis, multivariate analysis, TEM studies of the ultrastructure of the spore wall, like that of Thaithong (1982), and cultivation experiments, it may be wiser to use informal groups. Once sufficient data have been gathered hepaticologists should come to an agreement in defining the limits of subgenera, sections, species and subspecies in the Ricciae.

I am not well acquainted with the Ricciae of North America, Latin America, the Mediterranean and Australia, but for sub-Saharan Africa, I propose the following classification, which is quite similar to that of Perold (1991), which, being in a thesis, is not widely known or available. As yet, only informal groups are recognized; see also Perold (1995): *A survey of the Ricciaceae of tropical Africa.*

32. PEROLD (1995): sub-Saharan Africa

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

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

32.2.1 Subgenus *Riccia*: thallus dorsally with an epithelium of mostly thin-walled cells, echlorophyllose, uni- or bistratose or bearing free-standing cell pillars; air pores numerous, generally small, regular, intercellular spaces; assimilation tissue compact; thallus margins naked or bearing cilia or mammillate cells; spores single.

32.2.1.1 Section *Riccia*: epithelium uni- or bistratose.

32.2.1.1a Group Ciliatae: *R. trichocarpa*, *R. crozalsii*, *R. microciliata* O.H. Volk & Perold, *R. natalensis*. Epithelium unistratose; thallus margins ciliated.

32.2.1.1b Group Mammillatae: *R. mammifera* O.H. Volk & Perold. Epithelium unistratose; thallus margins, especially at the apex, with a row of mammillate cells.

32.2.1.1c Group Squamatae:

R. sorocarpa, *R. atropurpurea*, *R. lanceolata*, *R. nigerica*. Epithelium uni- or bistratose, generally with some cell walls thickened; thallus margins glabrous; scales not conspicuous.

R. congoana, *R. nigrella*, *R. limbata*, *R. angolensis*, *R. okahandjana*. Epithelial cells without thickened walls; thallus margins glabrous; scales large, dark, black or reddish black, to violet.

R. macrocarpa. Scales brown with violet blotches; idioblasts present throughout thallus. Sérgio (1991) has placed *R. campbelliana* in synonymy under *R. macrocarpa*.

R. pottsiana, *R. runssorensis*, *R. rosea* O.H. Volk & Perold, *R. radicosa*, *R. erubescens* Perold. Scales pink to red; idioblasts absent.

R. albolimbata, *R. alboporosa* Perold, *R. albornata* O.H. Volk & Perold, *R. argenteolimbata* O.H. Volk & Perold, *R. bicolorata* Perold, *R. lamellosa*, *R. montana* Perold, *R. saharensis* Steph. ex Ast, *R. somaliensis* Perold. Scales predominantly white or hyaline, often encrusted with calcium deposits.

32.2.1.1d Group Intermediatae: *R. discolor*, *R. symoensii*. Assimilation tissue medianly compact, air spaces widening toward wings.

32.2.1.2 Section *Pilifer*: epithelium in free-standing 2–5(6)-celled, uniseriate pillars, top cells variously shaped, soon collapsing, not regularly orientated; scales small to large, rounded and smooth at margins, rarely triangular and dentate or apically filiform.

R. alatospora O.H. Volk & Perold, *R. albomarginata* Bisch., *R. albovestita*, *R. ampullacea* Perold, *R. concava* Bisch., *R. elongata* Perold, *R. furfuracea* Perold, *R. hantamensis* Perold, *R. parvo-areolata*, *R. pulveracea* Perold, *R. simii* Perold, *R. trachyglossum* Perold, *R. vitrea* Perold. Scales rounded, margins smooth.

R. hirsuta. Scales triangular, apices split into several loose cellular strands.

R. villosa. Scales triangular, margins dentate.

32.2.2 Subgenus *Ricciella*: thalli dorsally with an epidermis of thin-walled, generally chlorophyllose cells; air pores mostly delimited, well spaced, fewer, often becoing lacunose; assimilation tissue spongy with polyhedral air chambers enclosed by unistratose cell plates; scales mostly hyaline or violet and inconspicuous, distant, often evanescent; sporangia deeply imbedded or bulging somewhat above or below; spores single.

32.2.2.1 Section *Spongodes*: thalli in rosettes; spongy.

32.2.2.1a Group Crystallina: *R. crystallina*, *R. cavernosa*, *R. vulcanicola* Eb. Fisch., *R. moenkemeyeri*, *R. huebeneriana*. Monoicous; spores completely or incompletely reticulate.

32.2.2.1b Group Cupuliferae: *R. cupulifera*, *R. frostii*. Dioicous; heterothallic with smaller male plants; spores foveolate or with vermiculate ridges.

32.2.2.1c Group Vesiculosa: *R. bullosa*, *R. garsidei*, *R. volkii*, *R. rubricollis*. Thalli rarely in rosettes, swollen to somewhat flatter, usually becoming cavernous; dorsally deeply grooved along entire length of branch or only apically; scales small, two-ranked.

32.2.2.2 Section *Ricciella*: plants terricolous or aquatic; thalli not in rosettes; branches linear, strap-shaped or 'ribbon'-like; not cavernous; scales ventral, one-ranked.

R. stricta, *R. purpurascens*. Sporangia bulging conspicuously ventrally.

32.2.3 Subgenus *Leptoriccia*: *R. membranacea*. Thalli thin and flat, ventral tissue vestigial; scales reduced or absent; spores spherical, small, ornamented with fine spinules.

32.2.4 Subgenus *Thallocarpus*: thalli in complete or incomplete rosettes; heterothallic; spores remaining in tetrads.

R. curtisii. Spores joined together by narrow band or ridge into tetrahedral tetrads; ornamentation with slender spicules up to 5 µm long.

R. perssonii. Spores joined by wide band into rhomboidal tetrads; ornamentation with stout spines 10–15 µm long.

32.2.5 Subgenus *Chartacea*: *R. schelpei*. 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.

32.2.6 Subgenus *Pannosae*: *R. tomentosa*. Dorsal epidermis with cellular outgrowths of very tall, hair-like outgrowths; 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 tetrads.

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