
Austral Hepaticae. 26. The Identity, Taxonomic Position, and Ecology of *Trichocolea julacea* Hatcher (Trichocoleaceae)

John J. Engel

Department of Botany, The Field Museum, Chicago, Illinois 60605-2496, U.S.A.

ABSTRACT. A new species, *Leiomitra julacea*, is proposed for the New Zealand *Trichocolea julacea*, which is invalid according to the *International Code of Botanical Nomenclature*. The species is described and illustrated.

The genus *Trichocolea* Dumortier is well represented in tropical montane areas and to a lesser extent the south temperate zone. Only a single species, *T. tomentella* (Ehrhart) Dumortier, occurs in temperate areas in the Northern Hemisphere, where it is disjunctly widespread in range. *Trichocolea tomentella* is the type of the genus.

Gottsche (1864: 132) subdivided *Trichocolea* into two sections, sect. *Hirtiflora* Gottsche (= sect. *Trichocolea*) and sect. *Laeviflora* Gottsche. He characterized section *Hirtiflora* as having a hairy "involucrum," i.e., the calyptra, which is fused with and surrounded by bracts and bracteoles. Three species were assigned to this section: *T. tomentella*, *T. mollissima* (Hooker f. & Taylor) Gottsche, and *T. lanata* (Hooker) Nees. The other section, *Laeviflora*, was defined as having a smooth calyptra, devoid of bracts, and contained one species, *T. tomentosa* (Swartz) Gottsche, which is therefore the type of the section. Lindberg (1875) created a new genus, *Leiomitra* Lindberg, which included *T. tomentosa* and a new species, *L. capillata* Lindberg. He distinguished the genus from *Trichocolea* in part by the lack of regularly pinnate branching, and on the characters cited by Gottsche for *Trichocolea* sect. *Laeviflora*. However, Gottsche's section was not cited as a synonym.

Leiomitra has been variously treated by subsequent authors. Spruce (1884–1885) recognized *Leiomitra* as a genus and included four neotropical species: *L. tomentosa* (Swartz) Lindberg, *L. flaccida* Spruce, *L. sphagnoides* Spruce, and *L. paraphyllina* Spruce. Stephani (1888) and Bescherelle (1893) also accepted the genus. Schiffner (1893–1895) treated *Trichocolea* as a genus and recognized Gottsche's sections as subgenera; *Leiomitra* Lindberg was cited as a synonym of subgenus *Laeviflora* (Gottsche) Schiffner. Schiffner's description of subgenus *Hirtiflora* (Gottsche) Schiffner emphasized

succubously oriented leaves, repeatedly pinnate branching, and the presence of a fleshy, wooly "calyptra" having both bracts and sterile archegonia inserted on it; the subgenus included six species. By contrast, subgenus *Laeviflora* had incubously oriented leaves, less regularly pinnate branching, and a "calyptra" that was both thin and smooth throughout, or at least in the upper portion. Schiffner included seven primarily neotropical species in subgenus *Laeviflora*, including *T. tomentosa*. Spruce (1895) was the first to treat *Leiomitra* as a subgenus, subg. *Leiomitra* (Lindberg) Spruce. Subgenus *Laeviflora* (Gottsche) Schiffner has less than a three-week priority over subgenus *Leiomitra* (Lindberg) Spruce (15 January vs. 5 February fide Stafleu & Cowan, 1985).

Leiomitra was included as a synonym of *Trichocolea*, without subgeneric status by, e.g., Stephani (1898–1924), who regarded the two genera as the same on developmental grounds; Verdoorn (1932); Evans (1939); Müller (1951–1958); Hatcher (1957); Fulford (1963); Gradstein (1989); Fulford and Sharp (1990); Gradstein and Florschütz-de Waard (1990); and Schuster (1966). Little (1949: 10) lectotypified *Leiomitra* Lindberg with *L. tomentosa* (while including the genus in the synonymy of *Trichocolea*). *Leiomitra* was recognized as a distinct genus by Schuster (1980, 1984) and by Grolle (1983). Schuster and Grolle placed both *Trichocolea* and *Leiomitra* in the Trichocoleaceae.

Schuster (1963) added a third genus to the Trichocoleaceae, *Eotrichocolea* Schuster, based on *Trichocolea polyacantha* (Hooker f. & Taylor) Gottsche et al. of New Zealand. Schuster (1980) discussed interconnections of the Trichocoleaceae with a group of genera that includes *Temnoma* in the Pseudolepicoleaceae Fulford & J. Taylor, and merged the two families into one family, Trichocoleaceae, with four subfamilies: Trichocoleoideae, Temnomoideae Schuster, Blepharostomatoideae Grolle, and Chaetocoleoideae Schuster (Schuster, 1980, 1984).

Hatcher (1958) described *Trichocolea julacea* Hatcher, based on a plant from Stewart Island, New Zealand. Known only from the protologue, this spe-

cies has remained somewhat of a mystery plant. Examination of the type, and material recently collected in New Zealand, reveals that the plant possesses characters that place it in *Leiomitra*, and a new combination is therefore required, as follows:

Leiomitra julacea Hatcher ex Engel, sp. nov. *Trichocolea julacea* Hatcher, Trans. Roy. Soc. New Zealand 85: 245. f. 30–36. 1958, nom. inval. (Art. 37). TYPE: New Zealand. Stewart Is.: Port Pegasus, Sawmiller's Arm, 1949, *Martin* 621 (holotype, F; isotype, UWM). Figure 1.

Plants spongy, distinctly julaceous, with all sides appearing as a mass of interwoven cilia, loosely creeping, chocolate brown (the shoot tips light green), the shoots to 2 mm wide. Branching irregularly sympodial to pseudodichotomous, the leading axis soon losing its dominance, the main shoot and branches alike in vigor. Stem lacking paraphyllia, hidden on all sides by interwoven leaf cilia. Rhizoids occasional, in tight bundles, from stem at immediate base of underleaves, the tips often branched. Leaves widely spreading but with lobes arching toward shoot apex, rather closely imbricate, distinctly succubously (almost longitudinally) inserted, the lamina twisted: ventral sector of leaf oriented parallel with substrate, the dorsal sector of leaf antically assurgent and the dorsal margin seen on edge, the leaves obtrapezoidal to subreniform, asymmetrically 4–6-lobed, the ventral pair of lobes largest, the dorsal lobe smallest. Lobes caudate, not 3-fid, the ventral pair of lobes 4–5 cells wide at base (tier immediately above sinus base), then 2–3 tiers of laterally juxtaposed cells basal to the uniseriate row of 6–10 cells; cells of uniseriate row \pm cylindrical, with dilated septa, 13–25 μm wide, 62–98 μm long, the cells toward base of uniseriate row rather thick-walled, the cells becoming progressively smaller and less thick-walled toward lobe apices, the cuticle of penultimate and terminal cells striolate-papillose, that of the remaining cells finely striolate; terminal cell of uniseriate row somewhat tapered, 10–12 μm wide, 68–90 μm long, slightly thick-walled in the tip; margins of lobes copiously armed with pairs of opposing cilia, the cilia of lobes and sinus bases repeatedly dichotomously branched, the branches of each dichotomy stiffly diverging, but the armature primarily directed adaxially and oriented at right angles to the leaf plane, the leaf thus appearing to have a stiffly ciliate adaxial leaf surface, the cilia ultimately forming a densely interwoven dendroid crown to the leaf; marginal cilia of lobe uniformly uniseriate throughout, the cells elongate, rather

thick-walled, the cuticle of cells toward base of ciliium striolate, the cuticle of cells toward and including terminal cell striolate-papillose; sinus bases plane and not reflexed. Disc slightly convex, asymmetric, 3–4 cells high at dorsal sinus, 5–6 cells high at ventral sinus (from base to sinuses); margins of disc with dichotomously branched cilia similar to those of lobes, the cilia often adaxially displaced and lying at right angles to the disc plane. Underleaves somewhat smaller than leaves, narrowly connate on both sides, cuneate, quadrifid, the marginal armature similar to leaves and likewise forming a mass of interwoven cilia; disc 3–4 cells high. Cells of disc thin-walled, strongly elongated, aligned in somewhat irregular tiers, in lamina middle 22–26 μm wide \times 84–108 μm long; cuticle markedly long striolate, with only a few papillae. Asexual reproduction lacking. Otherwise unknown.

Nomenclature. The name *Trichocolea julacea* is invalid according to the ICBN, Art. 37 (Greuter et al., 1994), which requires that after 1 January 1958 a holotype for new species must be indicated. Hatcher (1958) made no reference to a nomenclatural type for the species (see also Art. 7), but stated that “portions of the original collection,” gathered by Martin, are in four herbaria, including that of Martin followed by the number 621 in parentheses. The specimen retained by Hatcher (now at F) bears the locality that matches the protologue, but also includes the number 621 and “TYPE” on the label. That specimen is herein designated the holotype. The above description and accompanying illustration (Fig. 1) are based on this collection.

Distribution and ecology. Known only from the type collection and the Cascade ultramafic moraine in southern Westland Province. There the species occurs at ca. 135 m in an area of ultramafic rocks and outcrops with rather open vegetation consisting mainly of *Gleichenia*, *Lycopodium*, *Juncus*, the lichen *Cladina*, and scattered *Leptospermum*. The species forms thick, nearly pure mats on well-drained soil of slopes and vertical banks of drainage channels. Hatcher (1958) mentioned that the type was “epiphytic; on forest trees.”

Additional specimens examined. NEW ZEALAND. **South Island:** Westland Prov., Cascade Road, Cascade ultramafic moraine, W of Martyr Saddle, SSW of Jackson Bay, ca. 135 m, *Engel* 21779, 23001 (F).

Taxonomy. Only juvenile gynoecia are known for the species (the type), but the irregularly sympodial to pseudodichotomous branching pattern (with the leading axis soon losing its dominance) and the distinctly succubously to nearly longitudi-

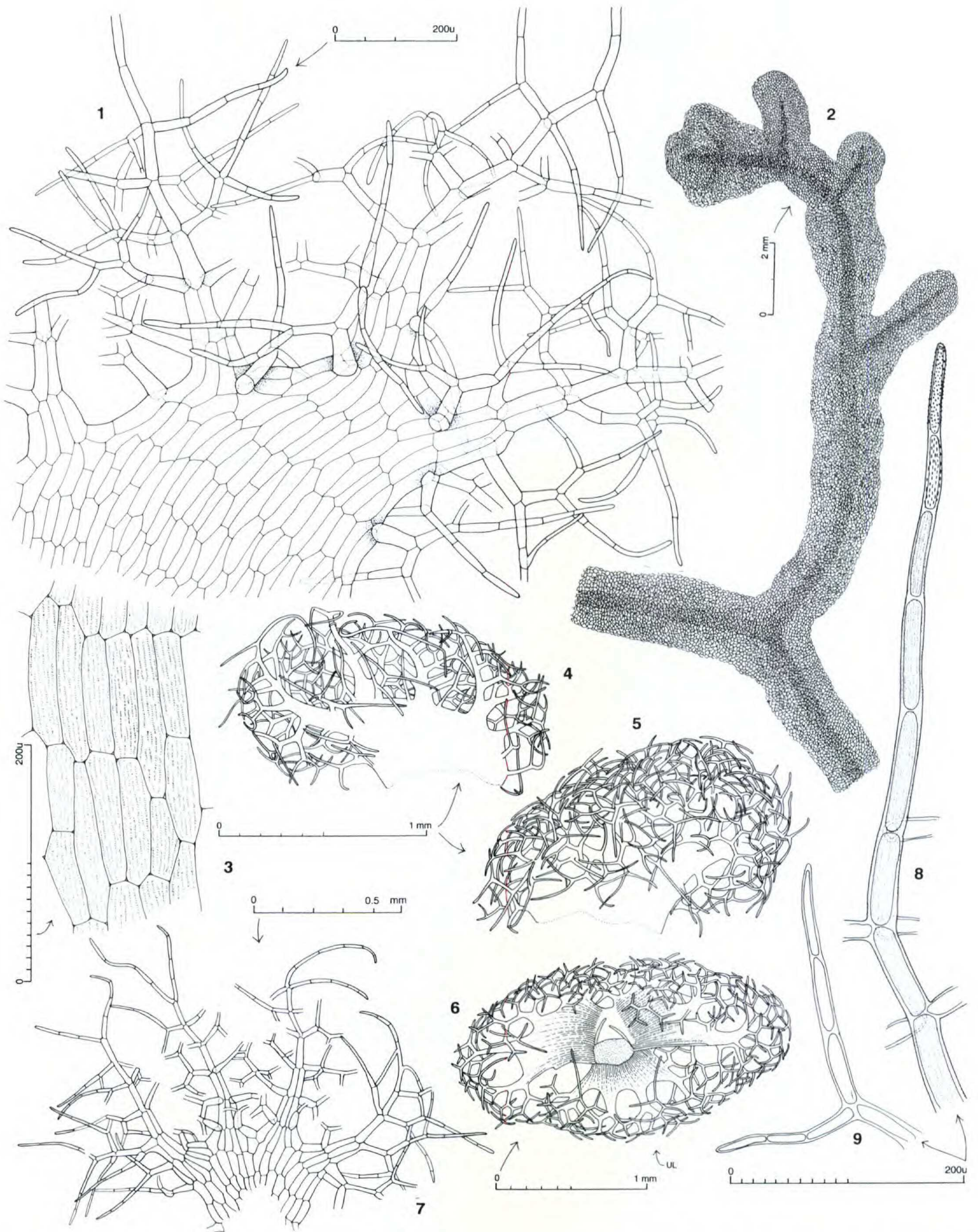


Figure 1. *Leiomitra julacea* Hatcher ex Engel. —1. Ventral sector of leaf, adaxial aspect (some portions of marginal armature not shown for clarity). —2. Shoot, dorsal view. —3. Median cells of lamina. —4. Leaf, adaxial view. —5. Leaf, abaxial view. —6. Cross section of shoot showing mass of interwoven, branched cilia (UL = underleaf) of 1 gyre. —7. Underleaf (some portions of marginal armature not shown for clarity). —8. Leaf lobe, distal sector. —9. Lateral armature of leaf lobe, distal sector. (All from holotype.)

nally inserted leaves are characters that place this species in *Leiomitra*. *Trichocolea* s. str. has regularly 2–3(4)-pinnate branching, with the main axis retaining its dominance and the leaf insertion varying from weakly succubous to weakly incubous.

The leaves of this species are remarkable for their development of a densely interwoven “basket-work” of cilia (Fig. 1: 4–6), which causes the axis and branches to appear spongy and julaceous (Fig. 1: 2); the cilia are repeatedly dichotomously branched and widely divergent (Fig. 1: 1), the ultimate divisions of each leaf forming a densely interwoven dendroid “crown.” Living plants, as well as the type, are brownish. Branching is irregularly sympodial to pseudodichotomous, as in *Leiomitra lanata* (Hooker) Schuster, but the form of the leaves will immediately distinguish this species. The species is readily distinguished in the field by the julaceous, wiry aspect of the plants coupled with the brownish color.

Leiomitra julacea and *L. lanata*, also of New Zealand, are the only south temperate members of the genus; all other species of *Trichocolea* reported from the south temperate belong to that genus (s. str.). The two New Zealand species of *Leiomitra* may be distinguished by the following key.

KEY TO NEW ZEALAND SPECIES OF *LEIOMITRA*

- 1a. Leaf lobes equally 3-fid, consisting of an adaxially divergent segment and a pair of abaxially divergent segments, each segment usually 1(2) times again 3-fid, ending in a pair of \pm equally divergent, uniseriate cilia; leaf disc 6–10 cells high; plants grass green to yellowish green; common, North and South Islands *L. lanata*
- 1b. Leaf lobes caudate, not 3-fid, the margins armed with pairs of opposing cilia, the cilia repeatedly dichotomously branched and forming a densely interwoven dendroid crown; leaf disc 5–6 cells high; plants brown; rare, Stewart Is. and southern Westland Prov. *L. julacea*

Acknowledgments. I thank Marlene Donnelly for preparing the habit figures for the illustration, and Gary Merrill for valued advice on the manuscript.

Literature Cited

Bescherelle, E. 1893. Énumération des hépatiques connues jusqu'ici aux Antilles françaises (Guadeloupe et Martinique). *J. Bot. (Morot)* 7: 174–180, 183–194.

Evans, A. W. 1939. The classification of the Hepaticae. *Bot. Rev. (Lancaster)* 5: 49–96.

Fulford, M. 1963. Manual of the Leafy Hepaticae of Latin America. Part I. *Mem. New York Bot. Gard.* 11: 1–172, pl. 1–37 (unnumbered).

——— & A. J. Sharp. 1990. The leafy Hepaticae of Mex-

ico: One hundred and twenty-seven years after C. M. Gottsche. *Mem. New York Bot. Gard.* 63: 1–86.

Gottsche, C. M. 1864. Hepaticae. *In: Triana & Planchon, Prodrum florae novo-granatensis. Ann. Sci. Nat. Bot., Ser. 5, 1: 95–198, pl. 17–20.*

Gradstein, S. R. 1989. A key to the Hepaticae and Anthocerotae of Puerto Rico and the Virgin Islands. *Bryologist* 92: 329–348.

——— & J. Florschütz de Waard. 1990. Results of a botanical expedition to Mount Roraima, Guyana. I. Bryophytes. *Tropical Bryology* 1: 25–54.

Greuter, W., F. R. Barrie, H. M. Burdet, W. G. Chaloner, V. Demoulin, D. L. Hawksworth, P. M. Jørgensen, D. H. Nicolson, P. C. Silva, P. Trehane & J. McNeill. 1994. International Code of Botanical Nomenclature (Tokyo Code). *Regnum Veg.* 131.

Grolle, R. 1983. Nomina generica Hepaticarum; References, types and synonymies. *Acta Bot. Fenn.* 121: 1–62.

Hatcher, R. E. 1957. The genus *Trichocolea* in North, Central and South America (Hepaticae). *Lloydia* 20: 139–185.

———. 1958. The genus *Trichocolea* in New Zealand. *Trans. Roy. Soc. New Zealand* 85: 237–246, figs. 1–3.

Lindberg, S. O. 1875. Hepaticae in Hibernia mense Julii 1873 lectae. *Acta Soc. Sci. Fenn.* 10: 467–559.

Little, E. L. 1949. Nomina conservanda proposals in Hepaticae. *Bryologist* 52: 1–22.

Müller, K. 1951–1958. Die Lebermoose Europas. *In: Rabenhorst's Kryptogamen-Flora*, ed. 3, 6, pp. 1–1365, figs. 1–514.

Schiffner, V. 1893–1895. Hepaticae (Lebermoose). Pp. 3–141, f. 1–73 *in: A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, Teil I (Abt. 3, 1 Hälfte): 1 (3), Leipzig. [Pp. 1–96, 10 Oct. 1893; pp. 97–144, 15 Jan. 1895.]*

Schuster, R. M. 1963. Studies on antipodal Hepaticae. I. Annotated keys to the genera of antipodal Hepaticae with special reference to New Zealand and Tasmania. *J. Hattori Bot. Lab.* 26: 185–309.

———. 1966. The Hepaticae and Anthocerotae of North America east of the hundredth meridian. Vol. 1. Columbia Univ. Press, New York.

———. 1980. New combinations and taxa of Hepaticae. I. *Phytologia* 45: 415–437.

———. 1984. Evolution, phylogeny and classification of the Hepaticae. Pp. 892–1070, f. 36–100 *in: R. M. Schuster (editor), New Manual of Bryology, Vol. 2. Hattori Botanical Laboratory, Nichinan.*

Spruce, R. 1884–1885. Hepaticae Amazonicae et Andinae. *Trans. & Proc. Bot. Soc. Edinburgh* 15: 1–308, pl. 1–4, 1884 (part I); i–xi, 309–589, pl. 5–22, 1885 (part II).

———. 1895. Hepaticae elliottianae, insulis Antillanis Sti Vincentii et Dominica a clar. W. R. Elliott, annis 1891–92, lectae, Ricardo Spruce determinatae. *J. Linn. Soc., Bot.* 30: 331–372, pl. 20–30.

Stafleu, F. A. & R. S. Cowan. 1985. Taxonomic Literature. A selective guide to botanical publications and collections with dates, commentaries and types. Vol. III: Sal-St. *Regnum Veg.* 112: 1–1066.

Stephani, F. 1888. Westindische Hepaticae. *Hedwigia* 27: 276–299.

———. 1898–1924. *Species Hepaticarum*. Genève & Bale, 6 vols.

Verdoorn, F. 1932. Classification of hepatics. Pp. 413–432 *in F. Verdoorn (editor), Manual of Bryology. The Hague.*