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A taxonomic revision of the family Stephaniellaceae (Marchantiophyta)

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Abstract – Stephaniellaceae (R.M. Schust.) R.M. Schust. is a small family that occurs in the high elevations of the Americas, from Mexico to northern South America and South Africa. This taxonomic revision is based on the examination of herbarium specimens from various parts of its range, and field work in Mexican localities. The taxonomic treatment provides a re-description and illustration of the family, its genera and species, and a taxonomic key based on gametophytic characters. Five species in two genera (*Stephaniella* and *Stephaniellidium*) are recognized. *Stephaniella* is characterized by hyaline leaves, abundant paraphyllia, and sporophyte developed within the perianth. *Stephaniellidium* is characterized by chlorophyllose leaves, scarce paraphyllia, and sporophyte developed within a marsupium.

Stephaniellaceae / *Stephaniella* / *Stephaniellidium* / liverworts / paraphyllia

INTRODUCTION

Schuster (2002) was the first to recognize the family Stephaniellaceae, a group of small and poorly known liverworts from high elevations from Mexico to northern South America and South Africa. Sördeström *et al.* (2016) recognized the family Stephaniellaceae. The status of the family has been confirmed by phylogenetic analyses based on morphological data (Juárez-Martínez *et al.,* 2016); however, it has not yet been tested by molecular data.

The Stephaniellaceae according to Schmitt and Winkler (1968) originally comprised a single genus (*Stephaniella*) with six species, namely, *Stephaniella paraphyllina* J.B. Jack*, S. boliviensis* Steph., *S. hamata* Steph.*, S. rostrata* U. Schmitt, *S. uncifolia* S. Winkl.*,* and *S. sleumeri* Müll. Frib. Winkler (1969) transferred the last named species to the monotypic genus *Stephaniellidium* which was validated afterwards (in Grolle, 1983) as *Stephaniellidium sleumeri* (Müll. Frib.) S. Winkl. *ex* Grolle (Juárez-Martínez *et al.,* 2016). According to the phylogenetic analysis by Juárez-Martínez *et al.* (2016) and the examination of herbarium specimens we conclude that *Stephaniella boliviensis* is a synonym of *S. paraphyllina,* and recognized four other species in *Stephaniella* and one of *Stephaniellidium.* Thus, the family includes five species in two genera.

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In addition to the species cited above, Arnell (1961) had described *Stephaniella mexicana* S.W. Arnell from Mexico (Popocatépetl volcano). However, the study of the holotype showed that the specimen was a mixture of *Stephaniellidium sleumeri* and *Gongylanthus liebmannianus* (Juárez-Martínez *et al*., 2016). Because of this, *S. mexicana* was excluded from this revision.

In order to complement the morphological information for the family, this study provides a re-description and illustration of the Stephaniellaceae, *Stephaniella* and *Stephaniellidium,* and their species, as well as a taxonomic key.

MATERIAL AND METHODS

Approximately, 200 herbarium specimens of Stephaniellaceae from B, BM, G, M, MEXU, MO, NY, and S were examined. Mexican material for study was collected by the first autor in Ajusco volcano (Mexico City); in Parque Nacional Izta-Popo and Nevado de Toluca volcano (Estado de Mexico); La Malinche volcano (Tlaxcala), and Pico de Orizaba (Veracruz). These specimens were deposited in MEXU.

TAXONOMIC TREATMENT

Stephaniellaceae (R.M. Schust.) R.M. Schust., *Nova Hedwigia Beiheft* 119: 584. 2002

Green, pale-yellow, grayish or grayish-green plants, compact, prostrate or erect, slightly or strongly adhered to the substrate, forming small patches or large mats. Stem 4-10 mm long, with cortical and medullary cells differentiated. Cortical cells in 2-5 layers, brown, smooth, thickened and usually larger than medullary cells. **Stolons** present (in *Stephaniella*) or absent (in *Stephaniellidium*). Stolons ventral-intercalary, with cortical and medullary cells differentiated. **Amphigastria** absent. **Rhizoids** dense, scattered throughout the stem, smooth, sometimes originating at the leaf base. **Stem-branching** scarcely, lateral-intercalary or lateral-terminal. **Stem paraphyllia** present, numerous (in *Stephaniella*) or scarce (in *Stephaniellidium*), filiform or foliose, erect or falcate. **Leaves** undivided, succubous, alternate, slightly or strongly imbricate, concave, hyaline (in *Stephaniella*) or green at least the basal and middle cells (in *Stephaniellidium*). Leaf areolation regular. Marginal postical cells strongly elongated forming a differentiated border; apical cells differentiated, the same size or larger than the mid-leaf cells; with cell walls thinner than or thicker than those of mid-leaf cells. **Trigones** absent. **Intermediate thickenings** poorly developed. Leaf insertion line transgressing the stem midline (interlocking merophytes). **Oil bodies** small, spherical, 3-8 per cell, weakly botryoidal-granular. **Dioicous**. **Gynoecia** terminal, on the stem tip, the inner plicate longitudinally, apex undivided, margin entire, serrulate or prorulose. **Perianth** present (in *Stephaniella*) or absent (in *Stephaniellidium*), with longitudinal folds and fused only at the base, apex lobed. Paraphyllia present in the gynoecia, longer than the paraphyllia on the stem. **Marsupium** lacking (in *Stephaniella*) or present (in *Stephaniellidium*). **Sporophyte capsule** cylindrical, capsule wall 2-layered. **Gemmae** not seen.

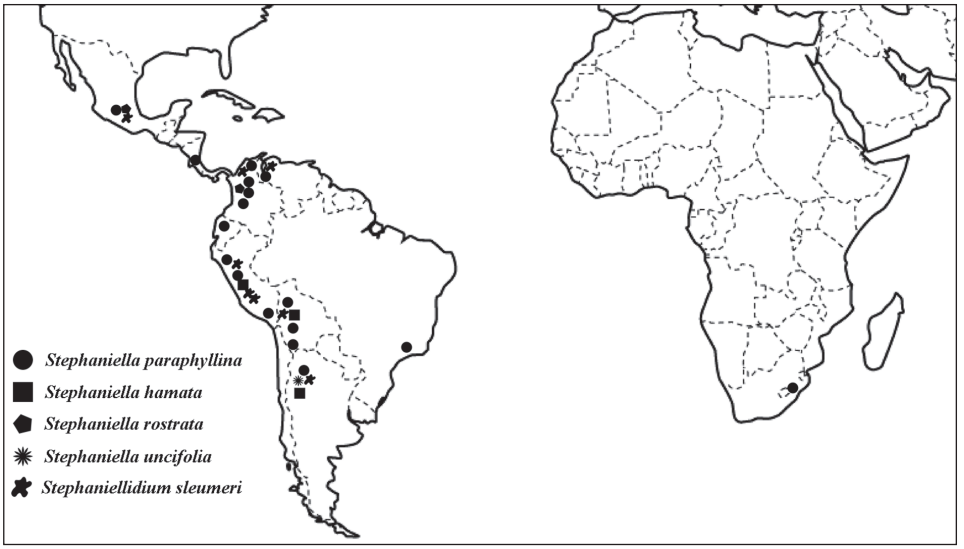


Fig. 1. Distribution map of the Stephaniellaceae and its species.

Distribution and ecology. Stephaniellaceae is a family distributed at high elevations (2100-4700 masl), from South America to Mexico (Gradstein *et al.,* 2001; Juárez-Martínez *et al.,* 2016) (Fig. 1). Also, *Stephaniella paraphyllina* is reported from South Africa (Arnell, 1961). Members of the Stephaniellaceae occur on compact soil. In Mexico, in alpine localities where the soil is not compact the members of Stephaniellaceae are absent, *e.g.* Pico de Orizaba, Veracruz. It is probable that in non-compacted soils the plants cannot become anchored.

Morphological considerations

The leaf form is a character difficult to examine and determine, because the merophytes and leaves are interlocking and easily broken. In this sense, the length and width as well as the postical and antical margins are difficult to determine. Figure 2 shows the general morphology of the leaf and where its measurements were obtained.

Schmitt and Winkler (1968) explained and discussed the degrees of separation between the leaf base and the stem. Although the authors found significant differences among species, this character was not included in this study due to the complexity of its measurement.

Schuster (2002, p. 587) provided a detailed description of the oil bodies in *Stephaniella;* their description here comes from that study. Oil bodies were only observed in a specimen of *Stephaniellidium sleumeri* (*Juárez-Martínez 352,* MEXU).

Schuster (2002) used the terms paraphyllia and paraphyses indistinctly. Schmitt and Winkler (1968) and Schuster (2002) cited the presence of filaments among the archegonia and antheridia, but those structures were not observed in the present study. The term paraphyllia in the gynoecia refers to the photosynthetic filaments only found among the female bracts.

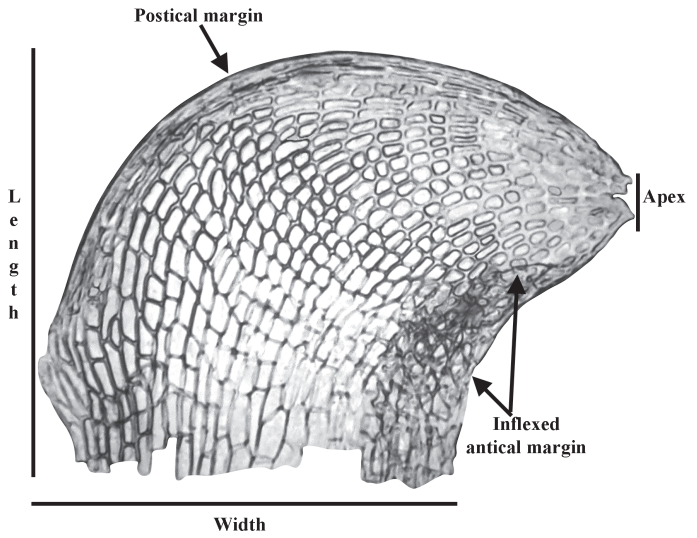


Fig. 2. Diagram of the leaf of *Stephaniella* indicating its morphology and where the measurements were obtained.

Schuster (2002) referred to the structure surrounding the archegonia as a "perianth-like structure". Schmitt and Winkler (1968), Schuster (2002) and Váňa *et al*. (2010) stated that *Stephaniella* had inner female bracts fused only at the base so that it is difficult to distinguish them as a perianth. Nevertheless, there were significant morphological differences between the external and the "inner female bracts" among the species of *Stephaniella.* Therefore, in this treatment, the "inner female bracts" and "perianth-like structure" are considered as a perianth.

Sporophytes are rarely found in *Stephaniella* and *Stephaniellidium*. However, Schuster (2002, p. 594) described the sporophyte of *Stephaniella uncifolia,* and Schmitt and Winkler (1968, p. 121) described the seta of *S. paraphyllina* which lacks differentiation of epidermal and medullary cells.

Since no archegonia and antheridia have been found on the same stem (*cf.* Schuster, 2002), the Stephaniellaceae may be considered as a dioicous taxon.

For a detailed description of the androecium see Schuster (2002).

Taxonomic key to the genera and species of Stephaniellaceae

1a. Leaves chlorophyllose, with longitudinal folds; leaf apex straight..... ..... **5. *Stephaniellidium sleumeri* (*Stephaniellidium*)**

1b. Leaves hyaline without longitudinal folds; leaf apex falcate.... **2. (*Stephaniella*)**

2a. Leaf base not decurrent; stem paraphyllia usually filiform. Apical cells of the perianth oblong, not sinuose **3**

2b. Leaf base decurrent; stem paraphyllia usually foliose. Apical cells of the perianth oblong-sinuose..... **4**

3a. Leaves oblate or ovate, wider than long or as wide as long. Leaf apex obtuse, entire ..... **1. *Stephaniella paraphyllina***

3b. Leaves ovate, longer than wide, sometimes as long as wide. Leaf apex acute, slightly serrulate or prorulose ..... **3. *Stephaniella rostrata***

4. Leaf blade plane; leaf apex obtuse to acute ..... **2. *Stephaniella hamata***

4. Leaf blade concave; leaf apex acute to apiculate.. **4. *Stephaniella uncifolia***

***Stephaniella* J.B. Jack,** *Hedwigia* 33: 11. 1894

Green, brown or grayish plants, usually pale, forming small patches or large mats. **Stem** poorly or well-differentiated in a 2-3 layered cortex, cortical cells smooth, larger and thicker-walled than medullary cells. **Stolons** geotropic ventral-intercalary, 5 mm to 4 cm long, differentiated in cortex and medulla, with scattered rhizoids, shorter than stem rhizoids, sometimes originating new branches. **Stem paraphyllia** filiform or foliose, chlorophyllose, sometimes branching near the base or in the middle; ending in a single triangular cell. **Leaves** echlorophyllose, antically secund (homomallous) with apex pointing toward the stem base, asymmetric, slightly or strongly imbricate. Cell walls smooth or papillose, at least near the leaf apex. Postical margin involute to plane, antical margin inflexed. Leaf apex falcate, involute or plane, obtuse or acute (rarely apiculate). Leaf longitudinal plicae lacking. **Oil bodies** observed only in the cells of the paraphyllia. **Gynoecia** on tip of leafy axes, capitate. Female bracts 2-3 pairs, the inner undivided, with longitudinal folds. **Paraphyllia of the gynoecia** becoming progressively longer than stem paraphyllia. **Perianth** exsert, narrowly ovate, only fused at the base, lobed at apex, longitudinally plicate, without paraphyses. **Androecia** (see Schuster, 2002). **Perigynium** present. **Marsupium** lacking. **Sporophyte** capsule cylindrical.

Morphological considerations

The species of *Stephaniella* sometimes form underground networks of stolons.

Schmitt and Winkler (1968) illustrated the leaf shape of *Stephaniella* as well-defined, which it is not always the case. It is frequently difficult to identify the species by the leaf shape only because it is a highly variable character. On the other hand, the leaves of *Stephaniella* are asymmetrical with a falcate apex, but rounded leaves near the stem apex were observed in specimens of *S. paraphyllina* and *S. hamata* (Figs 15, 31, 32, 34, 35).

Schuster (2002) emphasized remarkable differences in the number of cells in the paraphyllia of *Stephaniella rostrata, S. paraphyllina,* and *S. uncifolia*, but the examination of specimens and observations of Juárez-Martínez *et al.* (2016) show that this character was uninformative. In all species of *Stephaniella* the paraphyllia are usually longer near the gynoecia.

Schuster (2002, p. 587) described the morphology of the mature sporophyte capsule. In his description, the cell strata of the capsule wall have well-separated radial thickenings.

Androecia were not observed in the specimens examined.

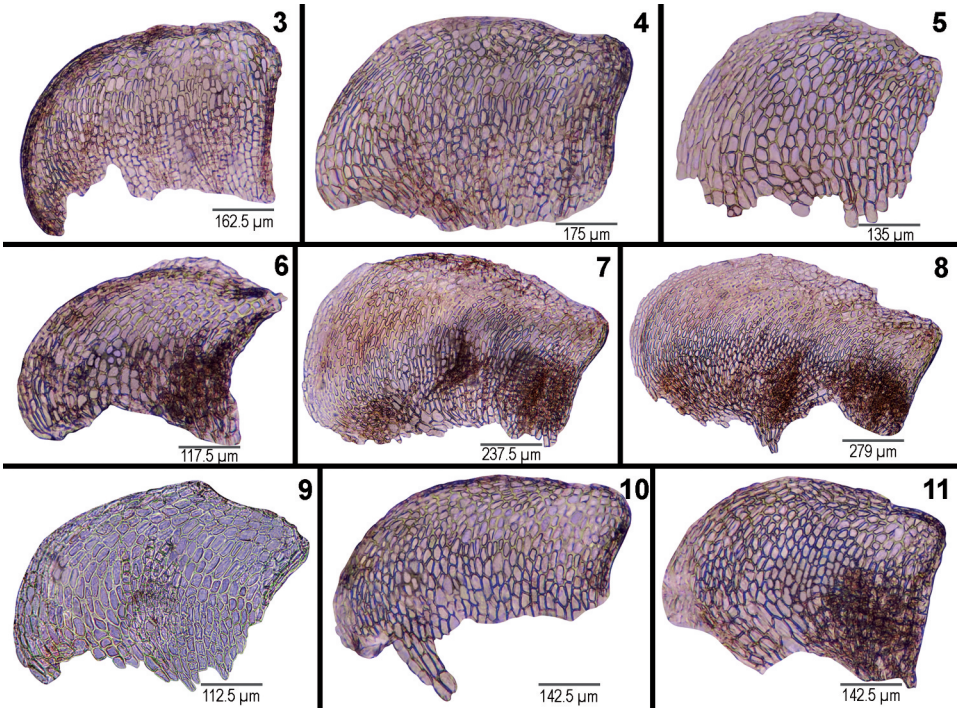
Note: L:W in the species description refers to the length to width ratio of a given structure.

When no collection number is available, the barcode number and the herbarium acronym are cited for specimen identification.

1. *Stephaniella paraphyllina* J.B. Jack, *Hedwigia* 33: 11, 1894 **Figs 3-30**

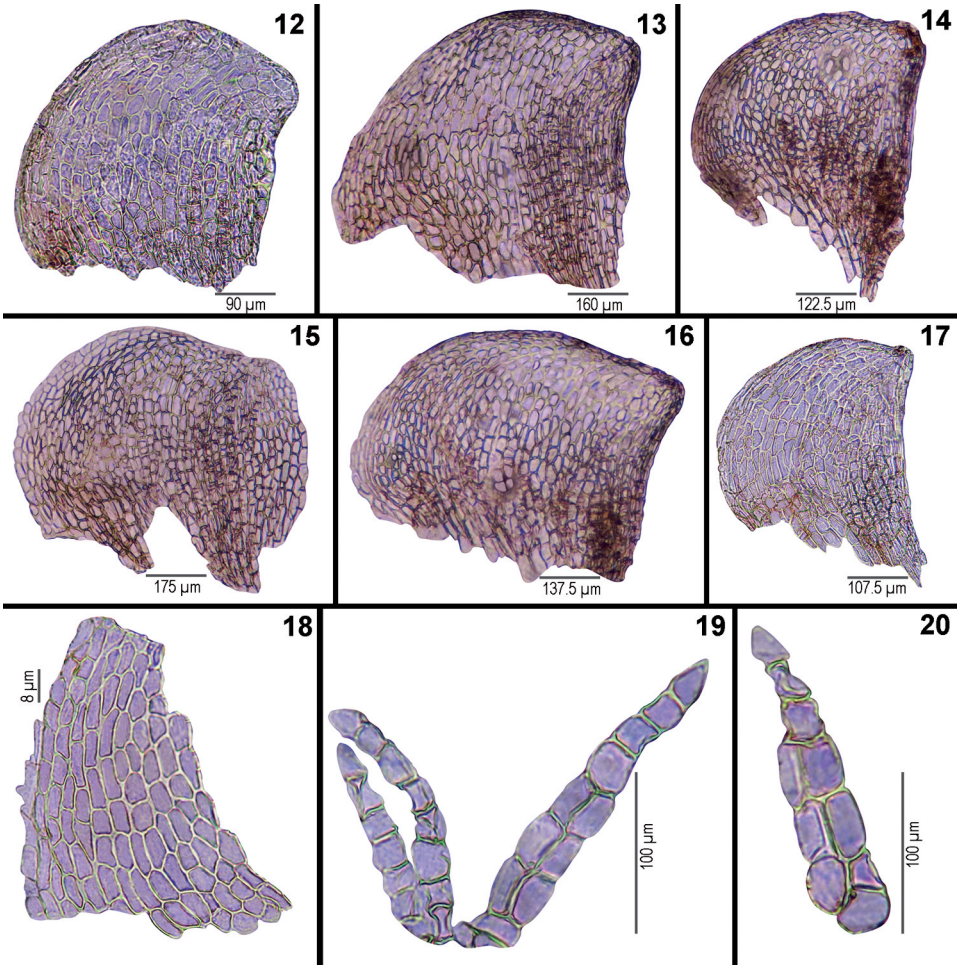
Type citation: Cordillera Argentino-Bolivianis. Cienega, alpine region, 1873, *Lorentz s.n.* (Lectotype designated by Juárez-Martínez, 2014 G-00120479!, isolectotype G!, M!).

Syn.: *Stephaniella boliviensis* Steph., *Bibliotheca Botanica* 87: 182, 1916, **syn. nov.**



Figs 3-11. *Stephaniella paraphyllina* J.B. Jack. **3-11.** Stem leaves.

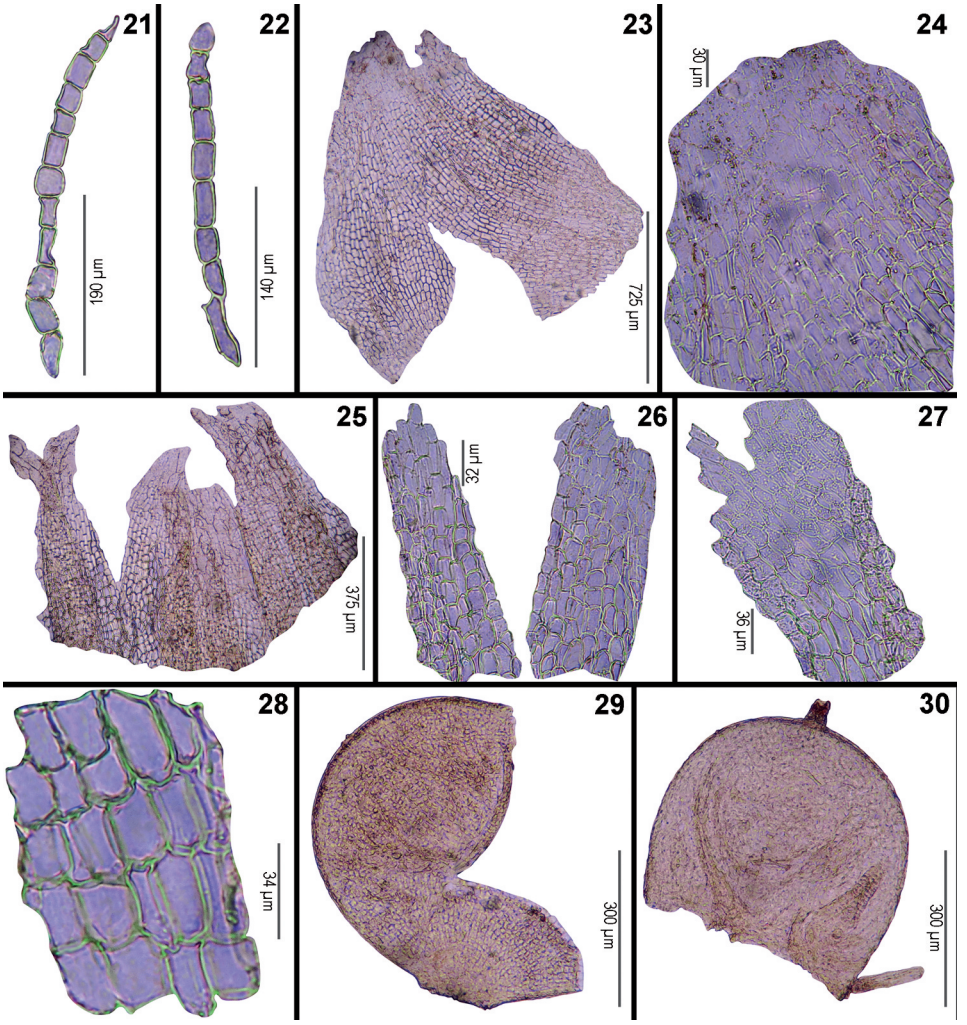
Plants mostly prostrate. **Stem** to 5 mm long, grayish to brown-pale, in section 130-160 (-220) µm diameter, weakly differentiated in cortex and medulla. Cortical cells in 2-3 layers, isodiametric to shortly oblong, brown to yellow-pale, thick-walled, 12-22 (-24) µm × 6-14 (-16) µm. Medullary cells shortly oblong to hexagonal, yellow-pale, thick-walled, but smaller than cortical cells, 10-18 (-20) µm × (6-) 8-10 (-16) µm. **Stolon** cross section 120-240 µm diameter. **Branching** lateral-intercalary, or frequently with ventral branches. **Stem paraphyllia** usually filiform, (90-) 150-250 (-290) µm long, (5-) 6-13 (-15) cells high, paraphyllia cells rectangular to quadrate, (10-12-) 14-30 (-32) µm long, smooth and thin-walled. **Leaves** strongly imbricate, concave, the apex or postical margin sometimes tinged red. Leaves falcate-reniform, wider than long, sometimes as long as wide, 300-750 µm × 430-900 µm, L:W ratio 1:1.4-1.8. Leaf insertion oblique, 350-500 (-570) µm. Leaf base not decurrent, antical and postical margins involute, sometimes plane, smooth. Leaf apex obtuse, usually involute, sometimes plane; when the antical margin is unfolded the apex is rounded; basal cells oblong-hexagonal, rhomboid and rectangular, thick-walled, (18-) 20-32 (-34-42) µm × 10-20 µm; mid-leaf cells oblong-rectangular, rhomboid, thick- or thin-walled, (18-) 20-30 (-38) µm × (8-) 10-14 (-18) µm; postical marginal cells elongate-rectangular, thin- to thick-walled, (22-) 26-40 (-52) µm × 6-12 (-14-16) µm, L:W ratio 3-6:1. Leaf cell walls smooth. **Gynoecia** ~2.2 mm high. **Female bracts** 2-3 pairs, the inner ovate-falcate, 1.4 mm × 1.1 mm, with entire margin, smooth, and apex acute; basal cells rectangular, quadrate, thin-walled, 22-38 (-40) µm × 12-20 µm; middle cells oblong, thin-walled, but thicker than basal cells, (20-) 26-38 µm × 14-20 µm; apical cells oblong, not sinuose, thick-walled,



Figs 12-20. *Stephaniella paraphyllina* J.B. Jack. **12-17.** Stem leaves. **18.** Marginal postical cells of the leaf. **19-20.** Paraphyllia of the stem.

24-30 (-36) µm × 12-18 µm. **Paraphyllia of the gynoecia** usually filiform, (470-) 580-910 (-1000) µm long, 12-21 cells high, rectangular to quadrate, 20-40 (-52) µm long, smooth and thin-walled. **Perianth** at least with 7 archegonia, with entire margin, the apex lobed, segments widely acute, smooth; basal cells rectangular and quadrate, thin-walled, 24-34 (-40) µm × (10-) 12-18 µm; middle cells oblong, thin-walled, 22-40 µm × 14-22 µm; apical cells oblong, no sinuose, thin-walled, 34-48 (-52) µm × 10-20 µm. Cell walls of the perianth smooth. **Androecium** not seen. **Immature sporophyte** with spherical capsule.

Distribution and ecology. *Stephaniella paraphyllina,* is the most common species of *Stephaniella;* its distribution is shown in Figure 1. It is distributed from northern Argentina to Mexico, and South Africa, at elevations from 3000 to 4000 masl; in Brazil and Sierra Nevada in Colombia, it has been found from 2000 to 2700 masl. *S. paraphyllina* occurs in paramos and puna, and in places where larger vegetation



Figs 21-30. *Stephaniella paraphyllina* J.B. Jack. **21-22.** Paraphyllia of the stem. **23**. Female bract. **24.** Apical and median cells of the female bract. **25.** Perianth. **26.** Perianth apical cells. **27.** Perianth basal cells. **28.** Perianth median cells. **29.** Immature sporophyte capsule. **30.** Calyptra and archegonia. (Figs 3-5, 13, 15, 18-20, *Herzog 4794,* S, G*;* Fig. 12, *Herzog 3750,* G*;* Fig. 17, *Herzog 3750,* M; Fig. 22, *Lorentz s.n.* G-00115491.)

is sparse. In Mexico, it occurs in alpine grassland above timberline, around 4000 masl, forming dense mats on soil or soil on rocks, in humid or wet, exposed or sheltered sites, often mixed with other species of the genus, *Stephaniellidium sleumeri* or *Gongylanthus*.

Specimens examined. MEXICO. Distrito Federal: Volcán Ajusco. *Karsten s.n.* (BM, M). **Estado de México:** Llano Grande, extremo NW del volcán Iztaccíhuatl, 3500 m, *C. Juárez-Martínez 117, 118a, 120 p.p.* (MEXU). La Joya, extremo SW del volcán Iztaccíhuatl. 8 km al N de Paso de Cortés, 3963 m, *A. Cárdenas S. 6754 p.p., 6756, 6757* (MEXU), *C. Juárez-*

Martínez 110 p.p. (MEXU). Outer N slope of the crater of Nevado de Toluca volcano, 4050 m, *T. Pócs 9548H* (MEXU). **Tlaxcala:** Mpio. San José Teacalco, Volcán La Malinche, ~4000 m, *C. Juárez-Martínez & J.A. Cruz-López 349, 350, 352 p.p.* (MEXU). **Veracruz:** Orizaba. *Karsten s.n.* (BM). **ARGENTINA. Prov. de Salta:** Cordillera, Cienega, *Lorentz 286, 324* (BM). Cordillera Argentino-Bolivianis, Cienega, alpine region. *Lorentz s.n.* (lectotype, G-00120479!), (isolectotype, G-00120478!, G-00115491!), (isolectotype, M-0182810!). **Prov. Tucumán:** Valle de Tafi, Potrerillo, 3200 m, *I.M. Lamb 5437* (B). **BOLIVIA. Depto. Cochabamba:** Catena Yanakaka, ca. 4600 m, *Herzog 3750* (lectotype of *Stephaniella boliviensis* M, isolectotype G, B). Llavetal, 4300 m, *Herzog 4794* (syntype of *S. boliviensis* G, M, S). **Depto. La Paz:** Along Rio Zongo. Lago Milluni, 3500-4000 m, *J. Duke, E. Smith & R. Larra 17368* (MO). Murillo, mina San Francisco, NE de Palca, 4380 m, *S. Churchill, M. Cano & J. Jiménez 24736 p.p.* (MO). **Depto. Potosí:** Chayanta. Cuenca Río Ravelo, cerca Sacsanta, 3160 m, *S. Churchill et al. 24706* (MO). Chayanta, cerca Sfiri, 3280 m, *S. Churchill et al. 24684* (MO). **BRASIL. Goiás:** Brasilia, 2100 m, *P. Dusén s. n.* (NY). **Río de Janeiro:** Serra do Itatiaia. 2100 m, *P. Dusén s. n.* B189285, B189287, B189289, 564 (S), *R. Douin s.n.* (M). **COSTA RICA. Prov. Cartago:** Volcano Irazú, Pacific side. *Ruth D. Svihla 464, duplicado* (NY). Cordillera de Talamanca, páramo Buenavista, 3400 m, *G. Dauphin 2922* (NY). **COLOMBIA. Depto. Bogotá:** páramo El Boquerón, 3500 m, *C. Troll 2168* (B, S). **Depto. Boyacá:** páramos al NW de Belén, cabeceras Quebrada Minas, filo divisorio entre la Laguna El Alcohol y la Laguna Negra, 4000 m, *A.M. Cleef 1948* (B, MEXU, NY). **Depto. Cundinamarca:** páramo de Chingaza, around Lagunita, along trail to St. Juanito, 3400 m, *S.R. Gradstein & E. Santana 4246* (B, MEXU, NY), *4261* (NY). Páramo El Tablazo, 3500 m, *B. M. Thiers 5497* (NY). **Depto. Magdalena:** Sierra Nevada de Santa Marta. Transecto del Río Buritaca, parte alta del Filo La Cumbre, 3750 m, *O. Rangel & A.M. Cleef 1019* (B, NY), *1020 p.p.* (NY), *S. Winkler C395* (M). S-flanke der Sierra Nevada de Santa Marta, oberhalb von San Sebastian, sparliches Bewuchsmit Ericaceen, 2700 m, *S. Winkler C206 p.p.* (S). **Depto. Santander:** páramo de la Rusia, an ole, Strasse von Duitama, 3350 m, *S. Winkler C512* (B, M). **ECUADOR. Prov. Cotopaxi:** Parque Nacional Cotopaxi. Burro Tabla Grande, Rio Cutuchi, 3400 m, *S.R. Gradstein & H.J. Sipman 121* (B, MEXU, MO, S). Parque Nacional Cotopaxi, along road from Pampa de Limpios to summit of Cotopaxi, 4100 m, *W.R. Buck 10055* (NY). **PERU. Depto. Arequipa:** Caylloma, along road Chivay to Sibaya. 3700-4000 m, *H. van der Werff, L. Valenzuela & E. Suclli 2099a* (MO). **Depto. Cajamarca:** Prov. Cajamarca. Ort. Las Lagunas. 3900 m, *P. & E. Hegewald 6207 p.p.* (MO). **Depto. Junín:** Prov. Jauja. Ort. La Oroya, Laguna bei den Minen «Gran Bretagne». *P. & E. Hegewald 5439* (MO). **SOUTH AFRICA.** KwaZulu-Natal: Sani Pass, Sani Top. 3000 m, *H.W. Matcham, J.G. Duckett & N.G. Hodgetts 4125a* (BM). **VENEZUELA.** Straβe von Valera nach Mérida. 3700 m, *Schäfer-Verwimp & Verwimp 12077 p.p.* (MO). **Mérida:** Sierra de Santo Domingo, páramo de Mucuchies: Passo El Aguila an der Straβe Merida-Valera, 3900 m, *H. Hertel 10436* (M).

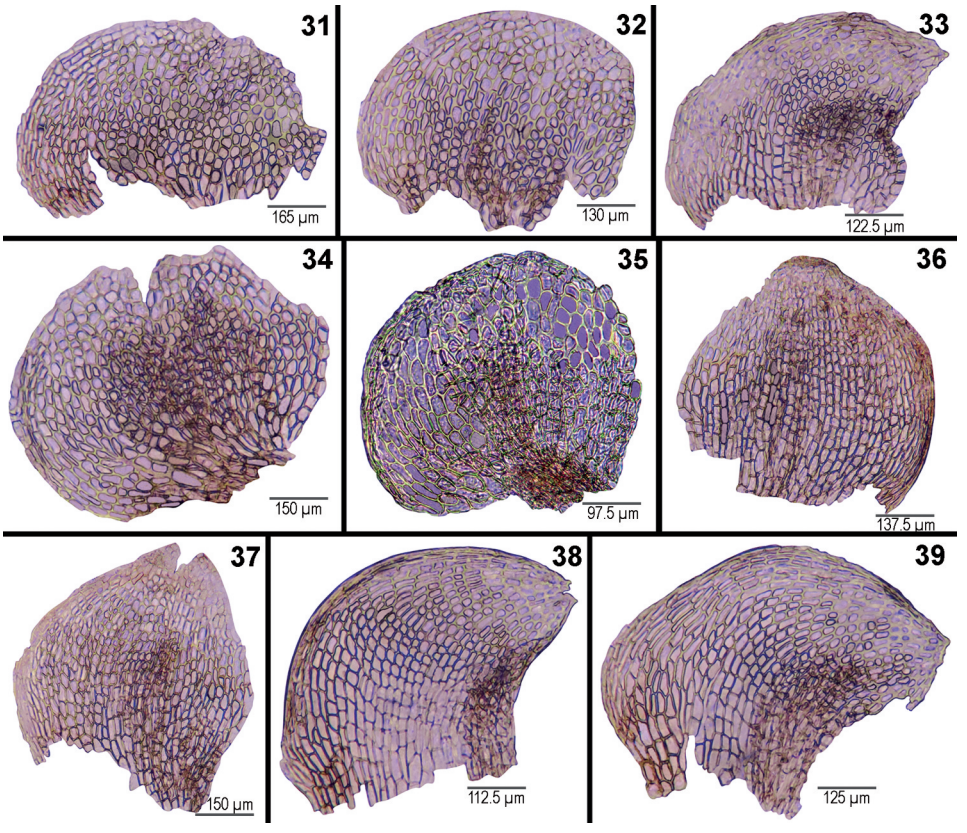
The shape of the leaves of *Stephaniella paraphyllina* shows high variation (Figs 3-17). As mentioned above, as in *S. hamata,* in *S. paraphyllina* rotund leaves (Fig. 15) were also observed. However, the rotund shape is caused by the antical margin that, when unfolded, has the appearance of a rounded leaf. This condition could occur in leaves near of the stem apex or in young stems. The rotund leaves are as wide as long, or slightly wider than long (450-550 μm × 520-540 μm). This condition was observed in *Juárez-Martínez 349* (MEXU).

On the other hand, in the protologue of *Stephaniella boliviensis*, Stephani described the marginal cells as crenate-protruding and the leaf margin as subdentate. Nevertheless, in the type specimens the marginal and apical cells are entire and smooth (Figs 3-5, 12, 13, 14, 17). In this sense, *S. paraphyllina* and *S. boliviensis* are very similar, and are distinguished only by the leaf shape: oblate in *S. paraphyllina* and ovate in *S. boliviensis* (Juárez-Martínez *et al*., 2016) (Figs 3-17). Accordingly, the synonymy of *S. boliviensis* under *S. paraphyllina*, as proposed Grolle (1967, on a label comment) is accepted.

2. *Stephaniella hamata* Steph., *Bulletin de l'Herbier Boissier ser.* 2, 1: 1024, 1901
Figs 31-49

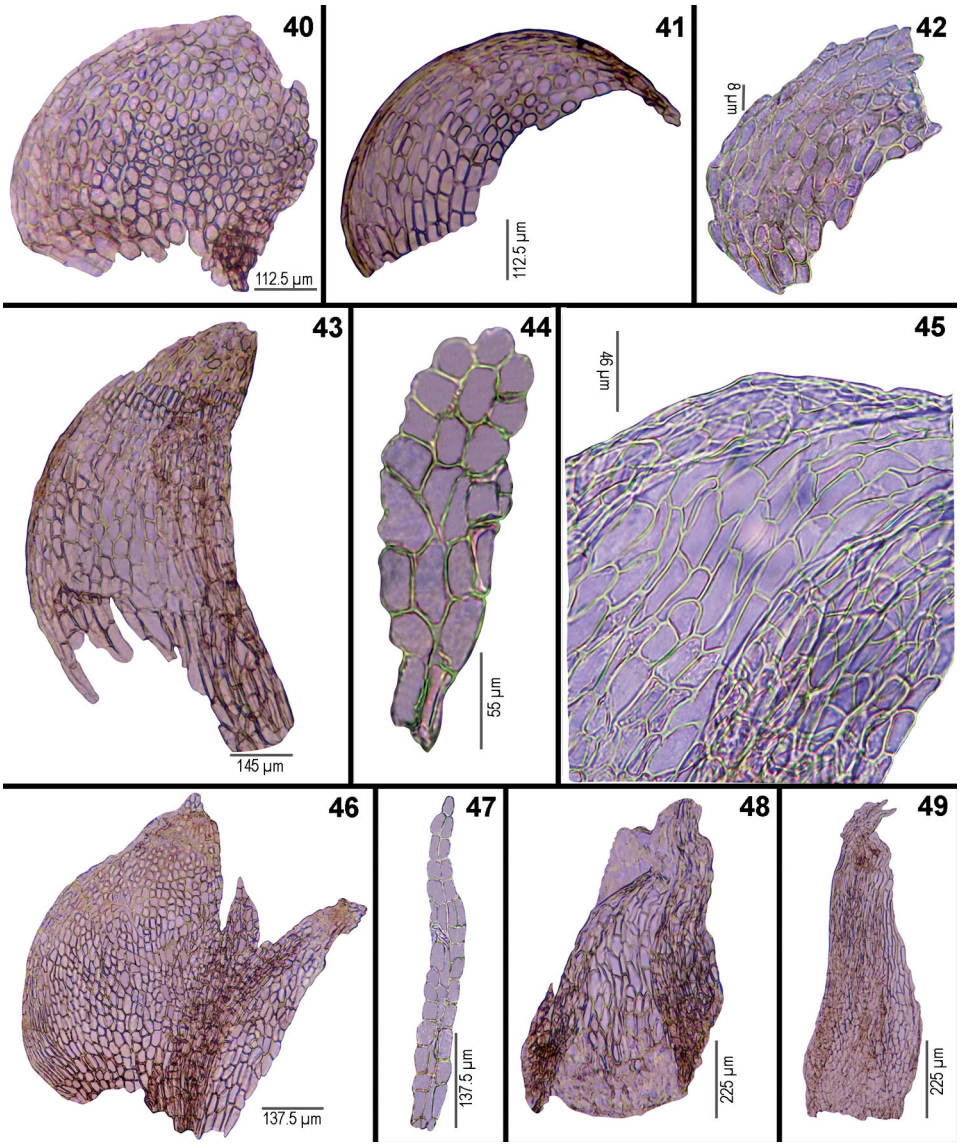
Type citation: Argentina. Córdoba, *Lorentz s.n.* (Lectotype designated by Juárez-Martínez, 2014 G-00069943!)

Plants postrate or erect. **Stem** to 7-10 mm long, yellow-pale, without reddish tinged, in section 170-190 µm in diameter, well-differentiated in cortex and medulla. Cortical cells in 2-3 layers, shortly oblong to isodiametric, brown, thick-walled, 14-20 (-22) µm × 10-12 (-16) µm. Medullary cells shortly oblong, brown, thin-walled, 16-18 µm × (8-) 10-14 µm. **Stolon** cross section 150-180 µm in diameter. **Branching** lateral-intercalary, ventral-intercalary, branches almost as long as the stem. **Stem paraphyllia** usually filiform, falcate or erect (spatulate), 160-260 µm long, several long cells, paraphyllia cells oblong-quadrate, 12-42 µm long, thick-walled, rough near the apex. **Leaves** loosely imbricate, nearly plane, not tinged red. Leaves ovate-falcate, slightly longer than wider or as long as wide, 460-600 µm × 400-600 µm, L:W ratio 1-1.2:1. Leaf insertion oblique, 250-350 µm. Leaf base decurrent, postical leaf margin slightly involute, antical margin inflexed, serrulate near the apex. Leaf apex obtuse to acute, plane. Leaf basal cells oblong-rectangular,



Figs 31-39. *Stephaniella hamata* Steph. **31-39.** Stem leaves (Figs 33, 38, 39, *Lorentz s.n.* G-00069943).

rhomboid, thin-walled, (18-20-) 24-34 (-38) µm × (10-) 14-18 (-20) µm; mid-leaf cells oblong-rectangular, quadrate, slightly thick-walled (14-) 20-30 (-34) µm × (10-) 12-16 (-22) µm; postical marginal cells strongly elongate, some of them linear, strongly thick-walled, 20-50 µm × 4-12 µm, L:W ratio 4-5 (-6):1. Cell walls of the leaf slightly papillose, usually near the apex. **Gynoecia** ~900 µm high. **Female**



Figs 40-49. *Stephaniella hamata* Steph. **40-49, 43.** Stem leaves. **41, 42.** Marginal postical cells of the leaf. **44.** Paraphyllia of the stem. **45.** Perianth median cells. **46.** Female bract. **47.** Paraphyllia of the gynoecia. **48, 49.** Perianth. (Figs 41, 49, *Lorentz s.n.* G-00069943).

bracts 2- pairs, the inner ovate-falcate, 850-600 μm long, with middle section toward the apex serrulate or prorulose, and apex acute; basal cells oblong-rectangular, thin-walled, (26-) 32-42 μm × 12-16 (-18) μm; middle cells shortly oblong, thin-walled, (22-) 26-30 (-38) μm × 10-16 μm; apical cells elongate to linear, strongly thick-walled, 20-26 (-30) μm × 4-8 μm. **Paraphyllia of the gynoecia** usually lanceolate to spatulate, 570-580 μm long, several cells long, oblong, 26-34 μm long, smooth and thin-walled. **Perianth** margin slightly serrulate, and the apex lobed, segments widely acute and slightly serrulate; basal cells oblong-elongate, thin-walled (22-) 30-34 (-46) μm × 14-18 (-22) μm; middle cells oblong-elongate, thin-walled, 24-32 μm × 12-18 μm; apical cells oblong-elongate, sinuose, thick-walled, (20-) 30-42 (-50) μm × 8-10 μm. Cell walls of the perianth smooth. **Androecium** not seen. **Sporophyte** not seen.

Distribution and ecology. *Stephaniella hamata* is only known from Argentina, Bolivia and Peru (Fig. 1), at elevations from 3595 to 4600 masl. Like other species of *Stephaniella, S. hamata* grows at high elevations, forming patches on soil or soil on rocks, mixed with species of *Gongylanthus* and mosses.

Specimens examined. ARGENTINA. Córdoba, *Lorentz s.n. G-00069943* (lectotype, G). **BOLIVIA.** *Herzog 4255* (G), ca. 4500-4600 m, *Herzog 3166* (B, M, S). **Depto. Chuquisaca:** Oropeza, entre 36-52 km al Oeste de Sucre, en la comunidad de Maragua, por el camino que va hacia el cerro con forma de cráter, 3595 m, *I. Linneo, S. Churchill et al. 747* (MO). **PERU. Depto. Junín:** Prov. Jauja. Ort. Laguna Huaylacancha, 4400 m, *P.& E. Hegewald 5875* (MO).

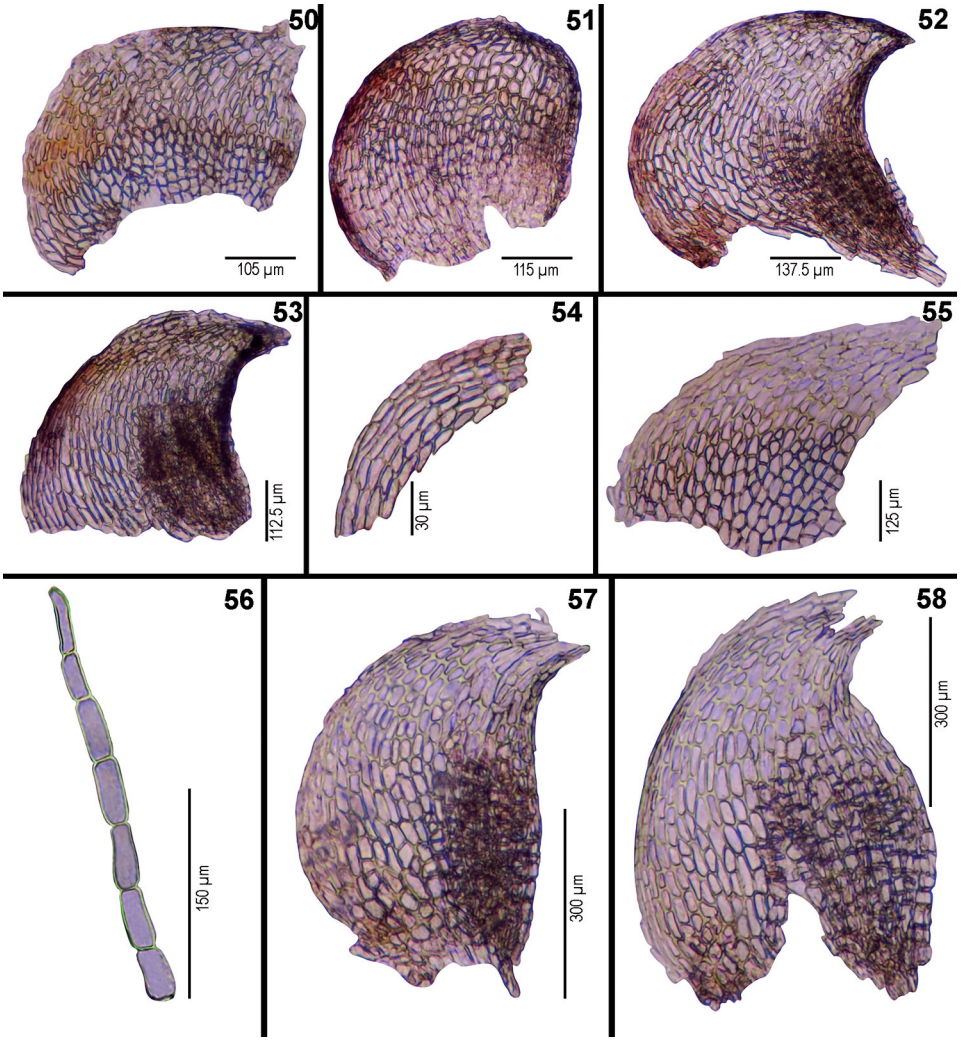
Schmitt and Winkler (1968) and Herzog (1926) illustrated *Stephaniella hamata* with rotund leaves. Nonetheless, according to the original description and the examination of type specimen, the leaves are clearly ovate-falcate (Fig. 33, 36-40, 43), not rotund. The only specimen of *S. hamata* with rotund leaves is *Herzog 4255* (G!) (Figs 31, 32, 34, 35).

On the other hand, Schmitt & Winkler (1968) proposed that *Stephaniellidium sleumeri* is a polyploid form of *S. hamata*, because of its large foliar cells. However, no morphological evidence was found to support this assumption and the phylogenetic analysis of Juárez-Martínez *et al*. (2016) did not show any relationship between *S. hamata* and *S. sleumeri.*

3. *Stephaniella rostrata* U. Schmitt, *Oesterreichische Botanische Zeitschrift* 115: 124, 1968 **Figs 50-69**

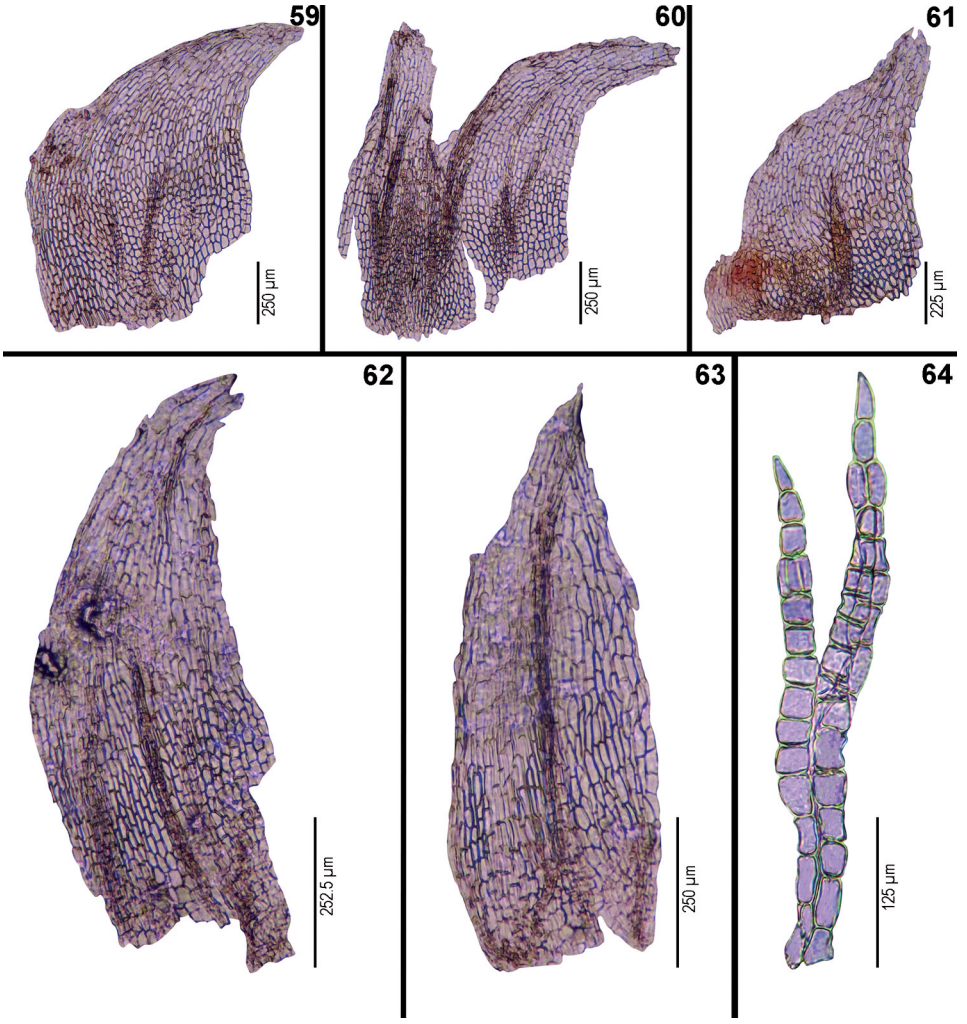
Type citation: Colombia, Páramo de la Rusia, and der Straβe von Duitama, 1967, *S. Winkler C513,* Herbarium S. Winkler, TUB. (Schmitt & Winkler, 1968: 127).

Plants erect. **Stem** ~4 mm long, yellow-pale, without a reddish tinge, in section 130-170 μm diameter, weakly differentiated in cortex and medulla. Cortical cells in 2 layers, oblong, yellow-pale, slightly thick-walled, (16-) 18-22 μm × 8-12 (-16) μm. Medullary cells shortly oblong, yellow-pale, thin-walled, (10-) 12-16 μm × 6-8 μm. **Stolon** cross section (140-) 200-250 μm diameter. **Branching** lateral-intercalary, sometimes new branches originating at the stem tip. **Stem paraphyllia** commonly filiform, (124-) 140-200 μm long, (3-) 7-11 (-12) cells high, paraphyllia cells quadrate to rectangular, (12-) 14-20 (-24) μm long, smooth and thin-walled. **Leaves** loosely imbricate, plane or slightly concave, sometimes tinged red. Leaves largely ovate-falcate, longer than wide, sometimes as long as wide, 450-550 (-600) μm × 300-350 (-500) μm, L:W ratio (1-) 1.5:1. Leaf insertion oblique, 150-280 (-300) μm. Leaf base not decurrent, antical and postical leaf margins slightly incurved, near apex slightly serrulate or prorulose. Leaf apex acute, prolonged. Basal



Figs 50-58. *Stephaniella rostrata* U. Schmitt. **50-53, 55, 57, 58.** Stem leaves. **54.** Marginal postical cells of the leaf. **56**. Paraphyllia of the stem.

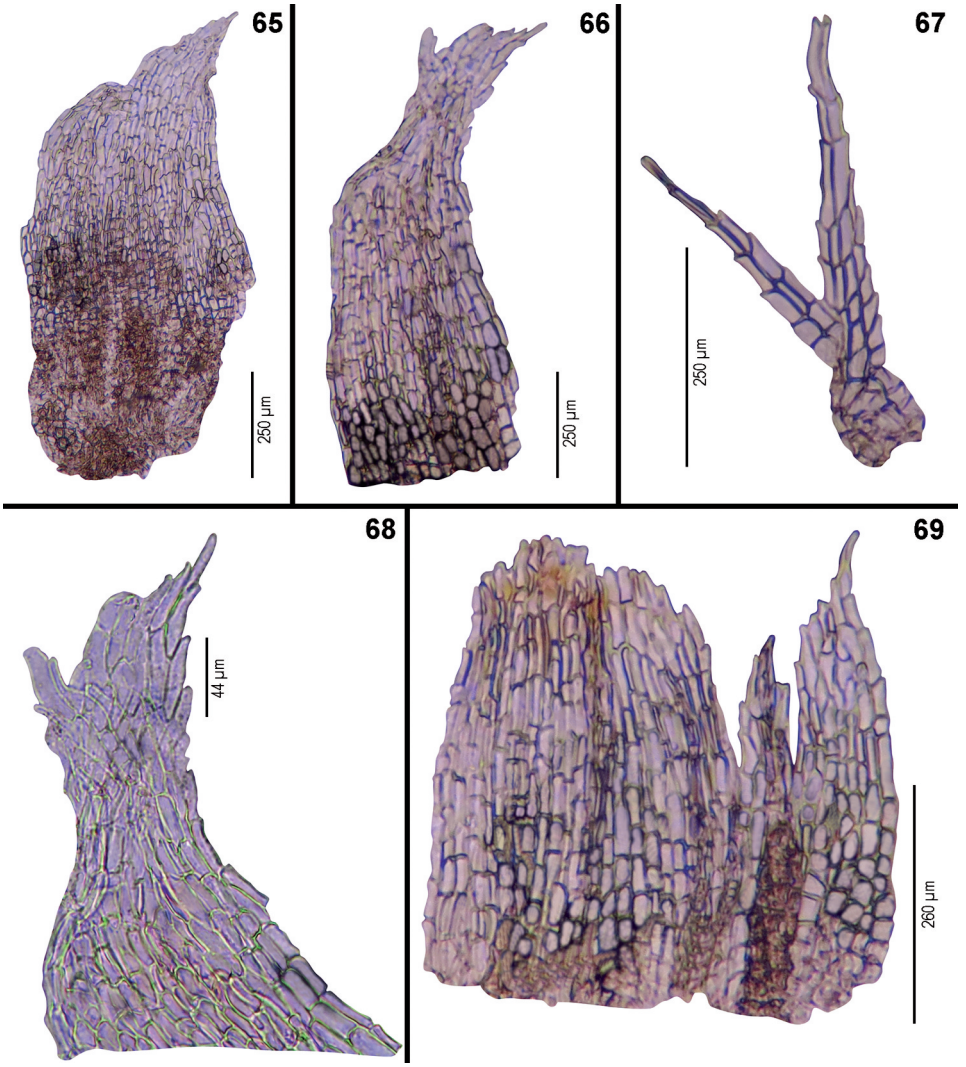
leaf cells rhomboid and/or hexagonal, thin-walled, 20-26 (-32) µm × (8-) 10-14 µm; mid-leaf cells oblong, thin- or slightly thick-walled, (18-) 24-30 (-36) µm × 10-18 µm; postical marginal cells strongly elongate, thick-walled, (26-) 28-40 (-46) µm × 6-10 (-12) µm, L:W ratio 3-5 (-7). Cell walls of the leaf smooth. **Gynoecia** ~1 mm high. **Female bracts** 2 pairs, the inner ovate-falcate, 900-1000 µm × 540 µm, with margin near the base entire, middle section toward the apex slightly serrulate, and apex acute; basal cells shortly oblong, thin-walled, (20-) 22-30 (-32) µm × 10-16 µm; middle cells oblong, thin-walled, 20-30 µm × 8-14 µm; apical cells oblong-elongate, rhomboid, not sinuose, thick-walled, (20-) 30-46 µm × 10-14 µm. **Paraphyllia of the gynoecia** usually filiform, (160-) 200-300 (-370) µm long, (8-) 11-16 (-21) cells high,



Figs 59-64. *Stephaniella rostrata* U. Schmitt. **59-63.** Female bract. **64.** Paraphyllia of the gynoecia.

isodiametric to oblong, (10-) 12-18 (-28) µm long, smooth and thin-walled. **Perianth** with entire margin to slightly serrulate and the apex lobed, segments acute to apiculate, slightly serrulate. Basal cells quadrate to shortly rectangular, thin-walled, 16-20 (-26) µm × (12-) 14-20 µm; middle cells elongate-rectangular, thin- or thick-walled, (20-) 22-32 µm × (-6) 8-12 µm; apical cells elongate-rectangular, not sinuose, thin- or thick-walled, 34-48 (-60) µm × (6-) 8-14 (-16) µm. Cell walls of the perianth smooth. **Androecium** not seen. **Sporophyte** not seen.

Distribution and ecology. *Stephaniella rostrata* is here reported from Mexico for the first time. It occurs in the Colombian paramos while in Mexico it occurs in the highlands in shrub vegetation and grasslands, above 3400 masl. It grows on soil, in exposed and humid sites.



Figs 65-69. *Stephaniella rostrata* U. Schmitt. **65, 66.** Perianth. **67.** Paraphyllia of the gynoecia. **68.** Perianth apical cells. **69.** Perigynium. (Fig. 50, *C. Juárez-Martínez 296,* MEXU; Figs 51, 52, *C. Juárez-Martínez 304*, MEXU; Figs 53, 54, *C. Juárez-Martínez 346,* MEXU; Figs 55, 56, 59-63, 67, *S.R. Gradstein & E. Santana 4252,* B*;* Figs 57, 58, 64, 65, 66, 68, 69, *O. Rangel & A.M. Cleef 1020,* NY).

Specimens examined. MEXICO. Estado de México: Volcán Nevado de Toluca, 4180 m, *C. Juárez-Martínez 296* (MEXU). Parque Nacional Iztaccíhuatl-Popocatépetl, 3900 m, *C. Juárez-Martínez 339 p.p., 341 p.p.* (MEXU). **Tlaxcala:** Mpio. San José Teacalco, Volcán La Malinche, ~4000 m, *C. Juárez-Martínez 346* (MEXU). **COLOMBIA. Depto. Cundinamarca:** páramo de Chingaza, around lagunita along trail to St. Juanito, 3400 m, *S.R. Gradstein & E. Santana 4252* (B, NY). **Depto. Magdalena:** Sierra Nevada de Santa Marta, Transecto del Río Buritaca, parte alta del Filo La Cumbre, 3750 m, *O. Rangel & A.M. Cleef 1020 p.p.* (NY).

In some Mexican specimens the leaves are red-tinged (Figs 50-53) and the postical marginal cells are longer than those from South America, (38-) 48-58 (-60) µm × 8-12 (-16) µm. In addition, the paraphyllia are longer (200-350 µm) and the paraphyllia cells are longer (22-30 (-36) µm) than those from South America. As in *S. paraphyllina* and *S. hamata, S. rostrata* sometimes has rotund leaves (Fig. 51).

Sometimes *Stephaniella rostrata* resembles *S. paraphyllina,* but they differ in the slightly serrulate or prorulose distal leaf margin of *S. rostrata* (Figs 57, 58).

4. *Stephaniella uncifolia* S. Winkl., *Oesterreichische Botanische Zeitschrift* 115: 124, 1968 **Figs 70-83**

Type citation: Argentinien, *Lorentz s.n.* Herbarium Stephani, M! (Lectotype, Schmitt & Winkler, 1968: 127).

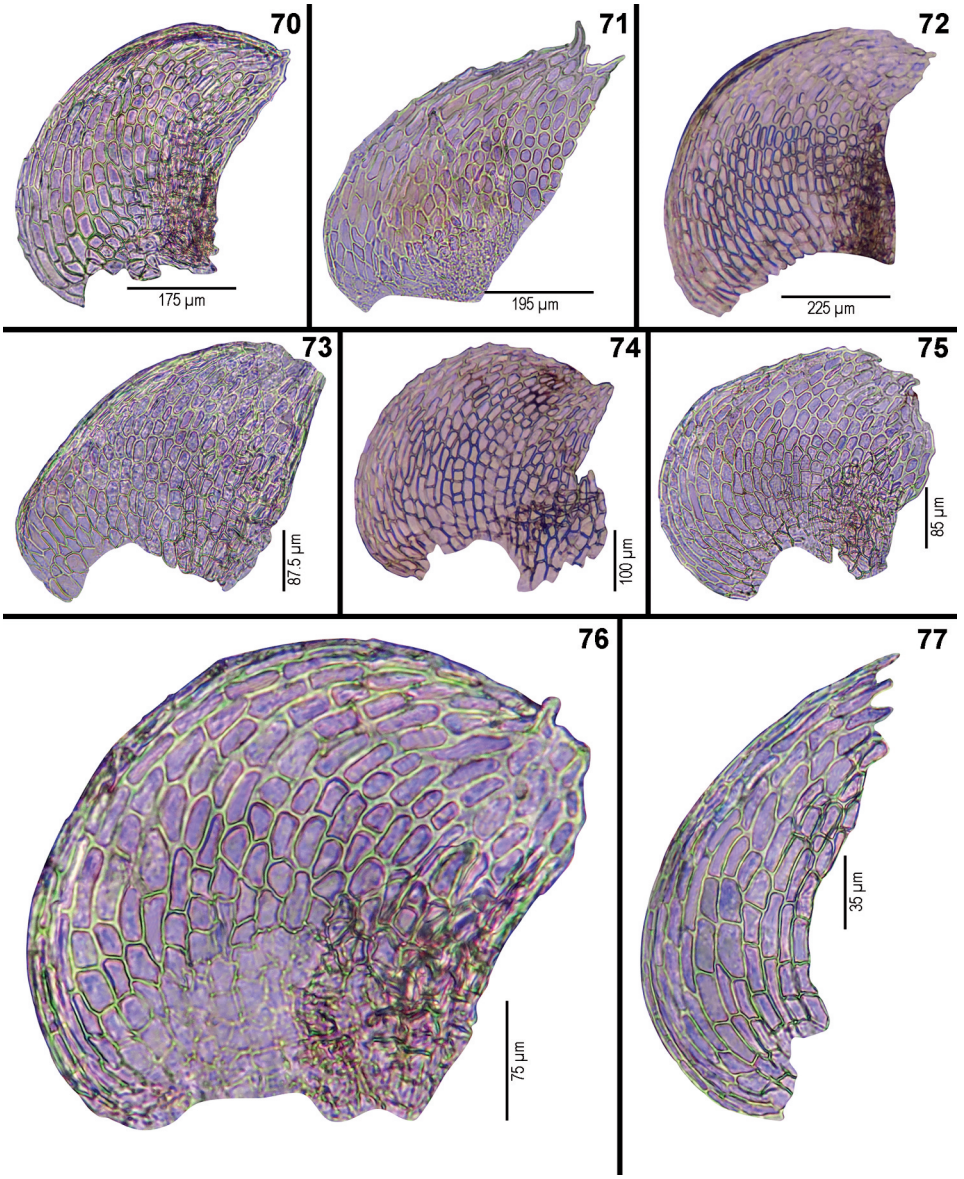
Plants erect. **Stem** up to 8 mm long, light brown, in section 110-120 µm in diameter, differentiated in cortex and medulla. Cortical cells in 2 layers, brown, shortly oblong to isodiametric, thick-walled, (8-) 12-16 µm × 6-10 µm. Medullary cells smaller than the cortical cells, thin-walled. **Stolon** cross section 160-210 µm in diameter. **Branching** lateral-intercalary. **Stem paraphyllia** usually foliose, erect or falcate, 140-240 µm long, more than 18 cells high, paraphyllia cells oblong to quadrate, (14-) 16-26 (-30) µm long, smooth and thick- or thin-walled. **Leaves** loosely imbricate, concave to almost plane, hyaline without red tinge. Leaves ovate-falcate, slightly wider than long, some leaves as wide as long, 400-500 µm × 390-550 µm, L:W ratio 1:1-1.2. Leaf insertion oblique, 200-250 µm. Leaf base decurrent, postical margin slightly involute or plane, antical margin inflexed, slightly serrulate near apex. Leaf apex acute, sometimes apiculate. Basal leaf cells rhomboid, hexagonal, thin-walled, 20-30 (-38) µm × (8-) 10-16 µm; mid-leaf cells oblong-rectangular or rhomboid, thick-walled, (16-) 18-28 µm × (6-) 8-14 µm; postical marginal cells strongly elongate, thick-walled, (22-) 26-46 (-58) µm × (4-) 6-10 (-12) µm; L:W ratio 3-7 (-8):1. Cell walls near leaf apex papillose, the remaining smooth. **Gynoecia** ~750 µm high. **Female bracts** 2 pairs, the inner ovate-falcate, 720 µm × 530 µm, with margin entire, serrulate or prorulose, middle section toward apex cell walls papillose, and apex acute. Basal cells oblong-rectangular, thin-walled, 30-42 µm × 10-18 µm; middle cells elongate-rectangular, elongate-rhomboid, slightly thick-walled, 30-40 µm × 10-14 µm; apical cells oblong-elongate, thick-walled, (26-) 28-42 (-44) µm × 6-12 µm. **Paraphyllia of the gynoecia** usually lanceolate, falcate or erect, 200-280 (-380) µm high, several cells long, oblong-rectangular, (20-) 22-36 (-38) µm long, cell walls smooth. **Perianth** margin slightly serrulate, apex lobed, segments acute, serrulate or prorulose. Basal cells oblong to rectangular, thin-walled, 22-30 (-32) µm × 8-12 (-14) µm. Middle cells oblong-rectangular, thin-walled, (24-) 26-40 (-44) µm × 8-12 µm. Apical cells elongate, sinuose, thick-walled, 26-46 (-54) µm × (6-) 8-10 (-12) µm. Cell walls of the perianth smooth. **Androecium** not seen. **Sporophyte** not seen.

Distribution and ecology. Specimen labels bear no habitat or ecological data.

Specimens examined. ARGENTINA. *Lorentz s.n.* (G-00265372, M-0182816).

The leaf shape in *Stephaniella uncifolia* and *S. rostrata* is very similar, but in *S. uncifolia* there are foliose paraphyllia (Fig. 79) and the perianth apical cells are oblong-sinuose (Figs 80-81).

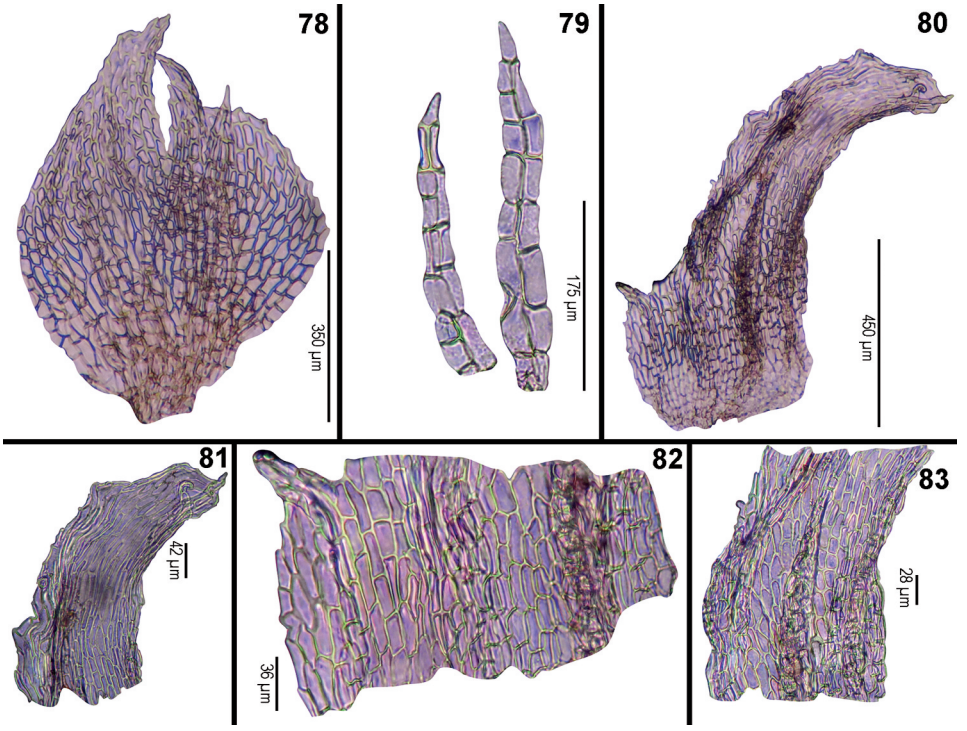
According to Schuster (2002) *Stephaniella uncifolia* has slightly plicate leaves, but no longitudinal folds were observed in the type specimens (Figs 70-76) of this taxon.



Figs 70-77. *Stephaniella uncifolia* S. Winkler. **70-76.** Stem leaves. **77.** Marginal postical cells of the leaf.

***Stephaniellidium* S. Winkl. *ex* Grolle,** *Acta Botanica Fennica* 121: 38. 1983

Green or green-pale plants, forming patches or large mats. **Stem** well-differentiated in a 2-5 layered cortex; cortical cells smaller than medullary cells, but with slightly thicker walls. **Stolons** lacking. **Stem paraphyllia** foliose. **Leaves** green, chlorophyllose, erect with apex pointing toward the stem tip, symmetric or little symmetric, strongly imbricate. Cell walls smooth. Postical and antical margins



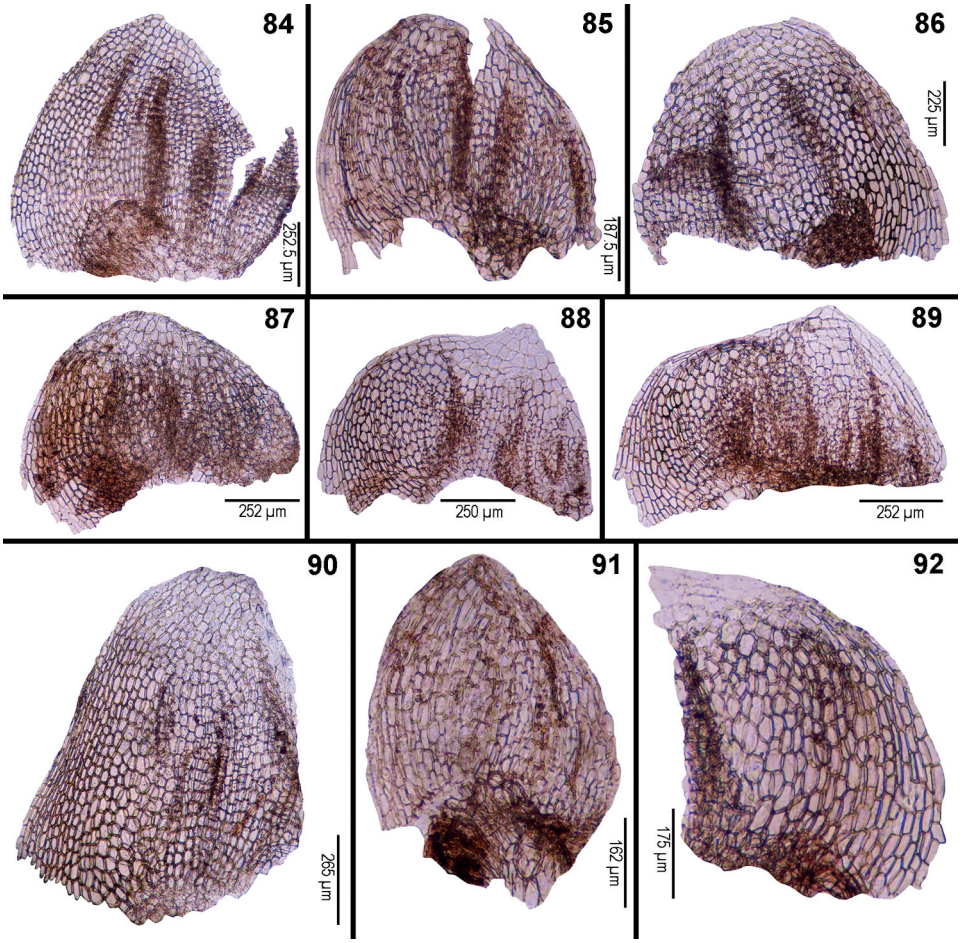
Figs 78-83. *Stephaniella uncifolia* S. Winkler. **78.** Female bract. **79.** Paraphyllia of the gynoecia. **80, 81.** Perianth. **82.** Perianth basal cells. **83.** Perianth median cells. (Figs 73-77, *Lorentz s.n.* M-0182816).

of the leaf slightly incurved to plane, entire. Leaf apex not falcate, plane, and obtuse or rounded in old leaves. **Oil bodies** in the basal and apical cells of the leaf and paraphyllia. Leaves longitudinally plicate. **Gynoecia** on the stem surface, near of the tip of the stem. **Female bracts** 1-2 pairs, the inner undivided, with longitudinal folds. **Paraphyllia of the gynoecia** foliose. **Perianth** lacking. **Androecia** with several antheridia per bract, the latter concave, morphologically similar to stem leaves. **Perigynium** not seen. **Marsupium** present. **Sporophyte** capsule cylindrical.

5. *Stephaniellidium sleumeri* (Müll. Frib.) S. Winkl. *ex* Grolle, *Acta Botanica Fennica* 121: 38. 1983. *Stephaniella sleumeri* Müll. Frib., *Revue Bryologique et Lichénologique* 20: 177, 1951 **Figs 84-96**

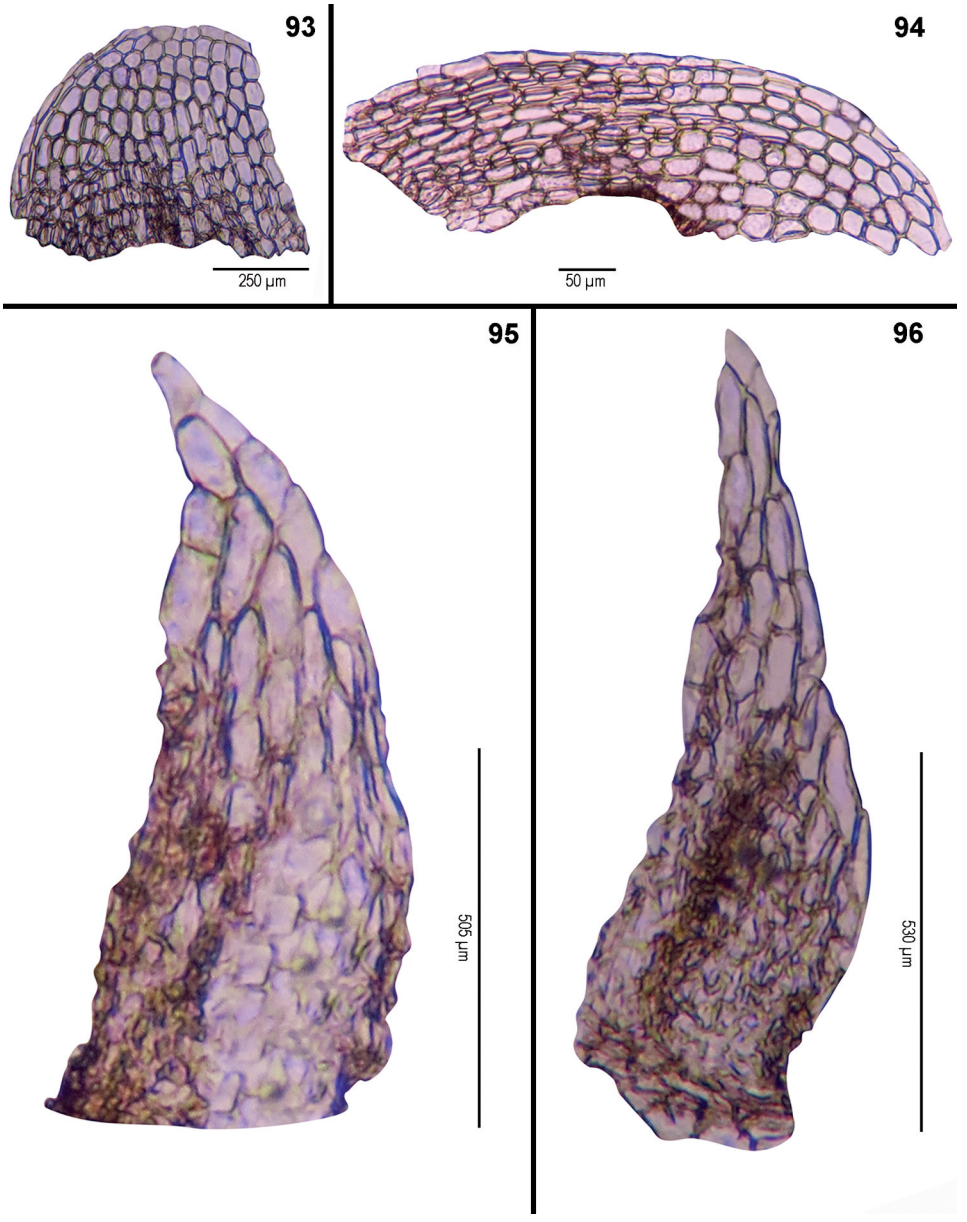
Type citation: Prov. Tucumán: Depto. Tafí, La Ciénega, Morro de las Aguadas, 1950, *Sleumer s.n.* (Lectotype designated by Juárez-Martínez, 2014 S! (B47665), isolectotype B! S!).

Plants prostrate. **Stem** up to 4 mm long, green or green-pale, in section ~180 µm diameter, differentiated in cortex and medulla. Cortical cells in 2-5 layers, oblong to isodiametric, yellow-pale, weakly thick-walled, smaller than medullary cells (12-) 16-20 µm × 8-14 (-18) µm. Medullary cells oblong to isodiametric, thin-walled, hyaline, (20-) 30-40 (-50) µm × 6-28 µm. **Branching** scarce, lateral-terminal, ventral branches lacking. **Stem paraphyllia** scarce, always foliose, 400-650 µm long, several long cells, paraphyllia cells oblong to hexagonal, isodiametric, (28-)



Figs 84-92. *Stephaniellidium sleumeri* (Müll. Frib.) S. Winkler ex Grolle. **84-91.** Stem leaves. **92.** Marginal postical cells of the leaf.

40-56 (-68) µm long, smooth and thin-walled. **Leaves** strongly imbricate, concave, young leaves green throughout, chlorophyllose; in mature leaves the apical cells are hyaline, red tinge lacking. Leaves widely ovate to reniform, longitudinally plicate, wider than long or as wide as long, rarely longer than wide, (550-) 600-1300 µm × (600-) 650-1500 µm, L:W ratio 1:1-1.4. Leaf insertion oblique, 600-800 µm; leaf base not decurrent. Leaf apex as in the genus. Basal cells oblong-hexagonal, circular, thin-walled, (26-) 34-62 (-78) µm × 16-36 (-46) µm; mid-leaf cells oblong-rectangular, isodiametric, thin-walled, (24-) 28-44 (-52) µm × (16-) 20-30 (-38) µm; postical marginal cells strongly elongate to linear, thin-walled, (40-) 44-90 µm × 10-20 (-24) µm, L:W ratio 3-5 (-6):1. **Oil bodies** 4-8 per cell, brown, ellipsoidal, granular. **Gynoecia** with female bracts smaller than stem leaves, the inner ovate, with margin entire, smooth, and apex undivided, acuminate or apiculate, not falcate. Other characters as in stem leaves. **Paraphyllia of the gynoecia** foliose, other characters as in paraphyllia of the stem**. Perianth** lacking. **Marsupium** near tip of the stem, *Calypogeia*-type, ~1 mm long, 400 µm width, with a few rhizoids. Marsupial channel



Figs 93-96. *Stephaniellidium sleumeri* (Müll. Frib.) S. Winkler ex Grolle. **93-94.** Marginal postical cells of the leaf. **95-96.** Paraphyllia of the stem. (Figs 85, 91, 95, 96, *Sleumer s.n.* B-47665, S).

with large circular cells, sometimes oblong, thin-walled, 52-80 µm in diameter. Archegonia 3-4 at the bottom of the marsupium.

Distribution and ecology. *Stephaniellidium sleumeri* is distributed in Mexico, Venezuela, Colombia, Bolivia, Peru, and northern Argentina at elevations from 3000

to 4000 masl. It occurs in puna vegetation and Andean paramos. In Mexico, *S. sleumeri* grows in alpine grassland and in subalpine habitats with *Festuca-Calamagrostis, Pinus hartwegii,* and *P. montezumae,* in *Abies* forests, and in oak forests. The species grows in patches or mats on soil or soil on rocks, humid, exposed or sheltered sites often mixed with *Stephaniella paraphyllina* and *Gongylanthus*.

Specimens examined. MEXICO. Distrito Federal: Cima, 3048 m, *C.G. Pringle 10681* (MEXU). **Estado de México:** La Joya, ladera SW del volcán Iztaccíhuatl, 3950 m, *A.T. Whittemore 4102* (MO), *A.M. Cleef & C. Delgadillo M. 10265* (MEXU). Volcán Iztaccíhuatl, La Joya, 3983 m, *C. Delgadillo M. 7673* (MEXU). La Joya, extremo SW del volcán Iztaccíhuatl, 8 km al N de Paso de Cortés, 3963 m, *C. Juárez-Martínez 110 p.p., 112, 114* (MEXU), *A. Cárdenas S. 6754 p.p., 6755* (MEXU). Parque Nacional Iztaccíhuatl-Popocatépetl, 3900 m, *C. Juárez-Martínez 319, 322, 323, 324, 326, 327, 332, 329, 331, 333, 334, 337, 338, 339 p.p., 340, 341 p.p.* (MEXU). Extremo NW del volcán Iztaccíhuatl, Llano Grande, 3320 m, *C. Juárez-Martínez 121* (MEXU); 3470 m, *A. Cárdenas S. 6760* (MEXU); 3500 m, *C. Delgadillo M. 7252* (MEXU), *A. Cárdenas S. 6759* (MEXU), *C. Juárez-Martínez 120 p.p.* (MEXU). Volcán Nevado de Toluca, ladera NW, 4180-4222 m, *C. Juárez-Martínez et al., 295, 298, 299, 300, 301, 306, 307, 308, 309, 311, 312, 313, 314, 315, 316, 317* (MEXU). Ladera S del cráter del Nevado de Toluca, 4221 m, *C. Juárez-Martínez et al., 318* (MEXU). **Morelos:** Alte Straβe Cuernavaca-México, nahe vor Tres Cumbres, 3000 m, *R. Düll 232* (B). Autobahn von (ca. 50 km hinter) Mexico nach Cuernavaca, 2100 m, *R. Düll 235a* (B). Tepozotlán, Cima de la Sierra de Alcaparrosa, 2660 m, *C. Juárez-Martínez 214* (MEXU). **Tlaxcala:** Mpio. San José Teacalco. Volcán La Malinche, ca. 4000 m, *C. Juárez-Martínez & J.A. Cruz-López 343, 344, 345, 347, 348, 351, 352 p.p.* (MEXU). **ARGENTINA. Prov. Tucumán:** Depto. Tafi. La Ciénega, Morro de las Aguadas. 2800 m, *Sleumer s.n.* (S-B47665! S-B47664!) (B-30 0012078!). **BOLIVIA. Depto. La Paz:** Murillo, mina San Francisco, NE de Palca, 4380 m, *S. Churchill, M. Cano & J. Jiménez 24736 p.p.* (MO). **COLOMBIA.** S-flanke der Sierra Nevada de Santa Marta, oberhalb von San Sebastian, 2700 m, *S. Winkler C206 p.p.* (S). **PERU. Depto. Cajamarca:** Prov. Cajamarca. Ort. Las Lagunas, 3900 m, *P. & E. Hegewald 6207 p.p.* (MO). **Depto. Cuzco:** Prov. Anta. Ort. Indahuacho, 3600 m, *P. & E. Hegewald 5672* (MO). **Depto. Junin:** Prov. Jauja. Ort. La Oroya, Laguna bei den Minen «Gran Bretagne», 4420 m, *P. & E. Hegewald 5447* (MO). **Depto. La Libertad:** Prov. Huamachuco. Ort. Sausacocha bei Huamachuco, ca. 3000 m, *P. & E. Hegewald 6038* (MO). **Depto. Ancash:** Prov. Recuay. Ort. Cordillera Blanca zwischen Recuay und Chiquian, 4100 m, *P. & E. Hegewald 7761* (MO). **VENEZUELA.** Straβe von Valera nach Mérida, 3700 m, *Schäfer-Verwimp & Verwimp 12077 p.p.* (MO).

Originally, *Stephaniellidium sleumeri* was included in the genus *Stephaniella,* but its transfer was supported by the presence of plicate leaves (Figs 84-92), lanceolate paraphyllia (Figs 95, 96), and the presence of a marsupium (Juárez-Martínez *et al*., 2016).

In some Mexican specimens of *Stephaniellidium sleumeri* (*C. Juárez-Martínez et al., 313, 314, C. Juárez-Martínez 323, 324, 327, 332,* MEXU), the postical marginal cells are not as long as given in this description, and they resemble *Gongylanthus liebmannianus*. However, the longitudinal plicate leaves and the presence of paraphyllia were constant characters in these specimens.

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