

***Lejeunea adpressa* Nees (Lejeuneaceae), a widely distributed species of tropical America**

*M. Elena REINER-DREHWALD**

*Georg-August-Universität Göttingen,
Albrecht-von-Haller-Institut für Pflanzenwissenschaften, Systematische Botanik,
Untere Karspüle 2, D - 37073 Göttingen, Germany*

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Abstract – *Lejeunea adpressa* Nees has ovate and entire-margined leaves, bifid underleaves and 5-keeled perianths, among other typical *Lejeunea* features. The high variability of the species is demonstrated by the numerous synonyms proposed here, including *Lejeunea magnoliae* Lindenb. & Gottsche, seven species and one var. of “*Lejeunea* subg. *Eulejeunea*” described by Spruce, *Eulejeunea setistipa* Steph., *Lejeunea longifissa* Steph. and “*L. caespitosa* sensu Schuster 1980”. Four names are lectotypified. The species is described, illustrated and its geographical distribution in tropical America is documented.

**Lejeuneaceae / Eulejeunea / Lejeunea / Lejeunea adpressa / L. caespitosa / L. longifissa /
tropical America / distribution / morphology / synonyms / taxonomy**

INTRODUCTION

Lejeunea longifissa, a typical *Lejeunea* with 5-keeled perianths, was described by Stephani (1912-1917) based on collections of Charles Wright from Cuba. The species was treated in detail by Evans (1918) and Schuster (1957) and its known geographical distribution extended to Puerto Rico and the tropical and subtropical parts of Florida (United States). Later, Jones (1972) included *Lejeunea longifissa* Steph. in his treatment of the African “*Lejeunea caespitosa* Lindenb.” group, as a possible synonym. This opinion was followed by Schuster (1980), where *Lejeunea longifissa* was now described and illustrated under the name *L. caespitosa* Lindenb. Consequently, *L. caespitosa* was considered to be a pantropical and highly variable species and it was cited in many checklists of tropical America and Africa.

Surprisingly, study of the type material of *L. caespitosa*, from the Cape of Good Hope in South Africa, proved that this taxon is conspecific with *Lejeunea capensis* Gottsche (Reiner-Drehwald & Schäfer-Verwimp, 2008). The latter species has inflated perianths without keels and is distributed in Sub-Saharan Africa, Madagascar, the Yemeni Arab Republic and tropical America, where it is common in south-eastern Brazil and rare and poorly known along the Andes (Jones, 1987; Giancotti & Vital, 1989; Schäfer-Verwimp, 1992; Grolle, 1995;

* Correspondence and reprints : mreiner@uni-goettingen.de

Wigginton & Grolle, 1996; Kürschner, 2000; Reiner-Drehwald & Schäfer-Verwimp, 2008).

For the American plants known as *Lejeunea longifissa* and “*Lejeunea caespitosa* sensu Schuster 1980”, *Lejeunea adpressa* Nees is considered to be the oldest name. Spruce (1884-1885) described 30 taxa under “*Lejeunea* subg. *Eulejeunea*”, including eight proposed here as new synonyms of *L. adpressa*.

The aim of the present paper is to describe *Lejeunea adpressa* based on type materials and numerous other collections from tropical America, propose new synonyms and lectotypifications, and discuss the variability of this widely distributed taxon.

SYSTEMATIC TREATMENT

Lejeunea adpressa Nees, in Gottsche, Lindenberg & Nees, *Syn. Hep.*: 380. 1845.
Figs 1-29

Type. Brazil. Pão Pereira, s.coll., „dedit Cl. Fischer“ (holotype, STR [gyn., male]).

Lejeunea magnoliae Lindenb. et Gottsche, in Gottsche, Lindenberg et Nees, *Syn. Hep.*: 763. 1847. Type. Mexico. „ad Mirador“, „in foliis Magnoliae“, Mar 1842, Liebmann 246 (**lectotype**, W [Lindenb. Hep. 6506, a few shoots, gyn.], **here designated**; isotypes, C [a few shoots, male, gyn.], G 21599 [*ex* Lindenb. Hep. 6506, 1 shoot, sterile]). **Syn. nov.**

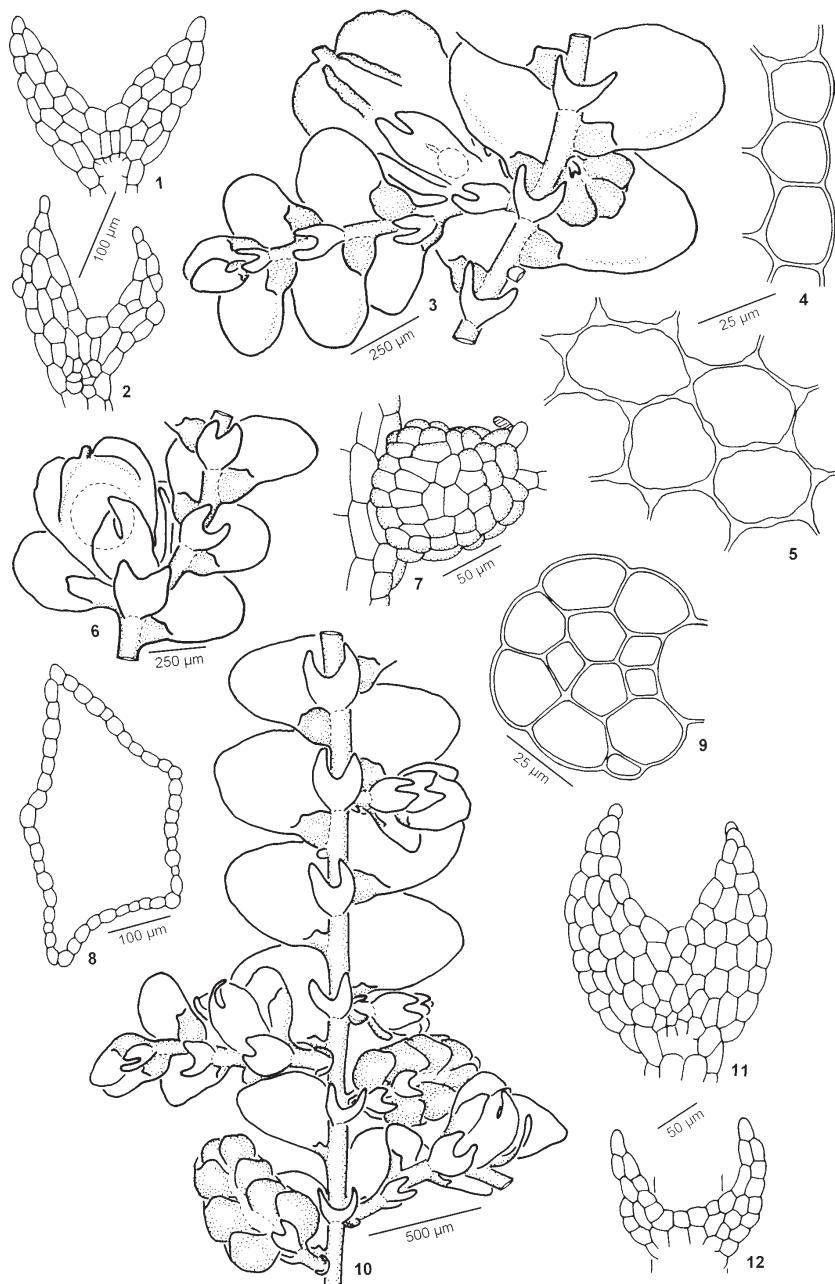
Lejeunea artocarpi Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 280. 1884. Type. Venezuela. San Carlos del Río Negro, “in cortice *Artocarpus edulis*”, Spruce s.n., Hepaticae Spruceanae: Amazonicae et Andinae (holotype, MANCH CC 18526 [autoicous, c.per.]; isotypes [all autoicous, c.per.], M, NY). **Syn. nov.**

Lejeunea carolensis Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 276. 1884. Venezuela. San Carlos del Río Negro, epiphyll, “cum Hookeria patrisii”, Spruce L486 (**lectotype**, MANCH CC 18530 [autoicous, c.per.], **here designated**; isolectotype, MANCH CC 18529 [autoicous, c.per.]). Brazil. “ad flumen Uaupés”, epiphyll, Spruce L 306 (paralectotype, MANCH CC 18531 [autoicous, c. per.]). **Syn. nov.**

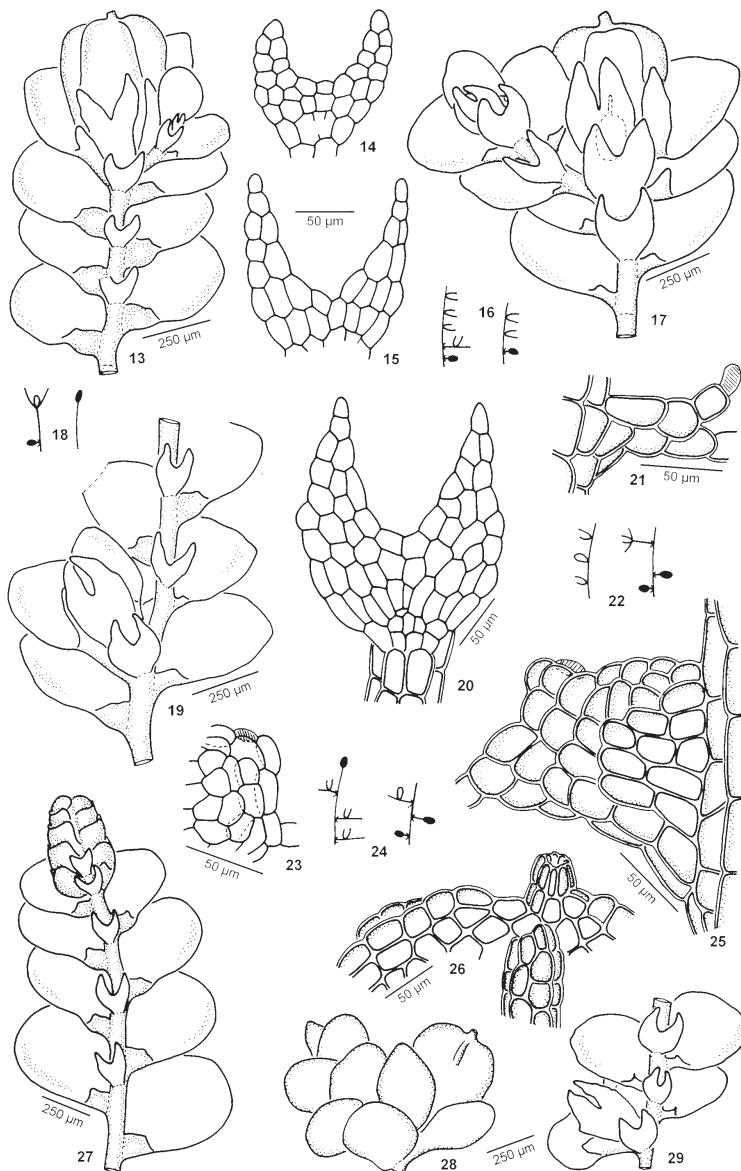
Lejeunea cauapunensis Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 283. 1884. Type. Venezuela. „ad rivulum Cauapuna, fl. Negro tributarium”, Spruce L 490 (holotype, MANCH CC 18535 [autoicous, c.per.], isotypes, MANCH CC 18537 [c. per.], MANCH CC 18536 [autoicous, c. per.]). **Syn. nov.**

Lejeunea coffeae Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 276. 1884. Type. Venezuela. San Carlos del Río Negro, epiphyll on *Coffea arabica*, Spruce L514 (holotype, MANCH CC 18587 [autoicous, c. per.]; isotype, MANCH CC 18586 [autoicous, c. per., Hep. Spruc.: Amaz. et And.]). **Syn. nov.**

Lejeunea drymophila Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 285. 1884. Type. Peru. Tarapoto, “in Melastomaceae folio”, Spruce L5m (**lectotype**, MANCH CC 18605 [autoicous, c.per.], **here designated**). Peru, Tarapoto, “in cortice” (paralectotypes [both autoicous, c.per.], MANCH CC 18607, 18604). Brazil. “Fl. Negro”, Spruce L 278 (paralectotype, MANCH CC 18600 [autoicous, c.per.]). **Syn. nov.**



Figs 1-12. *Lejeunea adpressa*. **1-2.** underleaves. **3.** shoot with perianth and androecium, ventral view. **4.** marginal leaf cells. **5.** median leaf cells. **6.** shoot with perianth, ventral view. **7.** lobule, in situ. **8.** cross section of perianth. **9.** cross section of stem. **10.** shoot with gynoecia and androecia, ventral view. **11-12.** underleaves. (1, 2, 8, 9: Verwimp 9013. 3, 7: Schäfer-Verwimp & Verwimp 22400/B : 4-6, 10-12: Schäfer-Verwimp & Verwimp 22432).



Figs 13-29. *Lejeunea adpressa*. **13, 17.** shoots with perianth, ventral view. **14-15, 20.** underleaves. **16, 18, 22, 24.** cladographs of fertile plants, solid ellipse = androecium, open ellipse = gynoecium with perianth, U = gynoecium without perianth. **19, 29.** shoots with gynoecium, ventral view. **21.** reduced lobule, in situ. **23.** detail of lobule apex. **25.** lobule. **26.** perianth apex with beak, dorsal view, detail of 28. **27.** shoot with androecium, ventral view. **28.** shoot with perianth, dorsal view. (13, 14, 18, 26, 28: Schäfer-Verwimp & Verwimp 14807/A. 15, 19: D. Griffin III s.n. (Jamaica). 16, 17, 20, 23: Acebey & Krömer 1029. 21, 29: Schäfer-Verwimp & Verwimp 14391/A. 22: Schäfer-Verwimp & Verwimp 17900/A. 24, 27: Frahm et al. 1410. 25: Reiner 773).

Lejeunea drymophila var. *macrostachya* Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 285. 1884. Type. Brazil. "Fl. Uaupés", Spruce L314 (**lectotype**, MANCH CC 18601 [c.per., scanty, in bad preservation state], **here designated**). **Syn. nov.** Note: two collections are cited in Spruce (1884-1885: 285): "ad fluvios Uaupés et Bombonasa". The only one found in MANCH is lectotypized here.

Lejeunea limbata Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 286. 1884. Type. Brazil. „S. Gabriel fl. Negro, in foliis vivis“, Spruce L465 (holotype, MANCH CC 18701 [autoicous, c.per.]; isotypes [both autoicous, c.per.], MANCH CC 18702, 18703). **Syn. nov.**

Lejeunea orbicularis Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 285. 1884. Type. Brazil. "fl. Negro, ad São Gabriel da cachoeria, in cortice", Spruce L65 (holotype, MANCH CC 18721 [autoicous, c.per.], isotypes, MANCH CC 18722, 18723, M, NY). **Syn. nov.**

Eulejeunea setistipa Steph., *Hedwigia* 35: 93. 1896. *Lejeunea setistipa* (Steph.) Steph., *Spec. hepaticae* 5: 759, 1915 (*non* Steph. ex Schiffn. 1893). Type: Brazil: "Brasilia", Ule 114 (holotype, G [autoicous, c.per.]). **Syn. nov.**

Lejeunea longifissa Steph., *Spec. hepaticae* 5: 745. 1915. Type. Cuba, 1188, Wright s.n. (holotype, G 9351 [autoicous, c. per.]; isotype, G s.n. [autoicous, c.per.]). **Syn. nov.**

Illustrations: Evans 1918 (as *Lejeunea longifissa*); Schuster 1957 (figs 42-44, as *L. longifissa*); Schuster 1980 (figs 709-710, as *L. caespitosa*); Stephani 1985 (2580, as *L. artocarpi*; 2582-2583, as *L. carolensis*; 2584-2585, as *L. cauapunensis*; 2590, as *L. coffeae*; 2598, as *L. drymophila*; 2621, as *L. limbata*; 2622, as *L. longifissa*; 2633, as *L. orbicularis*; 2650, as *Eulejeunea setistipa*).

Plants shiny, greenish to whitish in herbarium, 0.6-1.2(-1.4) mm wide, up to 6 mm long, irregularly branched or excurrent, with the main shoot longer than secondary branches (principally in epiphyll collections); branches of the *Lejeunea*-type, abundant or few, similar to the main shoot or smaller, collars large, most branches fertile. **Stems** 55-85 µm wide, epidermal cells in ventral view rectangular, 40-55 µm long, 16-20 µm wide; stems in cross section suborbicular, 7 epidermal cells surrounding 5-8 smaller medullary cells, epidermal cells 16-27 × 23-33 µm, medullary cells 9-15 × 9-18 µm, cell walls thin, hyaline; ventral merophyte 2 cells wide. **Leaves** contiguous to imbricate, obliquely to widely spreading. **Lobes** ovate, plane to slightly concave, 460-700 µm long, 350-550 µm wide, margin entire to slightly crenate, apex rounded to subacute, plane, dorsal margin arched, ventral margin ± straight. Marginal leaf cells quadrate to rectangular, 16-20 µm long and wide, median cells isodiametric to elongated, 23-27 µm long, 27-33 µm wide, basal cells elongated, 23-27 µm long, 36-50 µm wide; cell walls thin, trigones medium sized to large, intermediate thickenings 0-2 per wall, medium sized to large; cuticle smooth; oil bodies according to Schuster (1957: 413, as *L. longifissa*) segmented papillose, usually (2) 3-7 per cell, elliptical to linear, 2.5-3 × 8-11 µm to 4 × 5 µm, a few spherical, diameter about 4 µm. **Lobules** variable, when reduced only few cells large, ± rectangular, when developed oblong to suborbicular, strongly inflated, 115-180 µm long, 80-120 µm wide, ± 1/4 - 1/3 the lobe length, lateral margin incurved, 5-6 cells long, tooth short, hyaline papillae proximal, with or without a small notch on the proximal side of the tooth, apical margin straight to lunulate, 2-3 cells, keel slightly arched, entire, at the union with ventral margin of lobe slightly angled. **Underleaves** distant, ovate to oval, (80-)110-225 µm wide, 115-270 µm long, longer than wide, 1.5-2.8 x the stem width, 50-70 % bifid, sinus V- to U-shaped, lobes triangular to lanceolate, straight to connivent or ± divergent,

apex subacute, 1-2 cells in a row at the apex, 3-5 cells wide at the base, margins entire to crenate, occasionally with a small tooth formed by a protuberant cell, base cuneate, insertion line slightly arched, rhizoids often developed. **Autoicous**, often fertile. **Androecia** terminal on short branches without vegetative leaves at the base or terminal on the main shoot, 2-6(-9) pairs of bracts, bracts imbricate, hypostatic, 1-2 bracteoles at the base of the spike, 2 antheridia per bract. **Gynoecia** terminal on short branches or on the main shoot, with one sterile or fertile lejeuneoid innovation, 1-3(-5) gynoecia in a row, seldom with 2 innovations. Female bract lobes ovate, 430-490 µm long, 230-250 µm wide, margin entire, ± sinuate, apex rounded to subacute; bract lobules triangular to lanceolate, 215-280 µm long, 60-70 µm wide, margin entire, apex subacute, keel slightly arched, not winged; bracteoles oblong, 350-430 µm long, 180-215 µm wide, free or connate with the bract lobule on one side, bifid for 55-60 % of their length, sinus narrow, V-shaped, lobes ± lanceolate, mostly ± connivent. **Perianths** ± 1/3 its length emergent between the bracts, obovoid to obcordate, dorsally compressed, 0.45-0.70 mm long, 0.3-0.5 mm wide, 5-keeled, keels 1/3-1/2 as long as the perianth, dorsal keel shorter and less distinct, keels entire or irregularly 2-winged, wings short, 1 cell wide, ± crenate, beak 40-70(-100) µm (1-2 rows of cells) long. **Vegetative reproduction** not observed.

Distribution and ecology: *Lejeunea adpressa* is widely distributed in tropical America, from Mexico, tropical and subtropical parts of Florida (Evans, 1918; Schuster, 1957, 1980) and the West Indies to N Argentina. It is found from sea level to 1900 m in different forest types, often also in disturbed forests or secondary vegetation. *Lejeuna adpressa* forms small patches appressed to the substratum or growing intermingled among other Lejeuneaceae. It is found as an epiphyte on tree trunks, on small branches, on lianas or as an epiphyll.

Selected additional specimens examined:

MEXICO. Mirador, Mar 1842, Liebmann 236 pp., Hep. Lindenb. 6503 (W, G 21598).

COSTA RICA. Río Naranjo, Tonduz s.n. (G 11832, JE, both with the type of *Hygrolejeunea tonduzana*).

PANAMA. CHIRIQUÍ: Reserva Forestal La Fortuna, Hornito, sendero Quebrada Alemán, 1100-1200 m, Mar 1996, Reiner-Drehwald 960068 (PMA). **PANAMÁ:** NP Altos de Campana, sendero de interpretación, 8°40'N, 79°55'W, 850 m, Oct 1991, Salazar Allen 10815 (U, dupl. from PMA). Isla de Barro Colorado, 9°10'N, 79°50'E, Mar 1987, Salazar Allen & Chung 4678 (PMA). NP Chagres, Cerro Azul, Sendero El Cantar, 800 m, Mar 1996, Reiner-Drehwald 960122 (PMA).

CUBA. GUANTÁNAMO: Sierra del Purial, 6 km N of Puriales de Caujeri, S of Río Toa, Oct 1980, Pócs et al. 9185/BF (EGR). **ORIENTE:** Sierra Maestra, Pico Real del Turquino, 1800-1900 m, Dec 1969, Borhidi et al. s.n. (EGR).

JAMAICA. St. Mary, Castleton Gardens, 23 Jun 1968, D. Griffin III s.n. (U).

DOMINICAN REPUBLIC. MONSEÑOR NOUEL: Cordillera Central, 1200-1300 m, Nov 2003, S. & T.Pócs 03156/F (GOET, dupl. from EGR). **SANTIAGO:** Cordillera Central, San José de las Matas, between Montones Arriba and Mata Grande, 800 m, Apr 2007, Schäfer-Verwimp & Verwimp 27159 (herb. Schäfer-Verwimp).

WINDWARD ISLANDS. GUADELOUPE: Schäfer-Verwimp & Verwimp 22400 B, 22432.

DOMINICA: SW of the island, above Giraudel, May 1996, Schäfer-Verwimp & Verwimp 17900/A (herb. Schäfer-Verwimp). Roseau Valley, road from Laudat to Middleham Falls, 550 m, May 1996, Schäfer-Verwimp & Verwimp 17687 (herb. Schäfer-Verwimp).

COLOMBIA. RISARALDA: W side of Cordillera Occidental, above village of Jeguadas, W of Mistrato, 800 m, Jul 1992, Gradstein 8627 (U).

VENEZUELA. San Gabriel, Spruce s.n. (MANCH CC 18527, as *Lejeunea artocarpi*). San Carlos, Spruce L409 (MANCH CC 16967, as *Lejeunea solanicola*).

SURINAM. Area of Kabalebo Dam project, distr. Nickerie, 5°N, 58°W, 0-50 m, Nov 1981, *Bekker 1467b* (U).

FRENCH GUIANA. Village Saul, 3°37'N, 53°11'W, 200-400 m, Jun 1986, *Bekker 2248-5* (U).

ECUADOR. ESMERALDAS: road Ibarra – San Lorenzo, near Lita, 500 m, Aug 2004, *Schäfer-Verwimp et al. 24419/A* (herb. Schäfer-Verwimp). **PICHINCHA:** NW from Quito, road Quito-Mindo, km 62, S of Nanegalito, 1900 m, Aug 2004, *Schäfer-Verwimp et al. 24325/C* (herb. Schäfer-Verwimp). **TUNGURAHUA:** above Río Topo, between Baños and Puyo, 1170 m, Aug 2004, *Schäfer-Verwimp et al. 24235* (herb. Schäfer-Verwimp).

PERU. MADRE DE DIOS: NP Manu, near Palotoa and Sta. Cruz, road between Pilcopata and Shintuya, 500 m, Feb 2000, *Drehwald 994369* (herb. Drehwald, scanty). **SAN MARTÍN:** Prov. Lamas, road Yurimaguas-Tarapoto, km 107, 700 m, Sep 1982, *Bryotrop: Frahm et al. 1410* (U).

BRAZIL. AMAZONAS: Rio Juruá, Jun 1901, *Ule 547* (M, HBG, both as *Lejeunea drymophila*). **ESPÍRITO SANTO:** Vargem Alta, Rio Novo, Jul 1990, *Schäfer-Verwimp & Verwimp 13017* (herb. Schäfer-Verwimp). **PARANÁ:** Foz do Iguaçu, 160 m, Aug 1987, *Verwimp 9013* (herb. Schäfer-Verwimp). **SÃO PAULO:** Serra de Paranapiacaba, S of Capão Bonito, Mata Atlântica near Rio do Carmo, 540 m, Jul 1991, *Schäfer-Verwimp & Verwimp 14807/A* (herb. Schäfer-Verwimp). Litoral Norte, Ilha de São Sebastiao, 150 m, Apr 1991, *Schäfer-Verwimp & Verwimp 14391/A* (herb. Schäfer-Verwimp). Raposo Tavares, km 501, ca 65 km E of Presidente Prudente, 350 m, Feb 1988, *Schäfer-Verwimp 9437* (herb. Schäfer-Verwimp). Serra do Mar near Ubatuba, Fazenda Capricornio, 80 m, Dec 1986, *Schäfer-Verwimp 7859* (herb. Schäfer-Verwimp). Brotas, Mar 1966, *D. Vital 763* (U). Cited for São Paulo by Schiffner & Arnell 1964 (page 105 as *Lejeunea setistipa*, page 107 as *L. limbata*), not revised.

BOLIVIA. BENÍ: Prov. Ballivian, Serranía del Pilón Lajas, 450 m, *Gradstein 7105* (U). Prov. Ballivian, 15 km SW of San Borja, 250 m, Nov 1989, *Gradstein 7348* (GOET). **LA PAZ:** Prov. Nor Yungas, NP Cotapata, Estación Biológica Tunquini, 1600-1900 m, Aug 2001, *E. & U. Drehwald 10512* (LPB). Prov. Sud Yungas, Alto Bení, Sapecho, 500 m, Aug 1999, *Acebey & Krömer 1029* (GOET).

ARGENTINA. MISIONES: Dpto. Iguazú. Parque Nacional Iguazú, sobre ruta 101, 5 km al E del Arroyo Santo Domingo, *Reiner 999*, Aug 1986 (BA); idem, sobre ruta 101, picada frente a la Seccional Yacuiba, *Reiner 1030*, Aug 1986 (BA). Dpto. Eldorado. Puerto Piñares, Salto Elena, *Reiner 1106*, Aug 1986 (BA). Dpto. Montecarlo. Montecarlo, hostería ACA, *Reiner 766, 773*, Aug 1986 (BA).

Lejeunea adpressa is widely distributed in the neotropics and its morphological variation is high, which resulted in description of a large number of synonyms. The typical characteristics of this taxon are:

- Leaf cells thin-walled, with usually large and distinct trigones and intermediate thickenings (this feature is highly variable, and in some specimens the trigones are small and the intermediate thickenings are nearly absent).
- Leaf lobule variable, if well developed it is suborbicular, strongly inflated, with the lateral margin incurved.
- Deeply bifid underleaves, lobes lanceolate, straight to connivent, rarely divergent, sinus often U-shaped and wide, with or without lateral tooth.
- Perianth often obcordate, with the lateral keels strongly expanded and the dorsal keel very low and almost vestigial (perianth dorsally compressed).

Three collections from Cuba labelled *Lejeunea longifissa* are deposited in Stephani's herbarium (G). The collection bearing the same data as the *Icones Hepaticarum* (Stephani, 1985), namely "original" and "1188 ... Cuba, Wright", is considered to be the holotype. The envelope G s.n. includes two smaller ones, one with an isotype of *L. longifissa* and the other with *L. huctumalcensis* Lindenb. et Gottsche. In G 9352 only *L. huctumalcensis* was found (Reiner-Drehwald & Ilkiu-Borges, 2007).

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