



## A revision of *Archilejeunea* s.str. (Lejeuneaceae, Marchantiophyta)

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With 5 figures

**Abstract:** The genus *Archilejeunea* s.str. was taxonomically reviewed. Six species are recognized, including five species known in tropical America and one new species, *A. gradsteinii* known only from Africa. The new species differs from the closely related species *A. fuscescens* in the usually apiculate leaf apex, mostly double subfloral innovations, and female bract lobule 1/4–1/3 as long as the bract lobe. A key to the species of *Archilejeunea* is provided.

**Key words:** Africa, *Archilejeunea gradsteinii*, Hepaticae, new species, Ptychanthoideae, Sierra Leone.

### Introduction

*Archilejeunea* (Spruce) Steph. was first described as subgenus *Archi-Lejeunea* Spruce in the broadly defined genus *Lejeunea* Lib. Subsequently, Stephani (1888) reported a new species, *Archilejeunea erronea* Steph., and *Archi-Lejeunea* was raised to the generic level. However, *Archilejeunea erronea* was considered a synonym of *Leucolejeunea clypeata* (Schwein.) A.Evans (Gradstein & Geissler 1997) [ $\equiv$  *Cheilolejeunea clypeata* (Schwein.) W.Ye & R.L.Zhu]. Although many authors usually cited the genus as "(Spruce) Schiffn. 1893" and proposed to conserve "(Spruce) Schiffn. 1893" (Grolle 1995 p. 18, Gradstein & Geissler 1997), Söderström et al. (2014) have shown "(Spruce) Steph. 1888" to be a valid genus name free of conservation and the type of *Archilejeunea* sensu Spruce can be used for *Archilejeunea* Steph. 1888.

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*Archilejeunea* s.l. is a pantropical genus with about 20 species (Shi et al. 2014, Frey & Stech 2009). It was divided into two heterogeneous subgenera, i.e., *A. subg. Archilejeunea* (pyncnolejeuneoid innovations of gynoecia and never reduced leaf lobules) and subg. *Dibrachiella* (lejeuneoid innovations of gynoecia and often reduced leaf lobules) (Gradstein & Buskes 1985, Gradstein 1994, Wilson et al. 2007). Traditionally, *Archilejeunea* is characterized by the stems without an enlarged epidermis, isodiametric leaf cells with unpigmented walls, simple-triangular to radiate trigones, usually segmented oil bodies, presence of gynoecial innovations, and perianths with 4–5 smooth to weakly toothed keels (Gradstein 1994).

Recent molecular-phylogenetic studies reveal that *Archilejeunea* is not monophyletic (Wilson et al. 2007), and that *A. subg. Dibrachiella* should be raised to the generic level (Shi et al. in prep.). Morphologically, *Archilejeunea* s.str. (*A. subg. Archilejeunea*) is separated from *Dibrachiella* by the pyncnolejeuneoid innovations of gynoecia and never reduced leaf lobules. Morphological-anatomical characters and molecular-phylogenetic analyses reveal that *Archilejeunea* s.str. is sister to *Verdoornianthus* Gradst., a small genus from Amazonia (Gradstein 1994, Shi et al. in prep.) and *Dibrachiella* is closely related to the paleotropical *Ptychanthus* Nees and *Spruceanthus* Verd., and the East Asian endemic *Tuzibeanthus* S.Hatt. Both genera have tropical Afro-American distributions, but the range of *Archilejeunea* s.str. is much more restricted than that of *Dibrachiella*.

Here we present a taxonomic revision of *Archilejeunea* s.str. Six species of *Archilejeunea* were recognized, including a new species, *A. gradsteinii*, discovered from West Africa during our studies on the *Archilejeunea* specimens collected by E.W.Jones from Sierra Leone in 1971.

## Material and methods

About 300 herbarium specimens from BR, E, EGR, GOET, HSNU, PC, STU, and U were examined in the present study. Specimens were observed, measured, and illustrated with Olympus BX43 microscope and Nikon Y-IDT drawing tube instructions. Measurements were made as described in Zhu & So (2001) and Zhu & Gradstein (2005) and always represent the complete observed morphological variation of the plants. Cells and cross sections of the stem were examined and illustrated using cover slips, while shoots, leaves, underleaves, bracts, bracteoles, etc., were observed and illustrated without cover slips. Habitat data on the species were obtained from herbarium labels and literatures.

## Taxonomic treatment

*Archilejeunea* (Spruce) Steph., Hedwigia 27: 113. 1888.

*Lejeunea* subg. *Archilejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 88. 1884. *Lejeunea* subg. *Archilejeunea* Spruce sect. *Monotropella* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 89. 1884. *Archilejeunea* subg. *Monotropella* (Spruce) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 130. 1893. TYPE: *Archilejeunea ludoviciana* (Lehm.) P.Geissler & Gradst. subsp. *porelloides* (Spruce) Gradst. ( $\equiv$  *Lejeunea porelloides* Spruce).

Plants glossy yellowish-brown or dark brown in herbarium specimens, 1–3 mm wide. Stems slender, ventral merophyte 4–6(–8) cells wide; epidermis cells similar

to medullary cells; subepidermis absent. Vegetative branching of the *Lejeunea*-type. Microphyllous branches absent. Leaf margins entire; midleaf cells isodiametrical or longer than width, trigones rather thick, radiate and sometimes confluent; oil bodies segmented. Lobules never reduced, short rectangular with truncate apex and 0–1 teeth. Underleaves imbricate, rarely distant, 3–6 × stem width. Dioicous, rarely parioicous (*A. badia*). Androecia terminal or intercalary on elongated branches, bracts in (1–)4–11 pairs, bracteoles borne throughout the androecium. Gynoecia usually with a single, repeatedly fertile pycnolejeuneoid innovation (mostly double gynoecial innovations in *A. gradsteinii*), bracts and bracteoles entire; bracts as large as vegetative leaves or larger, lobe apex rounded to apiculate, lobules usually lanceolate-acuminate and 2/3 of lobe length (1/4–1/3 of lobe length in *A. gradsteinii*), never reduced; bracteoles ovate-oblong, apex entire to shortly bifid. Perianths (2–)4–5-keeled, keels smooth or slightly toothed, the ventral keels sometimes reduced in *A. fuscescens*.

*Archilejeunea* s.str. consists of six species: *Archilejeunea badia* (Spruce) Steph., *A. crispistipula* (Spruce) Steph., *A. fuscescens* (Lehm. & Lindenb.) Fulford, *A. ludoviciana* subsp. *ludoviciana*, *A. ludoviciana* subsp. *porelloides*, and *A. nebeliana* Gradst. & Schäf.-Verw. from tropical America, ranging from Costa Rica to southern Ecuador and eastern Brazil (Gradstein 1994); and *A. gradsteinii* from west Africa. The species mainly inhabits tree trunks or branches, rarely rotted logs (e.g. *A. fuscescens*) in lowland rainforests, common at altitudes of 0–550 m, sometimes up to 1075 m (Schäfer-Verwimp et al. 2013).

#### Key to the species of *Archilejeunea* s.str.

- 1 Leaf apex narrowly and obtusely pointed; cells of leaf lobule thin-walled and almost colorless ..... *A. nebeliana*
- 1' Leaf apex broadly rounded or apiculate; cells of leaf lobule moderately thick-walled and not colorless ..... 2
- 2 Leaf apex apiculate or rounded; lobules of female bract 1/4–1/3 × lobe length; mostly double gynoecial innovations; known from tropical Africa ..... *A. gradsteinii*
- 2' Leaf apex rounded; lobules of female bract 2/3 × lobe length; always single gynoecial innovations (paired innovations also present on the base of shoot in *A. ludoviciana* subsp. *porelloides*); known from tropical America ..... 3
- 3 Underleaf margins undulate; ventral leaf margin usually auriculate at the junction with the keel ..... *A. crispistipula*
- 3' Underleaf margins not undulate; ventral leaf margin never auriculate ..... 4
- 4 Leaves suborbicular, lobe apex often incurved, the angle between ventral leaf margin and the lobule keel usually less than 150°; ventral keels of perianth often reduced ..... *A. fuscescens*
- 4' Leaves ovate-oblong, lobe apex plane, the angle between ventral leaf margin and the lobule keel more than 150°; ventral keels of perianth well-developed ..... 5
- 5 Parioicous; leaf lobules strongly swollen, lobular tooth 1–4 cells long and 2–4 cells wide at base ..... *A. badia*
- 5' Dioicous; leaf lobules rather flat, lobular tooth lacking or present ..... 6
- 6 Leaf lobules 1/3–1/2 × lobe length, lobular tooth indistinct ..... *A. ludoviciana* subsp. *porelloides*
- 6' Leaf lobules 1/5–1/3 × lobe length, lobular tooth uniseriate, 1–2 cells long ..... *A. ludoviciana* subsp. *ludoviciana*

*Archilejeunea gradsteinii* X.Q.Shi & R.L.Zhu sp. nov.

Fig. 1

TYPE: Sierra Leone. Kenema District: Kambui Hills. Bambawo. 27 Mar. 1971, E.W.Jones 1528 (holotype, E! Barcode: 00018881, female).

*Archilejeunea gradsteinii* differs from *A. fuscescens* in its rounded or apiculate leaf apex, often double subfloral innovations, and the lobule of female bract  $1/4-1/3 \times$  lobe length.

DIOICOUS. PLANTS 1–1.5 cm long  $\times$  1.2–1.5 mm wide, yellowish-brown in herbarium specimens. STEMS in cross section orbicular in shape, 125–150  $\mu\text{m}$  in diam., composed of 12–14 thick-walled epidermal cells surrounding 21–23 similar medullary cells; ventral merophyte four cell rows wide. Branching of the *Lejeunea*-type. LEAVES imbricate, when dry widely spreading and flat, dorsal lobe ovate-oblong, ca.  $0.75 \times 0.5$  mm, apex rounded or usually apiculate, dorsal margin plane, arched, ventral margin plane or slightly incurved, forming an angle of ca.  $120-150^\circ$  with the keel. Lobe cell thin to moderately thick-walled, marginal cells quadrate to rectangular,  $10-20 \times 10-15$   $\mu\text{m}$ , median cells suborbicular to slightly elongate,  $15-33 \times 14-25$   $\mu\text{m}$ , basal cells hexagonal, longer than wide,  $20-45 \times 20-23$   $\mu\text{m}$ , trigones small to medium, simple-triangular, intermediate thickenings 0–1 per wall; oil bodies not seen. Lobules invariably well-developed, short-rectangular, ca.  $1/3 \times$  lobe length, apex truncate, with one short, outwardly pointing tooth consisting of 1 cell, tooth sometimes lacking. UNDERLEAVES contiguous to slightly imbricate, flat, suborbicular or reniform,  $0.25-0.32 \times 0.36-0.5$  mm,  $3-4 \times$  stem width, apex truncate, margins plane, insertion line shallowly curved. ANDROECIA terminal or intercalary on lateral branches or stem, bracts in 4–5 series, hypostatic,  $0.5-0.6 \times 0.3-0.4$  mm, apex rounded, margins entire, antheridia 2 per bract; male bracteoles slightly larger than underleaves, borne throughout the androecium. GYNOCIA with 2(–1) pycnolejeuneoid innovations, bracts suberect, lobe obovate to angular,  $0.8-1.0 \times 0.5-0.65$  mm, apex apiculate or obtuse, margins entire, lobules rectangular to ligulate, sometimes with the apex extending into a long, weird-looking extension,  $1/4-1/3 \times$  lobe length; bracteole oval,  $0.6-0.8 \times 0.3-0.57$  mm, apex obtuse to broadly rounded. PERIANTH immature. SPOROPHYTES and VEGETATIVE REPRODUCTIVE ORGANS not seen.

ETYMOLOGY: The species is dedicated to Dr. S.Robbert Gradstein, who has made an outstanding contribution to *Archilejeunea*.

*Archilejeunea* s.str. was previously known only from tropical America. *A. gradsteinii* is the first record of *Archilejeunea* s.str. from Africa. *A. gradsteinii* stands out by its rounded or usually apiculate leaf apex, mostly double innovations, and smaller lobule of the female bract, ca.  $1/4-1/3 \times$  lobe length. The species is similar to *A. fuscescens* which is extremely common in the lowland rain forests of Amazonia and the Guianas (Gradstein 1994). However, the latter differs in the constant rounded leaf apex, single gynoecial innovation, and larger lobules of the female bract, ca.  $2/3 \times$  lobe length. Moreover, the shoots of *A. fuscescens* are more robust (ca. 1.5–2.5 mm wide) and the margins of the underleaves are often recurved.

The leaves and leaf lobules of *Archilejeunea gradsteinii* also resemble *A. nebeliana*, which is the only other species in the *Archilejeunea* s.str. with pointed leaves. However, in *A. nebeliana*, the leaves become long pointed acuminate and cells of leaf lobule are colorless and thin-walled. Moreover, the female bracteoles in that species are bifid and the gynoecial innovations are single.

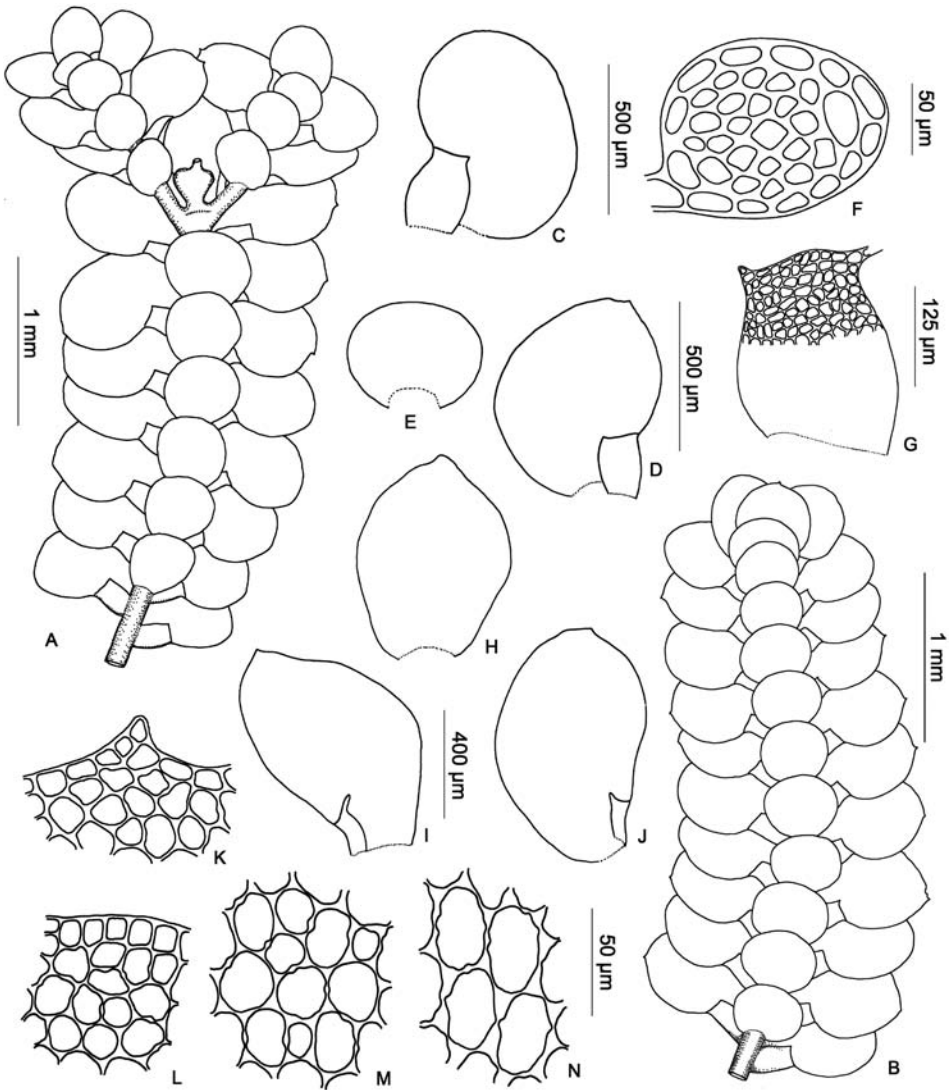


Fig. 1. *Archilejeunea gradsteinii*. A–B. Portion of shoots, ventral view. C–D. Leaves. E. Underleaf. F. Cross section of stem. G. Leaf lobule. H. Female bracteole. I–J. Female bracts. K–L. Apical marginal cells of leaf lobe. M. Median cells of leaf lobe. N. Basal cells of leaf lobe. (All from holotype, E.W.Jones 1528.)

SPECIMENS EXAMINED: SIERRA LEONE. Kenema District: Kambui Hills. Bambawo. 29 Mar. 1971, E.W.Jones 1547A (E).

DISTRIBUTION: Known only from the type locality in Sierra Leone, on tree trunks.

***Archilejeunea badia*** (Spruce) Steph., Sp. Hepat. 4: 711. 1911. Fig. 2. A–F

*Lejeunea badia* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 92. 1884. TYPE: Brazil. Rio Uaupés, IX. 1852. Spruce L104 (n.v.).

For further synonyms see Gradstein (1994).

ILLUSTRATION: Gradstein & Buskes (1985, p. 93, fig. 1b, e–f. as *Archilejeunea juliformis* (Nees) Gradst.); Stephani (1985, icones no. 793, no. 815 as *Archilejeunea recurvans* (Spruce) Steph.).

DESCRIPTION: Spruce (1884, as *Lejeunea badia*), Stephani (1911), Gradstein (1994).

*Archilejeunea badia* is recognized by the 1) paroicous sexuality, 2) strongly inflated leaf lobule with a remarkable tooth 3–5 cells long and (1–)2–4 cells wide at the base, and 3) lobule apex of the female bract usually with a long uniseriate tip (Fig. 2F).

*Archilejeunea ludoviciana* subsp. *porelloides* is similar to *A. badia*, but differs in its larger size (shoots 2.7–3.5 mm wide, only 1.5–2.5 mm wide in *A. badia*), dioicous sexuality, and lack of a distinct lobular tooth.

SPECIMENS EXAMINED: BRAZIL. Amazonas: Rio Negro, in arborum ramulis. Spruce s.n. isotype of *Lejeunea recurvans* Spruce (BR, E); Panuré fl. Uaupés, in cortice. Spruce s.n. (E).

DISTRIBUTION: Brazil and Guyana (Gradstein 1994). Often on small twigs, sometimes on leaf surface.

***Archilejeunea crispistipula*** (Spruce) Steph., Sp. Hepat. 4: 712. 1911. Fig. 2. G–K

*Lejeunea crispistipula* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 93. 1884. TYPE: Brazil. Amazonas: Rio Negro, Uanauaca, XII. 1851–1852, Spruce L60 (lectotype, designated by Gradstein & Buskes 1985, MANCH, n.v.).

ILLUSTRATION: Gradstein & Buskes (1985, p. 97, fig. 2. g–j); Stephani (1985, icones no. 797–798).

DESCRIPTION: Spruce (1884, as *Lejeunea crispistipula*), Stephani (1911), Gradstein & Buskes (1985), Gradstein (1994).

*Archilejeunea crispistipula* is separated from other *Archilejeunea* species by its glossy yellow plant, undulate underleaf margin, an angle of 90° between the ventral leaf margin with the lobule keel, and moreover, the ventral leaf margin usually "auriculate" at the junction with the lobule keel.

*Archilejeunea crispistipula* and *A. gradsteinii* are the smallest species in *Archilejeunea*, both with shoots 1.2–1.5 mm wide and ventral merophytes four cells wide. *A. gradsteinii* stands out by its usually apiculate leaf apex, plane underleaf margin, and mostly double innovations.

SPECIMENS EXAMINED: BRAZIL. Amazonas: Sao Gabriel fl. Negro, Spruce s.n. isosyntype of *Lejeunea crispistipula* (BR, E), in Campina forest, Km 60 along Manaus-Caracarái road, Griffin et al. 971 (HSNU).

DISTRIBUTION: Northern South America (Gradstein 1994). On tree trunks.

***Archilejeunea fuscescens*** (Lehm. & Lindenb.) Fulford, Bryologist 45: 174. 1942. Fig. 3

*Lejeunea fuscescens* Lehm. & Lindenb., Nov. Stirp. Pug. 7: 16. 1838. *Marchesinia fuscescens* (Lehm. & Lindenb.) Kuntze, Revis. Gen. Pl. 2: 837. 1891. TYPE: Peru (?). "in cortic. Chinae reg." ex hb. Hampe (n.v.).



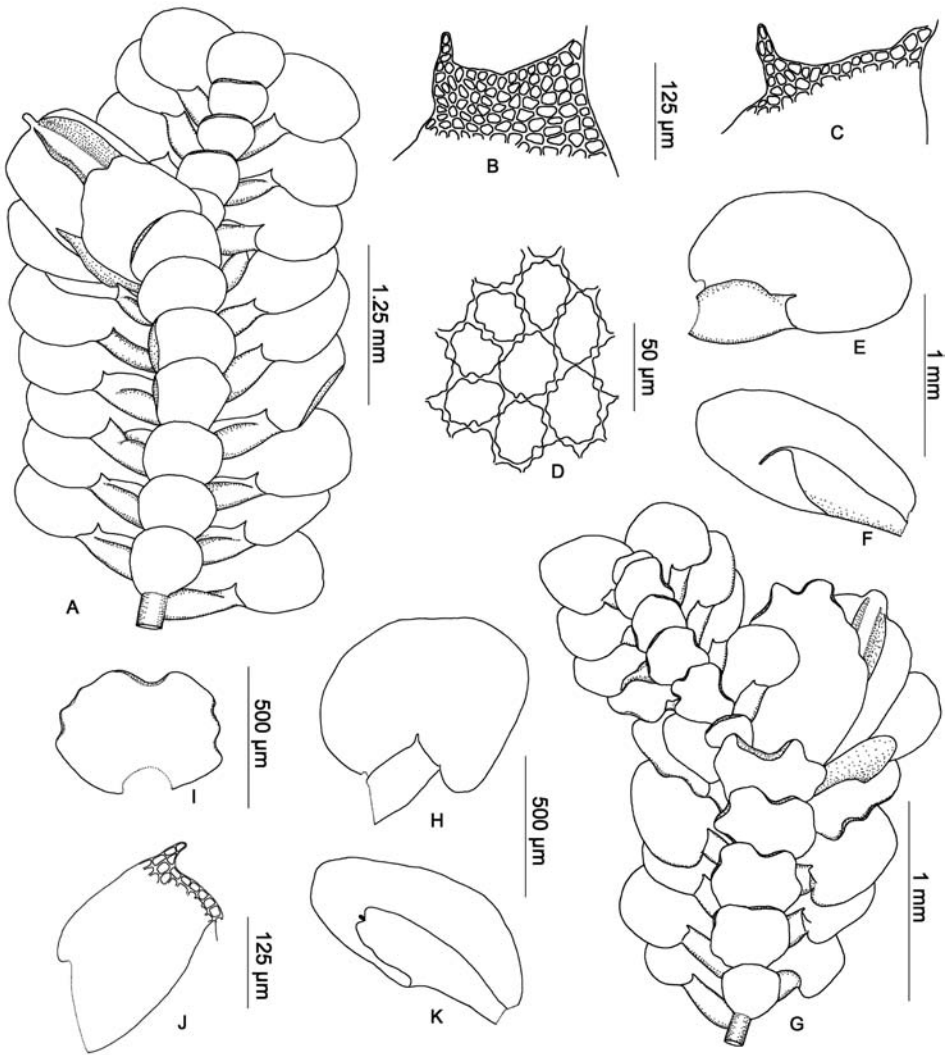


Fig. 2. A–F. *Archilejeunea badia*. A. Portion of shoot, ventral view. B–C. Leaf lobule apex. D. Median cells of leaf lobe. E. Leaf. F. Female bract. G–K. *Archilejeunea crispistipula*. G. Portion of shoot, ventral view. H. Leaf. I. Underleaf. J. Leaf lobule. K. Female bract. [A–F from Spruce s.n. (BR), G–K from Spruce s.n. (BR).]

For further synonyms see Gradstein (1994).

ILLUSTRATION: Gradstein (1994, p. 56, fig. 14); Gradstein & Ilkiu-Borges (2009, p. 54, fig. 28: A–C).

DESCRIPTION: Gradstein (1994), Gradstein & Ilkiu-Borges (2009).

*Archilejeunea fuscescens* is widely distributed in northern South America (Gradstein 1994). The species is characterized by the glossy brownish color, suborbicular leaf

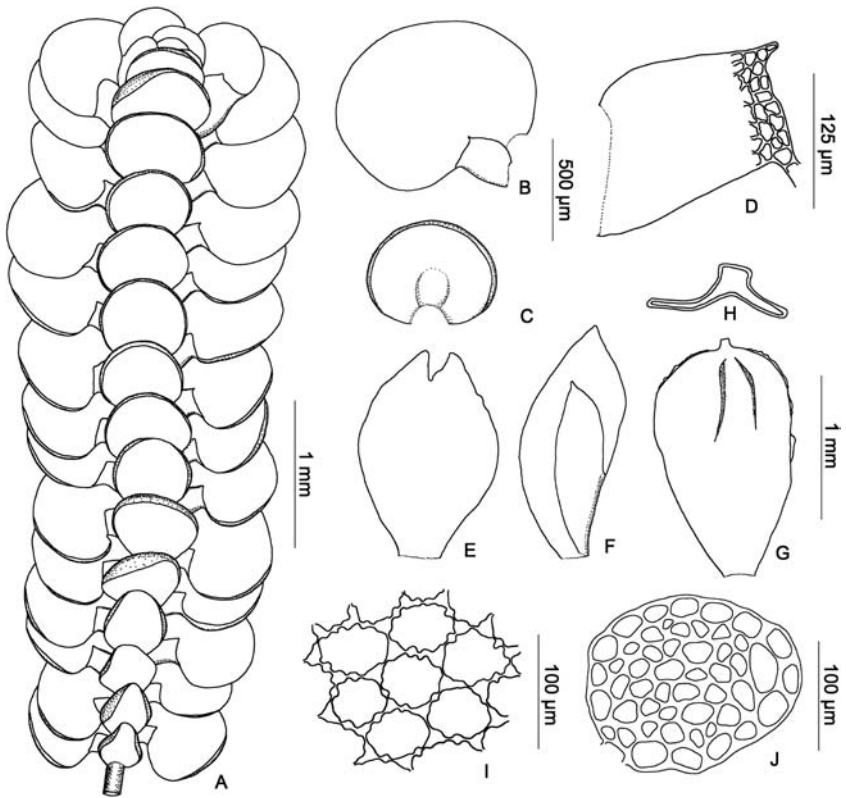


Fig. 3. *Archilejeunea fuscescens*. A. Portion of shoot, ventral view. B. Leaf. C. Underleaf. D. Leaf lobule. E. Female bracteole. F. Female bract. G. Perianth, ventral view. H. Cross section of perianth. I. Median cells of leaf lobe. J. Cross section of stem. (A from H.J. Cornelissen, H. ter Steege & S.R. Gradstein C070; B–J from S.R. Gradstein 4708.)

lobes, and often recurved underleaf apex. In addition, the ventral keels of the perianth are sometimes developed weakly, and tend to be reduced.

The differences between *Archilejeunea fuscescens* and *A. gradsteinii* are shown under the latter.

**SPECIMENS EXAMINED:** BRAZIL. Amazonas State: road Manaus-Itacoatiara km 27, Reserva Florestal Ducke. G.T. Prance et al. 11307 (BR, E). COLOMBIA. Amazon: Caquetá. L.V. Campos J5-C (HSNU). COSTA RICA. Heredia: "La Selva" Biological Station. A. Bernecker-Lücking 97–53. (E, EGR); Pantarenas: Osa Peninsula Rincón. S.R. Gradstein 9348, 9345 (HSNU). GUYANA. Mabura Hill: 180 km S of Georgetown. H.J. Cornelissen, H. ter Steege & S.R. Gradstein C070 (E, EGR); East Demerara district: Timehri, Dakara creek, Thompson farm. S.R. Gradstein 4708 (BR, E).

**DISTRIBUTION:** Bolivia, Brazil, Colombia, Costa Rica, French Guyana, Guyana, Peru, Suriname, Trinidad, and Venezuela (Gradstein 1994). On tree trunks and branches, occasionally on rotted logs.



*Archilejeunea ludoviciana* (Lehm.) P.Geissler & Gradst., J. Hattori Bot. Lab. 75: 202. 1994.

*Phragmicoma ludoviciana* Lehm., Nov. Stirp. Pug. 10: 11. 1857. TYPE: Tropical America, "in cortice Cinchonae," L.Dufour s.n. (n.v.).

*Archilejeunea ludoviciana* subsp. *ludoviciana*,

Fig. 4. A–H

For synonyms see Gradstein (1994).

DIOICIOUS. PLANTS 5 cm long, 2.5–3 mm wide, dull green to yellowish-brown in herbarium specimens. STEMS rather fragile, in cross section suborbicular in shape, 200–300  $\mu\text{m}$  in diam., composed of 22–24 thick-walled epidermal cells surrounding 55–65 thick-walled medullary cells, epidermal cells not larger than medullary cells; ventral merophyte 6–7 cell rows wide. Branching of the *Lejeunea* type, flagelliform branches lacking. LEAVES obliquely spreading at an angle of 60–80°, subimbricate; dorsal lobe ovate-oblong, 1.1–1.6  $\times$  0.7–0.8 mm, apex rounded, dorsal margin plane and arched, ventral margin slightly curved, forming a broad angle with the keel; margin cells suborbicular to hexagonal, isodiametrical, 20–30  $\times$  15–25  $\mu\text{m}$ , median cells longer than width, 30–40  $\times$  20–25  $\mu\text{m}$ , basal cells similar to median cells, 30–60  $\times$  20–30  $\mu\text{m}$ , trigones small to medium, simply to radiate, intermediate thickenings 0–2 per wall; oil bodies not seen. Lobules short rectangular, ca. 1/5–1/3  $\times$  lobe length, apex truncate, with one sharp, 1–2(–3) cells long tooth. UNDERLEAVES imbricate, rounded or longer than width, 0.8  $\times$  0.5–0.7 mm, 3–4  $\times$  stem width, apex truncate or emarginate, margins plane or weakly recurved, entire, insertion line arched. ANDROECIA terminal on lateral branches, bracts in 5–7 series, hypostatic, bracts lobe 0.80–1.00  $\times$  0.50–0.56 mm, apex rounded, margins entire, bract lobules 0.55–0.65  $\times$  0.30–0.35 mm, 2/3  $\times$  lobe length, antheridia 2 per bract; male bracteoles smaller than underleaves, borne throughout the androecium. GYNOECIA with 1 pycnolejeuneoid innovation, usually repeatedly fertile, the bracts and bracteoles in 2 series, bracts as long as vegetative leaves but much narrower, suberect, inner bract lobe oblong-lanceolate, 1.75–1.90  $\times$  0.58–0.72 mm, apex obtusely pointed or acuminate, margins entire, lobules lanceolate, 1.45–1.50  $\times$  0.37–0.40 mm, 2/3  $\times$  lobe length, apex apiculate; inner bracteole ovate-oblong, 1.75–2.10  $\times$  0.85–1.10 mm, apex bifid to 1/5 its length and the lobes narrowly acute; outer female bracteole about 1/2–2/3 as long as inner bracteole, ovate, apex shortly bifid and the lobes obtuse. PERIANTHS emergent, cylindrical-obovate, 2.2  $\times$  1.1 mm, with 5 almost smooth to irregularly subdentate keels. SPOROPHYTES not observed.

*Archilejeunea ludoviciana* subsp. *ludoviciana* is closely related to *A. ludoviciana* subsp. *porelloides*. The former, however, can be distinguished by the more slender plants and smaller leaf lobules (ca. 1/5–1/3  $\times$  lobe length) with an obvious tooth. In *Archilejeunea ludoviciana* subsp. *porelloides*, the plants are 2.7–3.5 mm wide, and the leaf lobules are ca. 1/3–1/2  $\times$  lobe length, without a distinct tooth.

Gradstein (1994) mentioned an unusual trait in the species that the distal end of the lobular free margin is truncate and connate with the leaf lobe across 1–2 cells. This character was not seen in the specimens cited below.

SPECIMENS EXAMINED: COLOMBIA. Chocó: Nuqui, El Amargal. S.R.Gradstein 8870 (HSNU). ECUADOR.

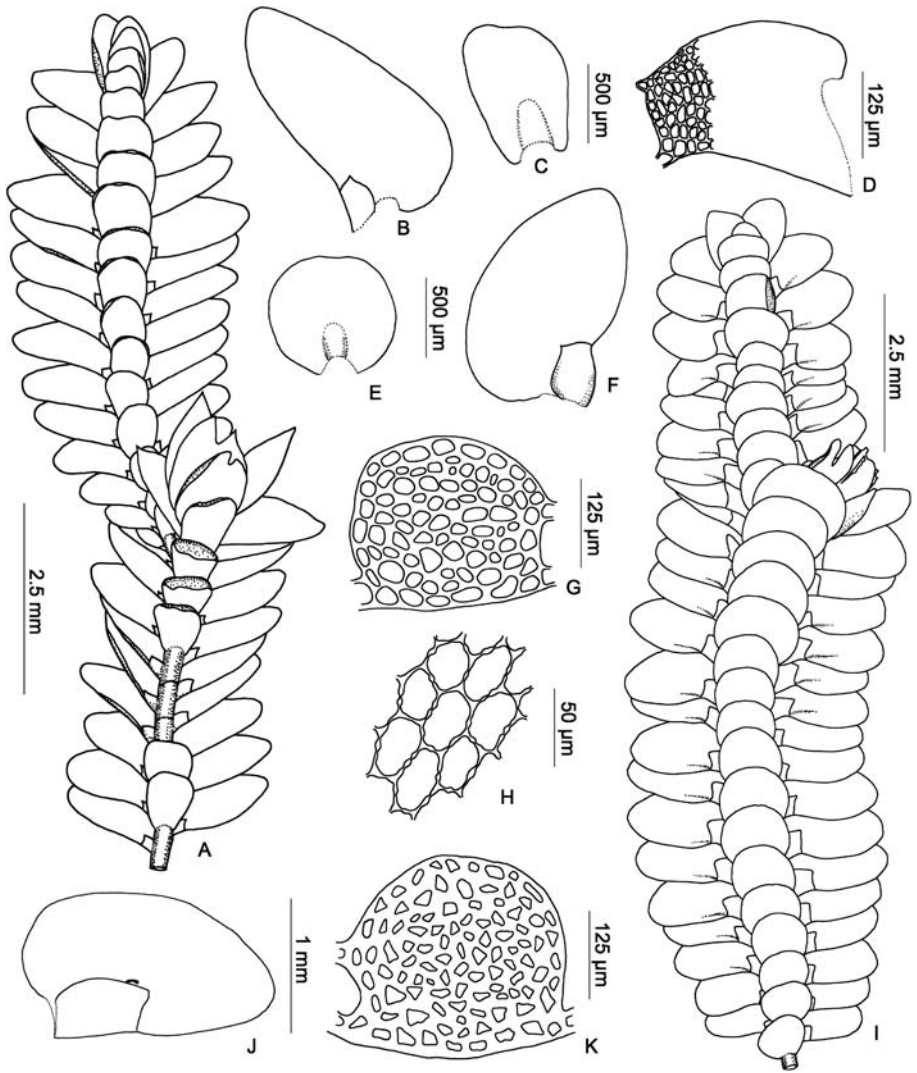


Fig. 4. A–H. *Archilejeunea ludoviciana* subsp. *ludoviciana*. A. Portion of shoot, ventral view. B, F. Leaves. C, E. Underleaves. D. Leaf lobule. G. Cross section of stem. H. Median cells of leaf lobe. I–K. *Archilejeunea ludoviciana* subsp. *porelloides*. I. Portion of shoot, ventral view. J. Leaf. K. Cross section of stem. [A–D from A. Schäfer-Verwimp 31733, E–H from S.R. Gradstein 8870, I–K from Spruce s.n. (BR).]

Napo: Tena, Estación Biológica Jatunasascha. A. Schäfer-Verwimp 31733 (PC, HSNU). VENEZUELA. Juan de Dios 28/B (BR).

DISTRIBUTION: Colombia, Ecuador, Panama, Venezuela (Gradstein 1994). On tree trunks.

*Archilejeunea ludoviciana* subsp. *porelloides* (Spruce) Gradst., Fl. Neotrop. Monogr. 62: 58. 1994. Fig. 4. I–K

*Lejeunea porelloides* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 90. 1884. *Archilejeunea porelloides* (Spruce) Schiffn., Hedwigia 33: 181. 1894. TYPE: Venezuela. Amazonas: San Carlos, Spruce L44 (lectotype, designated by Gradstein & Buskes 1985, MANCH, n.v.).

For further synonyms see Gradstein (1994).

ILLUSTRATION: Gradstein & Buskes (1985, p. 97 fig. 2a–f as *Archilejeunea porelloides*); Stephani (1985, icones no. 812–813 as *Archilejeunea porelloides*).

DESCRIPTION: Spruce (1884, as *Lejeunea porelloides*), Stephani (1911, as *Archilejeunea porelloides*), Gradstein & Buskes (1985, as *Archilejeunea porelloides*), Gradstein (1994).

*Archilejeunea ludoviciana* subsp. *porelloides* is the largest species of the genus. It can be easily recognized by the 1) robust size (2.7–3.5 mm wide, ventral merophyte 6–8 cells wide), 2) leaf lobule almost without a distinct tooth, and 3) cylindrical hyaline papilla at the proximal margin of the leaf lobule. The species is similar to *Archilejeunea ludoviciana* subsp. *ludoviciana*. For their differences see the latter.

An important morphological trait of *A. ludoviciana* subsp. *porelloides* is the absence of a distinct tooth of the leaf lobule. This character, however, is not stable. In several specimens (e.g. Venezuela. Amazonas: San Carlos. Spruce s.n. E00280573, E0028575) a lobular tooth 1–2 cells long is usually developed. Gradstein (1994, p. 60) reported leaf lobules with or without a tooth in a specimen of *A. ludoviciana* subsp. *ludoviciana*, and considered the two subspecies are closely related. Our studied confirmed his speculation.

The differences between *Archilejeunea ludoviciana* subsp. *porelloides* and *A. badia* are given under the latter.

SPECIMENS EXAMINED: BRAZIL. Amazonas: Km 130 along Manaus–Caracarai road, Rio Iages, in Campina forest. Griffin et al. 418 (HSNU). COLUMBIA. Amazonas: Rio Caquetá, near Araracoara. I. Wolf 1615 (HSNU). VENEZUELA. Amazonas: San Carlos. Spruce s.n. (BR, E).

DISTRIBUTION: Brazil, Columbia, Ecuador, Peru, Venezuela (Gradstein 1994). On tree trunks and twigs.

*Archilejeunea nebeliana* Gradst. & Schäfer-Verw., Cryptog. Bryol. 33(2): 108. 2012. Fig. 5

TYPE: Ecuador. Zamora-Chinchipec: ca 5 km S of Zamora, Parque Nacional Podocarpus, entrance Rio Bombuscara, sendero Mirador, 4°06,831'S, 78°58,017'W, on thin trunks in submontane rain forest, 1075 m alt., 25 Jan. 2011, A.Schäfer-Verwimp & M.Nebel 31924 (n.v.).

ILLUSTRATION: Gradstein & Schäfer-Verwimp (2012, p. 109, figs. 1–17).

DESCRIPTION: Gradstein & Schäfer-Verwimp (2012).

*Archilejeunea nebeliana* is easily recognized by the 1) narrowly and obtusely pointed leaves, 2) thin-walled leaf lobule cells, and 3) narrowly elongate female bracts.

The differences between *Archilejeunea nebeliana* and *A. gradsteinii* are given under the latter.

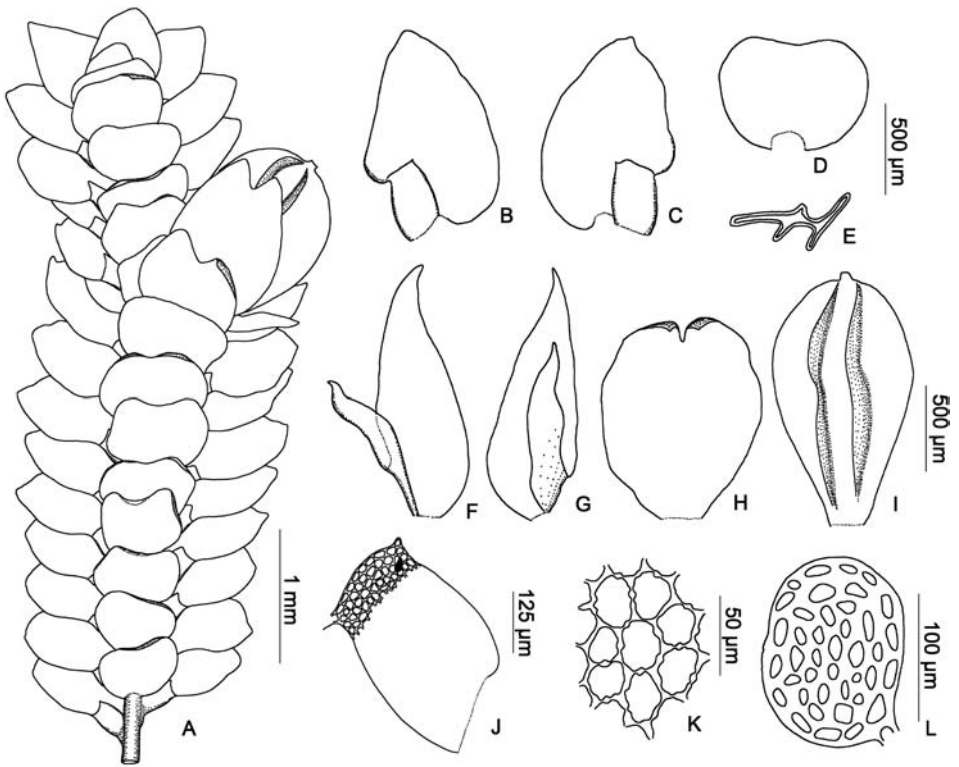


Fig. 5. *Archilejeunea nebeliana*. A. Portion of shoot, ventral view. B–C. Leaves. D. Underleaf. E. Cross section of perianth. F–G. Female bracts. H. Female bracteole. I. perianth, ventral view. J. Leaf lobule. K. Median cells of leaf lobe. L. Cross section of stem. (All from M.Nebel & A.Schäfer-Verwimp 111599.)

SPECIMENS EXAMINED: ECUADOR. Zamora-Chinchipe: Parque Nacional Podocarpus, Zugang Rio Bombuscara. M.Nebel & A.Schäfer-Verwimp 111599 (STU).

DISTRIBUTION: Ecuador (Gradstein & Schäfer-Verwimp 2012). On tree trunks or branches.

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