

The genus *Riccardia* (Aneuraceae) in Colombia and Ecuador

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Abstract – *Riccardia* is a large genus of thalloid liverworts and notoriously difficult in terms of species recognition. Thirty six species were recognized in the tropical Andes but many of these are not well-defined. In this paper fourteen species are accepted for Colombia and Ecuador; eighteen species and two varieties are reduced to synonymy. Descriptions and illustrations are provided for the accepted species together with a key and data on types, synonymy, geographical distribution, habitat and differentiating characters. *Riccardia palmata* and *R. multifida* are excluded from the flora of Colombia and Ecuador. The new combination *Riccardia latifrons* subsp. *parasitans* (Steph.) Gradst. & Reeb *comb. nov.* is proposed and eighteen new lectotypifications are made.

Andes / liverworts / *Riccardia* / synonymy / taxonomy / tropical America

INTRODUCTION

Riccardia Gray (Aneuraceae) is a large genus of thalloid liverworts with more than 300 accepted species worldwide (Söderström *et al.*, 2016). The genus has not been monographed and it is expected that a worldwide revision may lead to a considerable reduction of the number of accepted species (Preußing *et al.*, 2010). *Riccardia* is distinguished by the pinnately or palmately branched thalli with a rather narrow, 0.3-1.5(-2) mm wide main axis, archegonia and antheridia in two rows on short branches and a thin, four cells thick seta. The genus is closely related to *Aneura* Dumort. and *Lobatiriccardia* (Mizut. & S.Hatt.) Furuki, which differ from *Riccardia* in having broader and less branched thalli (usually more than 2 mm wide) and an 8-15 cells thick seta. In the older literature *Riccardia* is usually included in *Aneura* (e.g., Spruce, 1885; Stephani, 1898-1900).

The *Riccardia* species of Colombia and Ecuador have been studied by Spruce (1885), Stephani (1893, 1998-1900, 1916, 1917-1924), Meenks & De Jong (1985) and Meenks (1987). The latter author recognized 36 species in the tropical Andes, including 29 in Colombia and Ecuador, and provided a key to species together with type citations and brief notes on distribution and habitat. Due to the lack of species descriptions and illustrations, the treatment by Meenks (1987) has been difficult to use and the identities of the species have remained unclear. *Riccardia* species are morphologically highly variable and stable characters for species recognition are few (e.g., Meenks, 1987; Reeb & Bardat, 2014). Many characters

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used in Meenks' key such as growth form, branching pattern, thallus length, color, sexuality, habit and dentation are quite variable; the subdivision in the key into species with erect growth (members of the former genus *Acrostolia* Dumort.) and those with procumbent growth is marred by transitions (see also Spruce, 1885) and has been hard to use.

The difficulties with species identification has prompted us to revisit the taxonomy of *Riccardia* in the tropical Andes. Our study has been carried out in the framework of the project "Flora of the Liverworts and Hornworts of Colombia and Ecuador" (<https://www.researchgate.net/project/Flora-of-the-Liverworts-and-Hornworts-of-Colombia-and-Ecuador>). We have examined the types, as far as available, of almost all the species accepted by Meenks as well as about 150 additional herbarium specimens, most of them from Colombia and Ecuador but including some from neighbouring countries, from BM, G, GOET, MANCH, PC, QCA, STU and U. Our study focused essentially on morphological and anatomical characters but preliminary molecular evidence, available for several species, has also been taken into account (Schäfer-Verwimp *et al.*, 2013; Rabeau *et al.*, 2017; Reeb, in prep.). As a result, we have been able to recognize 14 species in Colombia and Ecuador, much fewer than recognized by Meenks (1987). The latter author had distinguished too many species, often with overlapping characters. Eighteen species and two varieties accepted by Meenks (1987) are reduced here to synonymy. Our treatment deals with all the species recognized by Meenks in the tropical Andes with the exception of *R. glaziovii* (Spruce) Meenks from southeastern Brazil and Bolivia (see under *R. pallida*) and a few additional taxa, most of which were doubtfully distinct. Comments on these taxa are given in the text. For each species accepted here a brief morphological description is provided together with data on types, synonyms, geographical distribution and habitat as well as a brief discussion of differentiating characters and taxonomic affinity. Habitat and distribution data are taken from herbarium labels and from the literature, especially Meenks (1987), Gradstein & Costa (2003), León-Yáñez *et al.* (2006), Schäfer-Verwimp *et al.* (2013) and Gradstein & Uribe-M. (2016). Eighteen taxon names are newly lectotypified following McNeill (2014).

Important characters for identification include shape and size of the main axis, presence or absence of a subepidermis, size of the epidermal cells relative to the inner cells, branching pattern, presence or absence of unistratose wings, size of the wing cells, and sexuality, even though considerable variation may be seen in some of these characters as noted above. In *R. hans-meyeri* and *R. poeppigiana*, for example, branch wings vary considerably in width and are sometimes absent. Direction of branches relative to the main axis varies from widely spreading to obliquely spreading to suberect. Obliquely to widely spreading branches form a "normal", pinnate pattern (varying from 1-4-pinnate) while suberect branches are frequently palmately arranged, e.g. in *R. latifrons* subsp. *parasitans*, *R. poeppigiana* and *R. hymenophytoides*. In aquatic or semi-aquatic plants (*R. cataractarum*), on the other hand, branching may be sparse or rudimentary, and thalli much elongated. *Riccardia poeppigiana* and *R. pallida*, finally, have typically deflexed branches. As to variation in sexuality, *R. regnellii* and *R. fucoides* are usually dioicous but sometimes monoicous whereas *R. hymenophytoides* is normally autoicous but occasionally apparently dioicous. The different sexual phenotypes had in the past usually been described as separate species.

Some important morphological traits had previously been overlooked or had received little attention. For example, *R. aberrans* is well-separated from other species by the densely papillose thallus whereas *R. digitiloba* (= *R. metzgeriiformis*)

and *R. cataractarum* (= *R. paramorum*) are well-characterized by small epidermal cells, 2-3× narrower than inner thallus cells. For identification complete plants including main axis and branches are required. A special problem in *Riccardia* is the fact that thallus cells may become collapsed in herbarium specimens. Meenks (1987) considered older herbarium materials therefore “almost useless for critical examination”. However, as shown by Rico (2011) this problem can be resolved by rehydration of the thallus with sodium hypochlorite.

Since *Riccardia* species are so variable, the present treatment should be considered a tentative one. Nevertheless, we hope that the key presented here may work better than the previous one. Since almost all the species recorded from the tropical Andes were included in this study, our treatment might be used also for other Andean countries. Further work, covering more material and including molecular analysis, is needed to ascertain the correct delimitation and distribution of the species of *Riccardia* in the region.

Key to species of *Riccardia* in Colombia and Ecuador

Two species of *Lobatiriccardia* described from Ecuador (Preußing *et al.*, 2010) are also included in the key since they may be confused with *Riccardia*.

1. Main axis (1.5-)2-5 mm wide, irregularly 1-pinnate, branches mostly very short and wide (ca. 1-2× as long as wide). Archegonia on receptacles at the thallus margin (not on short branches). Seta 8-15 cells thick..... (*Lobatiriccardia*) 2
1. Main axis 0.3-1.5(-2) mm wide, 2-4-pinnate, with short or long branches. Archegonia on short branches. Seta 4 cells thick..... (*Riccardia*) 3
2. Axis more than 10 cells thick in the middle (cross-section). Female receptacles extending beyond the thallus margin. On peaty soil in páramo (Ecuador), 3700-4100 m..... *Lobatiriccardia verdoornioides* Nebel *et al.*
2. Axis thinner, 7-10 cells thick in the middle. Female receptacles not extending beyond the thallus margin. In montane rainforest (southern Ecuador), ca. 1900 m *Lobatiriccardia oberwinkleri* Nebel *et al.*
3. Thallus cells covered by lamellate papillae..... *R. aberrans*
3. Thallus cells smooth.....4
4. Ultimate branches winged (wings 1-6 cells wide, ± unistratose, translucent).... 5
4. Ultimate branches not or scarcely winged (when in doubt try both leads)18
5. Main axis winged (sometimes only partly and very narrowly winged).....6
5. Main axis not winged (when in doubt try both leads)11
6. Plants prostrate, delicate. Axis 3-7 cells thick, dorsal surface of axis flat. Subepidermis lacking.....7
6. Plants ascending to erect, rather robust. Axis (7-)8-25 cells thick, dorsal surface of axis flat to convex. Subepidermis present or absent.....8
7. Branch wings as wide as or wider than the midrib. Surface cells on branches arranged in straight rows. Autoicous (rarely dioicous) *R. leptophylla*
7. Branch wings narrower than the midrib. Surface cells on branches often arranged in oblique rows. Dioicous or paroicous *R. regnellii*

8. Wing margins with ciliate teeth, the teeth 1-5 cells long, consisting of subquadrate to elongate cells. Branches obliquely spreading and short and plump
.....*R. ciliolata*
8. Wing margins entire or with short teeth, the teeth 0.5-1 cell long, consisting of a subquadrate cell. Branches widely spreading and long and slender, or obliquely spreading and short and plump9
9. Plants irregularly 1-2(-3)-pinnate. Axis very broad, mostly (0.8-)1-2 mm wide, plano-convex, gradually broadened towards the branch bases. Branches suberect to obliquely spreading, not deflexed, short and plump with a broad apex, branch base decurrent. Branch apex often with gemmae*R. wallisii*
9. Plants regularly 2-4-pinnate. Axis less than 1 mm wide, biconvex to rounded, not gradually broadened towards the branch bases. Branches widely spreading, often deflexed, long and slender, linear to subulate, branch base not decurrent. Gemmae absent 10
10. Wing cells large, 35-50 μm wide. All branches broadly winged. Wings of ultimate branches wider than the midrib.....*R. fucoidea*
10. Wing cells smaller, 20-30 μm wide. Primary branches narrowly and interruptedly winged. Wings of ultimate branches narrower than the midrib.*R. pallida*
11. Axis with a subepidermis (sometimes only weakly developed in *R. poeppigiana*). Plants erect or ascending, 2-4-pinnate, primary branches opposite or alternate12
11. Axis without subepidermis. Plants creeping or ascending, 1-3-pinnate, primary branches usually alternate13
12. Branches usually decurved, narrowed to the tip, ultimate branches winged but primary branches \pm without wing, wing cells 15-30(-35) μm wide*R. poeppigiana*
12. Branches straight, not narrowed to the tip, all branches regularly and broadly winged, wing cells 35-50 μm wide.....*R. fucoidea*
13. Stoloniform branches (\pm rounded in cross section) present in the lower half of the thallus. Branching in the upper half of the thallus palmate*R. hymenophytoides*
13. Stoloniform branches lacking, all branches clearly flattened. Branching mostly pinnate14
14. Axis broad, 0.8-2 mm wide. Branches short and plump, suberect to obliquely spreading, bases decurrent.....*R. wallisii*
14. Axis narrower, 0.3-0.8 mm wide. Branches linear or tongue-shaped, rather widely spreading15
15. Branch wings 2-5 cells wide, surface cells on branches often arranged in oblique rows. Branches often tongue-shaped. In lowland and montane forests, up to the páramo*R. regnellii*
15. Branch wings 1-2(-3) cells wide (wings lacking in older parts of the thallus), surface cells on branches in straight rows. Branches linear, rarely tongue-shaped. In upper montane forest and páramo, above 2000 m16
16. Epidermal cells distinctly narrower (2-3 \times) than medullary cells. Main axis rather thin, 4-7 cells thick, dorsal surface flat or concave. Gemmae absent. Rare species 17

16. Epidemis cells not or scarcely narrower than medullary cells. Main axis 6-12 cells thick, dorsal surface convex. Gemmae present. Very common in páramo *R. hans-meyeri*
17. Semi-aquatic, often growing submerged. Dioicous. Thallus elongate, to 5 cm long, remotely pinnate, branches mostly very short or reduced, linear, most branches without wing. Sexual branches winged *R. cataractarum*
17. On soil or rock, not semi-aquatic. Autoicous. Thallus shorter, 1-2 cm long, rather densely branched. Branches well-developed, long, linear or tongue-shaped, all branches narrowly winged. Sexual branches without wing *R. chamedryfolia*
18. Axis with a subepidermis. [Dioicous. Branches often decurved, long-linear or lanceolate. Epidermal cells \pm as wide as inner cells] *R. poeppigiana*
18. Axis without subepidermis 19
19. Monoicous, usually paroicous (with a small male branch at the base of the female branch). Branching in upper part of thallus palmate, branches linear to lanceolate. Epidermal cells on ultimate branches arranged in oblique rows. Main axis stoloniform [1-2 \times wider than high, biconvex to rounded]. Gemmae absent. Common in páramo *R. latifrons* subsp. *parasitans*
19. Dioicous, often sterile. Branching not palmate, all branches linear. Epidermal cells on ultimate branches arranged in straight rows. Main axis not stoloniform. Gemmae present or lacking 20
20. Epidermal cells not or scarcely narrower than medullary cells. Plants \pm symmetrically pinnate. Gemmae usually present. In páramo, common *R. hans-meyeri*
20. Epidermal cells distinctly narrower (2-3 \times) than medullary cells. Plants asymmetrically pinnate (branches varying considerably in length) 21
21. Gemmae absent. Axis thin, 4-6(-7) cells thick, upper surface flat (axis sometimes thicker at the base, biconvex). Sexual branches winged. Submerged in lakes or in marshes in páramo *R. cataractarum*
21. Gemmae present. Axis thicker, 6-12 cells thick, upper surface convex. Sexual branches not winged. In lowland or montane forest areas, below 3000 m, not growing submerged *R. digitiloba*

Riccardia aberrans* (Steph.) Gradst.*Figs 1-8**

Aneura aberrans Steph. – Type: Colombia, Antioquía, *Wallis s.n.* (lectotype, G-00282986!, designated here).

On very humid, shaded soil and between *Sphagnum* in shrubby páramo, ca. 2700-3600 m, apparently rare; in Colombia recorded from Antioquía (type) and Quindío (new), in Ecuador from Zamora Chinchipe (new). All further records of the species are probably erroneous and need to be checked (see below).

General distribution: northern Andes.

Plants monoicous, yellowish-green, rather robust, 2-4 cm long, irregularly 2(-3)-pinnate, branches alternate or opposite, curved downwards in older portions of stem. Axis plano-convex to slightly biconvex, 12-13 cells thick, inner cells large, thin-walled, hyaline, walls slightly thickened and brownish towards the epidermis and in internal parts of older thalli, a weak subepidermis of 1-2 cell-layers present, axis narrowly winged (wing 0-2 cells wide), wing becoming wider and more conspicuous towards the branch bases. Branches short and plump, obliquely

spreading, interruptedly winged, the wings lobed-undulate, to 5 cells wide, wing margins crenate or with a few teeth, wing cells thin-walled and very transparent, ca. 2× larger than epidermal cells. Thallus cells without oil bodies. Outer walls of epidermal cells densely lamellate-papillose. Gemmae not observed.

Riccardia aberrans is a very distinct but rare species that is readily recognized by the numerous lamellate papillae on the thallus surface. The papillae are particularly conspicuous on the hyaline wing cells of the branches and are protuberant on the margins. Another unique character of the species is the lack of oil bodies (observed in fresh material from Quindío, *Gradstein 12733*). By its papillose thallus surface *R. aberrans* is similar to *R. crassa* (Schwägr.) Nees from southern South America and Australasia and *R. aspera* Steph. from New Guinea. The species was misinterpreted by Meenks (1987) who apparently overlooked the presence of papillae. Specimens identified by the latter author as *R. aberrans* belong to *R. pallida* (collections from Peru) or *R. wallisii* (collections from Colombia).

Further specimens examined: **Colombia.** Quindío: Calarcá, páramo El Campanario, 4 May 2018, *Gradstein 12733* (HUQ). **Ecuador.** Zamora Chinchipe: Reserva Biológica San Francisco, *Holz 536* (QCA).

***Riccardia cataractarum* (Spruce) Schiffn.**

Figs 9-15

Aneura cataractarum Spruce – Type: Paraguay, «roches humides de la cascade de Mobatobi», June 1881, *Balansa 4245*, c. gyn. (lectotype MANCH!, designated here; isolectotype G-282999!). Further syntypes are listed in Meenks (1987). Since the specimen *Balansa 4245* is fertile (female) and fits the protologue well, it is chosen here as the lectotype.

Aneura uleana Steph. – Type: Brazil, Itajahi, “schattige Quelle”, *Ule 64*, c. andr. (lectotype G-00282959!, designated by Meenks, 1987; isolectotype G-002829658!).

Riccardia paramorum Meenks **syn. nov.** – Type: Colombia, Cundinamarca, páramo de Palacio, Lagunas de Buitrago, 3580 m, submerged in lake, 25 May 1972, *Cleef 4115* (holotype COL; isotypes G-417637!, U-0033761!).

Submerged in lakes and marshes and on wet soil in páramo, 3400-4000 m; in Colombia recorded from Boyacá, Cundinamarca and Meta, in Ecuador (new) from Napo (páramo Guamani). Elsewhere in the Neotropics the species has been recorded from lower elevations (130-3325 m), from lakes, ponds, bogs, marshes and wet rock in waterfalls (Meenks, 1987).

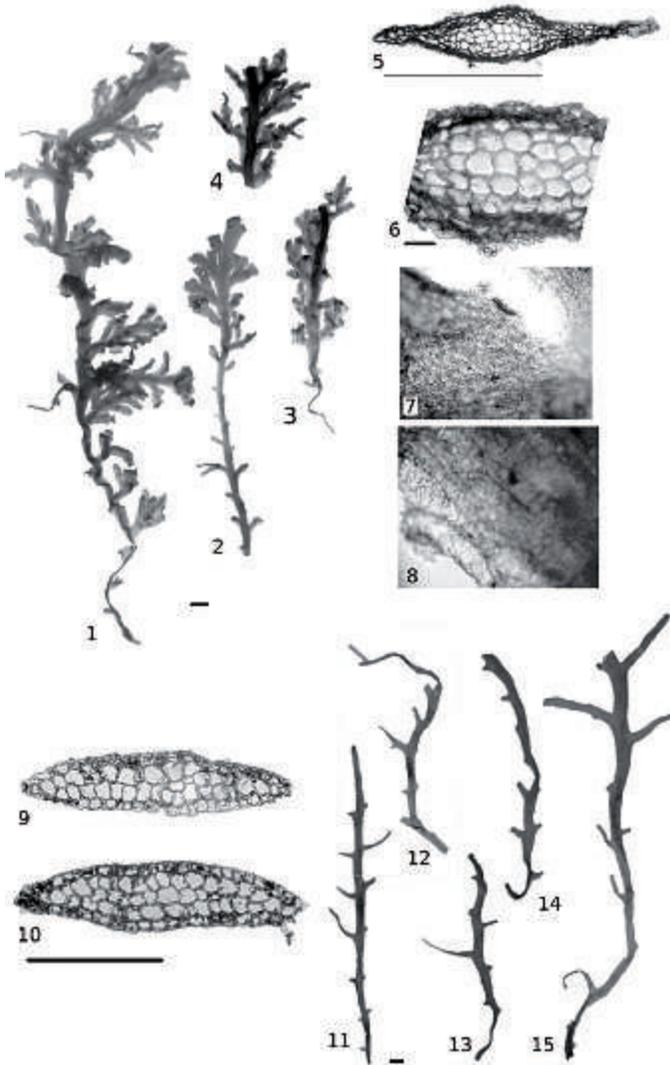
General distribution: West Indies (Dominican Republic, Dominica, Martinique), tropical Andes (Colombia to Bolivia), southern Brazil, Paraguay; probably more widespread and overlooked.

Further illustration: Gradstein & Costa (2003, Fig. 89F-G).

Plants dioicous, pale green to dark brown, 1-5 cm long, land form densely and irregularly 2-pinnate with short and long branches, water forms conspicuously elongate and distantly and often sparsely 2-pinnate, branches often short or rudimentary developed, wingless or with very narrow wings. Main axis planoconvex to slightly elliptical, 4-6(-7) cells thick, sometimes with a short biconvex base (10-15 cells thick) but soon becoming thin, cell walls thin or slightly thickened, epidermal cells ca. 2-5× longer than wide, flat (not mamilliose), much narrower (2-3×) than medullary cells in cross section, walls colorless to brownish, medullary walls ± colorless. Branches alternate to subopposite, highly variable in length and width, varying from short and broad (leaf-like) to long linear, wingless or with very narrow, 1-2-cells wide wings, margins entire, apex rounded or retuse, papillae

scattered on the ventral surface of the branches. Male branches and female branches usually winged. Gemmae not observed.

Riccardia cataractarum is a semi-aquatic species that is recognized by the elongate (to 5 cm long), rather flat and thin, irregularly 2-pinnate and more or less



Figs 1-15. *Riccardia aberrans* and *R. cataractarum*. – 1-8. *Riccardia aberrans*. 1-4. Habit. 5. Cross section of the main axis, middle. 6. Midportion of cross section of the main axis. 7-8. Portion of thallus surface, showing striate-papillose cells. – 9-15. *Riccardia cataractarum*. 9-10. Cross section of the main axis, middle. 11-15. Habit. (1-8 from Holz 536; 9-15 from isotype of *R. paramorum*). Scale bars: 1-4 = 1 mm, 5, 11-15 = 0.5 mm, 6 = 0.05 mm, 9-10 = 0.25 mm.

wingless, dioicous thalli with a small-celled epidermis (2-3× narrower than inner cells) and winged sexual branches. Sometimes the basal portion of the axis of primary branch is swollen and biconvex. The species exists as a water form and a land form; the water form is more elongate and less branched than the land form.

Further specimens examined: **Colombia.** Boyacá: páramo de la Sarna, *Cleef 9410* (GOET, U); Sierra Nevado del Cocuy, Ritacuba, *Bischler 2743* (PC), *ibid.*, Playitas, *Bischler 2888* (PC). **Ecuador.** Napo: páramo Guamani, wet páramo, *Meenks & De Vries 208* (QCA).

Riccardia chamedryfolia (With.) Grolle

Figs 16-22

Jungermannia chamedryfolia With. – Type: England (Grolle, 1976).

Riccardia pinnatifida (F. Weber) Trevis.

Riccardia sinuata (Hook.) Trevis.

Riccardia foliacea Meenks & C. De Jong **syn. nov.** – Type: Ecuador, Napo, páramo de Guamani, 4000 m, April 1982, *Meenks & De Vries 214*, very sparse, c. gyn. (holotype U-0033759!; isotype QCA-203238!).

On moist soil or rock in upper montane forest and páramo, 2700-4000 m; in Colombia recorded from Cundinamarca (Gottsche, 1864), in Ecuador from Loja (Schäfer-Verwimp *et al.*, 2013) and Pichincha (new).

General distribution: widespread in temperate regions of the Northern Hemisphere, scattered in the Tropics; in the Neotropics recorded from the West Indies, Brazil and a few times from the northern Andes.

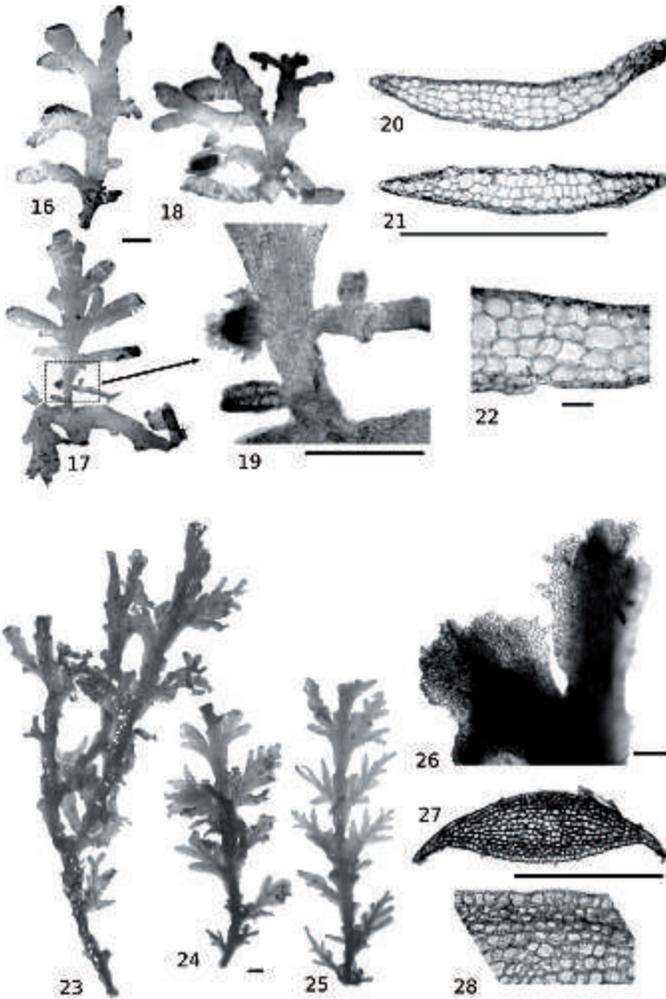
Further illustrations: Gradstein & Costa (2003, Fig. 89F-G), Paton (1999, Fig. 272), Schuster (1992, Fig. 883).

Plants monoicous, rather small, 1-2 cm long, 0.3-0.6 mm wide, prostrate, irregularly 1(-2)-pinnate, without stolons. Main axis without wing (rarely narrowly winged), 4-7(-8) cells thick, with flat to slightly concave dorsal side and convex ventral side, all cells thin-walled, epidermal cells smaller than medullary cells. Branches linear or tongue-shaped, with rounded to retuse tips, ultimate branches narrowly winged (wings lacking in older parts of the thallus), wings 1-2(-3) cells wide, margins entire. Oil bodies present in all epidermal cells, finely granular. Gemmae not observed.

Riccardia chamedryfolia has been overlooked in the northern Andes and is probably not rare in páramo. Its presence in the region, where it was first recorded by Gottsche (1864), has been confirmed by DNA sequences (Schäfer-Verwimp *et al.*, 2013). The species may be confused with *R. hans-meyeri* and *R. cataractarum* but the latter two species are dioicous. *Riccardia hans-meyeri* furthermore differs in the thicker axis with epidermal cells not or scarcely smaller than inner cells and more or less mamillate as well as the frequent presence of gemmae, and *R. cataractarum* by semi-aquatic growth, more elongate and much less branched thalli and winged sexual branches.

Riccardia foliacea is placed in the synonymy in *R. chamedryfolia* because of its plano-convex axis with epidermal cells smaller than medullary cells and its winged branches. The type material of *R. foliacea* is very scanty and contains only thalli with gynoecia; androecia have not been seen. The species was described because of its shortly tongue-shaped branches. The value of this character is dubious, however, as normal, linear branches also occur in this plant.

Further Andean specimens examined: **Ecuador.** Pichincha: páramo de Pichincha, ca. 4000 m, *Balslev & De Vries 3917* (QCA), *ibid.*, *Burghardt et al. 6662* (QCA, PC); Loja: Parque Nacional Podocarpus, above Cajanuma, 2880 m, *Schäfer-Verwimp & Nebel 31841* (QCA).



Figs 16-28. *Riccardia chamedryfolia* and *R. ciliolata*. – 16-22. *Riccardia chamedryfolia*. 16-18. Habit. 19. Portion of habit, showing male and female branch. 20. Cross section of the main axis, middle. 21. Cross section of ultimate branch. 22. Midportion of cross section of the main axis, middle. – 23-28. *Riccardia ciliolata*. 23-25. Habit. 26. Branches showing ciliate wings. 27. Cross section of the main axis, middle. 28. Midportion of cross section of the main axis, showing subepidermal and larger epidermal cells (16-22 from Schäfer-Verwimp & Nebel 31841; 23-28 from Schäfer-Verwimp & Nebel 31879). Scale bars: 16-18, 19, 23-25 = 1 mm, 20-21, 26-27 = 0.5 mm, 22 = 0.05 mm.

***Riccardia ciliolata* (Spruce) Horik.**

Figs 23-28

Aneura ciliolata Spruce – Type: Ecuador, Mt. Mulmúl, *Spruce s.n.* (lectotype MANCH, designated by Meenks, 1987).

On bark, rotten wood and humus, 2650-3750 m; in Colombia recorded from Antioquía, Arauca, Boyacá, Cauca, Chocó, Cundinamarca, Meta, Quindío (new) and Risaralda; in Ecuador recorded from Loja and Tunguragua.

General distribution: tropical Andes.

Further illustration: Spruce (1885, Pl. XIX).

Plants dioicous, robust, 3-10 cm long, 2-pinnate, branches obliquely spreading, short and plump. Main axis irregularly and narrowly winged, biconvex, 10-15 cells thick, with a subepidermis, dorsal epidermal cells \pm larger than subepidermal cells. Branches with a broad midrib and with narrow, irregular wings, apex of branches rounded to emarginate, wings on ultimate branches to 5 cells broad, wing cells 25-40 μ m wide, irregularly elongate-hexagonal, cells becoming conspicuously smaller to the margin, the margins sharply toothed by 1-5-cells long cilia made up of subquadrate to elongate cells. Oil bodies present in most epidermal cells, 4-7 per cell, but rare or absent in wing cells (Meenks & De Jong, 1985). Gemmae frequently present.

A very distinct species recognized by the robust thalli with obliquely spreading, short and plump, irregularly winged branches with sharply toothed-ciliate margins, the cilia being 1-5-cells long and made up of subquadrate to elongate cells.

Specimens examined: **Colombia.** Arauca: Sierra Nevada del Cocuy, Cleef 10168 (COL, GOET, U); Boyacá: El Arenal, Aguirre & Gradstein s.n. (GOET, U); Meta: Valencia, Bischler 1016 (PC); Quindío: Calarcá, páramo El Campanario, abundant, Gradstein s.n. (HUQ). **Ecuador.** Loja: Cajanuma, Schäfer-Verwimp & Nebel 31873, 31879 (QCA), *ibid.*, Burghardt et al. 7219 (QCA).

Riccardia digitiloba (Spruce) Pagán

Figs 42-50

Aneura digitiloba Spruce – Type: Brazil, Rio de Janeiro, Glaziou 7228, c.gyn. (isotypes G-00283000!, G-00283001!, G-00283002!, G-00283003!).

Riccardia calcarea (Steph.) Meenks (*Aneura calcarea* Steph.) **syn. nov.** – Type: Venezuela, Tovar, Goebel s.n. (lectotype G-00283006!, designated here).

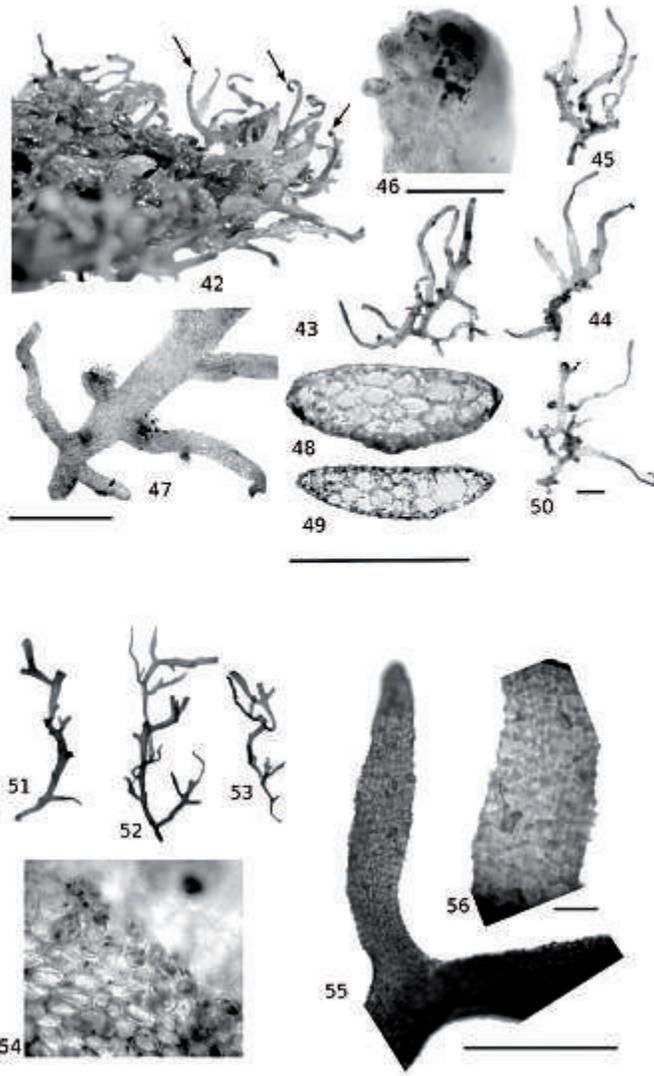
Riccardia metzgeriiformis (Steph.) R.M.Schust. (*Aneura metzgeriiformis* Steph.) **syn. nov.** – Type: Brazil, Rio de Janeiro, Glaziou 4566 (lectotype G-00282969!, designated here).

On rotten wood, tree base and rock in shaded and humid sites in lowland and montane forests, from sea level to ca. 3000 m; in Colombia recorded from Cundinamarca, Huila, Magdalena and Quindío; in Ecuador from El Oro, Loja, Napo, Pastaza (new) and Zamora Chinchipe.

General distribution: tropical America.

Plants dioicous, delicate, to 1 cm long, pale-green, prostrate, irregularly 2-pinnate to dichotomous, branches different in length, linear, sometimes becoming very long and attenuate (narrowed to the apex) and producing gemmae at the tip, branch bases sometimes rounded, stolon-like. Main axis without wing, ellipsoid, ca. 6-12 cells thick, medullary cells large, thin-walled, epidermal cells 3-4 \times smaller than medullary cells, thin-walled or somewhat thick-walled, sometimes a few large, swollen epidermal cells occurring mixed with the small epidermal cells. Branches linear, without wing or, occasionally, with a very narrow, 1(-2)-cells wide wing, margins \pm straight, apex rounded, straight or recurved. Sexual branches winged, sometimes prolonged by sterile innovations. Calyptra surface almost smooth. Gemmae usually abundantly produced at the thallus tips.

The small-celled epidermis and the delicate, pinnate to dichotomous thalli with linear, wingless or rudimentarily winged branches producing gemmae at the tips are the principal characters of *Riccardia digitiloba*. The large, hyaline medullary cells are readily visible below the small-celled epidermis, without cross sectioning. The gemmiparous branches are sometimes tapering to narrow tips. *Riccardia*



Figs 42-56. *Riccardia digitiloba* and *R. hans-meyeri*. – 42-50. *Riccardia digitiloba*. 42. Habit of a population, showing curved branch tips producing gemmae (arrows). 43-45, 50. Habit. 46. Branch tip with gemmae. 47. Portion of habit, showing two gynoecia, one gynoecium with a long innovation. 48. Cross section of the main axis, middle. 49. Cross section of ultimate branch. – 51-56. *Riccardia hans-meyeri*. 51-53. Habit. 54. Detail of branch surface with gemmae. 55-56. Branches with mamillate projections (42-50 from *Gradstein & Varón 11072*; 51-53, 55-56 from *Nebel & Kottke 03118*; 54 from *Price 20*). Scale bars: 43-45, 47, 50, 51-53, 55 = 0.5 mm, 46, 48-49 = 0.25 mm, 56 = 0.1 mm.

metzgeriiformis is a rather robust phenotype of *R. digitiloba* and *R. calcarea* is a very delicate phenotype.

The illustration of *R. digitiloba* in *Gradstein & Costa (2003)* showing an autoicous thallus with plump branches and a sporophyte arising from the dorsal surface of the thallus, is erroneous.

Further specimens examined: **Colombia.** Cauca: Gorgona I., 25 m, *Gradstein & Varón 11072* (GOET, PC). **Ecuador.** Loja: Parque Nacional Podocarpus, Cajanuma, 2900 m, *Nebel & Kottke 031340* (QCA); Pastaza: Baños-Puyo road, *Thiers 4719* (QCA). **Peru.** San Martín: Mt. Campana, *Spruce s.n.* (MANCH).

Riccardia fucoidea (Sw.) C.Massal.

Figs 29-41

Jungermannia fucoidea Sw. (*Aneura fucoidea* (Sw.) Spruce) – Type: Jamaica, *Swartz s.n.* (lectotype S-B25923!, designated here).

Riccardia andina (Spruce) Herzog (*Aneura andina* Spruce) **syn. nov.** – Type: Ecuador, Río Bombanasa, *Spruce s.n.* (lectotype MANCH n.v., designated by Meenks, 1987; isolectotype G-00283009!).

Riccardia bogotensis (Gottsche) Pagán (*Pseudoneura bogotensis* Gottsche, *Aneura bogotensis* [Gottsche] Steph.) **syn. nov.** – Type: Colombia, Cundinamarca, San Antonio, 1900 m, June 1860, *Lindig 1731* (isotype PC-0101708!).

Riccardia crassicaulis (Steph.) Meenks & C.De Jong (*Aneura crassicaulis* Steph.) **syn. nov.** – Type: Bolivia, Río Tocorani, 2200 m, *Herzog 4029* (lectotype G-00282978!, designated by Meenks, 1987).

Riccardia lepidomitra (Spruce) Gradst. (*Aneura lepidomitra* Spruce) **syn. nov.** – Type: Ecuador, Mt. Guayrapata, 2800 m, *Spruce H86* (lectotype MANCH!, designated here).

Riccardia papillata (Gottsche) Gradst. & Hekking (*Pseudoneura papillata* Gottsche, *Aneura papillata* [Gottsche] Steph.) **syn. nov.** – Type: Colombia, Manzanos, 2700 m, July 1860, *Lindig 1734* (lectotype PC-0101705!, designated here).

Riccardia plumiformis (Spruce) Meenks (*Aneura plumiformis* Spruce) **syn. nov.** – Type: Ecuador, Mt. Abitagua, *Spruce s.n.* (lectotype MANCH-cc2032!, designated by Meenks, 1987; isolectotype G-00282963!).

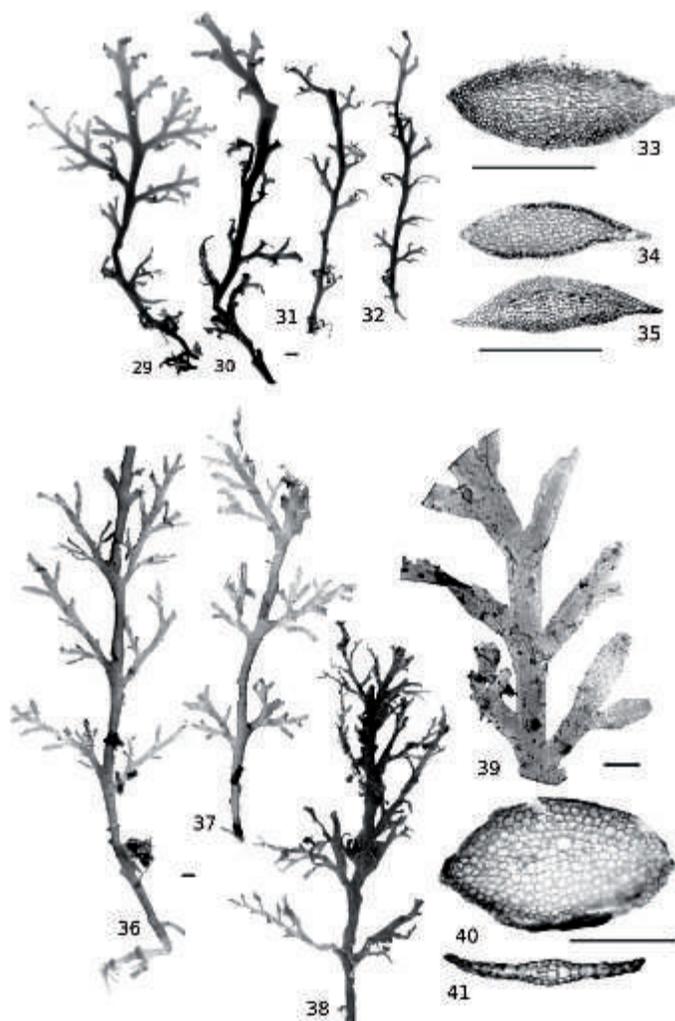
On humic soil, bark, rotten wood and rock in submontane and montane rainforests, cloudforests and páramo, (300-)1000-3900 m; in Colombia recorded from Antioquía, Boyacá, Cauca, Chocó, Huila, Magdalena, Meta, Nariño, Putumayo, Quindío, Risaralda, Santander and Tolima; in Ecuador recorded from Carchi (new), Loja (new), Los Ríos, Napo, Pastaza, Pichincha, Tunguragua and Zamora Chinchipe.

General distribution: tropical America.

Further illustration: Gradstein *et al.* (2001, Fig. 67E-F), Gradstein & Costa (2003, Fig. 88A-D).

Plants dioicous, rarely monoicous, growing upright, rather robust (but varying greatly in length), 2-10 cm long, regularly or irregularly (2-)3-4-pinnate, primary branches often subopposite, spreading at straight or oblique angles, branches usually straight (rarely deflexed), stolons present at the base. Main axis robust, biconvex to rounded, 10-25 cells thick, with a subepidermis, without wing or slightly winged at branch bases, rarely narrowly and interruptedly winged, margins entire, epidermal cells usually smaller than inner cells. Branches linear, straight, margins entire to crenate to toothed, with broad, transparent wings, the wings of ultimate branches wider than the midrib, wing cells large, ca. 35-50 µm wide and 40-75 µm long, hexagonal, thin-walled or slightly thickened, in straight rows. Male branches winged, margins crenate. Calyptra irregularly hairy. Gemmae not observed.

Riccardia fucoidea is a common neotropical-montane species that is readily recognized by the rather robust, ascending, regularly 3-4-pinnate thalli with a thick, rounded axis without wing or rudimentarily winged, all branches broadly winged, the wings 3-7 cells wide, made up of large hexagonal cells, ca. 35-50 µm wide, wings broader than the midrib on ultimate branches and with entire or toothed



Figs 29-41. *Riccardia fucoidea*. 29-32. Habit. 33. Cross section of the main axis, middle. 34-35. Cross section of a secondary branch. 36-38. Habit. 39. Detail of habit, showing axis and branches. 40. Cross section of the main axis, middle. 41. Cross section of ultimate branch. (29-35 from Holz 358; 36-41 from Burghardt 7011). Scale bars: 29-32, 36-39 = 1 mm, 33-35, 40-41 = 0.5 mm.

margins. Phenotypes of *R. fucoidea* with rudimentary wings on the axis can be confused with *R. pallida* but the branch wings in *R. pallida* are made up of smaller cells, 20-30 μm wide, and the wings are narrower, 2-4 cells wide, not wider than the midrib and usually only rudimentarily developed on the primary branches. Moreover, we have not observed stolons in *R. pallida*.

Riccardia andina and *R. lepidomitra* are small-sized phenotypes of *R. fucoidea*, *R. plumiformis* is a phenotype with primary branches spreading at oblique angles, *R. crassicaulis* is a phenotype with a very thick and slightly winged axis and *R. bogotensis* is a monoicous phenotype. *Riccardia papillata*, a further synonym of

R. fucoidea, was described based on three Lindig collections from Colombia (Manzanos, Lindig 1734; Fusagasuga, Lindig 2904; Cipacon, Lindig 1748). We have examined the syntypes from Manzanos and Fusagasuga (the specimen from Cipacon could not be traced) and found that the Manzanos material belongs to *R. fucoidea* whereas the Fusagasuga material belongs to *R. poeppigiana*. Since sporophytes, which were described in the protologue, are only present in the material from Manzanos we have selected this material as the lectotype.

Selected further specimens examined: Ecuador. Carchi: Awá reserve, 1330 m, Hoover et al. 2890 (QCA); páramo El Angel, Thiers 4453 (QCA). Loja: Parque Nacional Podocarpus, Cajanuma, Schäfer-Verwimp & Nebel 31760 (QCA), ibid., Burghardt 7011 (PC, QCA); Zamora Chinchipe: Reserva Biológica San Francisco, Holz 358, 501 (QCA), ibid., Burghardt 7212 (QCA), ibid., Sauer & Gradstein 146 (QCA).

Riccardia hans-meyeri (Steph.) Meenks & C.De Jong

Figs 51-56

Aneura hans-meyeri Steph. – Type: Ecuador, Chimborazo, El Altar, páramo region, 4000 m, H. Meyer 4223 (lectotype G-00282974!, designated by Meenks, 1987).

Riccardia hans-meyeri var. *dentata* Meenks **syn. nov.** – Type: Colombia, Cauca, Puracé, Laguna de San Rafael, 3315 m, 6 January 1972, Cleef & Fernandez 550e (holotype COL; isotype U!).

Riccardia columbica (Steph.) Gradst. & Hekking (*Aneura columbica* Steph.) **syn. nov.** – Type: Colombia, Primavera, 1904, Raap s.n. (lectotype G-00282979!, designated here).

On moist, humic soil, rotten wood and bogs in montane cloud forests and páramo, occasionally in running water, 2700-4500 m; in Colombia recorded from Boyacá, Cauca, Chocó, Huila, Meta, Quindío and Risaralda; in Ecuador from Azuay (new), Carchi (new), Chimborazo, Cotopaxi (new), Loja (new), Morona Santiago, Pichincha and Zamora Chinchipe.

General distribution: northern Andes.

Plants dioicous, small, 0.5-1.5 mm long, axis very slender, 0.2-0.6 mm wide, prostrate or growing upright in dense mats, regularly 2-pinnate, branches linear, obliquely to widely spreading, alternate or subopposite, little narrower than the axis, cells the thallus surface flat or mamilllose, sometimes with projecting tips (especially on the ventral thallus surface), walls thin or slightly thickened, especially the transverse walls. Main axis without wing, biconvex, 6-12(-17) cells thick, without subepidermis, dorsal and ventral epidermal cells similar in size and scarcely smaller than medullary cells, often with brownish walls in older portions of the thallus, medullary cells with colorless or yellowish walls, thin or thickened. Branches linear, plano-convex, margins entire to crenate, apex rounded or retuse, often recurved, wings present or absent, 0-2(-3) cells wide, marginal wing cells sometimes enlarged, walls thin-walled or thickened. Oil bodies present in all epidermal cells, 1-2(-8?) per cell. Mucilage papillae present on ventral surface of branches and occasionally also on the dorsal surface. Gemmae frequently produced at the retuse thallus tips, 2-celled, thin-walled.

Riccardia hans-meyeri is a characteristic species of páramo that is recognized by the delicate, creeping, regularly or irregularly 2-pinnate, dioicous thalli with narrowly winged or wingless branches, and by the biconvex axis with epidermal cells scarcely smaller than inner cells. The epidermal cells are sometimes mamilllose and the walls of the epidermal cells can be colorless or brownish pigmented, and thin or somewhat thickened. *Riccardia hans-meyeri* can be confused with *R. latifrons* subsp. *parasitans*, which is also common in páramo, but *R. latifrons* subsp.

parasitans differs in palmate branching, paroicous sexuality, and epidermal cells of the main axis usually narrower than inner cells and orientated obliquely towards the thallus margin on ultimate branches.

Riccardia columbica, recorded a few times from Colombia, is a small phenotype of *R. hans-meyeri* with plants only 5 mm long. The voucher specimen of *R. columbica* cited in Gradstein & Uribe (2016) has a thin and broadly winged thallus with male and female branches growing mixed, and irregular branching with some tongue-shaped branches, and belongs to *R. regnellii*.

Further specimens examined: **Colombia.** Boyacá: Sierra Nevada del Cocuy, *Bischler* 2793, 2834 (with stoloniform axis), 2999 (PC); Quindío: Calarcá, páramo El Campanario, *Gradstein* 12732 (HUQ). **Ecuador.** Azuay: El Cajas, *Price* 20 (QCA); Carchi: páramo El Angel, *Ramsay et al.* 2006, 2024 (QCA), *ibid.*, *Thiers* 4438 (PC, QCA); Cotopaxi: Parque Nacional Llanganates, *Burghardt* 6719 (QCA); Loja: Parque Nacional Podocarpus, Cajanuma, *Nebel & Kottke* 031118, 031119 (QCA); Napo: páramo de Guamani, *Meenks* 235 (GOET, U); Pichincha: páramo de Pichincha, *Burghardt et al.* 6654, 6673 (QCA).

***Riccardia hymenophytoides* (Spruce) Meenks**

Figs 57-62

Aneura hymenophytoides Spruce – Type: Peru, Mt. Campana, 1200 m, *Spruce s.n.* (lectotype G-00282970!, designated here). As type material is lacking in the Spruce herbarium in MANCH (L. Loughtman, pers. com.), the isotype in Geneva is selected as the lectotype.

Riccardia sprucei (Steph.) Meenks & C.De Jong (*Aneura sprucei* Steph., *Aneura pectinata* Spruce nom. illeg.) **syn. nov.** – Type: Venezuela, “Río Cauapuna, Fl. Negro,” *Spruce s.n.* (lectotype MANCH-cc1700!, designated by Meenks & De Jong, 1985).

Riccardia regnellii auct. (e.g., Hell, 1969; Gradstein & Costa, 2003), non typus (see Gradstein & Reeb, 2018).

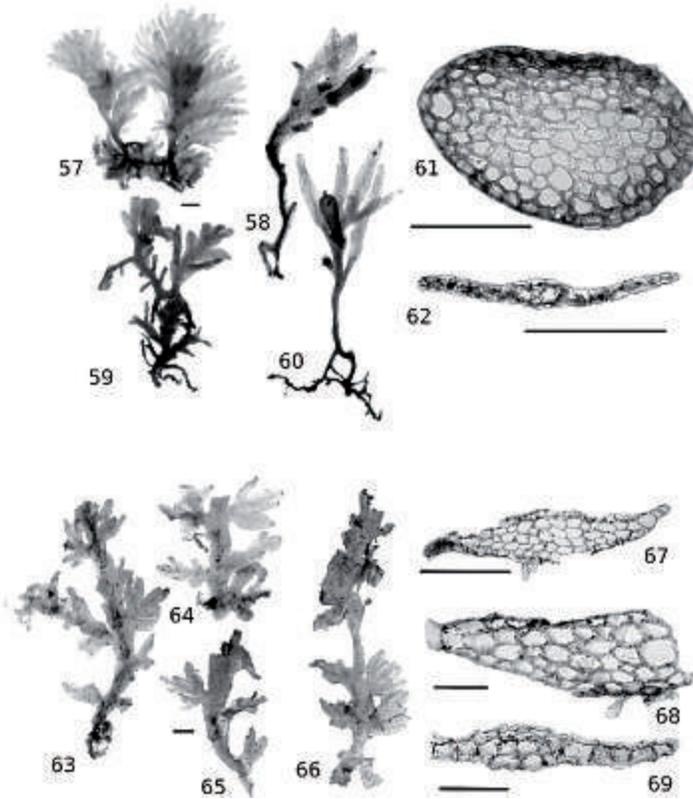
On rotten wood, shaded soil and rock in montane rainforest, (200-)500-3000 m; in Colombia recorded from Chocó, Magdalena, Meta (new), Quindío, Risaralda and Santander; in Ecuador (new) from Pichincha.

General distribution: West Indies, tropical Andes, Guianas, Brazil (Amazonia).

Further illustration: Gradstein & Costa (2003, Fig. 88H-J as *R. regnellii*), Gradstein & Ilkiu-Borges (2009, Fig. 9H-I as *R. sprucei*).

Plants monoicous (but occasionally apparently dioicous), pale green, small to rather robust, ca. 1-2 cm long, ascending from a creeping base, 2-pinnate, usually palmate in the upper part with suberect branches, short or long stoloniform branches present on the lower part of the axis. Main axis not winged, broadly ellipsoid to rounded, stolon-like, in cross section, 7-15 cells thick, without subepidermis, all cells thin-walled, epidermal cells smaller than medullary cells. Branches flat, linear or tongue-shaped, mostly suberect, with broad transparent wings, the wings 4-8 cells wide, broader than the midrib. Calyptra covered by thick-walled papillae. Gemmae not observed.

Riccardia hymenophytoides is usually monoicous but some populations are unisexual (e.g., the lectotype). The species varies considerably in size and becomes more robust towards higher elevation (e.g., Ecuador, *Gradstein et al.* 6792). *Riccardia sprucei* is a rather delicate phenotype from low elevation. *Riccardia hymenophytoides* was nested in a *R. fucoidea* – *R. plumiformis* clade in molecular analysis (*Rabeau et al.*, 2017) but clearly differs from *R. fucoidea* in the creeping axis without subepidermis and in palmate branching. The species is maintained here as a separate taxon pending the results of further analyses.



Figs 57-69. *Riccardia hymenophytoides* and *R. leptophylla*. – 57-62. *Riccardia hymenophytoides*. 57-60. Habit. 61. Cross section of the main axis. 62. Cross section of ultimate branch. – 63-69. *Riccardia leptophylla*. 63-66. Habit. 67-68. Cross section of the main axis. 69. Cross section of ultimate branch. (57, 61-62 from Gradstein et al. 6792; 58, 60 from the lectotype; 59 from Romero 001; 63-69 from the isotype of *Aneura allionii*). Scale bars: 57-60, 55 = 1 mm, 61, 69 = 0.1 mm, 62 = 0.25 mm, 63-66 = 0.5 mm, 67, 68 = 0.05 mm.

Further specimens examined: **Colombia.** Meta: Villavicencio, Caña Parrado, Romero 001 (PC). **Ecuador.** Pichincha: near Lloa, ca. 2900 m, Gradstein et al. 6792 (G, QCA, U); Zamora Chinchipe: Reserva Biológica San Francisco, Holz 434 (QCA). **Peru,** San Martín: Tarapoto, Spruce s.n. (MANCH-cc2095), Mt. Campana, Spruce s.n. (MANCH-cc2091, PC), Mt. Guyarapurina, Spruce s.n. (MANCH-cc2092).

***Riccardia latifrons* (Lindb.) Lindb. subsp. *parasitans* (Steph.) Gradst. & Reeb
comb. nov. Figs 85a-91**

Aneura parasitans Steph., Biblioth. Bot. 87: 175, 1916; *R. parasitans* (Steph.) Meenks & C.De Jong – Type: Bolivia, “In einem Torfmoor der Cerros de Malaga”, ca. 4000 m, June 1911, Herzog 4374, paroicous (lectotype G-00282964!, designated here; isolectotype PC!; further dupls. in L, MANCH and S according to Meenks, 1987).

Aneura pulvinata Steph. nom. illeg. – Type: Bolivia, Quebrada de Cunucu, 900 m, Herzog s.n. (lectotype G-00282991!, designated here).

On humic soil, rock and rotten wood in upper montane cloud forest and páramo, sometimes growing submerged, 2600-4500 m; in Colombia recorded from Antioquia, Arauca, Boyacá, Chocó, Cundinamarca, Huila, Meta and Risaralda; in Ecuador recorded from Cotopaxi, Loja, Napo and Pichincha.

General distribution: tropical Andes, usually at high elevation.

Plants paroicous or autoicous, small, to 1 cm long, with a prostrate main axis and numerous small ascending branches, 2(-3)-pinnate to palmate, primary branches widely to obliquely spreading, ultimate branches suberect and forming a palmate branching pattern. Main axis without wing, swollen, stoloniform, biconvex to rounded, 1-2× wider than thick, 10-15 cells thick, without subepidermis, epidermal cells subquadrate, narrower than medullary cells, thin-walled or slightly thick-walled, flat to slightly mamilliose, trigones absent. Branches ligulate to lanceolate, wingless or with a rudimentary, 1-cell wide wing, margins entire, apex rounded, epidermal cells on ultimate branches usually orientated obliquely towards the margin. Male branches usually developed on the side of the female branch (paroicous), more rarely separate (autoicous). Gemmae not seen.

Riccardia parasitans (Steph.) Meenks & C.De Jong is a small species characteristic of páramo that stands out by the monoicous, often paroicous, sexuality, frequently palmate branching in the upper part of the thallus, wingless branches, a stoloniform, 10-15 cells thick axis and absence of gemmae. The epidermal cells of the ultimate branches are typically orientated obliquely towards the thallus margin. *Riccardia parasitans* is morphologically quite similar to *R. latifrons* (Lindb.) Lindb. a widespread holarctic species that is not known with certainty from the Tropics (records from Cuba and Panama [Schäfer-Verwimp *et al.*, 2013] must be verified), and Schäfer-Verwimp *et al.* (2013) identified a specimen of *R. parasitans* from southern Ecuador as *R. latifrons*. The identification was supported by molecular data. *Riccardia parasitans* clearly differs from *R. latifrons*, however, in its thicker, stoloniform main axis. In the holarctic plants the main axis is 5-8(-9) cells thick and not stoloniform (Furuki, 1991; Schuster, 1992; Paton, 1999). Since *R. parasitans* and *R. latifrons* differ in one morphological character and in geographical range, they are treated here as subspecies.

An important character of *R. latifrons* is the absence of oil bodies in the epidermis. We have not been able to examine the oil bodies of *R. latifrons* subsp. *parasitans* but Meenks & De Jong (1985) reported the presence of oil bodies in the epidermis. This observation needs confirmation.

Further specimens examined: **Colombia.** Boyacá: Sierra Nevada del Cocuy, 4000-4500 m, *Bischler* 2838, 2859, 2986, 3001 (PC); Cundinamarca: Sibaté, *Meenks et al.* 86 (GOET, U as *R. papillata*). **Ecuador.** Loja: Parque Nacional Podocarpus, above Cajanuma, along trail to Mirador, 2900 m, *Nebel & Schäfer-Verwimp* 111550 (as *R. latifrons*); Pichincha: páramo de Pichincha, *Burghardt et al.* 6518, 6564, 6642 (QCA), páramo de Papallacta, *Burghardt et al.* 6512 (QCA), *ibid.*, *Schäfer-Verwimp & Nebel* 32192 (QCA).

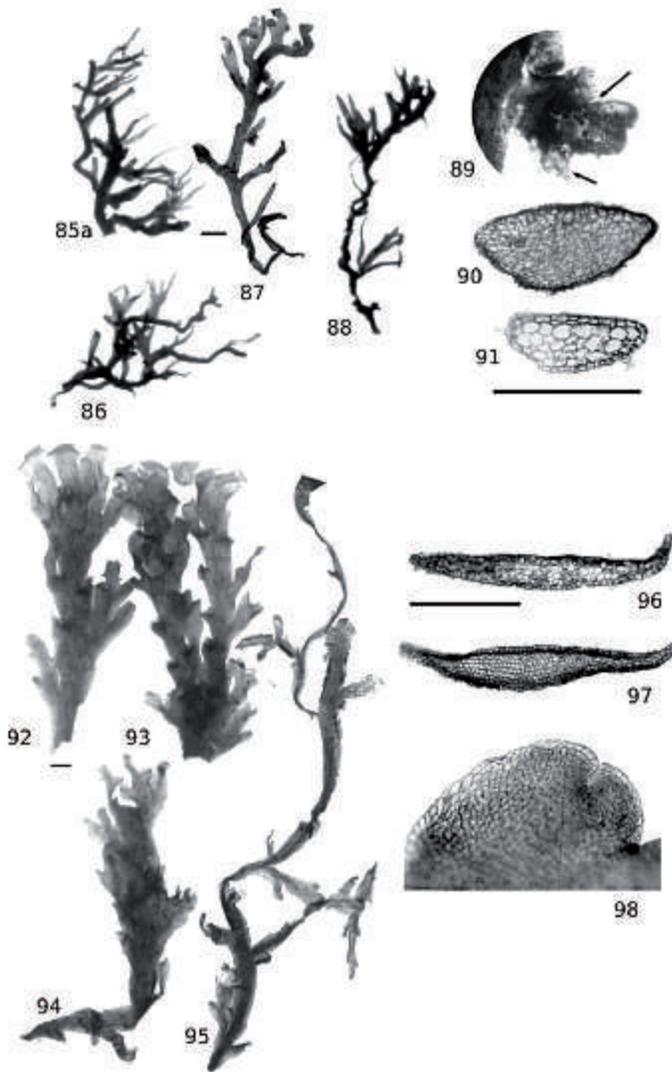
***Riccardia leptophylla* (Spruce) Herzog**

Figs 63-69

Aneura leptophylla Spruce – Type: Venezuela, Amazonas, San Carlos del Río Negro, *Spruce* H31c (lectotype MANCH-cc1817, designated by Meenks, 1987).

Aneura allionii Steph. – Type: Ecuador, Gualaquiza, Río Guriapa, February 1909, *Allioni s.n.* (isotype PC!).

? *Riccardia tenuicula* (Spruce) Meenks (*Aneura tenuicula* Spruce) (type not seen).



Figs 85a-98. *Riccardia latifrons* subsp. *parasitans* and *R. wallisii*. – **85a-91.** *Riccardia latifrons* subsp. *parasitans*. **85a-88.** Habit. **89.** Gynoecium with two androecial branches (arrows), paroicous sexuality. **90.** Cross section of the main axis. **91.** Cross section of ultimate branch. – **92-98.** *Riccardia wallisii*. **92-95.** Habit. **96-97.** Cross sections of the main axis. **98.** Apex of ultimate branch, showing narrow wing. (85a-86, 88-89 from the isolectotype; 87, 90-91 from Schäfer-Verwimp & Nebel 32192; 92-98 from Gradstein *et al.* 12608). Scale bars 85a-88 = 1 mm, 90-91, 96-97 = 0.5 mm, 92-95 = 1 mm, 98 = 0.25 mm.

On trunk bases and rotten wood in moist lowland and montane forests up to the páramo, 100-3350 m; in Colombia recorded from Antioquia, Boyacá, Chocó, Cundinamarca, Huila, Risaralda and Santander; in Ecuador from Cotopaxi, Los Ríos, Morona Santiago and Zamora Chinchipe.

General distribution: tropical America.

Plants monoicous (rarely dioicous), delicate, less than 1 cm long, translucent, prostrate, 2-pinnate to palmate. Axis 3-6 cells thick, plano-convex to elliptical, winged, wings 1-3 cells wide, epidermal cells smaller than inner cells. Branches linear or tongue-shaped, broadly winged, wings as wide as or wider than the midrib, the midrib sometimes vanishing below apex. Epidermal cells on branches in straight rows. Gemmae present.

Riccardia leptophylla is one of the smallest neotropical *Riccardia* species. It is very close to *R. regnellii* and might be conspecific with the latter but is preliminarily maintained here as a separate species as we have seen only very little material. Differences with *R. regnellii* are given in the key. Further study of this species, including a molecular comparison with *R. regnellii*, is recommended. *Riccardia tenuicula* (Spruce) Meenks, also described from Amazonia, is probably a synonym of *R. leptophylla*.

Riccardia pallida (Spruce) Meenks & C.De Jong

Figs 70-76

Aneura pallida Spruce – Type: Ecuador, Chimborazo, 1500 m, August 1860, *Spruce H84* (lectotype MANCH-cc1276!, designated here).

Riccardia boliviensis (Steph.) Meenks (*Aneura boliviensis* Steph.) **syn. nov.** – Type: Bolivia, Cochabamba, Incacorral, 2200 m, January 1908, *Herzog s.n.*, Bryotheca Levier 6080 (lectotype G-00283008!, designated here).

Riccardia capillacea (Steph.) Meenks & C.De Jong (*Aneura capillacea* Steph.) **syn. nov.** – Type: Bolivia, Cochabamba, Tablas, 3400 m, *Herzog 2786* (lectotype G-00282981!, designated by Meenks, 1987).

Riccardia capillacea var. *dentata* Meenks **syn. nov.** – Type: Colombia, Risaralda, Macizo del Tamaná, 3500 m, 7 February 1983, *van Reenen & Aguirre C4837* (holotype COL; isotype U!).

Riccardia herzogiana (Steph.) Meenks & C.De Jong (*Aneura herzogiana* Steph.) **syn. nov.** – Type: Bolivia, Quebrada de Pocona, ca. 2800 m, April 1911, *Herzog 5132* (lectotype G-00282972!, designated here).

Riccardia trichomanoides (Spruce) Meenks (*Aneura trichomanoides* Spruce) **syn. nov.** – Type: Ecuador, Canelos, *Spruce s.n.* (lectotype MANCH-cc2069!, designated here).

On rough bark, rotten wood, humic shaded soil and in *Sphagnum* bogs, in humid montane forests and páramo, 1400-4000 m; in Colombia recorded from Antioquía, Arauca, Boyacá, Casanare, Cauca, Chocó, Cundinamarca, Huila, Magdalena, Meta, Quindío, Risaralda, Santander and Tolima; in Ecuador from Azuay, Carchi, Chimborazo, Pastaza, Pichincha (new) and Zamora Chinchipe.

General distribution: tropical Andes.

Plants dioicous, robust but very slender, to 6 cm long, regularly to irregularly 2-4-pinnate, growing upright or pendent, primary branches often deflexed, opposite or alternate, stolons lacking. Main axis 0.5-0.75 mm wide, usually biconvex, 8-12 cells thick, with a subepidermis (sometimes only weakly developed) and with a narrow, interrupted, 1-2(-3) cells wide wing (part of the axis without wing), axial wing cells quadrate to narrowly rectangular, 15-30 µm wide and 25-80 µm long, thin-walled, without trigones. Primary branches narrowly, interruptedly winged like the axis, ultimate branches very thin, linear to subulate, straight or deflexed, with a conspicuous, 2-4 cells wide wing, the wings as wide as or narrower than the midrib, wing cells elongate-hexagonal, ca. 20-30 µm wide and 30-50 µm long, in straight or oblique rows, thin-walled with small trigones, ultimate branch margins entire to crenate to remotely toothed, teeth 0.5-1(-2) cells long. Oil bodies finely granular, 1-4

per cell, present in 60-70% of the epidermal cells (Meenks & De Jong, 1985). Antheridial branches winged, the wing toothed or subentire. Gynoeical branches subtended by 1-2 sterile innovations, margins with scale-like paraphyses. Gemmae not observed.

Riccardia pallida is close to *R. fucoidea* but differs in smaller wing cells. Moreover, the axis and primary branches in *R. pallida* are narrowly and interruptedly winged, the wings on ultimate branches are not broader than the midrib and stolons seem to be lacking. *Riccardia trichomanoides* and *R. herzogiana* are robust, 3-4-pinnate phenotypes of *R. pallida* and *R. capillacea* is a delicate, 2-pinnate phenotype with remote, deflexed branches.

Riccardia glaziovii (Spruce) Meenks, distributed in southeastern Brazil and Bolivia (Meenks, 1987; Gradstein & Costa, 2003), is very close to *R. pallida* and possibly a synonym of the latter. This needs further study.

Further specimens examined: **Colombia.** Cauca: Valle de las Papas, 2910 m, *Bischler 1020* (GOET, U). **Ecuador.** Azuay: páramo de Patacocho, *Gradstein et al. 12661* (PC, QCA); Loja: El Tiro, *Kottke & Nebel 031123* (QCA), *ibid.*, *Schäfer-Verwimp & Nebel 32071* (QCA); Pichincha: páramo de Papallacta, ca. 4000 m, *Burghardt et al. 7348* (QCA, PC); Zamora Chinchipe: Reserva Biológica San Francisco, *Burghardt 6892* (QCA). **Peru,** Chachapoyas: *Frahm et al. 1178, 1485* (GOET, U as *R. aberrans*).

Riccardia poeppigiana (Lehm. & Lindenb.) Meenks & C. De Jong

Figs 77-85

Jungermannia poeppigiana Lehm. & Lindenb. – Type: Peru, *Pöppig s.n.* (lectotype S-B28716!, designated here; isolectotypes G-00282994!, G-00282024!).

Riccardia algooides (Taylor) Meenks (*Metzgeria algooides* Taylor) **syn. nov.** – Type: Ecuador, Pichincha, in woods on the western side of Mt. Pichincha, 1847, *Jameson 170*, c. andr. (lectotype FH-01146768!, designated here; isolectotype BM-001007726!).

Riccardia cervicornis (Spruce) Gradst. & Hekking (*Aneura cervicornis* Spruce) **syn. nov.** – Type: Ecuador, Pichincha, *Spruce s.n.* (lectotype MANCH, designated by Meenks, 1987; isolectotype G-00283004!). – Syntype: Ecuador, Tunguragua, *Spruce s.n.* (G-00283005!).

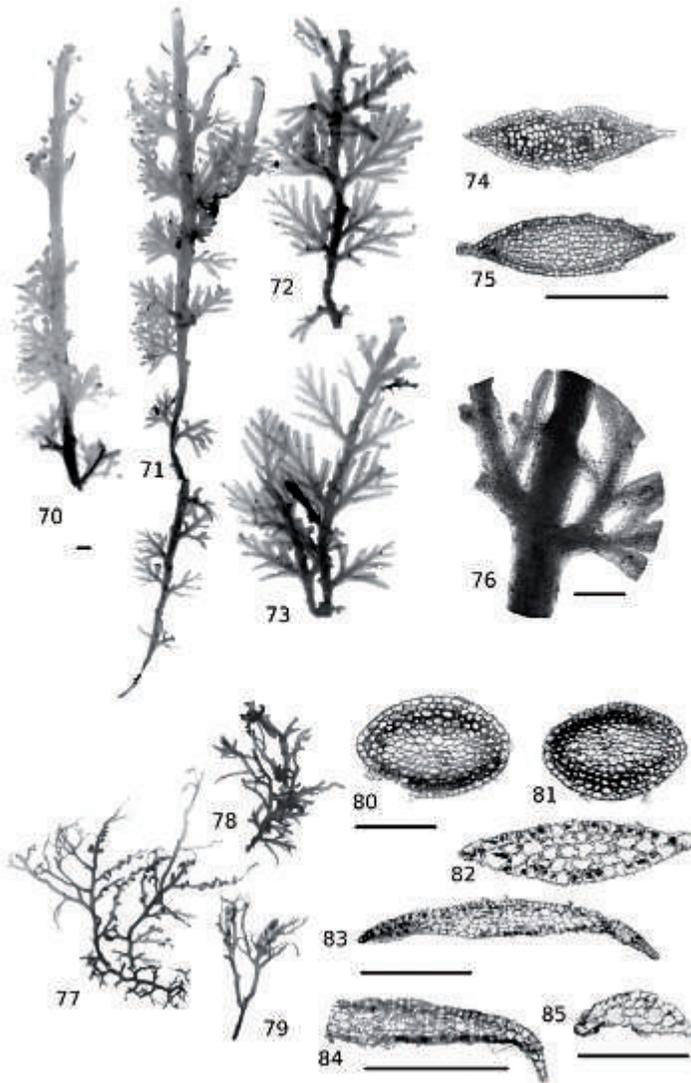
Riccardia squarrosa (Steph.) Gradst. (*Aneura squarrosa* Steph.) – Type: Colombia, Antioquía, páramo de Sonsón, 1874, *Wallis s.n.* (lectotype G-00282960!, designated here).

Riccardia papillata auct. (non lectotypus).

On loamy soil, rotten wood and twigs in montane forests and páramo, also in running water, (1200-)2500-4200 m; in Colombia recorded from Antioquía, Boyacá, Cesar, Chocó, Cundinamarca (new), Huila, Meta (new), Risaralda, Santander, Tolima and Valle; in Ecuador from Azuay (new), Pichincha and Tunguragua.

General distribution: probably widespread in tropical America.

Plants dioicous, medium-sized, ascending to erect, 1.5-10 cm long, the ascending shoots rather densely 2-3-pinnate, branches suberect or spreading, alternate or opposite, usually curved downwards. Main axis without wing, ellipsoid to distinctly biconvex, 8-22 cells thick, with a subepidermis especially in older portions of the axis, epidermal cells as large as inner cells or slightly smaller. Primary branches ± without wings, often deflexed, ultimate branches narrowly linear to laneolate and narrowed to the tip, curved, winged or not winged, the wings 0-4 cells wide, narrower than the midrib, the wing cells rather small, 15-35 µm wide, margins entire to irregularly crenate, marginal cells as large as or smaller than adjacent cells and sometimes slightly thicker-walled, apex rounded or retuse. Oil bodies present in



Figs 70-85. *Riccardia pallida* and *R. poeppigiana*. – 70-76. *Riccardia pallida*. 70-73. Habit. 74-75. Cross sections of the main axis, middle. 76. Portion of axis with a few branches, showing wings. – 77-85. *Riccardia poeppigiana*. 77-79. Habit. 80-81. Cross sections of the main axis, middle. 82. Cross section of the main axis, upper portion. 83-85. Cross sections of ultimate branches. (70-71, 74-76 from Gradstein *et al.* 12661; 72-73 from Schäfer-Verwimp & Nebel 32071; 77, 79-81, 83-85 from Gradstein *et al.* 12709; 78, 82 from Burghardt *et al.* 6760). Scale bars 70-73, 76, 77-79 = 1 mm, 74-75 = 0.5 mm, 80-85 = 0.25 mm.

60-70% of the epidermal cells, finely granular, 1-10 per cell, globose to ellipsoid (Meenks & De Jong, 1985). Male branches with crenulate wings (1-4 cells wide). Female branches short and broad, with lacinate margins. Gemmae often present on the tips of the ultimate branches.

Riccardia poeppigiana, described from Peru in 1834, is the earliest tropical Andean species described in *Riccardia*. Very characteristic are the upright growing, 2-3-pinnate plants with decurved, \pm wingless primary branches. The plants vary considerably in size, the branches are tapering to narrow tips or not, and the wings of the ultimate branches vary in width and are sometimes absent; they are narrowly winged in the type material. Integrated molecular and morphological analysis may clarify the status of *R. poeppigiana* as broadly defined here. A robust, conspicuously winged phenotype from Pichincha has been described as *R. algooides* and a \pm unwinged phenotype as *R. cervicornis*. Plants with broadly winged ultimate branches may be confused with *R. fucoidea* but in the latter species the branches are not decurved, the primary branches are also winged, the branch tips are broad and the wing cells are larger. Moreover, *R. fucoidea* lacks gemmae.

Riccardia poeppigiana is largely restricted to upper montane forest and páramo, above 2500 m. A specimen from low elevation (1200 m) in the Pastaza river valley (*Thiers 4727*, QCA) resembles *R. poeppigiana* but differs in very broad, 4-5 cells wide branch wings.

Selected further specimens examined: **Colombia**. Boyacá: Guicán, Corralites, 4000 m, *Bischler 2985* (PC); Casanare: road Socha – Sácama, *Gradstein et al. 12709* (UPTC, PC); Cundinamarca: La Aguadita, *Meenks 78* (GOET, U as *R. papillata*); Meta: Nevado de Sumapaz, *Cleef 7756* (GOET, U as *R. wallisii*); Risaralda: St. Rosa de Cabal, *van Reenen 882* (GOET, U). **Ecuador**. Azuay: El Cajas, 4000 m, *Wooller 11B* (QCA); Cotopaxi: Parque Nacional Llanganates, ca. 4000 m, *Burghardt et al. 6760, 6851* (QCA); Loja: Parque Nacional Podocarpus, Cajanuma, *Nebel & Kottke 031120* (QCA as *R. lepidomitra*), El Tiro, *Nebel & Kottke 031122* (QCA as *R. lepidomitra*); Napo: páramo Guamani, *Meenks & De Vries 209* (QCA); Pichincha: Quito, *Jameson s.n.* (BM-000735834); above Quito, 1857, *Saettone s.n.* (PC); summit of Pichincha, *Jameson s.n.* (BM00-1007725).

***Riccardia regnellii* (Ángstr.) G.K.Hell**

Figs 99-112

Pseudoneura regnellii Ángstr. – Type: Brazil, Minas Gerais, Caldas, *Regnell s.n.* (lectotype S-B260631!, designated by Gradstein & Reeb, 2018; isotype G-00282990!).

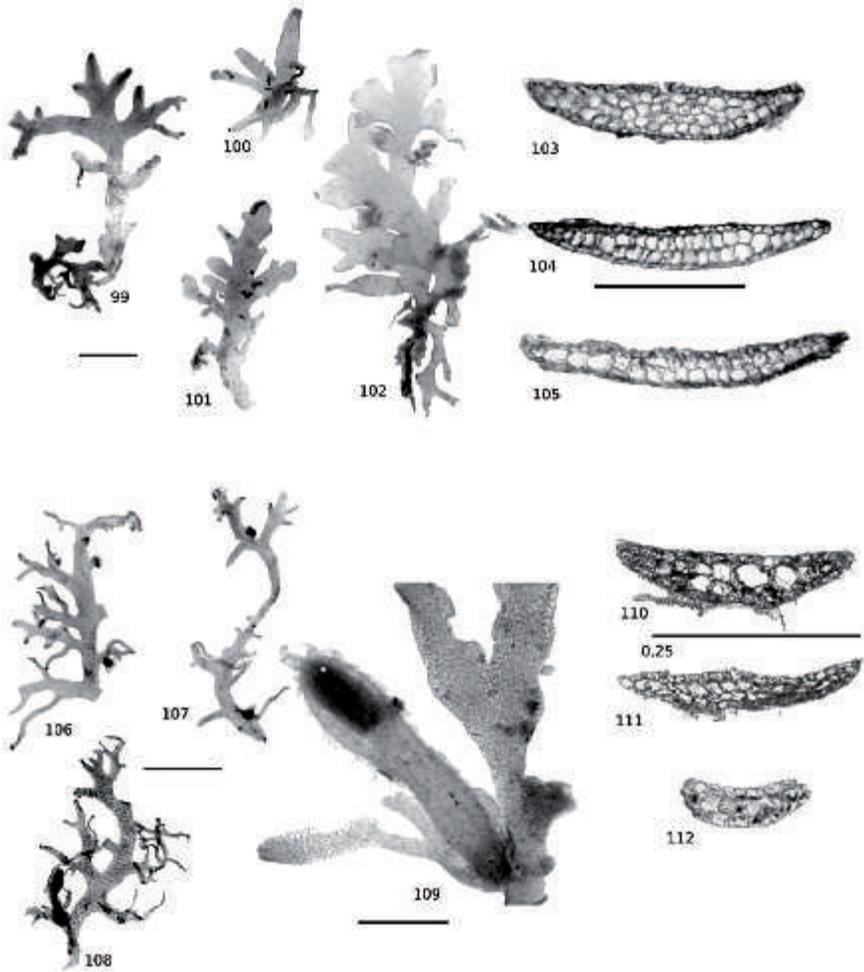
Riccardia amazonica (Spruce) Gradst. & Hekking (*Aneura amazonica* Spruce). – Type: Venezuela, San Carlos del Río Negro, “in trunco putrido”, *Spruce H16* (lectotype MANCH-cc1680!, designated by Meenks & Pócs, 1985).

On decaying wood, soil, tree bases and rock in lowland and montane rainforests, from sea level to ca. 3700 m; in Colombia recorded from Amazonas, Boyacá, Cauca, Chocó, Cundinamarca, Huila, Magdalena, Risaralda, Santander (new) and Vaupés; in Ecuador from Esmeraldas, Loja, Napo, Pastaza and Zamora Chinchipe.

General distribution: widespread in tropical South America; also in the West Indies.

Further illustrations: Gradstein *et al.* (2001, Fig. 67G-H as *R. amazonica*), Gradstein & Ilkiu-Borges (2009, Fig. 9E-G as *R. amazonica*).

Plants dioicous, rarely paroicous, 0.5-1.5 cm long, prostrate, irregularly 1-2-pinnate, without stolons. Axis 4-7 cells thick, plano-convex, epidermal cells smaller than inner cells, wing absent or narrow, 1-2 cells wide. Branches flat, variable in shape, often tongue-shaped and narrowed to the apex, broadly winged, wings narrower than the midrib, margins straight or curved, apex rounded or retuse, wing cells thin-walled or slightly thickened, margin cells not conspicuously larger than adjacent cells; surface cells of branches arranged in oblique rows. Oil bodies present in almost all epidermal cells, 1-2 per cell. Apex of the calyptra umbonate. Gemmae occasionally present at branch tips.



Figs 99-112. *Riccardia regnellii*. 99-102, 106-108. Habit. 103-104, 110-111. Cross sections of the main axis. 105, 112. Cross sections of ultimate branches. 109. Detail of female thallus, showing sporophyte and umbonate calyptra. (99-105 from *Nebel & Kottke 031128*; 106-112 from *Cleef 6264*). Scale bar 99-102, 106-109 = 1 mm, 103-105, 110-112 = 0.25 mm.

Riccardia regnellii is a common and variable tropical South American species that was generally called *R. amazonica*, which is a synonym of *R. regnellii* (Gradstein & Reeb, 2018). The plants described and illustrated as *R. regnellii* by Hell (1969) and Gradstein & Costa (2003) belong to *R. hymenophytoides*. *Riccardia regnellii* (= *R. amazonica*) has also been recorded from Africa but Reeb & Bardat (2014) found that the African plant belong to a different species that should be called *R. longispica* (Steph.) E.W.Jones (Gradstein & Reeb, 2018). Dioicous plants of *R. regnellii* are sexually dimorphous with male thalli usually being slightly smaller and more elongate than female thalli (Reeb & Bardat, 2014). Male and female thalli may occur mixed in the same mat.

Selected further specimens examined: **Colombia.** Cundinamarca: páramo between Cogua and San Cayetano, 3680 m, *Cleef 6264* (GOET as *R. columbica*, PC); Santander: *Gil 2234* (UPTC). **Ecuador.** Esmeraldas: near Quingue, ca. 100 m, *Burghardt 6573* (QCA); Zamora-Chinchipec: Reserva Biológica San Francisco, *Holz 438* (GOET, QCA), Parque Nacional Podocarpus, Río Bombuscara, 1000 m, *Nebel & Kottke 031127, 031128, 031131* (QCA), *ibid.*, *Schäfer-Verwimp 31934* (QCA).

Riccardia wallisii (Steph.) Gradst.

Figs 92-98

Aneura wallisii Steph. – Type: Colombia, Antioquía, páramo de Sonson, *Wallis s.n.*, ex hb. K. Müller (holotype G-00282956!).

Riccardia smaragdina Meenks & C.De Jong **syn. nov.** – Type: Colombia, Cundinamarca, Subachoque, La Pradera, páramo de Pena Negra, on rotten bark in primary upper montane forest, 3390 m, 28 March 1982, *Meenks 192* (holotype COL; isotype U!).

? *Riccardia judithae* Meenks & C.De Jong (type not available).

? *Riccardia reginae* Meenks & C.De Jong (type not available).

On humic soil, bark, rotten wood and rock in upper montane forests and páramo, also among *Sphagnum* in bogs, 2300-4000 m; in Colombia recorded from Antioquía (type), Chocó, Cundinamarca, Meta, Quindío, Risaralda and Santander (Meenks, 1987 as *R. smaragdina*); in Ecuador from Cotopaxi, Loja, Pichincha and Zamora Chinchipec.

General distribution: tropical Andes (Colombia to Bolivia).

Further illustration: Meenks & De Jong (1985, Fig. 7 as *R. smaragdina*).

Plants dioicous, prostrate to ascending, 1-6 cm long, irregularly 1-2(-3)-pinnate to palmate, stolons absent. Axis rather robust, (0.6-)1-2 mm wide, widened towards branch bases, surface of spotted by brownish-colored cells, plano-convex to slightly ellipsoid, 6-14 cells thick in the middle, subepidermis absent or present, 0-2-cells wide, epidermal cells as large as inner cells or smaller; axis irregularly winged, wings 1-6 cells wide, wing cells quadrate to rectangular, varying in size, 20-50 µm wide, margin cells often thick-walled. Branches alternate, suberect to obliquely spreading, gradually arising from the axis and with as decurrent base, short and plump with a broad apex, little narrower than the axis, not deflexed, irregularly winged, wings narrow or broad, 1-7 cells wide, wing margin cells thin-walled or thick-walled, margins entire or crenulate, branch apex truncate to retuse. Male and female branches ± winged, female branches plump, short and broad, solitary or in pairs, with lacinia. Gemmae frequently present at branch tips.

Riccardia wallisii is a variable species that is recognized by the irregularly winged thallus with a rather broad and flat, plano-convex to slightly ellipsoid axis and with rather short and plump, obliquely spreading branches with decurrent bases and broad tips. The axis is often widened towards the branch bases and the axial surface is frequently spotted by brownish-colored cells in dry material. The wings vary considerably in width and a subepidermis is present or absent.

Robust plants with a rudimentary wing were described as *R. smaragdina*, which is a synonym. Based on the original descriptions and illustrations, *R. judithae* Meenks & C.DeJong and *R. reginae* Meenks & C.DeJong are probably also synonyms of *R. wallisii*. The types of *R. judithae* and *R. reginae* were on loan during the time of this study and could not be made available. The records of *R. aberrans* from *Sphagnum* bogs of Colombia (Meenks, 1987) refer to *R. wallisii*.

Further specimens examined: **Colombia.** Cundinamarca: La Galera, páramo de Palacio, *Meenks et al. 154* (GOET, U as *R. aberrans*), Subachoque, páramo de Peña Negra, *Meenks 175, 178* (GOET, QCA, U as *R. aberrans*). **Ecuador.** Cotopaxi: Parque Nacional Llanganates, Laguna Anteojos, ca. 4050 m, *Burghardt et al. 7853* (QCA), *7385* (QCA, PC);

Loja: Parque Nacional Podocarpus, Cajanuma, 2900 m, *Nebel & Kottke 031117* (QCA as *R. parasitans*); Pichincha: Papallacta Pass, in remnant *Polylepis pauta* forest, ca. 4000 m, *Schäfer-Verwimp & Nebel 32161* (QCA), *ibid.*, *Gradstein et al. 12608* (PC, QCA); Zamora Chinchipe: Reserva Biologica San Francisco, ca. 2100 m, *Nebel & Kottke 031129, 031330* (QCA).

Excluded records

Riccardia multifida (L.) Gray – Colombia (Gottsche, 1864). This widespread holarctic species is very rare in South America where it has been recorded from Brazil (Gradstein & Costa, 2003). The identity of the old Colombian record could not be verified because the material is lost (Meenks, 1987).

Riccardia palmata (Hedw.) Carruth. – Colombia (Gottsche, 1864). This common holarctic species is not known with certainty from the Tropics; records from Mexico (Gottsche, 1863) and Cuba (Schuster, 1992) probably refer to *R. digitiloba*, which is common in Cuba. The identity of the old Colombian record could not be verified because the material is lost (Meenks, 1987).

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