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A systematic monograph of the genus *Thysananthus* (Lejeuneaceae, Marchantiophyta)

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Abstract

A world-wide revision of the liverwort genus *Thysananthus* (Marchantiophyta: Lejeuneaceae) leads to the recognition of fifteen species in two sections: sect. *Thysananthus* (eleven species) and sect. *Vittatae* (four species). The genus is monophyletic with the inclusion of *Dendrolejeunea fruticosa* and *Mastigolejeunea pancheri*, and lacks synapomorphies. Morphological characters of *Thysananthus* are non-exclusive, and include *Lejeunea*-type branching, epidermal cells mostly as large as medullary cells, leaves convolute when dry, leaf cells elongate, trigones cordate, oil bodies segmented, underleaves often adnate to leaves, innovations lejeuneoid, and female involucre (incl. perianths) usually toothed. The two sections are characterized by the absence versus presence of a vitta. Species are defined by the possession of two or more independent, diagnostic morphological characters and monophyly. Based on phytochemical and molecular evidence *T. gottschei*, previously considered a synonym of *T. convolutus*, is resurrected as a distinct species. One variety, *T. gottschei* var. *continuus*, is newly described, and the new combinations *T. convolutus* var. *laceratus* and *T. retusus* subsp. *sellingii* are proposed. A key to the species of the genus *Thysananthus* is provided and each species is fully described and illustrated, with complete synonymy and detailed data on habitat and distribution. *Thysananthus* is pantropical in distribution, with four species ranging into warm temperate regions; the centre of diversity of the genus is in Southeast Asia. The species grow as epiphytes in moist lowland and montane forests, and include ecological specialists (shade epiphytes, sun epiphytes) as well as generalists.

Key words: Lejeuneaceae, liverwort, Marchantiophyta, monograph, *Thysananthus*

Introduction

The genus *Thysananthus* Lindenberg ex Lehmann (1844: 24) was firstly described in 1844. Later, Spruce (1884) published *Thysano-Lejeunea* Spruce (1884: 105) as one of his 37 subgenera of *Lejeunea* Libert (1820: 373), a genus which was almost equivalent to the present family Lejeuneaceae. The subgenus *Thysano-Lejeunea* was more or less equivalent to *Thysananthus* and was classified in the “Holostipae” Spruce (1884: 74) because of its undivided underleaves. Spruce included seven species in *Lejeunea* subg. *Thysano-Lejeunea*: *L. amazonica* Spruce (1884: 106), *L. dissoptera* Spruce (1884: 108), and *L. pterobryoides* Spruce (1884: 109) from tropical America, and *L. comosa* (Lindenberg ex Lehmann 1844: 25) Spruce (1884: 108), *L. convoluta* (Lindenberg in Gottsche *et al.* 1845: 288) Spruce (1844: 106), *L. reniloba* (Gottsche in Gottsche *et al.* 1845: 301) Spruce (1844: 106), and *L. spathulistipa* (Lindenberg in Gottsche *et al.* 1845: 287) Spruce (1844: 106) from Southeast Asia.

In Species Hepaticarum, Stephani (1912a) recognized 34 species in *Thysananthus*, the group having been restored to generic rank by Schiffner (1893), replacing “*Thysano-Lejeunea*”. Fourteen species of *Thysananthus* were newly described in his treatment, of which only two, however, have survived subsequent revisions (including this revision), *T. appendiculatus* Stephani (1912a: 794) and *T. mollis* Stephani (1912a: 798).

Distribution and ecology:—Endemic to New Caledonia; 400–700 m; on tree trunks in lowland rain forests.

Representative specimens:—**New Caledonia.** SOUTH: Mé Amméri, *Guillaumin & Baumann-Bodenheim 8902, 9136* (G, GOET); Rivière Blanche, *Guillaumin & Baumann-Bodenheim 11900* (G, GOET); Rivière Bleue, *Guillaumin & Baumann-Bodenheim 10893* (GOET); Koghis Mts., Bouo summit, *Hürlimann 2111* (G, GOET, U); Pourina, *Hürlimann 2647c* (GOET).

Subspecific variation:—*Thysananthus retusus* subsp. *sellingii* differs from subsp. *retusus* in the much greater length of lobule, which is 5 × longer than wide. *Thysananthus sellingii* is treated here as a subspecies of *T. retusus* because it is separated from the latter by only one diagnostic morphological character and by its different geographical range.

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Appendix I. Excluded Taxa

- Thysananthus africanus* Stephani (1886: 93). Type: EQUATORIAL GUINEA. Bioko [“Fernando Po Island”]: “*Mönkemeyer 545*” (holotype G!) = *Caudalejeunea africana* (Steph.) Schiffner (1893: 129)
- Thysananthus brasiliensis* Arnell in Schiffner & Arnell (1964: 118). Type: BRAZIL. “São Paulo: prope Salto Grande do Rio Paranapanema, ca. 500 m, ...Hb. W”, *Schiffner 2199* (holotype W) (not seen) = *Caudalejeunea lehmanniana* (Gottsche in Gottsche *et al.* 1845: 325) A.Evans (1907: 554), syn. fide Gradstein (1994): 121.
- Thysananthus crispatus* Stephani (1924: 567). Type: NEW GUINEA. “*Ledermann s.n.*” (holotype G) (not seen); Icon. Steph. nr. 10175 = *Spruceanthus polymorphus* (Sande Lacoste 1854: 420) Verdoorn (1934a: 155), syn. fide Verdoorn (1934a): 155.
- Thysananthus elongatus* (Austin) Evans (1900: 423). *Phragmicoma elongata* Austin (1869: 225). Type: HAWAII. “*Andersson s.n.*” (isotype G!) = *Spruceanthus polymorphus* (Sande Lacoste 1854: 420) Verdoorn (1934a: 155), syn. fide Verdoorn (1934a): 155.
- Thysananthus evansii* Fulford (1941: 34). Type: BELIZE. Punta Gorda: collector unknown (holotype CINC) (not seen) = *Fulfordianthus evansii* (Fulford) Gradstein (1992a: 46).
- Thysananthus fragillimus* Herzog in Handel-Mazzetti (1930: 45). Type: CHINA. Setchwan: “... auf dem Lungdschu-schan, bei Huili, 3000 m,...”, 24 March 1914, *Handel-Mazzetti 971* (not seen) = *Spruceanthus semirepandus* (Nees 1830: 39) Verdoorn (1934a: 153), syn. fide Verdoorn (1934a): 153.
- Thysananthus frauenfeldii* Reichardt (1866: 958). Type: FRENCH POLYNESIA. Tahiti, Novara expedition, *Jelinek s.n.* (isotype G!) = *Mastigolejeunea frauenfeldii* (Reichardt) Verdoorn (1934b: 230).
- Thysananthus lehmannianus* (Nees) Stephani (1912a: 785). *Phragmicoma lehmanniana* Nees in Gottsche, Lindenberg & Nees (1845: 302). Type: JAMAICA. “Hb. Lehmann” (not seen) = *Spruceanthus semirepandus* (Nees 1830: 39) Verdoorn (1934a: 153), syn. fide Geissler & Gradstein (1994): 202.
- Thysananthus mexicanus* Taylor (1848: 199). Type: ECUADOR. “on Pichincha, February 1847, *W. Jameson s.n.*” (not seen) = *Brachiolejeunea laxifolia* (Taylor 1847: 341) Schiffner (1893: 128), syn. fide Gradstein (1994): 172.
- Thysananthus moenkemeyeri* Stephani (1895: 234), *nom. nud.* = *Caudalejeunea africana* (Stephani 1886: 93) Schiffner (1893: 129), syn. fide Vanden Berghen (1948): 96.
- Thysananthus mutabilis* Sande Lacoste ex Verdoorn (1934a: 156), *nom. inval.* [Art. 34.1 (c)]. Material: ? = *Spruceanthus polymorphus* (Sande Lacoste 1854: 420) Verdoorn (1934a: 155), syn. fide Verdoorn (1934a): 155.
- Thysananthus oblongifolius* Chen & Wu (1964: 227). Type: CHINA. Yunnan: Jing-hong, 1100 m, 29 August 1936, *Wang 9445* (not seen) = *Caudalejeunea recurvistipula* (Gottsche in Gottsche *et al.* 1845: 326) Schiffner (1893: 129), syn. fide Zhu & So (2001): 97.
- Thysananthus obovatus* Yang (1963: 24). Type: TAIWAN. “Hualien Hsien, Mt. Tsing-shui, December 1961”, *T. Shimizu & M.T. Kao 317* (not seen) = *Spruceanthus semirepandus* (Nees 1830: 39) Verdoorn (1934a: 153), syn. fide Kitagawa (1981): 71.
- Thysananthus obtusifolius* Stephani (1912a: 792). Type: NEW CALEDONIA. (holotype G); Icon. Steph. nr. 10199, *syn. nov.* = *Spruceanthus polymorphus* (Sande Lacoste 1854: 420) Verdoorn (1934a: 155). Verdoorn (1934a) considered *T. obtusifolius* a synonym of *Spruceanthus*. Judging from the original description and the drawing of *T. obtusifolius* of Stephani’s “*Icones Hepaticarum Ineditae*”, this is *S. polymorphus*.
- Thysananthus olivaceus* Stephani ex Arnell (1962: 349), *nom. inval.* [Art 32.1(d)]. Material: ECUADOR. “Prov. Guayas: Rio Daule, below Pichincha, Hacienda Santa Barbarita (4737)” (not seen); Icon. Steph. nr. 10225: Brazil, Rio Branco, *Ule 655*, *syn. nov.* = *Bryopteris filicina* (Swartz 1788: 145) Nees in Gottsche, Lindenberg & Nees (1845: 284). Judging from the drawing of *T. obtusifolius* of Stephani’s “*Icones Hepaticarum Ineditae*”, which shows one leaf and one underleaf, this is *B. filicina*.
- Thysananthus ophiocephalus* Taylor (1846: 384). Type: NEW ZEALAND. “Bay of Islands”, *Sinclair s.n.* (holotype FH!; isotype S!), *syn. nov.* = *Archilejeunea olivacea* (Hooker & Taylor 1844: 568) Stephani (1912a: 734). Stephani (1912) considered *T. ophiocephalus* a synonym of *Mastigolejeunea anguiformis* (Hook.f. & Taylor) B.M.Thiers & Gradst. Judging from the type specimens, this is *A. olivacea*.
- Thysananthus paucidens* Stephani (1912a: 793). Type: HAWAII. (not seen); Icon. Steph. nr. 10203 = *Spruceanthus polymorphus* (Sande Lacoste 1854: 420) Verdoorn (1934a: 155), syn. fide Verdoorn (1934a): 155.