

**Studies on Lejeuneaceae subfam. Ptychanthoideae  
(Hepaticae) IV. *Verdoornianthus*, a new  
Genus from Amazonas, Brazil**

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Abstract. *The new Amazonian liverwort genus Verdoornianthus is considered to be a specialized derivative of the widespread tropical genus Archilejeunea. Differences are the absence of innovations, the dull, suberect leaves, the tristratose rhizoid pad and the larger size of the lobule of the female bracts in Verdoornianthus. There are two species, V. marsupiifolius (Spruce) comb. nov. (Lejeunea marsupiifolia Spruce) from the upstream part of the Rio Negro and V. griffinii sp. nov. from Manaus.*

For several years I have been puzzled by a South American species of liverworts collected by Spruce along the Rio Negro in Amazonas, and described as *Lejeunea* (subg. *Acrolejeunea*) *marsupiifolia* Spruce in his monumental Hepaticae of the Amazon and the Andes (1884). In his original publication Spruce compared the species with *Lejeunea torulosa* (Lehm. & Lindenb.) Spruce—lectotype of the genus *Acrolejeunea* (Spruce) Schiffn. (Gradstein, 1974)—from which it was said to differ by the structure of the free margin of the leaf lobule and by the perianth, which has 7–9 plicae in *L. torulosa* and only 4(–5) plicae in *L. marsupiifolia*. Spruce noticed a resemblance in its perianth to *Lejeunea hasskarliana* (Gott.) Spruce, a species now assigned to *Schiffneriolejeunea* Verdoorn (Gradstein, 1975).

Superficially *Lejeunea marsupiifolia* does resemble *Schiffneriolejeunea*, e.g. by its dull brownish color, its leaves, which are more or less suberect and convoluted when dry and subsquarrose when moist, and by the absence of innovations. However, as I showed in my treatment of the genera of Ptychanthoideae (Gradstein, 1975), *Schiffneriolejeunea* has elongated leaf-lobe cells with cordate trigones and therefore belongs in the tribus Ptychantheae. *Lejeunea marsupiifolia* on the other hand has more or less isodiametric cells with equally bulging or broadly radiate trigones, which indicates a relationship to genera of the tribus Archilejeunae.

I have long hesitated to transfer the species to a better systematic position since the old, fragmentary (but fertile!) type material was the only collection known. Fortunately, I have now at hand recent material of a plant quite close to *Lejeunea marsupiifolia*, collected by Dr. Dana Griffin et al. on the campus of the University of Manaus, Brazil. This plant differs from *Lejeunea marsupiifolia* by its lobule structure and is therefore described as a new species. Although the two species are only known from one collection each, their general structure seems distinct enough to permit the description of a new genus for their accommodation. I am pleased to dedicate this genus to Professor Frans Verdoorn, nestor of Hepaticology and former student of Ptychanthoideae (Verdoorn, 1934), at the occasion of his 70th birthday.

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**Verdoornianthus** Gradst. *gen. nov.*

Type: *Lejeunea marsupiiifolia* Spruce.

Ab *Archilejeunea* differt innovationibus nullis, foliis tristis in sicco suberectis, rhizoideis e disco elongato tristrato, bracteis gynoecii lobulis maioribus suffultis.

Plants autoicous, rather dull olive-brown to dark-brown when dry, loosely creeping on bark among other species of Lejeuneaceae or forming dense mats. Leafy stems up to 1.5 cm long, 1.3–1.7 mm wide, irregularly pinnate with exclusively *Lejeunea*-type branching (*Frullania*-type not seen!). Stem c. 0.15 mm in diameter, the ventral merophyte 4–8 cells wide; dorsal cortical cells arranged in straight longitudinal rows, quadrate to rectangular, 30–70 × 25–30 μm, the walls thickened; ventral cortical cells narrower and with more strongly thickened walls, 30–75 × 15–25 μm; stem in transverse section with 12–16 cortical cells surrounding 14–18 medullary cells, the dorsal cortical cells slightly larger and thinner-walled than the ventral cortical cells and the medullary cells: dorsal cortical cells 20–24 μm, ventral cortical cells 12–20 μm, medullary cells up to 18 μm in diameter and tapering to narrow ends in longitudinal section, all cell walls without pigmentation.

Leaves imbricated, when dry appressed to the stem and more or less convoluted, suberect on branches and more obliquely spreading on stems, when moist curving upwards distally and becoming falcate and often more or less squarrose, but not spreading widely. Lobe ovate-obovate, 0.9–1.2 × 0.7–0.8 mm the dorsal base straight or semicordate, the margins entire and more or less undulate, the apex widely rounded, plane, the ventral margin plane or incurved; median cells subisodiametric-hexagonal, 25–33 × 20–28 μm, towards the base larger and more elongated with more deeply yellowish-brown walls (suggesting a vitta), 40–50 × 30 μm at the margins subquadrate, c. 18–20 μm; trigones large, bulging with convex sides, often broadly radiating along one or two adjacent walls but not becoming confluent, the intermediate thickenings suborbicular, frequently present on longer cell walls, one on each wall, rarely two in basal cells; cuticle smooth; ocelli absent; oil bodies not seen. Lobule large, c. ½ the length of the lobe, conspicuously inflated along the curved keel, the apex with one, often incurved, tooth, the hyaline papilla soon vanishing (not seen).

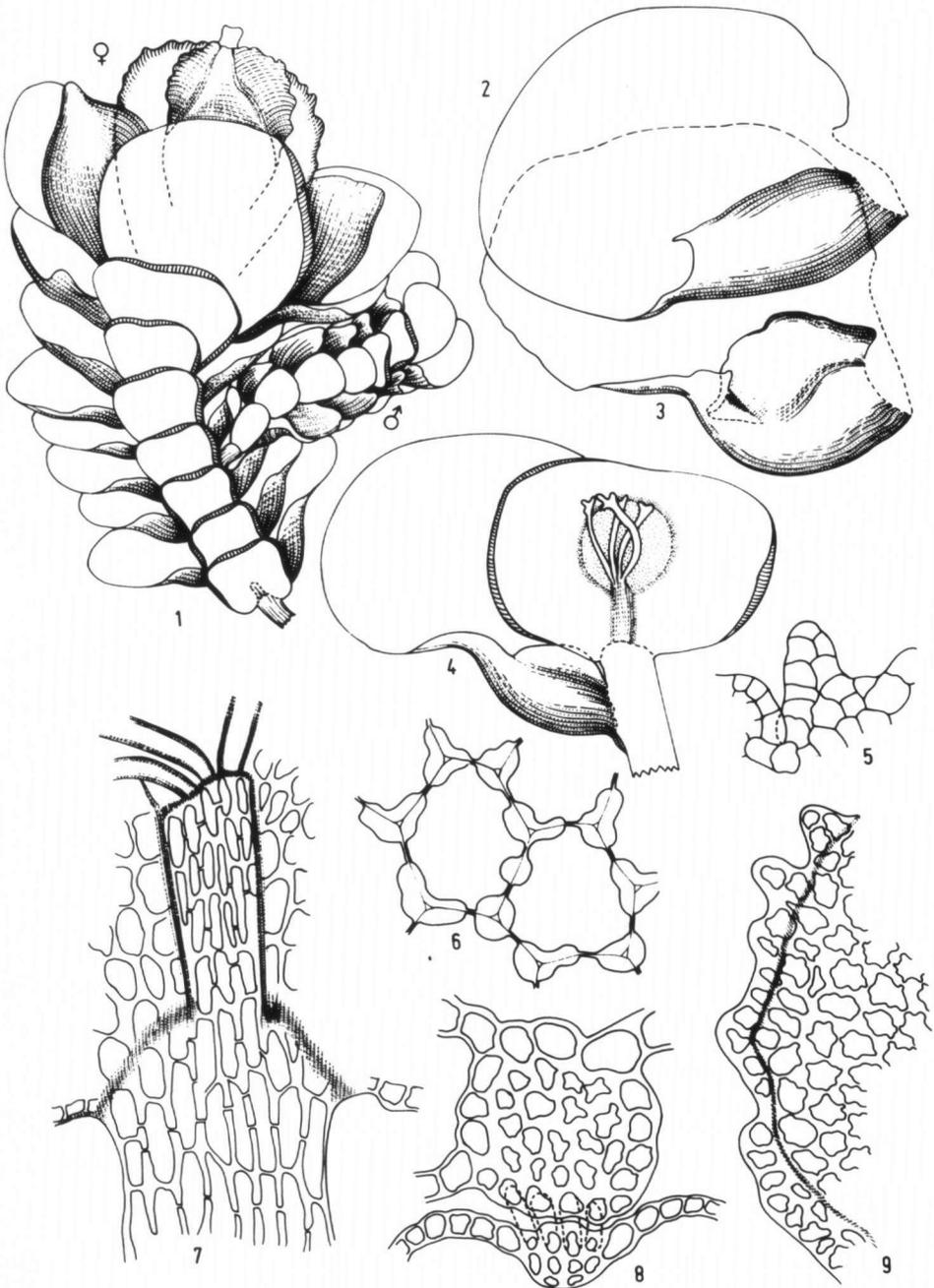
Underleaves large, imbricated, when spread out transversally ovate, 0.75–1 × 0.5–0.6 mm, 4–6 × the width of the stem, gibbous, the apex undivided and broadly truncate, the margins ± recurved (plane on branches), the bases straight to rounded, the insertion line shallowly curved; underleaf base with four superior central cells and a distinctly swollen, tristratose, elongated 100–150 μm long primary rhizoid disc, the rhizoid tufts originating from the tip of the rhizoid disc somewhat above the base of the underleaf.

Androecia terminal or intercalary on short or long branches, the bracts and bracteoles in 3–6 series, the bracts suberect becoming smaller towards the apex of the spike, unequally bilobed with large, hypostatic lobules and a sharp keel which is rough by projecting cells; antheridia 2(?) per bract. Gynoecia terminal on short branches or on leading stems, without innovations, the bracts and bracteoles in 1–2 series, the inner bract slightly larger than leaves, the lobe narrowly obovate, 1.2 mm long, with broadly rounded apex and entire, ± undulate margins, the lobule large, suberect, ligulate, 1 mm long, channeled with the margins recurved, the apex narrowly rounded; inner bracteole very large, broadly obovate, 1.2 × 1 mm, the apex rounded or retuse, the margins undulate, plane or slightly recurved. Perianth emergent, obcuneate, 1.2 mm long, bilaterally compressed with the ventral side more or less swollen, in the upper half with 4 sharp plicae: 2 lateral and 2 ventral (according to Spruce a small dorsal plica sometimes present in *V. marsupiiifolius*), the plicae roughened on their backs with sinuose to dentate wing-like projections; beak c. 6 cells long.

Calyptra entirely enveloping the young sporophyte, the upper portion 2(–3)-stratose, the lower portion 3–7-stratose, the outer cells about twice as wide as the inner cells, the calyptal stalk very short.

Mature sporophyte (seen in *V. marsupiiifolius*) exerted up to 2 mm above the perianth, the capsule splitting to near its base into four valves; valves widely spreading, bistratose, the outer cells with large nodulose trigones and intermediate thickenings (except for the centro-basal cells which are thin-walled), the inner cells covered by a golden-brown fenestrate sheath of thickening; elaters with one brownish spiral.

Sporeling (seen in *V. griffinii*) of the *Lopholejeunea*-type, protonema globose, of 10–12 cells, primary leaves in one series, very small, primary underleaves absent, juvenile leaves large, subequally bifid with strongly convex-cucullate lobes. Vegetative reproduction not seen.



FIGURES 1-9. *Verdoornianthus*. — 1-2. *V. griffinii*. — 1. Portion of fertile stem with gynoecium and male branch,  $\times 25$ . — 2. Leaf,  $\times 55$ . — 3-9. *V. marsupitifolius*. — 3. Leaf,  $\times 55$ . — 4. Leaf and underleaf, showing rhizoids,  $\times 55$ . — 5. Apical tooth of lobule, seen from inside,  $\times 215$ . — 6. Median leaf cells,  $\times 600$ . — 7. Underleaf base and rhizoid pad in surface view,  $\times 215$ . — 8. Transverse section of stem and underleaf base, showing 3-stratose rhizoid pad,  $\times 215$ . — 9. Upper portion of lateral perianth keel, showing rudimentary wing,  $\times 215$ .

*Verdoornianthus marsupiifolius* (Spruce) Gradst. *comb. nov.* (FIG. 3-9)

*Lejeunea* (subg. *Acrolejeunea*) *marsupifolia* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 118. 1884.

*Ptychocoleus marsupiifolius* (Spruce) Steph., Spec. Hep. 5: 35. 1912.

Type: AMAZONAS, Rio Negro, leg. Spruce (MANCH holo, FH).

In the original publication, the type locality of *Lejeunea marsupiifolia* Spruce is cited as "S. Gabriel, juxta fl. Negro cataractis, in arborum ramulis." São Gabriel is a little Brazilian village along the Rio Negro, near the junction with the Rio Uaupés, where Spruce collected from 15 January to 20 August 1852 (Spruce, 1908). Whether the material indeed came from this locality is dubious, because the handwritten label of the type collection in Spruce's herbarium (MANCH) reads: "S. Carlos, in ramulis, L 464." San Carlos is a village along the upstream part of the Rio Negro in Venezuela, near the Brazilian and Colombian borders, where Spruce collected in 1853. A vivid description of the two localities is found in Spruce's eminently useful diary of his Amazonian travels, edited posthumously by A. R. Wallace (Spruce l.c.).

Since the handwriting on the label, in pencil, is typically that of Spruce, it is hard to decide which of the two citations is correct. It thus remains uncertain whether the species was collected in Brazil or Venezuela.

*Verdoornianthus marsupiifolius* is easily recognized by its peculiar lobule, which is sharply folded near apex while the free margin projects into the sac (Fig. 3). Stephani (1912) called attention to this structure in a footnote (p. 36): "Die auffallende Ausbildung des oberen Randes (am lobulus folii) hat Spruce nicht gesehen; sie ist soweit meine Erfahrung reicht einzig in ihre Art." Since both Stephani and Spruce failed to describe the lobule adequately, a new description is called for:

Lobule ovate-orbicular, 0.45-0.5 × 0.35-0.45 mm, about half the length of the leaf lobe, strongly inflated along the keel and rather abruptly flattened towards the free margin, the flattened portion about as wide as the inflated portion but narrower in branch leaves; free margin strongly arched, plane, at apex deeply projecting into the sac through sharp folding of the lobule, the apical portion of the free margin, including the broad and blunt tooth (3 cells long, 2 cells wide), becoming totally invisible; hyaline papilla not seen; keel strongly arched, not decurrent, at an angle of 90-120° with the ventral margin of the lobe.

*Verdoornianthus griffinii* Gradst. *sp. nov.* (FIG. 1-2)

A *V. marsupiifolii* differt lobulis rectangulatis omnino inflatis apice non inflexis, carina leviter arcuata versus marginem ventralem angulum 150° formans.

Type: BRAZIL, AMAZONAS, Campus of the Instituto Nacional de Pesquisas sa Amazonia at Manaus. Secondary terra firme forest, elev. 30 m. On living trunk with *Acrolejeunea emergens* and *Pycnolejeunea callosa*. Dana Griffin III, Daniel M. Vital & Olga Yano 1-70-A, July-August 1974 (FLAS holo, U, hb. Grolle).

Although known only from type material, this plant is so distinct from *V. marsupiifolius* that I do not hesitate to describe it as a new species. Habitually the two species are rather similar but the lobule in *V. griffinii* is much narrower, rectangular in shape (0.5 × 0.2 mm), not flattened towards the free margin, and lacking the peculiar apical fold. The apical tooth is much slenderer (2-3 cells long, 1 cell wide) and clearly visible, whereas the keel is only shallowly curved and at a much wider angle (c. 150°) with the ventral margin of the lobe. Although the available material is of recent date, no trace of a hyaline papilla could be found. The material of *V. griffinii* differs further by the underleaves which are about 1 mm wide (0.75 mm is *V. marsupiifolius*), by the dorsal leaf base which is more strongly arched and often extending beyond the stem,

and by the rhizoid pad which is somewhat smaller in size, c. 100  $\mu\text{m}$  long (150  $\mu\text{m}$  in *V. marsupifolius*). These are only minor differences, which might fail to hold when further specimens turn up.

#### GENERIC AFFINITY

*Verdoornianthus* is a member of the tribe Archilejeuneae Gradst. because the leaf cells are isodiametric and the cell walls have equally bulging or radiate trigones. The rays of the trigones are wide and blunt, which is typical for *Archilejeunea* and its allies (*Archilejeunea*-complex sensu Gradstein, 1975). Among the genera of the *Archilejeunea*-complex (*Archilejeunea*, *Phaeolejeunea*, *Spruceanthus*, *Tuzibeanthus*), *Archilejeunea* seems most closely related to *Verdoornianthus*. Important mutual characteristics are the large leaf lobule with only one tooth, the entire, rounded leaves and bracts, purely *Lejeunea*-type branching, brownish color when dry and a 4-5-carinate perianth with rough keels. Differences are mainly the absence of innovations, the much larger size of the lobule of the female bracts, the tristratose rhizoid pad, and the leaf position in *Verdoornianthus*. Moreover, the leaves in *Verdoornianthus* are dull whereas in *Archilejeunea* they are somewhat glossy.

Most significant generically is the absence of innovations. In *Archilejeunea* they are either one or two per gynoeceum and none of the other genera assigned to the *Archilejeunea*-complex lacks innovations. Within the subfamily Ptychanthoideae presence or absence of innovations is a stable generic character and it is only in unfertilized gynoeceia that exceptions to this rule have been shown to occur (Gradstein, 1975). Rhizoid pad anatomy is a relatively new character in Lejeuneaceae taxonomy (Winkler, 1970) and its generic significance has not yet quite been established. My unpublished data show that *Archilejeunea* has a bistratose rhizoid pad, which seems to be the more common type in Ptychanthoideae. Tristratose rhizoid pads have so far only been found in *Symbiezidium*, *Odontolejeunea* and *Caudalejeunea* (Winkler l.c., Gradstein l.c.).

With respect to leaf position, *Verdoornianthus* is unique among Archilejeuneae and approaches the tribe Ptychantheae by its leaves being more or less suberect and convoluted when dry. In all other genera of Archilejeuneae the leaves are widely spreading both in the dry and in the wet state. In Ptychantheae, however, the entire leaf spreads outwards widely when moistened, whereas in *Verdoornianthus* the leaf retains its suberect direction except for the distal portion which curves upwards and becomes falcate or even squarrose. Thus it appears that the absence of strong outward movement of the leaves upon moistening is the main character for distinguishing members of the tribe Archilejeuneae from those of the Ptychantheae habitually. I venture to presume that the observed differences in leaf behavior are caused by differences in cell wall structure (as is apparent from the observed differences in cell and trigone shape). Further studies are necessary to verify this assumption.

Besides a close relationship to *Archilejeunea*, a relationship apparently more remote to *Lopholejeunea* should be noted. Both *Verdoornianthus* and *Lopholejeunea* are lacking innovations and have somewhat similar perianths, although in *Lopholejeunea* the perianth keels are usually strongly winged. Habitually the two genera are very different: *Verdoornianthus* is dull brownish when dry, lacking any trace of secondary pigmentation, whereas *Lopholejeunea* is very shiny and always shows some blackish secondary pigmentation of the cell walls, the plants being dark green or entirely black. Other differences include the shape of the trigones, the leaf position, the rhizoid pad and the female bracts.

With respect to the size of the stem cortex cells, *Verdoornianthus* is somewhat

intermediate between *Archilejeunea* and *Lopholejeunea*: in *Lopholejeunea* the cortical cells are usually larger than in *Verdoornianthus*, whereas in *Archilejeunea* they tend to be smaller and more rectangular. Both *Lopholejeunea* and *Archilejeunea* have an asymmetric cortex (Bischler, 1965), which is often brownish pigmented, whereas in *Verdoornianthus* the cortex lacks brownish pigmentation.

Summing up, it appears that *Verdoornianthus* is most closely related to *Archilejeunea*. It can be looked upon as a specialized derivative of an Archilejeuneoid ancestor which evolved by loss of innovations, increase in size of the lobule of the female bract, elaboration of the rhizoid pad and gradual increase in the size of the cortical cells, associated with loss of cortical pigmentation. By their present day distribution the two genera are quite contrasting. *Archilejeunea* is almost pantropical and represented in Amazonas by several common and widespread neotropical species (around Manaus they are among the most common liverworts). *Verdoornianthus*, on the other hand, is only known from two isolated Amazonian populations.

#### LITERATURE CITED

- BISCHLER, H. 1965. Recherches sur l'anatomie de la tige chez les Lejeuneaceae II. Les sous-familles Lejeuneoideae, tribu Ptychantheae, Nipponolejeuneoideae et Myriocoleoideae. Rev. Bryol. Lichénol. 33: 399-458.
- GRADSTEIN, S. R. 1974. Studies on Lejeuneaceae subfam. Ptychanthoideae I. Nomenclature and taxonomy of *Ptychocoleus*, *Acrolejeunea* and *Schiffneriolejeunea*. Jour. Hattori Bot. Lab. 38: 327-336.
- . 1975. Studies on Lejeuneaceae subfam. Ptychanthoideae III. A taxonomic monograph of the genus *Acrolejeunea* (Hepaticae), with an arrangement of the genera of Ptychanthoideae. Biblioth. Bryophyt. 4, 162 pp., Vaduz.
- SPRUCE, R. 1884. Hepaticae Amazonicae et Andinae. Trans. Proc. Bot. Soc. Edinburgh 15: i-xi, 1-590.
- . 1908. Notes of a Botanist on the Amazon & Andes. (ed. by A. R. Wallace). 2 vols., 1060 pp., London.
- STEPHANI, F. 1912. *Ptychocoleus*. Species Hepaticarum V: 19-60. Geneva.
- VERDOORN, F. 1934. Studien über Asiatische Jubuleae (De Frullaniaceis XV-XVII). Ann. Bryol. Suppl. 4: I-XII, 1-231.
- WINKLER, S. 1970. Zur Anatomie der Rhizoidplatten neotropischer Lejeuneaceen. Rev. Bryol. Lichénol. 37: 47-55.