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A taxonomic review of the Amazonian rheophyte  
*Schusterolejeunea* Grolle (Lejeuneaceae:  
Cololejeuneinae), with two new combinations

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# A taxonomic review of the Amazonian rheophyte *Schusterolejeunea* Grolle (Lejeuneaceae: Cololejeuneinae), with two new combinations

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## ABSTRACT

*Schusterolejeunea inundata* (Spruce) Grolle is a widespread, yet poorly known species restricted to riparian habitats of the Amazon Basin in northern South America. Since its original description by Richard Spruce in 1884, phenotypic differences among populations convinced the original author to split the taxon into two varieties. An extensive review of *Schusterolejeunea* Grolle specimens hailing from disparate regions of the Amazon Basin has provided convincing evidence of discontinuities among leaf, lobule, and perianth morphology offering support for a novel taxonomic proposal. In the present review, the genus *Schusterolejeunea* encompasses two species, *S. inundata* and the newly elevated species *Schusterolejeunea saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov., which differs from *S. inundata* by its oblong leaves, with large rectangular to oblong lobules, that cover  $\frac{1}{3}$ - $\frac{2}{3}$  of the leaf lobe, and the perianth with five indistinct low keels. The variety *Schusterolejeunea inundata* var. *fontinaloides* (Spruce) A.M.Sierra & C.E.Zartman, comb. nov. is considered a distinct taxon, distinguished from *S. inundata* var. *inundata* by its ovate leaves, and lobules on the primary stem triangular with a longer keel extending 6-12 cells long. For each taxon, we present a detailed morphological description, current geographical distribution, and illustrations.

## KEY WORDS

Brazil,  
Rio Negro,  
igapó forest,  
liverworts,  
Lejeuneaceae,  
lectotypification,  
new status,  
new combinations.

## RÉSUMÉ

*Revue taxonomique du rhéophyte amazonien Schusterolejeunea Grolle (Lejeuneaceae: Cololejeuneinae), avec deux nouvelles combinaisons.*

*Schusterolejeunea inundata* (Spruce) Grolle est une espèce répandue, mais mal connue, limitée aux habitats riverains du bassin amazonien dans le nord de l'Amérique du Sud. Depuis sa description originale par Richard Spruce en 1884, les différences phénotypiques entre les populations ont convaincu l'auteur original de diviser le taxon en deux variétés. Un examen approfondi des spécimens de *Schusterolejeunea* Grolle provenant de régions disparates du bassin amazonien a fourni des preuves convaincantes de discontinuités entre la morphologie des feuilles, des lobules et du périanthe, soutenant une nouvelle proposition taxonomique. Dans la présente revue, le genre *Schusterolejeunea* considère deux espèces, *S. inundata* et l'espèce nouvellement élevée *Schusterolejeunea saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov., qui diffère de *S. inundata* par ses feuilles oblongues, avec de grands lobules rectangulaires à oblongs, qui couvrent  $\frac{1}{3}$ - $\frac{2}{3}$  du lobe de la feuille, et le périanthe à cinq carènes basses indistinctes. La variété *Schusterolejeunea inundata* var. *fontinaloides* (Spruce) A.M.Sierra & C.E.Zartman, comb. nov. est considérée comme un taxon distinct, se démarquant de *S. inundata* var. *inundata* par ses feuilles ovales et ses lobules sur la tige primaire triangulaire avec une carène plus longue s'étendant sur 6 à 12 cellules de long. Pour chaque taxon, nous présentons une description morphologique détaillée, la répartition géographique actuelle et des illustrations.

## MOTS CLÉS

Brésil,  
Rio Negro,  
forêt d'igapo,  
hépatiques,  
Lejeuneaceae,  
lectotypification,  
statut nouveau,  
combinaisons nouvelles.

## INTRODUCTION

When Spruce (1884) first described and illustrated the species *Lejeunea inundata* Spruce, he recognized two varieties that principally differ in their leaf and lobule shape (*Lejeunea inundata* var. *fontinaloides* Spruce and *Lejeunea inundata* var. *saxorum* Spruce). Nearly a century later, Schuster in Kachroo (1967) described a new genus *Cladocolea* R.M.Schust. (nom. illeg., art. 52.1, Turland *et al.* 2018) to accommodate *Lejeunea inundata* due to its unique morphological characters not observed in other genera of Lejeuneaceae. Subsequently, Grolle (1980) proposed the name *Schusterolejeunea* Grolle to replace *Cladocolea* R.M.Schust., thus the new combination *Schusterolejeunea inundata* (Spruce) Grolle was proposed. Grolle (1980) synonymized under the name of *S. inundata*, the variety *Lejeunea inundata* var. *saxorum* Spruce, and the name *Potamolejeunea sprucei* Steph. proposed by Stephani (1914) and described from the same type specimen.

Morphologically, the genus *Schusterolejeunea* stands out from other genera of Lejeuneaceae by its short leaf insertion composed of three cells, leaves two times longer than wide, lobules forming a flat fold against the lobe, never saccate, and underleaves one per leaf pair (Gradstein *et al.* 2001). *Schusterolejeunea* (synonym: *Cladocolea*) was considered phylogenetically close to the genus *Myriocolea* Spruce (subfamily Myriocoleoideae) R.M.Schust. due to their shared gynoecia patterns and innovations (Schuster 1963). For example, *Schusterolejeunea* typically presents pycnolejeuneoid-type innovations, and less commonly lejeuneoid or *Radula*-type (Thiers 1984). Cladistic analyses using morphological data, placed *Schusterolejeunea* within the clade of Cololejeuneinae Gradst., principally based on its short leaf insertion: a synapomorphy of this subtribe (Gradstein *et al.* 2003; Gradstein 2013). Within the subtribe Cololejeuneinae, the genus *Schusterolejeunea* shares similar morphological characters with

some species of *Cololejeunea* (Spruce) Steph. For example, *Cololejeunea* subgenus *Protolejeunea* R.M.Schust. (Schuster 1963), which includes *Cololejeunea dauphinii* R.L.Zhu (Morales & Dauphin 1998; Zhu 2006) and *Cololejeunea vuquangensis* Pócs & Ninh (Pócs & Ninh 2005), shares an erect or creeping growth habit and large flat lobules without teeth, but *Cololejeunea* lacks underleaves. The rheophyte *Cololejeunea stotleriana* Gradst., Ilk.-Borg. & Vanderp. (*Schusterolejeunea andina* Gradst. & Ilk.-Borg., nom. inval., in León-Yáñez & Gradstein 2011), due to its wide-spreading oblong leaves, large flat lobules, and numerous androecia and gynoecia clustered in small branches, also resembles *S. inundata*, but differs from the latter in the presence of gemmae, 3-5 cells wide ventral merophytes, and the absence of underleaves (Gradstein *et al.* 2011). Nonetheless, the phylogenetic position of the genus *Schusterolejeunea* remains unclear as the genus has yet to be included in molecular analyses (Gradstein 2020).

The distribution of *Schusterolejeunea* remains unclear, as it has been sparsely collected over time and space across its distributional range. Most Brazilian collections were made nearly half a century ago and include *c.* 40 samples, the vast majority of which come from the Rio Negro Basin in northern South America (Costa *et al.* 2017; CRIA 2021). However, *Schusterolejeunea* has also been collected in Amazonian tributaries outside the Rio Negro, such as those found in the states of Pará (Lisboa & Ilkiu-Borges 2001), and Rondônia. Collections from a transition zone between Amazonia and the Cerrado (Santos & Ilkiu-Borges 2022), and the Cerrado biome in the Maranhão state (Peralta *et al.* 2011) have also given this genus an extra-Amazonian distribution.

Specimens collected by the authors from the Rio Branco (Roraima state) show particularly curious morphologies which include extremely large oblong lobules covering  $\frac{2}{3}$  of the leaf lobe area; an undescribed variation for *Schusterolejeunea* in

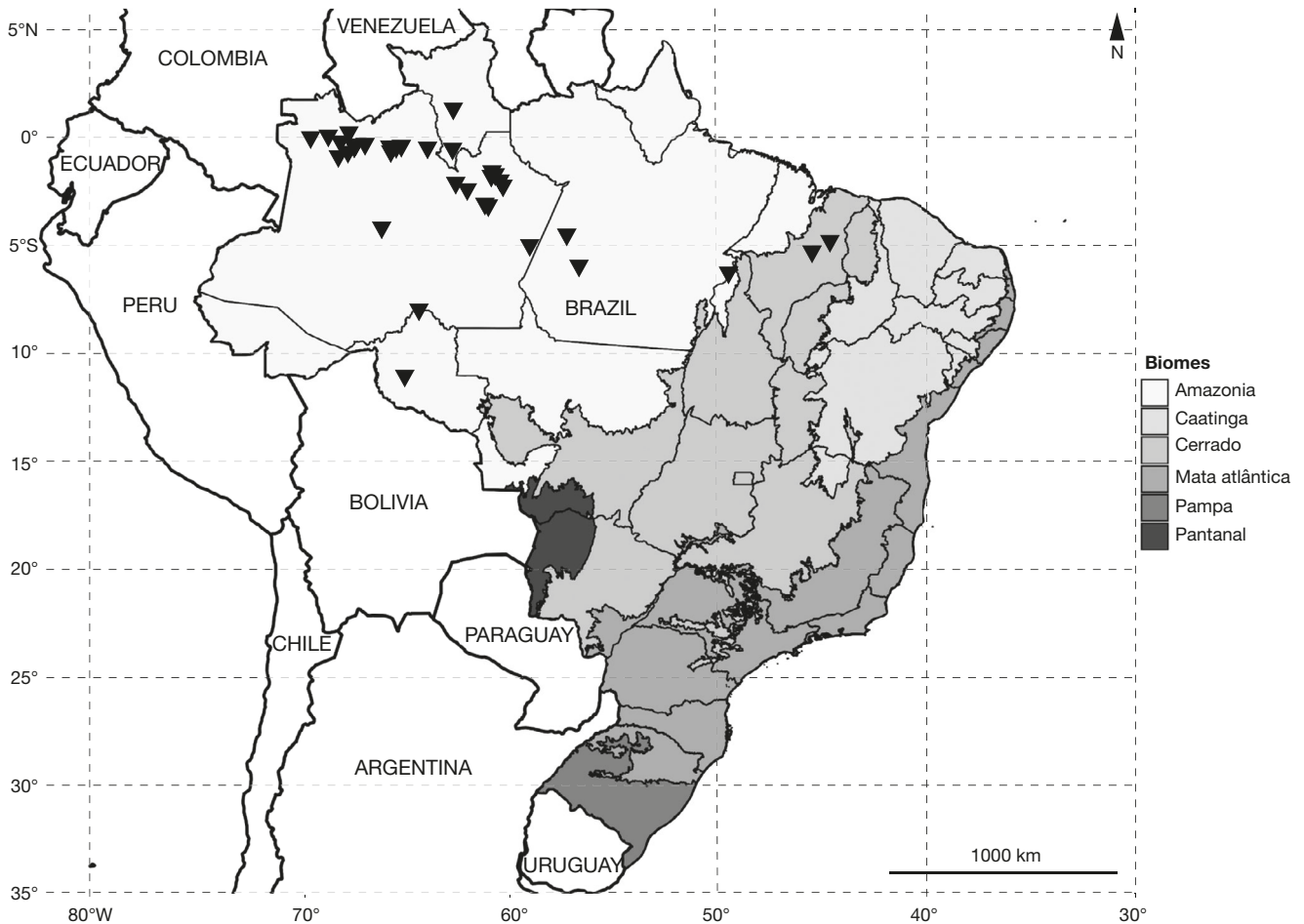


Fig. 1. — Geographical distribution of the genus *Schusterolejeunea* Grolle in the Brazilian biomes from the complete herbarium records. Each triangle represents the location of an herbarium record.

all previous descriptions of this taxon (Gradstein *et al.* 2001; Gradstein & Costa 2003; Gradstein 2016, 2021; Bastos 2020). Comparing these specimens with the protologue and the type material, the observed differences corresponded to a variety described by Spruce (1884). Due to the novel character and the high phenotypic plasticity within the taxon, we revised the genus to refine the taxonomic understanding of this species complex.

The present work aims to characterize the morphological variation of the genus *Schusterolejeunea* across its distribution range in the Brazilian Amazon, based on recently collected specimens and herbarium material from the Instituto Nacional de Pesquisas da Amazônia (INPA), Brazil. Specimens were compared to the type material deposited at the herbarium of the University of Manchester (MANCH), United Kingdom, and the description of the protologue in Spruce (1884). Herein, we present an updated taxonomic treatment of *Schusterolejeunea*, which considers two species, *S. inundata* and the newly elevated species *Schusterolejeunea saxorum* (Spruce) A.M.Sierra & C.E.Zartman, *stat. nov.*, *comb. nov.* Also, the variety *Schusterolejeunea inundata* var. *fontinaloides* (Spruce) A.M.Sierra & C.E.Zartman, *comb. nov.* is considered a distinct taxon.

## MATERIAL AND METHODS

For the revision of the genus *Schusterolejeunea* we examined the specimens from the herbariums of MANCH and INPA. Additionally, we collected samples along the Rio Negro between Manaus and São Gabriel da Cachoeira, and two of its major tributaries: the middle Rio Uaupés in Amazonas, and the Rio Branco near the Serra da Mocidade National Park in Roraima. Field observations were gathered for all collections. In total, we examined 56 specimens representing more than 65% of the known collections to date (Appendix 1).

The distribution of *Schusterolejeunea* in the Brazilian states was compiled from the Brazilian Flora 2020 (Bastos 2020; Costa & Peralta 2021). We subsequently added the specimens studied from the INPA herbarium, as well as the records archived on *speciesLink* Network database (CRIA 2021) and additional references (Lisboa & Ilkiu-Borges 2001; Peralta *et al.* 2011; Sierra *et al.* 2018a; Santos & Ilkiu-Borges 2022). Using this approach, we were able to maximize the number of samples identified as *Schusterolejeunea* to complement its Brazilian distribution (Fig. 1). We further described the morphological variation of each sample and compared it to the type specimens, and its original description, to classify *Schusterolejeunea*

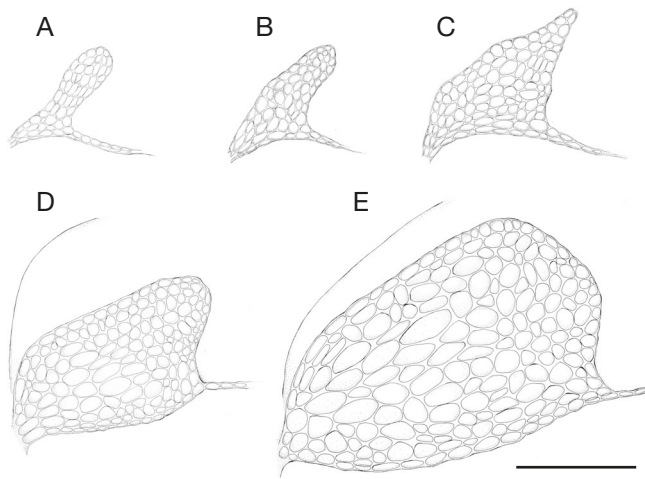


FIG. 2. — *Schusterolejeunea* Grolle leaf lobule variation: **A, B**, *S. inundata* var. *inundata* (Spruce) Grolle (lingulate); **C**, *S. inundata* var. *fontinaloides* (Spruce) A.M.Sierra & C.E.Zartman, comb. nov. (triangular); **D, E**, *S. saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov. (rectangular to oblong). Scale bar: 150 µm.

taxa following the taxonomic treatment provided below. All samples were georeferenced using geographical coordinates retrieved from GPS. When samples lacked geographical coordinates, georeferencing methods were estimated using Google Earth based on the locality description from herbarium labels. For each taxon, we provide a detailed description, illustration, and Brazilian distribution, along with comments on its ecology and habitat. All botanical records included for the distribution map and the specimens examined are listed in the Appendix 1, with their herbarium information.

## TAXONOMY

Family LEJEUNEACEAE Rostovzev

Genus *Schusterolejeunea* Grolle

*Journal of Bryology* 11: 105-106 (Grolle 1980).

## DESCRIPTION

Plants small to medium size, 1-2.5 mm wide, pale to dark green, creeping to loosely pendent. Stems in cross-section with seven cortical and three medullary thick-walled cells, epidermis slightly enlarged, without hyalodermis. Ventral merophytes are composed of two cells. Leaf lobes obliquely spreading, elliptical, ovate to oblong, 1.5-4 (5) times as long as wide, apices rounded, plane, margins entire, bases of the lobe very narrow, insertion line only 2-3 cells long. Cells pellucid, thin-walled, trigones rare, oil bodies finely granular, 2-4 per cell; ocelli absent. Lobules plane, small to large, variable in shape, when small narrowly lingulate with a narrow base (*S. inundata* var. *inundata*: Fig. 2A, B), or triangular (fin-shaped) (*S. inundata* var. *fontinaloides* (Spruce) A.M.Sierra & C.E.Zartman, comb. nov.: Fig. 2C), when large rectangular to oblong (*S. saxorum* (Spruce) A.M.Sierra & C.E.Zartman,

stat. nov., comb. nov.: Fig. 2D, E); hyaline papilla terminal at the apices. Underleaves small (rarely absent in *S. saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov.) narrower than the stems, longer than wide, narrowly bifid with erect lanceolate lobes ending in 3-5 uniseriate cells, sinus deeply V-shaped, rarely asymmetrical with one reduced lobe forming a triangular fold consisting of nine cells. Autoicous. Gametoezia numerous along the gametophyte, with either one antheridia or gynoecia branch located below almost every leaf insertion along both sides of the stem (Thiers 1984). Antheridia on short lateral branches, spikes with 2-6 (8) imbricate pairs of perigonal bracts; bracts ovate bilobed, and emarginate at the apices. Bracteoles arise as underleaves for each bract pair. Gynoecia 2-4 in a monochasial row, each gynoecium with one pycnolejeuneoid or lejeuneoid innovation which is again fertile (except for the outermost one). Perianths obpyriform to obovate, inflated, with five distinct (*S. inundata*) or indistinct low keels (*S. saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov.). Without vegetative reproduction.

### *Schusterolejeunea inundata* (Spruce) Grolle (Fig. 3)

*Journal of Bryology* 11: 105 (Grolle 1980).

LECTOTYPE. — **Brazil**. Est. Amazonas, fl. Negro, supra cataractas, ad arbores riparias, leg. *Spruce L319* (lecto-, designated in Grolle 1980, MANCH!; isolecto-, G).

SPECIMENS EXAMINED. — **Brazil**. Amazonas, Presidente Figueiredo, Rio Uatumã, 1°57'45.4"S, 59°27'40.6"W, corticicola umbrófila na margem do igapó, 21.II.1978, *Ivo P. et al. 3431* (INPA!); Heliofita coletado em tronco de palmeira, na margem da beira do igapó, 21.II.1978, *Ivo P. et al. 3432* (INPA!); Rio Uatumã a 4 km da Cachoeira, 1°57'45.4"S, 59°27'40.6"W, sobre galhos de árvore da beira do igapó, 20.II.1978, *Lisboa P. 1096* (INPA!); Santa Isabel do Rio Negro, Rio Cauaburi, 0°15'S, 65°55'W, 3.VII.1979, *Schuster 79-10-288* (INPA!, NY); São Gabriel da Cachoeira, Igarapé Ia Mirim, above the camp to Morro dos Seis Lagos, 0°17'06"N, 66°40'36"W, abundant on rock, twigs and leaves along the river, 1.IX.2011, *Zartman C.E. 8751* (INPA!, SP!); Roraima, Caracará, Parque Nacional Serra da Mocidade, Rio branco, 1°23'03.7"N, 61°39'23.0"W, 4.III.2017, *Zartman C.E. 9867* (INPA!, PMA!); Rondônia, Guajará-Mirim, Pacáas Novos, along the Rio Pacáas novos, between its confluence with the Rio Mamoré and the first rapids, 10°51'40.8"S, 65°16'21.5"W, Varzea forest, epiphyll, immersed in river by rising water, 8-13.III.1978, *Reese W.D. 13291* (INPA!, NY); on twigs under water in the river, 8-13.III.1978, *Reese W.D. 13288* (INPA!, NY); Pará, Serra do Cachimbo, Serra Maze and vicinity, 1208-1229 km north of Cuiabá along Cuiabá-Santarém highway (BR 163), c. 5°55'S, 55°40'W, 100-200 m a.s.l., on mature, tall, humid forest on steep slopes and valleys, with occasional igarapés and igneous rock exposures, 18-22.V.1983, *Reese W.D. 16797* (INPA!, NY). See Appendix 1.

DISTRIBUTION. — *Schusterolejeunea inundata* is distributed in the Amazon Forests of Brazil, Colombia, Guyana, Peru, and Venezuela (Grolle 1980; Gradstein *et al.* 2001; Dauphin *et al.* 2008; Gradstein 2021). In Brazil, it occurs in northern region (Gradstein *et al.* 2001), in the states of Amazonas, Pará (Lisboa & Ilkiu-Borges 2001; Santos & Ilkiu-Borges 2022), Maranhão (Peralta *et al.* 2011), Rondônia and Roraima.



FIG. 3. — *Schusterolejeunea inundata* (Spruce) Grolle: **A-D**, gametophytes in ventral view, showing androecia and gynoecia branches; **E**, lobule; **F**, underleaf; **G**, mid leaf cells. Micrography from Zartman C.E. 8751. Scale bars: A-C, 400  $\mu$ m; D, 200  $\mu$ m; E, F, 150  $\mu$ m; G, 100  $\mu$ m.

**HABITAT.** — The species *Schusterolejeunea inundata* is restricted to seasonally inundated habitats in the Amazon and Cerrado biomes as a rheophyte. It forms extensive dark mats on rocks, tree branches, exposed roots, and leaves that are seasonally submerged by black water tributaries (Gradstein & Costa 2003; Gradstein 2020). It

was also collected at the edge of the crater lakes of ancient volcanic origin at the Morro dos Seis Lagos (Amazonas state) (Appendix 1).

**ILLUSTRATIONS.** — Spruce 1884; Kachroo 1967 (figs 4; 5) as *Cladocolea inundata* (Spruce) Schust.; Gradstein *et al.* 2001 (fig. 53J-L);

Gradstein & Costa 2003 (fig. 65A-C); Thiers 1984 (fig. 21); Lisboa & Ilkiu-Borges 2001 (fig. 7).

#### DESCRIPTION

##### *Habit*

Plants small to medium in size, 1-2.5 mm wide, pale to dark green, creeping to loosely pendant, highly branched, with numerous gametangia, usually with fertile innovations. Branches *Lejeunea*-type.

##### *Stems*

Primary stems 120-135 µm in diameter, in cross-section with seven cortical and three medullary cells, cortical cells 25-45 µm in diameter, medullary cells 25-30 µm in diameter; stems with thick-walled cells, epidermis slightly enlarged, without hyalodermis; ventral merophytes two cells wide.

##### *Leaves*

Obliquely spreading, elliptical, (350) 600-1420 (1600) µm long, (160) 280-770 µm wide, 1.5-4 (5) times as long as wide, apices rounded, plane, margins entire, bases of the lobes very narrow, insertion line only 2-3 cells long. Cells pellucid, thin-walled, trigones rare, oil bodies finely granular, 2-4 per cell; ocelli absent. Basal laminal cells long rectangular to fusiform (16-50 × 9-20 µm), mid laminal cells short rectangular, quadrate, rarely long to short hexagonal (10-25 × 10-20 µm), marginal cells mostly quadrate to short rectangular (10-30 × 10-16 µm).

##### *Lobules*

Small narrowly lingulate with a narrow base, plane, narrowly ligulate, 200-418 µm long, 73-116 µm wide, covering 1/8 of the leaf lobes length, keels straight, formed by 2-5 cells, apex rounded broadly expanded (beyond the keel), standing obliquely upward or erect, parallel to stem. Teeth reduced, formed by two cells with a marginal hyaline papillae terminal at the lobule apex.

##### *Underleaves*

Small narrower than the stems (14-27 cells), 2-3 × longer than wide (150-280 × 55-90 µm), narrowly bifid with erect lanceolate lobes composed of 3-10 cells long, sinus deeply V-shape, lobes at base composed of 2-4 cells wide. Rhizoids brown, up to 11-16 µm wide and thick walls 3 µm wide.

##### *Autoicous*

Gametoecia numerous along the gametophyte. Antheridia on short lateral branches, spikes with 2-6 (8) imbricate pairs of perigonal ovate and bilobed bracts, which are emarginated at their apices. Bracteoles arise as underleaves for each bract pair.

Gynoecia 2-4 in a monochasial row, each gynoecium with one pycnolejeuneoid or lejeuneoid innovation which is again fertile (except for the outermost one). Perianths obpyriform, inflated, with five distinct keels, two ventral and three dorsal keels, margins entire. Sporophytes with a 595 µm long and 90 µm thick articulated seta. Capsules globular. Capsule valves with a plurifenestrate pattern. Elaters 1-3 per valve, one attached to the apical cells and others to the margins near

the apex of the valve, 165-195 µm long, and 8-14 µm wide with sinuous, incrassated walls, without real spiral bands. Spores green and variable in shape, spherical to rectangular (50-85 × 25-35 µm), and surface verruculose.

#### COMMENTS

In the field, it can be recognized by its dark green color with a loose and straggling habit, hanging from twigs, or in the base of trees and rocks in black water seasonally flooded igapó forests. Under the dissecting scope, it can be distinguished by its regularly pinnate, and narrow leaves which are widely spaced on their branches. The combination of its short leaf insertion, elongate elliptical to oblong leaves with a flat lobule, small underleaves, and five-keeled perianths in dense clusters, distinguish it from other rheophytic liverworts in the region.

*Schusterolejeunea inundata* var. *fontinaloides*  
(Spruce) A.M.Sierra & C.E.Zartman, comb. nov.  
(Fig. 4)

*Lejeunea inundata* var. *fontinaloides* Spruce, *Transactions and Proceedings of the Botanical Society of Edinburgh* 15: 278 (Spruce 1884).

LECTOTYPE. — **Brazil**. Est. Amazonas, Paricatuba, leg. Spruce s.n. (lecto-, designated in Grolle 1980, MANCHI!; isolecto-, G).

SPECIMENS EXAMINED. — **Brazil**. Amazonas, along the Rio Cauaburi between the Rio Negro and the Cachoeira do Carangueijo, 0°15'00"S, 65°55'00"W, mostly rocky flood plain forest, 3.VII.1979, *Buck W.R.* 2314 (INPA!, NY); Rio Negro, igarapé Foibara, vicinity of first cachoeira of the Igarapé Foibará of Rio Negro, 0°16'00"S, 66°35'00"W, Terra firme forest, 22.VII.1979, *Buck W.R.* 2627 (INPA!, NY); *Schuster R.M.* 79-21-1135 (INPA!, NY); Santa Isabel do Rio Negro, Rio Cauaburi, 0°15'00"S, 65°55'00"W, *Schuster* 79-10-295 (INPA!, NY); Ilha Acarabu, at the mouth of the Rio Marié, 0°25'00"S, 66°25'00"W, Marshy forest, 4.VII.1979, *Schuster R.M.* 79-11-302 (INPA!, NY); Manaus, Rio Negro, igapó forest in the island in front of the Praia da Lua, 3°01'56.5"S, 60°09'44.7"W, epiphyte on trunk in seasonal inundated forest (igapó), 25.XI.2017, *Sierra A.M.* 4583, 4582, 4586 (INPA!, PMA!); São Gabriel da Cachoeira, Rio Negro, banco de areia frente da cidade de São Gabriel da Cachoeira, 0°08'29.2"S, 67°05'04.1"W, sobre rochas sazonalmente inundável, 14.XII.2017, *Sierra A.M.* 4642 (INPA!); Rio Negro, 20 km descendo da cidade de São Gabriel da Cachoeira, Ilha Cariuari, 0°11'45.8"S, 67°00'10.9"W, floresta de igapó, 17.XII.2017, *Sierra A.M.* 4713, 4724 (INPA!, PMA!), 4714, 4718, 4720 (INPA!, SP!), 4719 (INPA!, SP!, PMA!), 4710 (INPA!); Rio Uaupés, Sitio São Paulo, 0°02'50.3"N, 68°29'05.7"W, epífita sobre ramos na margem do rio, 21.XII.2017, *Sierra A.M.* 5055, 5063 (INPA!, PMA!), 5056, 5059 (INPA!, SP!, PMA!); São Gabriel da Cachoeira, Rio Negro, Ilha em frente a São Gabriel da Cachoeira, 0°07'49.0"S, 67°05'21.1"W, sobre pedra na ilha, 20.VII.1979, *Yano O.* 2103 (INPA!, SP); Rio Negro, Temenduí, 0°22'00"S, 64°42'00"W, sobre rochas grandes submersas na água, 29.VI.1979, *Yano O.* 1536 (INPA!, SP); Rio Negro, São Tomé, Margem do rio, 0°22'00"S, 64°10'00"W, 29.VI.1979, *Yano O.* 1528 (INPA!, SP); Rio Negro, Ilha Acarabu, 0°40'00"S, 66°40'00"W, sobre raízes de plantas submersas na água, 4.VII.1979, *Yano O.* 1640 (INPA!, SP); Rio Negro, NW de São Gabriel da Cachoeira, em tronco submerso na água, 21.VII.1979, *Yano O.* 2139 (INPA!); Novo Airão, Parque Nacional Jaú, Carabinani river, 2°02'38"S, 61°33'28"W, rheophyte on sand along the Carabinani river, X.2007, *Zartman C.E.* 7547, 7544 (INPA!). See Appendix 1.



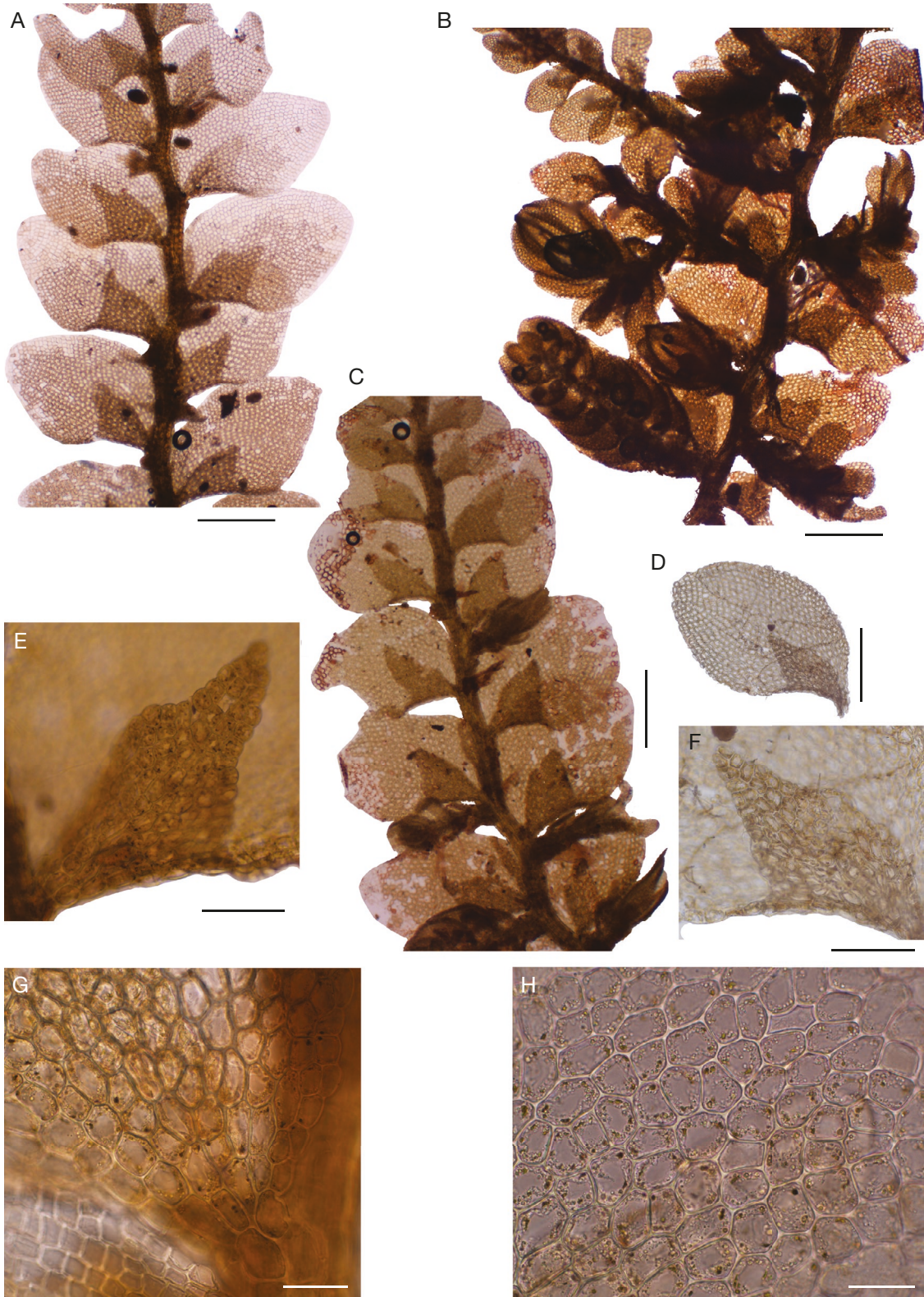


FIG. 4. — *Schusterolejeunea inundata* var. *fontinaloides* (Spruce) A.M.Sierra & C.E.Zartman, comb. nov.: **A-C**, gametophyte in ventral view, showing androecia and gynoecia branches; **D**, single leaf detail; **E, F**, lobule close-up; **G**, leaf insertion showing basal leaf cells; **H**, mid leaf cells. Micrography from Sierra A.M. 4582. Scale bars: A-D, 400  $\mu$ m; E, F, 100  $\mu$ m; G, H, 50  $\mu$ m.

**DISTRIBUTION.** — *Schusterolejeunea inundata* var. *fontinaloides* (Spruce) A.M.Sierra & C.E.Zartman, comb. nov. is relatively common in the Brazilian Amazon. It is known from several localities in the state of Amazonas along the Rio Negro Basin (including the type locality), and in the Rio Pacaás Novos in Rondônia.

**HABITAT.** — *Schusterolejeunea inundata* var. *fontinaloides* (Spruce) A.M.Sierra & C.E.Zartman, comb. nov. occurs in fast-flowing streams in black water seasonally flooded igapó forests in the Amazonas state, as well as white water várzea forests along Rio Pacaás Novos in Rondônia state (Appendix 1). It grows attached to rocks, tree branches, roots, trunks, and leaf surfaces.

#### DESCRIPTION

##### *Habit*

Plants small to medium in size, shoots up to 2 cm long and 1-2.5 mm wide, pale to dark green or yellow, creeping to loosely pendant, highly branched, with numerous gametangia, usually with fertile innovations. Branches *Lejeunea*-type.

##### *Stems*

Primary stems in cross-section with seven cortical and three medullary thick-walled cells, epidermis slightly enlarged, without hyalodermis; ventral merophytes two cells wide.

##### *Leaves*

Distant to continuous, patent, obliquely spreading, to suberect (45° with stem) insertions short composed of two ventral and 3-4 dorsal cells, ovate, (350) 600-1200 µm long, (160) 280-570 µm wide, (1.5) 2-5 times as long as wide, apices rounded, plane, margins entire, dorsal margins arched, ventral lobe margins slightly to widely arched after the lobule keel. Cells with numerous chloroplasts, oil bodies finely granular, 2-4 per cell. Leaf lobe cells hexagonal, quadrate, or rectangular, thin-walled, trigones small, intermediate thickenings scarce, cuticles smooth. Basal laminal cells hexagonal to rectangular (16-50 × 9-24 µm), mid laminal cells short, rectangular to quadrate, rarely hexagonal (10-30 × 10-25 µm), marginal cells mostly quadrate to short rectangular (10-23 (30) × 10-19 µm). Stylus unicellular.

##### *Lobules*

Small, usually well-developed, broadly expanded, arching obliquely upward or erect parallel to the stem, triangular or fin shaped, (170) 250-510 µm long, (80) 130-200 µm wide, covering less than ¼ of the leaf lobes, with a narrow base, keels straight to arched, formed by 6-12 cells; apices rounded. Teeth inconspicuous, formed by two cells with a marginal hyaline terminal papilla at the lobule apex.

##### *Underleaves*

Small, narrower than the stem, 2-6 × longer than wide, (140-360 × 50-115 µm) narrowly bifid with erect lanceolate lobes composed of 3-13 cells long, lobes at base composed of 2-4 cells wide, sinus deeply V-shaped. Rhizoids brown or hyaline, up to 11-16 µm wide and thick-walled (3 µm wide).

##### *Autoicous*

Androecia numerous, on short lateral branches at both sides of the stem. Spikes (420-1100 (1700) × 350-570 µm) with

2-4 (8) imbricate pairs of perigonal bracts; bracts ovate bilobed, and emarginate at the apices. Bracteoles arise as underleaves for each bract pair.

Gynoecia on short lateral branches originating at the bases of vegetative leaves, 2-4 in a monochasial row with 1-3 innovations of the pycnolejeuneoid type, which is again fertile (except the outermost one). Female bracts (630-750 µm), short, obovate, bilobed, entire margins with emarginated or obtuse apices; lobules lingulate, with rounded apices. Bracteoles like the underleaves. Perianths obpyriform (580) 630-720 × 250-430 µm, with five distinct keels ⅔ of the perianth length, keel margin entire or crenulated by bulging cells, beak short 2-celled.

#### COMMENTS

This variety is easily distinguished by its ovate leaves which are 1.5-2.5 × longer than wide, small lobules, covering less than half of the leaf lobe, usually triangular with the keel extending to 6-12 cells. Within an individual specimen, this taxon may show morphological variability among primary and secondary branches, as some secondary shoots may present small elliptical leaves with lingulate lobules. However, primary stem characters hold to the above description.

#### *Schusterolejeunea saxorum*

(Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov. (Fig. 5)

*Lejeunea inundata* var. *saxorum* Spruce, *Transactions and Proceedings of the Botanical Society of Edinburgh* 15: 278 (Spruce 1884).

**LECTOTYPE.** — **Brazil.** Est. Amazonas, San Carlos, in saxis fl. Negro inundatis, leg. *Spruce L331/c* (lecto-, designated here, MANCH!).

**SPECIMENS EXAMINED.** — **Brazil.** Amazonas, São Gabriel da Cachoeira, Rio Marié, Marauna, 0°40'00"S, 66°45'00"W, 5.VII.1979, *Schuster R.M. 79-13-381* (INPA!); Rio Uaupés, próximo a comunidade de São Pedro, 0°06'43.9"N, 67°39'19.1"W, 19.XII.2017, *Sierra A.M. 4760* (INPA!, PMA!); Rio Uaupés, sítio São Paulo, 0°02'50.3"N, 68°29'05.7"W, epífita sobre ramos ao margem do rio, 21.XII.2017, *Sierra A.M. 5057* (INPA!, PMA!), *5062* (INPA!, SP!, PMA!); São Gabriel da Cachoeira, 0°40'00"N, 66°40'00"W, sobre galhos submersas na água, 5.VII.1979, *Yano O. 1734* (INPA!, SP!); Rio Negro, Igarapé Foibara, 0°16'18"S, 66°35'00"W, sobre pedras na cachoeira, 22.VII.1979, *Yano O. 2150* (INPA!, SP!); Amazonas, Novo Airão, Parque Nacional Jaú, Carabinani river, 2°02'38"S, 61°33'28"W, X.2007, *Zartman C.E. 7542* (INPA!); Roraima, Caracarái, Parque Nacional Serra da Mocidade, Rio Branco, 1°23'26.2"N, 61°40'19.2"W, 4.III.2017, *Zartman C.E. 9790, 9888, 9889, 9892, 9787* (INPA!, PMA!), *9890, 9794* (INPA!, SP!), *9891* (INPA!, SP!, PMA!), *9832* (INPA!). See Appendix 1.

**DISTRIBUTION.** — *Schusterolejeunea saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov. is distributed in Amazonas and Roraima states. It is restricted to northern Amazonian tributaries of the Rio Negro: Rio Uaupés, Rio Jaú, Rio Marie (Amazonas state), and Rio Branco (Roraima state) (Appendix 1).

**HABITAT.** — This species is restricted to larger tributaries of the Rio Negro where it grows attached to rocks, branches, and tree trunks subject to seasonally flooding in igapó forests.

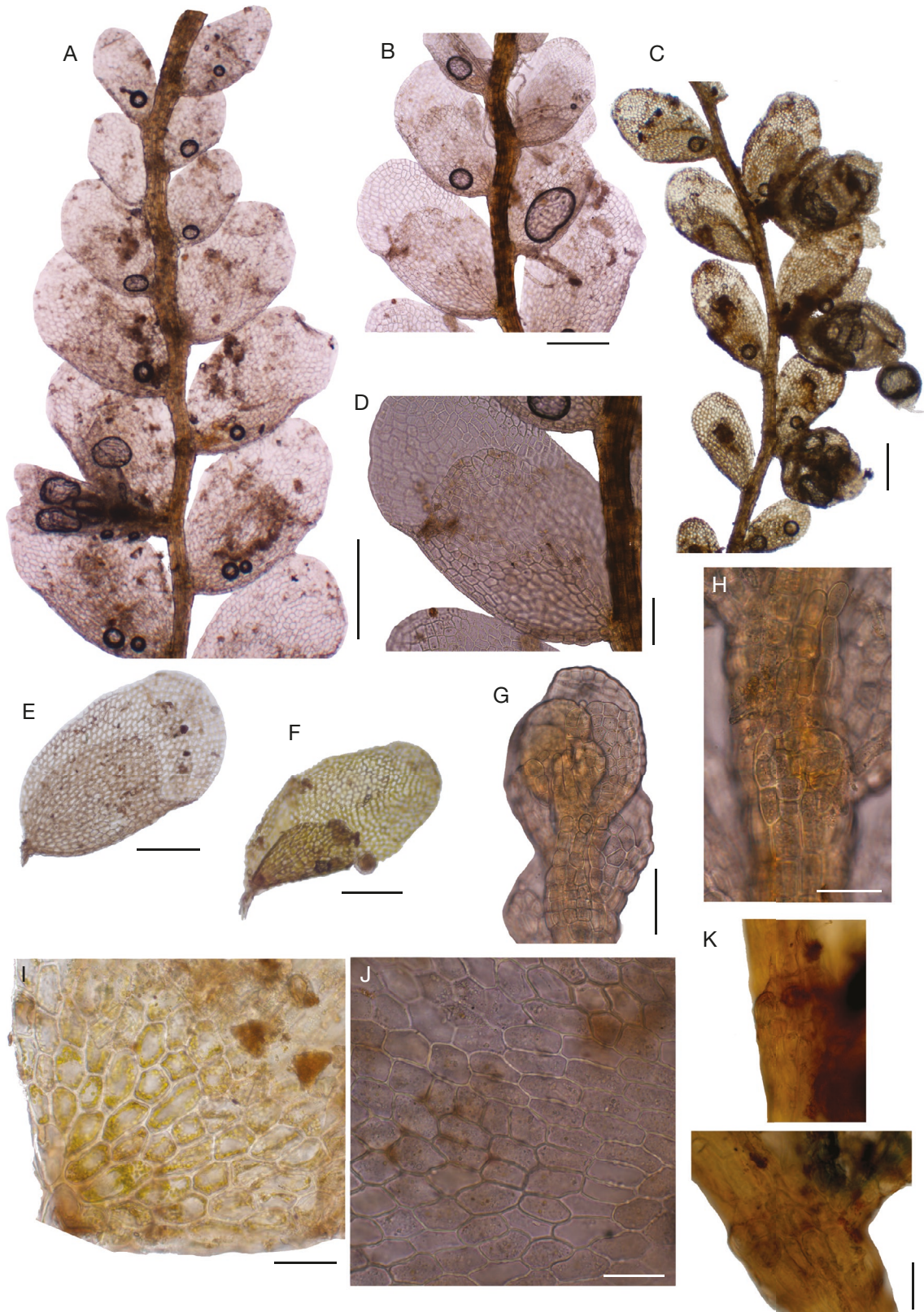


FIG. 5. — *Schusterolejeunea saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov.: **A-C**, gametophyte in ventral view, showing androecia and gynoecia branches; **D**, lobule close-up; **E, F**, single leaf detail, showing lobule shape variation; **G**, underleaf at apices; **H**, underleaf in mid portion of branches; **I**, leaf insertion showing basal leaf cells; **J**, mid leaf cells; **K**, rhizoids buds on basal portion of branches. Micrography from Zartman C.E. 9890. Scale bars: A, 400 µm; B, C, E, F, 200 µm; D, 100 µm; G-J, 50 µm; K, 40 µm.

## DESCRIPTION

### Habit

Plants small to medium in size, shoots up to 2 cm long and 0.2–1.5 mm wide, dark yellow to greenish-yellow when fresh, light brown when dry, pendent from leafless stoloniferous branches, shoots attenuate to the apices. Shoots highly branched, with numerous gametangia, usually with fertile innovations. Branches *Lejeunea*-type.

### Stems

Primary stems 60–75 µm in diameter, in cross-section with 6–7 cortical and three medullary cells, cortical cells 22 µm in diameter, medullary cells 18 µm in diameter; thick-walled cells, epidermis slightly enlarged, hyalodermis lacking; ventral merophytes two cells wide.

### Leaves

Distant, obliquely spreading to slightly erect, insertions short composed of two ventral and 3–4 dorsal cells, lobes (200) 600–790 (870) µm long, (150) 370–455 µm wide, oblong, 2–3 as long as wide, apices widely rounded to truncate, plane, margins entire. Ventral margins slightly arched. Cells with numerous chloroplasts, oil bodies finely granular, 2–4 per cell; leaf lobe cells rectangular, subquadrate to irregularly polygonal, irregular in shape and size, thin walls, trigones small, intermediate thickenings scarce, cuticles smooth. Apical marginal leaf cells (sub)quadrate (15–25 × 14–25 µm), dorsal marginal cells rectangular to sigmoid-quadrate (13–29 × 9–15 µm), ventral marginal cells irregularly hexagonal (21–35 × 18–25 µm), mid laminal cells hexagonal (18–30 × 15–20 µm), with scarce intermediate thickenings, basal cells long rectangular to hexagonal (26–53 × 14–27 µm), with scarce intermediate thickenings. Stylus unicellular.

### Lobules

Large, well developed, forming a flat fold against the leaf lobe, rectangular to oblong (150) 400–560 µm long, (90) 260–340 µm wide, covering  $\frac{1}{3}$ – $\frac{2}{3}$  of leaf lobes, free margin plane, slightly inflated along the keel, slightly crenate by bulging cells, apices rounded-truncate. Teeth inconspicuous, formed by two cells with a marginal hyaline papillae terminal at the lobule apex.

### Underleaves

Small and narrower than the stem, composed of 14–27 cells, (115) 275–450 × (62) 95–125 µm, 3× longer than wide, narrowly bifid with erect lanceolate lobes 8–11 cells long, and 3–5 at lobe base, ending in a 3–5 uniseriate cell, sinus deeply V-shape, rarely asymmetrical with one lobe reduced, forming a triangular fold of nine cells; underleaves usually absent along the basal portion of the stem. Rhizoids hyaline, up to 13 µm wide, and thick walls 4 µm wide.

### Autoicous

Androecia usually on short lateral branches originating at the base of vegetative leaves, or on long terminal branches. Short spikes 590–640 × 465–520 µm with 4–5 imbricate pairs of perigonial bracts, 320–360 × 170–195 µm, bracts emarginated at the apex.

Gynoecia on short lateral branches originating at the base of vegetative leaves, in a monochasial row with 1–3 innovations. Female bracts short 330–400 × 295–330 µm, obovate, bilobed, margins entire, with emarginated or obtuse apices. Bracteoles like the underleaves. Perianths obovate 630 × 460 µm, inflated with indistinct keels, at the apex with five indistinct low keels, at the apex slightly swollen forming short auricles, beak short 2-celled.

## COMMENTS

It is readily recognized by its large rectangular to oblong lobules covering greater than half of the leaf lobe length, and its obovate perianth with indistinct keels. Lobule size varies within and between samples. Along a single shoot, the lobule may only cover  $\frac{1}{3}$  of the leaf surface in some instances and up to  $\frac{2}{3}$  of the leaf surface in other cases. However, lobules are always rectangular to oblong in *S. saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov., contrary to *S. inundata* var. *fontinaloides* (Spruce) A.M.Sierra & C.E.Zartman, comb. nov. in which its lobules are triangularly shaped covering less than  $\frac{1}{4}$  of the leaf surface.

## RESULTS AND DISCUSSION

Due to high levels of phenotypic plasticity and homoplasy, rheophytic liverworts are exceptionally challenging to identify and even more difficult to assign accurately phylogenetically (Gradstein *et al.* 2011; Heinrichs *et al.* 2012; Yu *et al.* 2014). Moreover, undescribed phenotypic variation adds to the challenges in their specific identifications. Within the Lejeuneaceae, *Schusterolejeunea* may be confused with the rheophyte *Cololejeunea stotleriana* from the Río Nangaritzá, Ecuador. Indeed, Gradstein *et al.* (2011) highlight the morphological similarities among *C. stotleriana* and *Schusterolejeunea*, in light of its widely spreading oblong leaves with a large flat lobule and the gametophytes with high fertility, with numerous androecia and gynoecia. However, *C. stotleriana* is a more robust plant with 3–5 cells wide ventral merophyte and produces vegetative propagules (gemmae), whereas *Schusterolejeunea* is characterized by two cells wide merophyte and lacks vegetative propagules.

Riparian habitats in tropical regions remain woefully underexplored and systematic inventories of these unique environments demonstrably lead to myriad discoveries of new taxa, distributional extensions, unique ecological properties, and insights into their conservation status (Shevock *et al.* 2017). Amazonian rheophytic liverworts are still undercollected, leaving a large gap in their current known distribution. For example, there remains a single known collection of *Cephalantholejeunea temnanthoides* (R.M.Schust.) R.M.Schust. (Reiner-Drehwald & Weis 2001). Likewise, two other Amazonian species are only known from their type locality and a few recently discovered localities: *Cheilolejeunea polystachya* (Spruce) Gradst. & Ilk.-Borg., and *Ceratolejeunea temnantha* (Spruce) Reiner-Drehwald (Sierra *et al.* 2018b; Bastos & Gradstein 2020). For *Schusterolejeunea*, the records come from

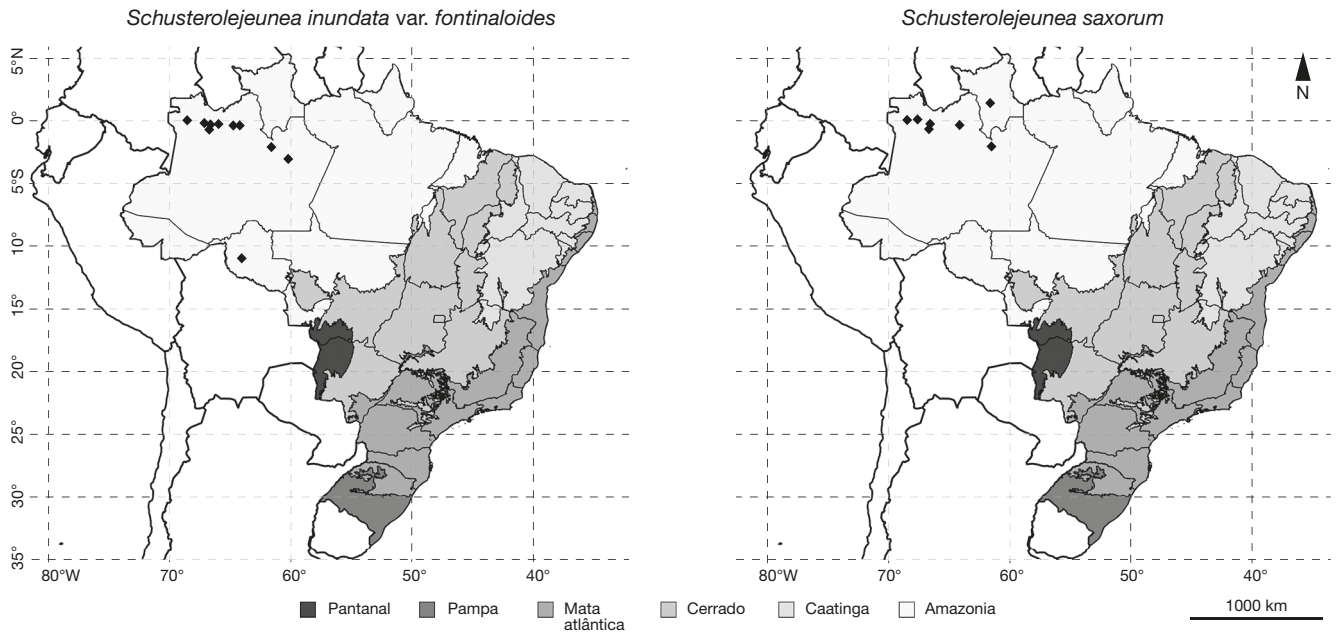


Fig. 6. — Geographical distribution of the new proposed variety *Schusterolejeunea inundata* var. *fontinaloides* (Spruce) A.M.Sierra & C.E.Zartman, comb. nov., and new species *Schusterolejeunea saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov. in the Brazilian biomes. Each rhombus represents the location of an herbarium sample studied.

collections made during Amazonian explorations in the 1980s (Costa *et al.* 2017), and a second wave in the past decades till these days, thus extending this taxon's distribution to highly disparate localities across northern South America (Lisboa & Ilkiu-Borges 2001; Peralta *et al.* 2011; Costa 2017; Sierra *et al.* 2018a; Gradstein 2021; Santos & Ilkiu-Borges 2022).

The present revision represents an updated and reliable taxonomic treatment of *Schusterolejeunea* across its entire range that will surely aid to better understand the morphological variation in this unique genus. Herein, we describe in detail the phenotypic variation of *Schusterolejeunea inundata* (*sensu lato*): notorious for its high plasticity in leaves, lobules, underleaves, androecia, and gynoecia characters. We conclude that the varieties described by Spruce (1884) are indeed readily distinguishable, as demonstrated by the key and descriptions presented here. The morphological differences between *S. inundata* and *S. saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov. are conspicuous, therefore we have subsequently considered them as two distinct species. Herein, we elevate *S. saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov. to species rank, a taxon which is considerably less common and geographically restricted to the Rio Negro and its northern tributaries in the Amazonas and Roraima states (Fig. 6). On the other hand, *Schusterolejeunea inundata* is widely distributed across both the Amazonian and the Cerrado biomes in several Brazilian states. Among populations, *S. inundata* shows high morphological variability. For example, we observed that separate samples collected in proximity represent either *S. inundata* with small lingulate lobules, or *S. inundata* var. *fontinaloides* (Spruce) A.M.Sierra & C.E.Zartman, comb. nov. with larger triangular lobules, but on its secondary shoots lingulate lobules were observed. In

summary, *S. inundata* is a highly variable species, with leaves varying from elliptical to ovate, and lobules from small lingulate to medium triangular shaped, while the perianth always presents five distinct keels reaching  $\frac{2}{3}$  of its length. Based on the distinct leaves and lobules variation observed within *S. inundata*, the variety *S. inundata* var. *fontinaloides* (Spruce) A.M.Sierra & C.E.Zartman, comb. nov. merits its systematic rank as originally proposed Spruce (1884) following the considerations for species variety by Gradstein (1975).

The available information suggests that both species, *S. inundata* and *S. saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov., are widely distributed in the Brazilian Amazon Forest but are threatened by anthropogenic activities, such as the deforestation of inundated habitats (igapó forest) and river dam construction projects (Resende *et al.* 2020). Of the specimens studied of *S. inundata*, several were collected forty years ago in areas that have suffered deforestation (Rondônia and Pará), or anthropogenic alteration in the flooding regimens due to dam construction (Uatumã river, Amazonas state). Illegal gold mining, as well as deforestation, have also dramatically increased sediments and mercury (Hg) runoff in the waters of many of the hydrological basins within the Amazon. This is the case of the Tapajós river (Pará) and its tributaries (Lino *et al.* 2019; RAISG 2020), where *S. inundata* is known to occur (Lisboa & Ilkiu-Borges 2001). Such changes in the habitat conditions where *Schusterolejeunea* occurs inevitably impact the survivability of such riparian taxa. Monitoring projects utilizing rheophytic bryophytes as bioindicators in proximity of large-scale projects involving intensive anthropogenic activities in riparian habitats would be essential to understand their impacts on the native biodiversity of these unique habitats.

KEY TO THE SPECIES IN THE GENUS *SCHUSTEROLEJEUNEA* GROLLE

1. Leaves oblong, lobules large (rectangular to oblong), covering  $\frac{1}{3}$ - $\frac{2}{3}$  of the leaf lobe, perianth with five indistinct low keels ..... *Schusterolejeunea saxorum* (Spruce) A.M.Sierra & C.E.Zartman, stat. nov., comb. nov.
- Leaves elliptical to ovate, lobules small to medium in size covering up to  $\frac{1}{4}$  of the leaf lobe, perianth with five distinct keels reaching  $\frac{2}{3}$  of the perianth length .....
2. Leaves elliptical, lobules on the primary stem always lingulate with a narrow base, keel extending < 6 cells .....
- Leaves ovate, lobules on the primary stem triangular (form of a shark's fin), keel extending > 6-12 cells .....

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APPENDIX

APPENDIX 1. — Species identification and herbarium information for specimens identified with the name *Schusterolejeunea* Grolle in Brazil. Specimens examined are highlighted in **bold**.

Taxa	Specimen number	Herbarium	Longitude	Latitude	Country	State	City	Locality
<i>Schusterolejeunea inundata</i> (Spruce) Grolle	<i>Braga, P.I.S. 3431</i>	INPA	–	–	Brazil	Amazonas	Presidente Figueiredo	Rio Uatumã de igapó no lado esquerdo do rio. Na margem do igapó
	<i>Braga, P.I.S. 3432</i>	INPA	–	–	Brazil	Amazonas	Presidente Figueiredo	Rio Uatumã de igapó no lado esquerdo do rio. Na margem da beira do igapó
	<i>Buck, W.R. 3052</i>	NY	-60	-2	Brazil	Amazonas	Presidente Figueiredo	Along Igarapé Caititu, c. 3 hours upstream from Rio Uatumã by motor
	<i>Buck, W.R. 3078</i>	NY	-60	-2	Brazil	Amazonas	Presidente Figueiredo	Along E shore of Rio Uatumã just downstream from Cachoeira do Tucumã
	<i>Buck, W.R. 3191</i>	NY	-60	-2	Brazil	Amazonas	Presidente Figueiredo	Along W shore of Rio Uatumã at junction of Rio Pitinga
	<i>Buck, W.R. 2781</i>	NY	-59	-2	Brazil	Amazonas	Presidente Figueiredo	Along Rio Uatumã at Cachoeira Morena
	<i>Buck, W.R. 3075</i>	NY	-60	-2	Brazil	Amazonas	Presidente Figueiredo	Along E shore of Rio Uatumã just downstream from Cachoeira do Tucumã
	<i>Costa, D.P. et al. 4059</i>	MNHN NY	-63	-8	Brazil	Amazonas	Barcelos	Rio Demene, braço do Rio Aracá
	<i>Fife, A.J. 17</i>	UEMA	-45	-5	Brazil	Maranhão	Caxias	São João stream, 60 km S of Humaitá on road to Porto Velho
	<i>Pic &amp; Conceição 23</i>	UEMA	-45	-5	Brazil	Maranhão	Caxias	Riacho Prata – Buriti Corrente
	<i>Pic &amp; Conceição 29</i>	UEMA	-44	-5	Brazil	Maranhão	Caxias	Riacho Prata – Buriti Corrente
	<b><i>Ivo et al. 3431</i></b>	INPA!	-59	-2	Brazil	Amazonas	Presidente Figueiredo	Rio Uatumã
	<b><i>Ivo et al. 3432</i></b>	INPA!	-59	-2	Brazil	Amazonas	Presidente Figueiredo	Rio Uatumã
	<b><i>Lisbôa, P.L.B. 1096</i></b>	INPA!	-59	-2	Brazil	Amazonas	Presidente Figueiredo	Rio Uatumã 4 Km da Cachoeira. Beira do igapó
	<i>Lisbôa et al. 6841</i>	MG	-56	4	Brazil	Pará	São Luís do Tapajós, Itaituba	Margem do Rio Tapajós, vegetação ribeirinha
	<i>Nelson, B.W. 1331</i>	NY	-58	-5	Brazil	Amazonas	Manaus	Rio Parauari between Agua Mineral and Calcarío
	<b><i>Reese, W.D. 13291</i></b>	INPA!, NY	-64	-11	Brazil	Rondônia	–	Along the Rio Pacaas Novos, between its confluence with the Rio Mamoré and the first rapids
	<b><i>Reese, W.D. 16797</i></b>	INPA!, NY	-56	-6	Brazil	Pará	Serra do Cachimbo	Serra Maze and vicinity; 1208-1229 km N of Cuiabá along Cuiabá-Santarém highway (BR 163)
	<b><i>Reese, W.D. 13288</i></b>	INPA!, NY	-64	-11	Brazil	Rondônia	–	Along the Rio Pacaas Novos, between its confluence with the Rio Mamoré and the first rapids
	<b><i>Reese, W.D. 16797</i></b>	INPA!, MO	-56	-6	Brazil	Pará	Serra do Cachimbo	Serra Maze and vicinity; km 1226 along Cuiabá-Santarém highway (BR-163)
	<i>Santos J.C.S. 961</i>	MG	-49	-6	Brazil	Pará	São Geraldo do Araguaia	Martírios-Andorinhas Mountain Ridge. On riparian forest. Growing on living trunk
	<i>Schuster, R.M. 79-7-173</i>	NY	-65	-0	Brazil	Amazonas	–	Collected along the Rio Negro between Manaus and São Gabriel da Cachoeira, Temendui Lagoon
	<i>Schuster, R.M. 79-6-154</i>	NY	-64	-0	Brazil	Amazonas	–	Collected along the Rio Negro between Manaus and São Gabriel da Cachoeira, Tapereira (cemetery and old fort) and São Tomas (stony beach)
	<i>Schuster, R.M. 79-10-274</i>	NY	-66	-0	Brazil	Amazonas	–	Collected along the Rio Negro between Manaus and São Gabriel da Cachoeira, along Rio Cauaburi between Rio Negro and Cachoeira do Carangueijo
	<i>Schuster, R.M. 79-7-182</i>	NY	-65	-0	Brazil	Amazonas	–	Collected along the Rio Negro between Manaus and São Gabriel da Cachoeira, Temendui Lagoon
	<i>Schuster, R.M. 79-6-153</i>	NY	-64	-0	Brazil	Amazonas	–	Collected along the Rio Negro between Manaus and São Gabriel da Cachoeira, Tapereira (cemetery and old fort) and São Tomas (stony beach)
	<i>Schuster, R.M. 79-7-182</i>	MICH	-65	-0	Brazil	Amazonas	–	Temendui Lagoon, on edge of Rio Negro
	<b><i>Schuster, R.M. 79-10-288</i></b>	INPA!, NY	-66	-0	Brazil	Amazonas	Santa Isabel do Rio Negro	Rio Cauaburi



## Appendix 1. — Continuation.

Taxa	Specimen number	Herbarium	Longitude	Latitude	Country	State	City	Locality
	Soares, A.E.R.; Carvalho- Silva, M. 1122	UB	-62	-0	Brazil	Roraima	Rorainópolis	Próximo ao Rio Branco, Rio Catrimani, afluente do Rio Branco, área alagável parcela 2
	<b>Spruce, R. L39</b>	MANCHI, G	-65	-4	Brazil	Amazonas	–	Fl. Negro, supra cataractas, ad arbores riparias
	Yano, O. 1693	UFPE	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Marié, Estirão de Piramirim
	Yano, O. 1693	SP	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Estirão de Piramirim, Rio Marié
	Yano, O. 9470	SP	-60	-3	Brazil	Amazonas	Manaus	Boca do Tarumã Mirim
	Yano, O. 1455	SP	-61	-2	Brazil	Amazonas	–	Paraná-Conceição, divisa com Tauatú
	Yano, O. 1643	SP	-67	-0	Brazil	Amazonas	Bom Jardim do Amazonas	Ilha Acaburu
	<b>Zartman, C.E. 8751</b>	INPA!, SP!	-67	0	Brazil	Amazonas	São Gabriel da Cachoeira	Igarapé la Mirim, above the camp to Morro dos Seis lagos, on rock in river, abundant on rock, twigs and leaves in the area
	<b>Zartman, C.E. 9867</b>	INPA!, PMA!	-62	1	Brazil	Roraima	Caracarái	Parque Nacional Serra da Mocidade, Rio branco
<i>Schusterolejeunea inundata</i> var. <i>fontinaloides</i> (Spruce) A.M.Sierra & C.E.Zartman, comb. nov.	<b>Buck, W.R. 2627</b>	INPA!, NY	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Negro, vicinity of first cachoeira of Igarapé Foibará of Rio Negro
	<b>Buck, W.R. 2314</b>	INPA!, NY	-66	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Along Rio Cauabari between the Rio Negro and Cachoeira do Carangueijo
	<b>Schuster, R.M. 79-11-302</b>	INPA!, NY	-66	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Ilha Acarabu, Rio Marié, at mouth of Rio Marié
	<b>Schuster, R.M. 79-21-1135</b>	INPA!, NY	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Igarapé Foibará, at first cachoeira
	<b>Schuster, R.M. 79-10-295</b>	INPA!, NY	-66	-0	Brazil	Amazonas	Santa Isabel do Rio Negro	Rio Cauaburi
	<b>Sierra, A.M. 4583</b>	INPA!, PMA!	-60	-3	Brazil	Amazonas	Manaus	Rio Negro igapó forest on island in front of Praia da Lua
	<b>Sierra, A.M. 4582</b>	INPA!, PMA!	-60	-3	Brazil	Amazonas	Manaus	Rio Negro igapó forest on island in front of Praia da Lua
	<b>Sierra, A.M. 4586</b>	INPA!, PMA!	-60	-3	Brazil	Amazonas	Manaus	Rio Negro igapó forest on island in front of Praia da Lua
	<b>Sierra, A.M. 4714</b>	INPA!, SP!	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Ilha Cariuari, 20 km descendo o Rio Negro
	<b>Sierra, A.M. 4713</b>	INPA!, PMA!	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Ilha Cariuari, 20 km descendo o Rio Negro
	<b>Sierra, A.M. 4720</b>	INPA!, SP!	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Ilha Cariuari, 20 km descendo o Rio Negro
	<b>Sierra, A.M. 4642</b>	INPA!	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Ilha ao frente da cidade
	<b>Sierra, A.M. 4724</b>	INPA!, PMA!	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Ilha Cariuari, 20 km descendo o Rio Negro
	<b>Sierra, A.M. 4718</b>	INPA!, SP!	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Ilha Cariuari, 20 km descendo o Rio Negro
	<b>Sierra, A.M. 5063</b>	INPA!, SP!	-68	0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Uaupés. Sitio São Paulo. Na margem do rio
	<b>Sierra, A.M. 5056</b>	INPA!, PMA! SP!	-68	0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Uaupés. Sitio São Paulo. Na margem do rio
	<b>Sierra, A.M. 4719</b>	INPA!, PMA!, SP!	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Ilha Cariuari, 20 km descendo o Rio Negro
	<b>Sierra, A.M. 4710</b>	INPA!	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Ilha Cariuari, 20 km descendo o Rio Negro
	<b>Sierra, A.M. 5055</b>	INPA!, PMA!	-68	0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Uaupés. Sitio São Paulo. Na margem do rio
	<b>Sierra, A.M. 5059</b>	INPA!, SP!, PMA!	-68	0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Uaupés. Sitio São Paulo. Na margem do rio
	<b>Spruce, R. s.n.</b>	MANCHI, G	–	–	Brazil	Amazonas	–	Paricatuba, leg.
	Yano, O. 2139	INPA!	–	–	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Negro, NW de São Gabriel da Cachoeira
	Yano, O. 1528	INPA!, SP	-64	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Negro, São Tomé (Margem do rio)
	Yano, O. 1640	INPA!, SP	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Negro, Ilha Acarabu
	Yano, O. 2103	INPA!, SP	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	São Gabriel da Cachoeira, Rio Negro, Ilha em frente a São Gabriel da Cachoeira
	Yano, O. 1536	INPA!, SP	-65	-0	Brazil	Amazonas	Santa Isabel do Rio Negro	Temenduí, Rio Negro
	<b>Zartman, C.E. 7544</b>	INPA!	-62	-2	Brazil	Amazonas	Novo Airão	Parque Nacional Jaú. Carabinani river
	<b>Zartman, C.E. 7547</b>	INPA!, SP!	-62	-2	Brazil	Amazonas	Novo Airão	Parque Nacional Jaú. Carabinani river

Appendix 1. — Continuation.

Taxa	Specimen number	Herbarium	Longitude	Latitude	Country	State	City	Locality
<i>Schusterolejeunea saxorum</i> (Spruce)	<b>Schuster, R.M. 79-13-381</b>	INPA!, NY	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Marié
A.M.Sierra & C.E.Zartman, stat. nov., comb. nov.	<b>Sierra, A.M. 4760</b>	INPA!, PMA!	-68	0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Uaupés. Proximo a comunidade de São pedro
	<b>Sierra, A.M. 5062</b>	INPA!, PMA!, SP!	-68	0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Uaupés. Sitio São Paulo. Na margem do rio
	<b>Sierra, A.M. 5057</b>	INPA!, PMA!	-68	0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Uaupés. Sitio São Paulo. Na margem do rio
	<b>Spruce, R. L331/c</b>	MANCHI, G	-	-	Brazil	Amazonas		San Carlos, in saxis fl. Negro inundatis, leg.
	<b>Yano, O. 1734</b>	INPA!, SP	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Marié, Marauna
	<b>Yano, O. 2150</b>	INPA!, SP	-67	-0	Brazil	Amazonas	São Gabriel da Cachoeira	Rio Negro, igarapé Foibará
	<b>Zartman, C.E. 9790</b>	INPA!, PMA!	-62	1	Brazil	Roraima	Caracaraí	Parque Nacional Serra da Mocidade, Rio Branco
	<b>Zartman, C.E. 9888</b>	INPA!, PMA!	-62	1	Brazil	Roraima	Caracaraí	Parque Nacional Serra da Mocidade, Rio Branco
	<b>Zartman, C.E. 9889</b>	INPA!, PMA!	-62	1	Brazil	Roraima	Caracaraí	Parque Nacional Serra da Mocidade, Rio Branco
	<b>Zartman, C.E. 9890</b>	INPA!, SP!	-62	1	Brazil	Roraima	Caracaraí	Parque Nacional Serra da Mocidade, Rio Branco
	<b>Zartman, C.E. 9891</b>	INPA!, PMA!, SP!	-62	1	Brazil	Roraima	Caracaraí	Parque Nacional Serra da Mocidade, Rio Branco
	<b>Zartman, C.E. 9892</b>	INPA!, PMA!	-62	1	Brazil	Roraima	Caracaraí	Parque Nacional Serra da Mocidade, Rio Branco
	<b>Zartman, C.E. 9794</b>	INPA!, SP!	-62	1	Brazil	Roraima	Caracaraí	Parque Nacional Serra da Mocidade, Rio Branco
	<b>Zartman, C.E. 9787</b>	INPA!, PMA!	-62	1	Brazil	Roraima	Caracaraí	Parque Nacional Serra da Mocidade, Rio Branco
	<b>Zartman, C.E. 9832</b>	INPA!	-62	1	Brazil	Roraima	Caracaraí	Parque Nacional Serra da Mocidade, Rio Branco
	<b>Zartman, C.E. 7542</b>	INPA!	-62	-2	Brazil	Amazonas	Novo Airão	Parque Nacional Jaú, Carabinani river