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TAXONOMÍA Y FILOGENIA DE LA FAMILIA STEPHANIELLACEAE (MARCHANTIOPHYTA)

TESIS

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DOCTORA EN CIENCIAS

PRESENTA:

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COORDINACIÓN

Dr. Isidro Ávila Martínez
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Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Biología Evolutiva y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día 18 de abril de 2016, se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la alumna **JUÁREZ MARTÍNEZ CATALINA** con número de cuenta **99180537** con la tesis titulada: **"Taxonomía y filogenia de la familia Stephaniellaceae (Marchantiophyta)",** realizada bajo la dirección del **DR. CLAUDIO DELGADILLO MOYA:**

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Sin otro particular, me es grato enviarle un cordial saludo.

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RESUMEN

El número de especies de hepáticas a nivel mundial oscila entre 5,000 y 8,000. Para México se reconocen 573 especies, subespecies y variedades; de éstas, 78 especies y variedades de hepáticas foliosas se encuentran en el Valle de México (~13% de la flora nacional de hepáticas). De manera adicional y como parte del estudio de la flora de hepáticas foliosas del Valle de México se observó que las Anastrophyllaceae, Southbyaceae, Gymnomitriaceae y Stephaniellaceae son familias características de las altas elevaciones (>3,000 m snm) de la región. En particular los miembros de Stephaniellaceae (*Stephaniella* y *Stephaniellidium*) son casi exclusivos de altas elevaciones donde toleran luz y radiación UV excesivas, escasez de agua y grandes fluctuaciones de temperatura durante el día. Inicialmente, *Stephaniella* y *Stephaniellidium* fueron colocados en las Gymnomitriaceae y posteriormente se elevaron a nivel de familia. Recientemente, con evidencia molecular, *Stephaniella* y *Stephaniellidium* se incluyeron en las Arnelliaceae. A través de la revisión de ejemplares de herbario, del análisis filogenético y de la revisión taxonómica de Stephaniellaceae, se tipifican algunas especies de la familia, y se evalúan sus relaciones con las Arnelliaceae, Southbyaceae, Gymnomitriaceae, y entre los géneros y especies de Stephaniellaceae. Este estudio muestra que Stephaniellaceae es un grupo monofilético apoyado por dos sinapomorfías: presencia de parafilios y presencia de pliegues longitudinales en las brácteas femeninas y que incluye cinco especies en dos géneros. El género *Stephaniella* se corrobora como monofilético y *Stephaniellidium* como su grupo hermano. La relación entre *Stephaniella uncifolia* S. Winkler y *S. hamata* Steph. está fuertemente apoyada por los valores de Jackknife. De acuerdo con las observaciones morfológicas y al análisis filogenético *Stephaniella boliviensis* Steph. es sinónimo de *S. paraphyllina* J.B. Jack. La revisión taxonómica de la familia, incluye una clave taxonómica, así como la descripción e ilustración de las especies. La posición taxonómica de *Stephaniella* y *Stephaniellidium* y los cambios en su clasificación se deben a la complicada morfología del grupo, a la ausencia virtual de estructuras sexuales y a las pocas colecciones disponibles. Sin embargo, este análisis apoya la elevación de *Stephaniella* y *Stephaniellidium* a la categoría de familia como Stephaniellaceae y se confirma la presencia de parafilios y la presencia de pliegues longitudinales en las brácteas femeninas como caracteres diagnósticos de la familia.

ABSTRACT

The number of the species of liverworts ranges between 5,000 and 8,000 worldwide. In Mexico 573 species, subspecies and varieties are recognized. Seventy eight of them are leafy liverworts distributed in the Valley of Mexico (~13% of the Mexican leafy liverwort flora). In addition, as part of the research of the flora of leafy liverworts of the Valley of Mexico it was observed that the Anastrophyllaceae, Southbyaceae, Gymnomitriaceae, and Stephaniellaceae are families inhabiting the high elevations (~3,000 m asl) in the region. The Stephaniellaceae (*Stephaniella* and *Stephaniellidium*) are almost exclusively found in high elevations where they tolerate excessive light and UV radiation, water stress and temperature fluctuations during the day. Initially, *Stephaniella* and *Stephaniellidium* were included in the Gymnomitriaceae, but later were elevated to family category. Recently, with molecular evidence, both genera were thought to be related to the Southbyaceae. Through the examination of herbarium specimens, the phylogenetic analysis, taxonomic revision, typification some species and the relationships of the Stephaniellaceae with the Arnelliaceae, Southbyaceae, Gymnomitriaceae, and between genera and species of the Stephaniellaceae were evaluated. This analysis shows that the family includes five species in two genera, and was resolved as a monophyletic group supported by two synapomorphies: presence of paraphyllia and of longitudinal folds in female bracts. *Stephaniella* was resolved as monophyletic and *Stephaniellidium,* as its sister group. The relationship between *Stephaniella uncifolia* S. Winkler and *S. hamata* Steph. is strongly supported by Jackknife values. According to the phylogenetic analysis and morphological observations, *Stephaniella boliviensis* Steph. is as synonym of *S. paraphyllina* J.B. Jack. The revision includes a taxonomic key along with descriptions and illustration of the species of Stephaniellaceae. The proposed taxonomic position of *Stephaniella* and *Stephaniellidium* and the changes in their classification reflect their complex morphology, the virtual absence of sexual structures and few collections available for study. However, this analysis supports the elevation of *Stephaniella* and *Stephaniellidium* to the family category as Stephaniellaceae. The presence of paraphyllia and the presence of longitudinal folds in the female bracts were corroborated as the diagnostic characters for the family.

INTRODUCCIÓN GENERAL

No hay acuerdo sobre el número de especies de hepáticas (División Marchantiophyta) que hay a nivel global, pero en opinión de varios autores, éste oscila entre 5,000 y 8,000 especies (Crandall-Stotler et al., 2009; Gradstein et al., 2001; Shaw & Renzaglia, 2004; Söderström et al., 2016). Esta diversidad puede ser agrupada por su forma de crecimiento: hepáticas foliosas (Jungermanniidae), hepáticas talosas simples (Metzgeriidae) y hepáticas talosas complejas (Marchantiidae) (Shaw y Renzaglia, 2004). Las hepáticas foliosas representan aproximadamente el 85% de la diversidad total de Marchantiophyta.

Para México, los únicos trabajos florísticos sobre hepáticas son los de Bourell (1986, 1992), Equihua y Pócs (1999), Fulford y Sharp (1990), Gottsche (1863), Parker (1954), Stephani (1909) y Svihla (1940, 1941). Con base en los trabajos anteriores y en registros en la bibliografía briológica, Delgadillo y Juárez-Martínez (2014) contabilizaron y reconocieron 592 especies y variedades de hepáticas (Anexo 1). Desde entonces, su número se ha ajustado a 573 especies, subespecies y variedades, de acuerdo a revisiones y monografías recientes, de las cuales 490 son foliosas y 83 talosas. El número de especies de hepáticas mexicanas es preliminar debido a que actualmente existen diferentes criterios taxonómicos sobre muchos grupos, además de la exploración deficiente del territorio nacional, y de ejemplares de herbario y publicaciones frecuentemente sin datos precisos de colecta.

El Valle de México es una de las zonas florísticamente mejor conocidas del país, como se refleja en diversas publicaciones (e.g., Calderón de Rzedowski & Rzedowski, 2010; Cárdenas & Delgadillo, 2009; Rzedowski & Calderón de Rzedowski, 1989, 1993; Velázquez & Romero, 1999). Sin embargo, para las hepáticas del Valle de México la información proviene únicamente de Parker (1954), quien reportó tres especies y seis géneros de hepáticas foliosas, y de Delgadillo y Cárdenas (2009) que reportan 15 especies de hepáticas talosas y tres foliosas.

El estudio más reciente sobre hepáticas mexicanas se enfoca en las foliosas (Anexo 2), en el cual se reconocen 75 especies y tres variedades incluidas en 25 familias. Las familias Anastrophyllaceae, Southbyaceae, Gymnomitriaceae y Stephaniellaceae son hepáticas foliosas características de altas elevaciones (>3,000 m snm) del Valle de México. De las familias anteriores, los miembros de Stephaniellaceae son de particular interés porque son casi exclusivos de las altas elevaciones y tienen formas de vida únicas que les permiten tolerar luz y radiación UV excesivas, falta de agua y grandes fluctuaciones de temperatura durante el día.

Estudios previos sobre taxonomía y morfología de *Stephaniella* y *Stephaniellidium* (e.g. Schmitt & Winkler, 1968; Schuster, 2002; Winkler, 1969), muestran que su posición familiar, relaciones genéricas y entre especies no son claras. El estudio de ambos géneros puede resolver el significado evolutivo de sus caracteres morfológicos y servir como marco de referencia para estudiar la fotosíntesis bajo estrés o posibles adaptaciones a condiciones ambientales extremas.

Finalmente, se debe mencionar que algunos conceptos morfológicos ampliamente utilizados en la literatura briológica, también incluidos en este estudio, son los mismos que se usan en las plantas vasculares (e.g. perianto, androceo, gineceo, brácteas, hojas, tallo, etc.). Sin embargo, las estructuras no son homólogas, porque en el caso de las hepáticas dichas estructuras pertenecen a la fase gametofítica del ciclo de vida. Los glosarios de Magill (1990) y Malcolm y Malcolm (2000) pueden aclarar dudas sobre los conceptos utilizados en este trabajo.

Por lo anterior, el objetivo de este trabajo es ofrecer un panorama general sobre la diversidad de Marchantiophyta en México y proporcionar herramientas (claves y descripciones) para el estudio de las hepáticas foliosas del Valle de México. También, esclarecer las relaciones filogenéticas entre los miembros de Stephaniellaceae, así como realizar la revisión taxonómica de la familia, como ejemplos de las actividades importantes para el conocimiento de nuestra flora.

OBJETIVOS GENERALES

-Conocer y catalogar las especies de hepáticas de México.

-Recopilar bibliografía y generar herramientas para el estudio de las hepáticas mexicanas.

-Aplicar las herramientas generadas a un área particular del Valle de México.

-Seleccionar y estudiar un grupo de hepáticas foliosas de la flora mexicana, como forma de aplicar herramientas filogenéticas y taxonómicas.

CAPÍTULO 1. “CLADISTIC ANALYSIS OF THE STEPHANIELLACEAE (MARCHANTIOPHYTA) BASED ON MORPHOLOGICAL DATA”

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Research Article

Cladistic analysis of the Stephaniellaceae (Marchantiophyta) based on morphological data

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This work evaluates the phylogenetic relationships between Stephaniellaceae, Arnelliaceae, Southbyaceae, and Gymnomitriaceae, and between genera and species of the Stephaniellaceae. We analysed morphological data obtained from herbarium specimens and from the literature under the parsimony criterion using equal weightings and implied weightings. The inclusion of *Stephaniella* and *Stephaniellidium* within Arnelliaceae, Southbyaceae or Gymnomitriaceae is not supported in this analysis. The clade Stephaniellaceae had a moderately high Jackknife support and the family was characterized by the following synapomorphies: presence of paraphyllia and presence of longitudinal folds in female bracts. Within the Stephaniellaceae, *Stephaniella* is corroborated as monophyletic and *Stephaniellidium* is resolved as its sister group. The relationship between *Stephaniella uncifolia* Winkler and *Stephaniella hamata* Stephani was strongly supported in both analyses while the relationship between *Stephaniella paraphyllina* Jack and *Stephaniella boliviensis* Stephani was weakly supported. With these results, *S. boliviensis* is proposed as a synonym of *S. paraphyllina.* We propose changes in the taxonomic position of *Stephaniella* and *Stephaniellidium* and in their classification in consideration of the complex morphology of the species and the lack of sexual structures and collections.

Key words: Arnelliaceae, equal weighting, implied weighting, Gymnomitriaceae, Southbyaceae, *Stephaniella*, *Stephaniellidium*

Introduction

Stephaniella Jack (Jack, 1894) and *Stephaniellidium* S. Winkler ex Grolle (*in* Grolle, 1983) (suborder Jungermanniineae, Jungermanniopsida) are genera of leafy liverworts distributed in high elevations (2,100–4,700 m asl) (Fig. 1–6), from South America to Mexico (Gradstein, Churchill, & Salazar-Allen, 2001) and South Africa (Arnell, 1963). *Stephaniella* and *Stephaniellidium* grow on soil or soil-covered rocks, on rather dry or moist, exposed sites, in the *Espeletia* zone in the paramos (Schuster, 2002). In Mexico, the species grows sheltered by grasses and mixed with species of *Gongylanthus*.

These genera were placed in the Gymnomitriaceae in the newly established subfamily Stephanielloideae (Schuster, 1984). However, morphological and molecular evidence suggests that they do not belong in this family (Crandall-Stotler, Stotler, & Long, 2009; De Roo, Hedderson, & Söderström, 2007; Schuster, 2002). According to Schuster (2002), most genera in the Gymnomitriaceae have adaptive traits typical of taxa inhabiting alpine and exposed sites (e.g., echlorophyllose leaves, leaf insertion lines dorsally transgressing the stem midline, long-stalked antheridia, gynoecia and bud-like female bracts). It is thought that the whitish echlorophyllose leaves reflect light thus preventing damage by radiation (higher in the upland habitats) to the innermost photosynthetic structures. However, this hypothesis has not been tested in the light of physiological studies.

A variable number of oil bodies in the leaf cells, the presence of paraphyllia, and the cylindrical sporophyte capsule, are characteristics that exclude *Stephaniella* and *Stephaniellidium* from the Gymnomitriaceae. Consequently, Schuster (2002) elevated the Stephanielloideae to family category as Stephaniellaceae (Table 1).

Recently, *Stephaniella* and *Stephaniellidium* were placed in the Arnelliaceae by De Roo et al. (2007) and Crandall-Stotler et al. (2009); their inclusion was supported by the analysis of the *trn*G intron, the presence of a *Calypogeia*-type marsupium, and a cylindrical sporophyte

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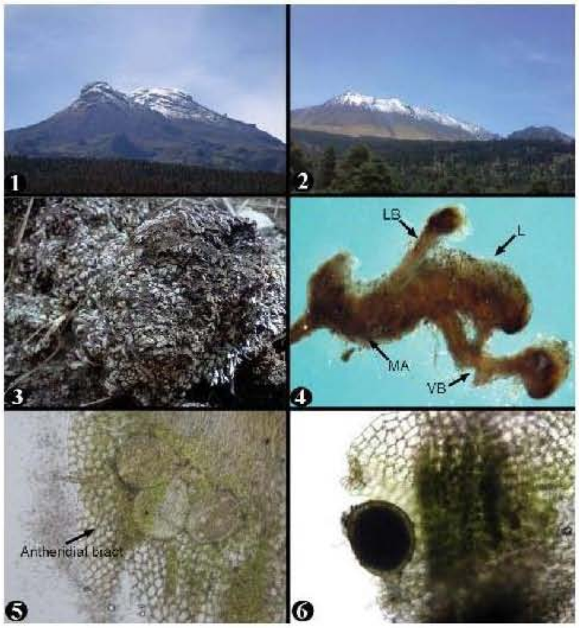


Figs. 1–6. Habitat of *Stephaniella* and *Stephaniellidium*: (1) Alpine area of the Iztaccíhuatl volcano, (2) Nevado de Toluca volcano. (3) Habit of *Stephaniella paraphyllina.* (4) Lateral view of the gametophyte of *Stephaniella boliviensis* showing the branching –type. VB, ventral branch; LB, lateral branch. (5) Antheridia group in *Stephaniellidium sleumeri*. The arrow indicates the position of the antheridial bract. (6) Antheridium of *S. sleumeri.* The pedicel is evident.

capsule with a bistratose wall. Later, Váňa, Grolle, and Long (2012), suggested that the Arnelliaceae was a monotypic family with the single species *Arnellia fennica* (Gottsche) Lindb. and the genera *Gongylanthus* and *Southbya* form the separate family Southbyaceae. Also, they indicated that *Stephaniella* and *Stephaniellidium* differ from Arnelliaceae and Southbyaceae by the presence of ventral-intercalary leafless stolons, alternate and mostly echlorophyllose leaves, leaf insertion lines dorsally transgressing the stem midline, presence of paraphyllia (chlorophyllose filaments) and long-stalked antheridia, and leaf-like bracts fused only at the base. However, Shaw et al. (2015) demonstrated that the voucher specimen of *Stephaniella paraphyllina* used by De Roo et al. (2007) was misidentified, and it was *Gongylanthus liebmannianus.* Because of this, the phylogenetic affinities of *Stephaniella* and *Stephaniellidium* remained unresolved.

Within Stephaniellaceae, Schmitt and Winkler (1968) recognized six species of *Stephaniella*, namely, *Stephaniella boliviensis* Steph., *Stephaniella hamata* Steph., *Stephaniella paraphyllina* J.B. Jack, *Stephaniella rostrata* U. Schmitt, *Stephaniella sleumeri* Müll. Frib., and *Stephaniella uncifolia* S. Winkl. Later, Winkler (1969) transferred *S. sleumeri* to the monotypic genus *Stephaniellidium* which was validated afterwards (in Grolle, 1983) as *Stephaniellidium sleumeri* (Müll. Frib.) S. Winkl. ex Grolle. Winkler based his decisions on the presence of plicate leaves, lanceolate paraphyllia, and the presence of a marsupium. In this regard, Schuster (2002) stressed the difficulty of separating

Table 1. Classification of *Stephaniella* and *Stephaniellidium* and the other genera included in our analysis according to different authors. The first column indicates the number of species currently recognized within each genus and the species included in the analysis. Váňa et al. (2013) transferred *Herzogobryum teres* to *Syzygiella* from the Adelanthaceae.

# sp. per genus/ # sp. included in the analysis	Genus	Classification according to Crandall-Stotler et al., 2009	Classification according to Váňa et al., 2012	Classification according to Vaňa et al., 2010	Classification according to Schuster, 2002
1/1	*Arnellia*	Arnelliaecae	Arnelliaceae		Arnelliaceae
12/9	*Gongylanthus*		Southbyaceae		
5/5	*Southbya*				
5/5	*Stephaniella*		¿?		Stephaniellaceae
1/1	*Stephaniellidium*				
3/0	*Acrolophozia*	Gymnomitriaceae	Gymnomitriaceae	Gymnomitriaceae	Gymnomitriaceae
5/1	*Apomarsupella*				
27/1	*Gymnomitrion*				
5/1	**Herzogobryum teres*				
27/1	*Marsupella*				
1/0	*Nanomarsupella*				
1/0	*Nothogymnomitrion*				
1/0	*Paramitrion*				
1/0	*Poeltia*				
2/0	*Prasanthus*				
1/0	*Lophonardia*			Lophoziaceae	

Stephaniella from *Stephaniellidium* based mainly on vegetative characters. Furthermore, he cited morphological similarities of the apex and margin of leaves of *S. sleumeri* and *S. rostrata*, and between the plicate leaves of *S. sleumeri* and *S. uncifolia.* According to him, it is necessary to clarify the relationship between the species of *Stephaniella* and *Stephaniellidium.* Currently, Schuster (2002), Schmitt and Winkler (1968), and Winkler (*in* Grolle 1983) recognize five species of *Stephaniella* and one of *Stephaniellidium.*

In the recent studies by Laenen et al. (2014) and Shaw et al. (2015), *Stephaniella* or *Stephaniellidium* were not included in their analyses. Shaw et al. (2015) provided the first phylogenetic reconstruction with molecular data of Jungermanniineae. Although the sampling was extensive and they included 163 species of 57 genera, the authors did not include *Stephaniella* and *Stephaniellidium.*

Members of *Stephaniella* and *Stephaniellidium* have life forms unique among liverworts that allow them to tolerate excessive light and UV radiation, lack of water and large temperature fluctuations during the day and thus colonize highlands. The phylogenetic study of both genera may resolve the evolutionary significance of these morphological characters. Thus, species of these genera could be model organisms to study photosynthesis under stress or possible adaptations to high mountain environments.

In this paper we attempt to assess the phylogenetic relationships between the species and genera of Stephaniellaceae and establish their relationships with the Arnelliaceae, Southbyaceae (*sensu* Váňa et al., 2012) and the Gymnomitriaceae using morphological data.

Materials and methods

Taxon sampling

For the ingroup, all species of the Stephaniellaceae were included, i.e., we examined five species of *Stephaniella* and the single species of *Stephaniellidium*. *Stephaniella mexicana* S.W. Arnell was excluded from the analysis because the holotype is a mixture of *S. sleumeri* and *Gongylanthus liebmannianus* (Lindenb. & Gottsche) Steph. Species of the monotypic family Arnelliaceae, nine of 12 species of *Gongylanthus* and four species of *Southbya* (Southbyaceae) were examined. In this study, we recognize 12 species of *Gongylanthus* while Váňa et al. (2012) recognized 10 species and placed *Gongylanthus renifolius* and *G. scariosus* within *G. ericetorum*, but did not do it within a phylogenetic framework. We consider that *G. ericetorum* differs from *G. renifolius* and *G. scariosus* in the epidermal cells of the stem and papillose leaves, the plane leaf surface, symmetric leaves and the entire margins of the female bracts. Three species of the Gymnomitriaceae and one species of Adelanthaceae were included in the analysis. Although in some morphological analyses (e.g., Crandall-Stotler et al., 2009; Schuster 1996; Váňa, Söderström, Hagborg, Von Konrat, & Engel, 2010) *Herzogobryum teres* is placed in the Gymnomitriaceae, other authors, on the basis of molecular and morphological characters, transferred *Herzogobryum teres* to the genus *Syzygiella* as part of the Adelanthaceae (Shaw et al., 2015; Váňa, Söderström, Hagborg, & Von Konrat, 2013). Therefore, in this analysis, this taxon will be treated as *Syzygiella teres.*

The outgroup selection follows the phylogenetic hypothesis of De Roo et al. (2007). Members of the Acrobolbaceae, Blepharidophyllaceae, and Solenostomataceae were selected for the outgroup. *Anthelia julacea* (L.) Dumort. was selected as the functional taxon to root the tree.

The number of species included in this analysis and the number of species per genus are cited in Table 1.

Morphological characters

Coding and editing of the data matrix was performed with WinClada ver. 1.00.08 (Nixon, 2002) (Appendix 1, online supplemental material, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2015.1103322). The data matrix was completed mainly from personal observations on herbarium specimens (B, BM, G, M, MEXU, MO, NY, and S) and in a few cases from the literature (e.g., Arnell, 1963; Burghardt & Gradstein, 2008; Grolle, 1965, 1966; Paton, 1999; Schmitt &Winkler, 1968; Schuster, 1969; 1974, 2002; Váňa, 1980, 2004; Váňa et al., 2012).

Phylogenetic analyses

A parsimony analysis under equal weights (EW) was performed. The topologies were found using TNT version 1.1 (Goloboff, Farris, & Nixon, 2003). A heuristic search with 4,000 replicates of Wagner trees constructed with random taxon addition followed by TBR branch swapping was performed; 10 trees were saved on each replicate and a further TBR was conducted to completion saving up to 10,000 trees. The trees were opened in WinClada (Nixon, 2002), where unsupported nodes were collapsed. The suboptimal and duplicate trees were discarded. All the most parsimonious trees were visually compared and summarized using a strict consensus tree constructed in WinClada (Nixon, 2002).

A second parsimony analysis under implied weights (IW) (Goloboff, 1993) was performed using TNT with similar parameters as those described above. The IW analysis was executed in order to assess the influence of different weighting schemes of homoplasy in the phylogenetic hypotheses; these hypotheses were then compared with the topologies obtained under equal weights. The use of IW considers that the most parsimonious hypotheses are those that maximize the fit of the characters on a topology by minimizing homoplasy. The IW was considered as an option without morphological *a priori* or *posteriori* assumptions. This procedure was performed for values of *k* from 1–15. For each value of *k*, the trees with best fit of the data were summarized using a strict consensus tree.

In order to compare the phylogenetic hypotheses obtained by EW and IW, the auto-consistent trees (those that were obtained in the EW and in the IW analyses) were identified from the non auto-consistent trees. To find them, the duplicate and the trees longer than the most parsimonious ones under EW (187 steps) were deleted from among the 15 strict consensus trees obtained on each implied weighting scheme using WinClada (Nixon, 2002). To perform these comparisons, the unsupported nodes were first collapsed on all trees. This procedure resulted in two most parsimonious trees. These two trees were summarized in a strict consensus tree.

In both analyses, characters two and six were treated as binary-additive, all others characters were treated as non-additive. Unambiguous optimization was performed to assess the character state evolution. The character states were mapped on the consensus tree using WinClada (Nixon, 2002) only if that optimization was supported also in all of the most parsimonious trees.

Additionally, a Jackknife analysis was executed in Nona (Goloboff, 1999) spawn through WinClada (Nixon, 2002), re-sampling the matrix 2000 times with TBR set to 2000 replications holding 10 trees on each of them.

A single character removal analysis was executed in Nona (Goloboff, 1999) spawn through WinClada (Nixon, 2002) using the same searching parameters as those applied for the EW analysis. This procedure retrieves the consensus of the most parsimonious trees obtained by progressively removing each of the characters in a matrix, hence resulting in as many consensus trees as characters in a matrix. By comparing the length of each of these consensus trees to the length of the consensus of the EW analysis it is possible to know if a character reduces conflict in the original matrix (longer consensus after removing it) or introduces conflict (shorter consensus after removing it).

Results

The data matrix contained 53 potentially informative characters (50 gametophytic and three sporophytic); 37 characters are binary and 16 characters are multistate and two of them were coded as additive (2, 6). A list of the characters used in this analysis and comments associated to the coding are given in Appendix 2 (see supplemental material online). The matrix has a total of 1590 cells, with 149 cells (9%) of them coded as missing (?) and 112 cells (7%) as inapplicable (-).

Parsimony analysis using equal weighting

The parsimony analysis resulted in 117 most parsimonious trees (MPTs) with a length of 187 steps (Ci = 0.41, Ri = 0.64). The strict consensus tree (Fig. 7) was poorly resolved, but Stephaniellaceae and *Gongylanthus* (excluding *Gongylanthus ericetorum* (Raddi) Nees) were supported as monophyletic.

Relationships within the *Stephaniella* + *Stephaniellidium* clade (Fig. 7)

The *Stephaniella* + *Stephaniellidium* clade was supported by two synapomorphies: presence of paraphyllia and presence of longitudinal folds in female bracts, while the apparent synapomorphy of strongly imbricated leaves is in fact an artefact of the polytomy. In addition, the clade

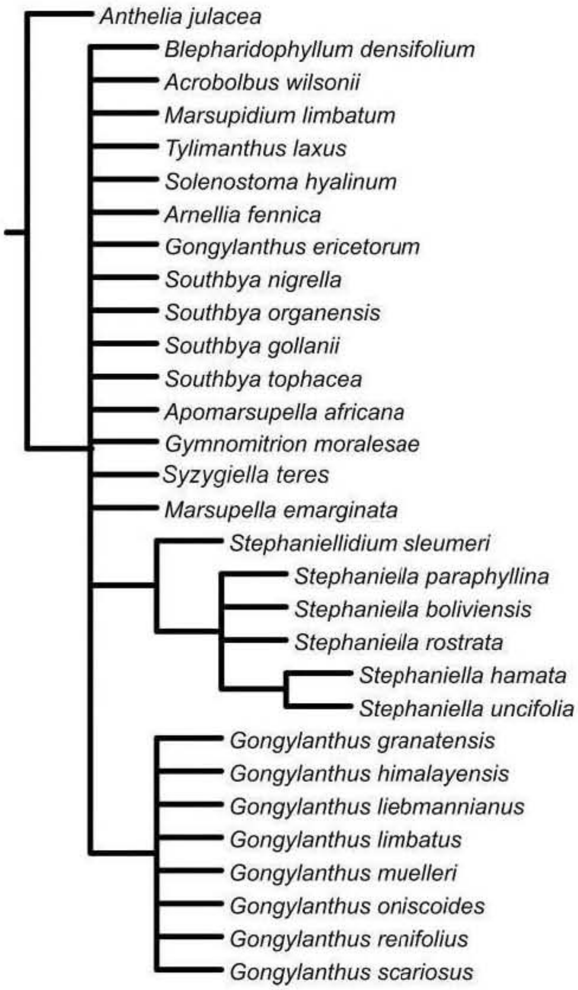


Fig 7. Strict consensus of the 117 most parsimonious trees (L = 187; Ci = 0.41; Ri = 0.64) under equal weighting.

is supported by homoplastic character states such as the insertion line of the leaves transgressing the stem midline, postical margin of the leaf differentiated, and sporophyte capsule cylindrical.

The *Stephaniella* clade was supported by two synapomorphies: absence of chlorophyllose leaves and female bracts with falcate apex. The relationships among the species of *Stephaniella* were poorly resolved. *S. paraphyllina*, *S. boliviensis* and *S. rostrata* formed a polytomy, while *S. hamata* and *S. uncifolia* formed a clade clustered by homoplastic characters. In some of the most parsimonious trees, *S. rostrata* was clustered with the *S. paraphyllina* + *S. boliviensis* clade, and this relationship was supported by the synapomorphic character state of filiform paraphyllia. However, in other equally parsimonious trees, *S. rostrata* was clustered with the *S. hamata* + *S. uncifolia* clade, and this was supported by two synapomorphies (foliar margin serrulate and female bracts with margin serrulate). The homoplastic character states supporting the relationship of the *S. hamata* + *S. uncifolia* clade were epidermal cells as large as the medullary cells, decurrent leaf base, leaf cell walls papillose, foliar apex acute, foliar margin serrulate, foliose paraphyllia, and apical cells of the perianth oblong-sinuose.

Relationships within the *Gongylanthus* clade (Fig. 7)

This clade was supported by six homoplastic character states (opposite and not united leaves, postical margin of the leaf differentiated, foliar margin involute, presence of marsupium, sporophyte capsule cylindrical, and absence of perygynium). However, the relationships among the species were unsolved. In all most parsimonious trees *G. ericetorum* was excluded from the *Gongylanthus* clade.

Review of the most parsimonious trees

The Southbyaceae was paraphyletic; *Southbya* always included *Arnellia fennica* (Gottsche & Rabenh.) Lindb., *Blepharidophyllum densifolium* (Hook.) Ångstr. ex C. Massal, and *G. ericetorum*.

The Gymnomitriaceae was monophyletic and they were related to *Syzygiella teres*.

Among the most parsimonious trees, *Solenostoma hyalinum* (Lyell) Mitt. was related to all groups included in the analysis. Although this taxon can be considered a wildcard because its position was variable among the most parsimonious trees, this behaviour cannot be explained by ambiguity (missing, inapplicable, or polymorphic data).

Relationships among families

In the consensus of all 117 most parsimonious trees, the phylogenetic relationships among families were unsolved; even so, these topologies showed only five general patterns of family relationship as explained below:

1. Southbyaceae as sister to Stephaniellaceae. This relationship is supported by two synapomorphies (leaves with postical margin differentiated and female bracts with apex not divided).
2. Stephaniellaceae and Gymnomitriaceae + Adelanthaceae form a clade. This relationship is supported by three synapomorphies (insertion line of the leaves transgressing the stem midline, presence of ventral stolons, and female bracts with apex undivided).
3. Stephaniellaceae segregated from all groups. The character states leaves imbricate strongly, presence of paraphyllia, and presence of longitudinal folds in female bracts are synapomorphies. Line insertion of the leaves transgressing the stem midline, leaves with postical margin differentiated and sporophyte capsule cylindrical are homoplastic characters.
4. Stephaniellaceae and *Solenostoma hyalinum* form a clade, in turn sister to Southbyaceae. One homoplastic character supports the relationship (epidermal cells smaller than medullary cells).
5. Stephaniellaceae nested within Gymnomitriaceae + Adelanthaceae. Two synapomorphies support this clade (insertion line of the leaves transgressing the stem midline and foliar margin inflexed).

Parsimony analysis using implied weighting

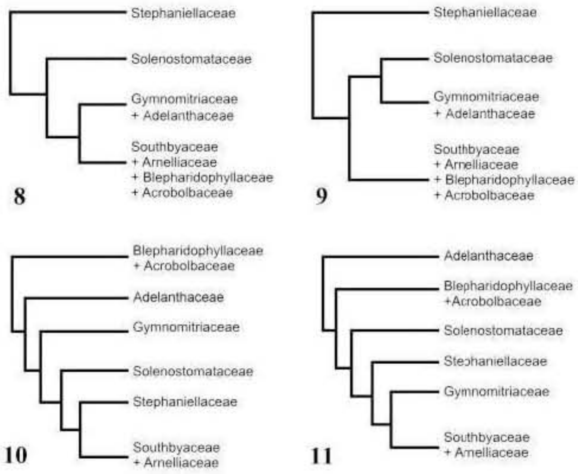
The length, consistency, retention index, homoplasy adjustment, and fit of the characters for the trees with best fit for each of the k values was analysed (Table 2). Under implied weighting, the *Stephaniella* + *Stephaniellidium* clade was recovered in the analyses with $k = 1-15$ (Fig. 8–11, Fig. 12). This clade and the *Stephaniella* clade were recovered and supported by the same synapomorphies resulting from equal weightings. In all the trees, *Stephaniellidium* was also recovered as sister to *Stephaniella*.

The relationships among the species of *Stephaniella* differed from those obtained with equal weightings (compare Fig. 7 and Fig. 12). Except for the tree obtained with $k = 1$, in all other trees *Stephaniella rostrata* was recovered as sister to the *Stephaniella paraphyllina* + *Stephaniella boliviensis* clade; this relationship was supported by filiform paraphyllia as a synapomorphy. The *S. paraphyllina* + *S. boliviensis* clade was supported by one homoplastic character (foliar apex obtuse). The *Stephaniella hamata* + *Stephaniella uncifolia* clade was supported by

Table 2. Number of trees (most parsimonious as MPTs), length (L), consistency index (CI), retention index (RI), fit (Fit) and homoplasy adjustment (HA) related to the trees found in the analyses of Stephaniellaceae. EW = equal weighting; IW = implied weighting; k = concavity function for the weighting in the IW.

Analysis	MPTs	L	CI	RI	Fit	HA
EW	117	187	0.41	0.64	–	–
IW $k = 1$	2	199	0.392	0.603	26.37	26.63
IW $k = 2$	4	196	0.398	0.613	31.88	21.12
IW $k = 3$	4	196	0.398	0.613	35.36	17.64
IW $k = 4$	1	193	0.404	0.623	37.81	15.19
IW $k = 5$	2	187	0.417	0.643	39.67	13.33
IW $k = 6$	1	187	0.417	0.643	41.16	11.84
IW $k = 7$	1	187	0.417	0.643	42.34	10.66
IW $k = 8$	2	187	0.417	0.643	43.30	9.70
IW $k = 9$	2	187	0.417	0.643	44.11	8.89
IW $k = 10$	1	187	0.417	0.643	44.79	8.21
IW $k = 11$	1	187	0.417	0.643	45.37	7.63
IW $k = 12$	2	187	0.417	0.643	45.87	7.13
IW $k = 13$	2	187	0.417	0.643	46.31	6.69
IW $k = 14$	2	187	0.417	0.643	46.70	6.30
IW $k = 15$	2	187	0.417	0.643	47.05	5.95

the same homoplasies as with equal weighting. In the trees obtained with $k = 1-15$ values, *S. rostrata* was sister to the *S. paraphyllina* + *S. boliviensis* clade (Fig. 12); this relationship was supported by one synapomorphy (filiform paraphyllia).



Figs. 8–11. Patterns of family relationships under implied weighting. 8, 9) Stephaniellaceae is segregated from all groups: 8) Solenostomataceae is segregated from Gymnomitriaceae and Adelanthaceae, 9) Solenostomataceae and Gymnomitriaceae + Adelanthaceae form a clade. 10) Stephaniellaceae and Southbyaceae + Arnelliaceae form a clade. 11) Stephaniellaceae is the sister group of Gymnomitriaceae + Adelanthaceae and Southbyaceae + Arnelliaceae.

In all analyses, Southbyaceae were recovered as paraphyletic. Arnelliaceae was always nested in Southbyaceae; and in most analyses, the Blepharidophyllaceae and Acrobolbaceae were also nested within Southbyaceae (Fig. 8–11, Fig. 12).

Relationships within the *Gongylanthus* clade

This clade was recovered as monophyletic in the analyses with values of $k = 5-15$ (Fig. 12), supported by two homoplastic characters (sporophyte capsule cylindrical and absence of perigynium), except for the exclusion of *G. ericetorum* from the *Gongylanthus* clade. In these trees, the relationships among species of *Gongylanthus* were better resolved as compared with the equal weighting analysis.

The Gymnomitriaceae was monophyletic (Fig. 12). In the analyses with $k = 5-15$, *Syzygiella teres* was the sister group of Gymnomitriaceae. In the analyses with $k = 1-4$, *S. teres* was not related with Gymnomitriaceae. Characters that exclude it from the family were foliar margin crenulate and presence of amphigastria.

As with equal weighting, the position of *S. hyalinum* was very variable among the strict consensus trees for all k values.

Relationships among families

Under implied weighting three patterns of relationship at family level were found for Stephaniellaceae (Fig. 8–11), as explained below:

(1) The Stephaniellaceae is segregated from all groups (Figs 8, 9). Presence of paraphyllia and female bracts with longitudinal folds are synapomorphies that exclude the group from the other families.
(2) The Stephaniellaceae and Southbyaceae + Arnelliaceae form a clade (Fig. 10). This relationship is supported by one synapomorphy (leaves with postical margin differentiated) and one homoplastic character (cells of the leaves with regular areolation).
(3) The Stephaniellaceae is the sister group of Gymnomitriaceae + Southbyaceae + Arnelliaceae (Fig. 11). These groups are supported by one homoplastic character (insertion line of the leaves transgressing the stem midline).

Auto-consistent trees

Two auto-consistent tree (L = 187; Ci = 0.41; Ri = 0.64) were obtained among the implied weighting analyses using k values from 1–15. Fig. 13–17 shows the consensus tree from both trees. As expected by the reduction of

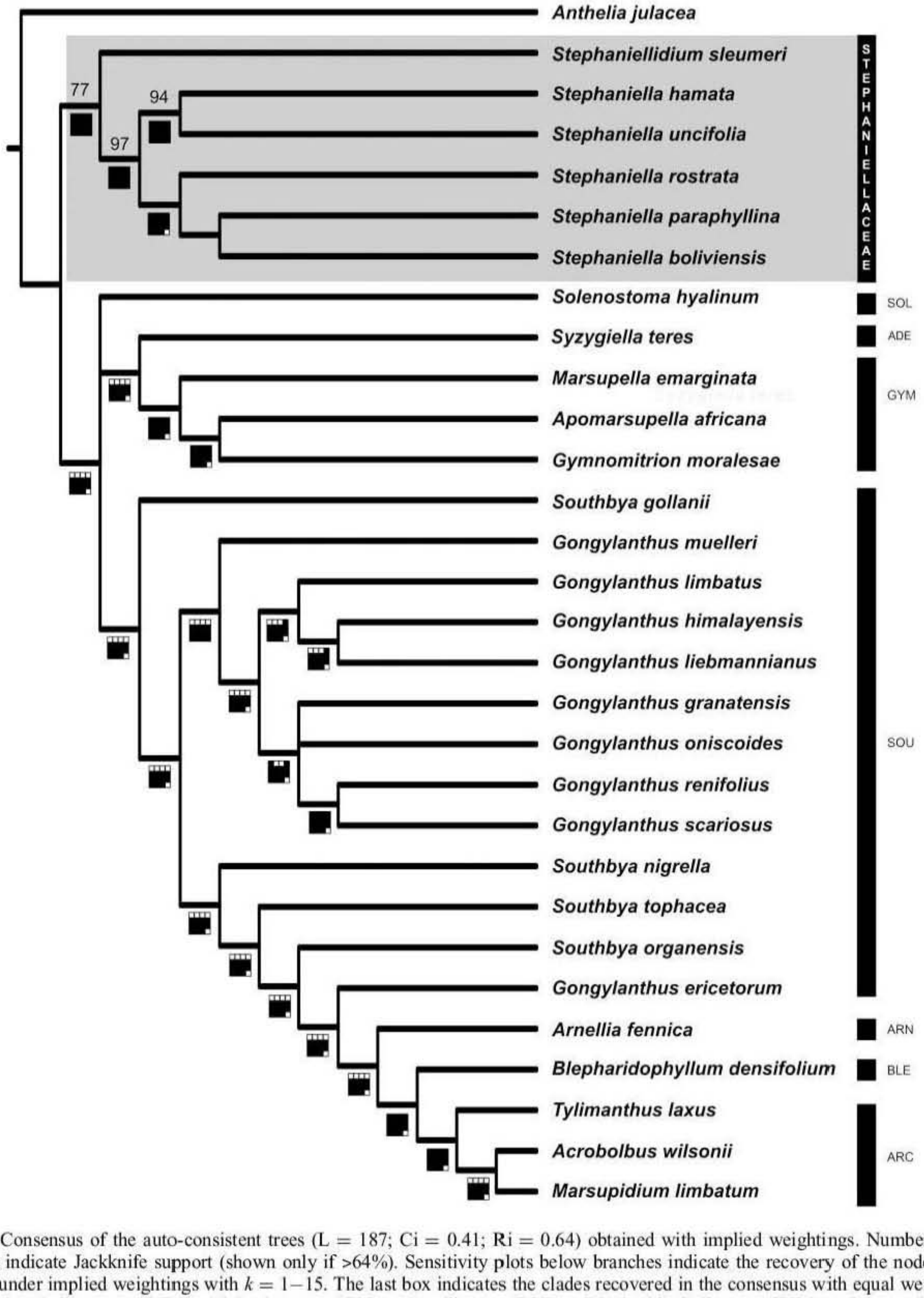
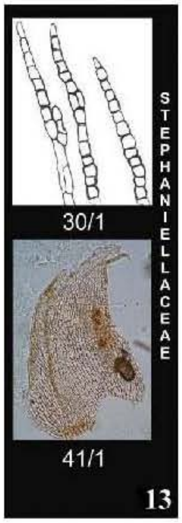
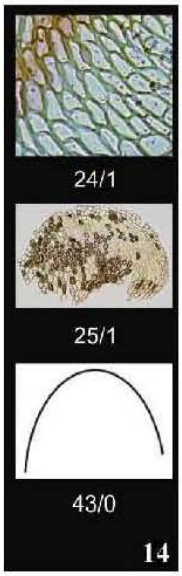
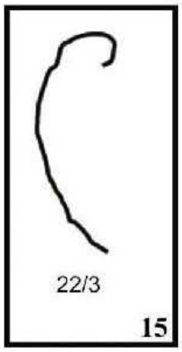
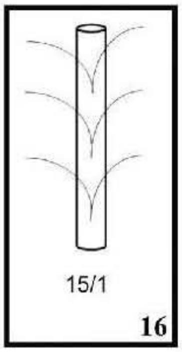


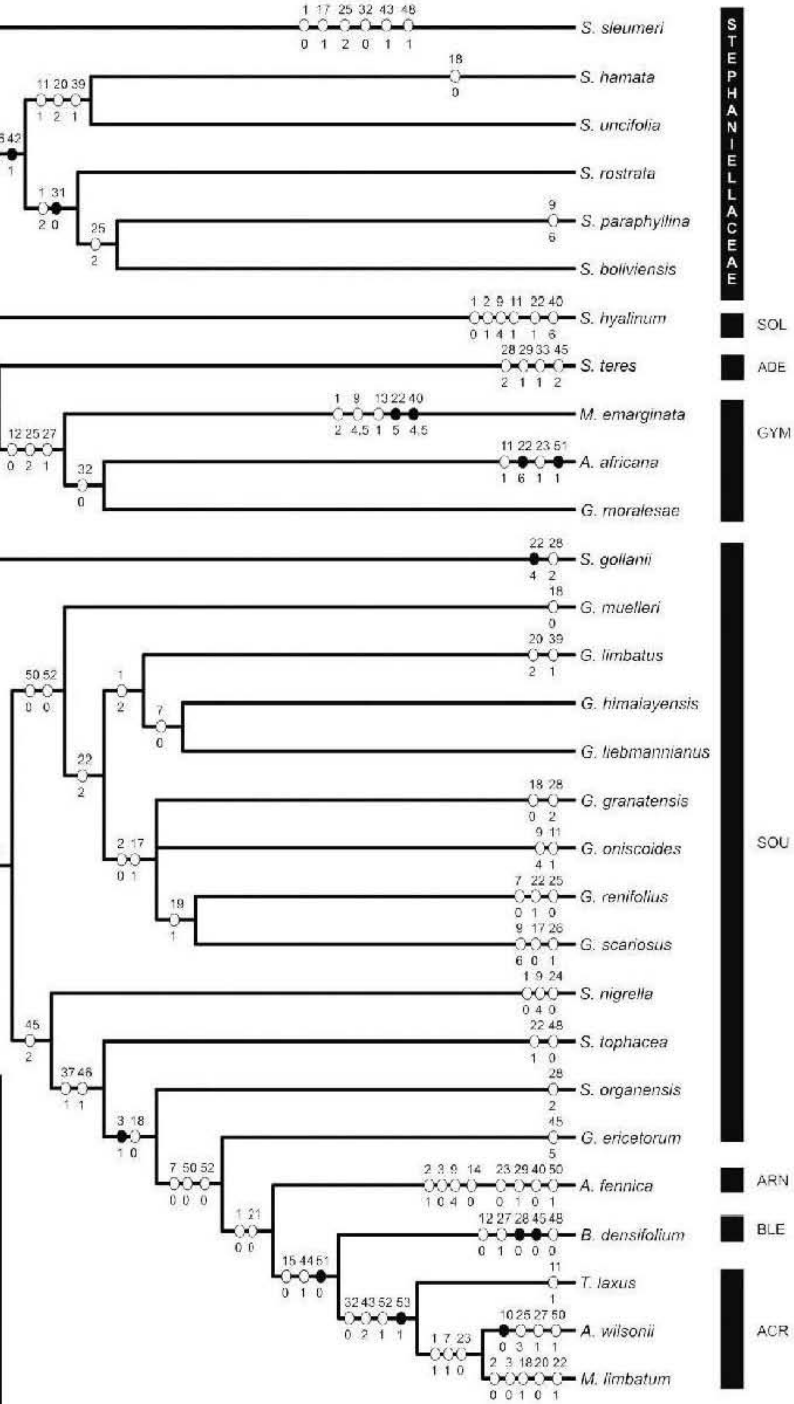
Fig. 12. Consensus of the auto-consistent trees (L = 187; Ci = 0.41; Ri = 0.64) obtained with implied weightings. Numbers above branches indicate Jackknife support (shown only if >64%). Sensitivity plots below branches indicate the recovery of the nodes in the analysis under implied weightings with $k = 1-15$. The last box indicates the clades recovered in the consensus with equal weightings. ACR = Acrobolbaceae; ADE = Adelanthaceae; ARN = Arnelliaceae; BLE = Blepharidophyllaceae; GYM = Gymnomitriaceae; SOL = Solenostomataceae; SOU = Southbyaceae.











Figs. 13–17. Auto-consistent consensus among the tree under implied weightings, showing the character states that support the branches. The numbers above the circles indicate the characters according to **Appendix 2 (**see supplemental material online); the numbers below the circles indicate the character states. The black circles show the synapomorphic character states and the white circles show the homoplastic character states. Synapomorphies for the four major clades are illustrated. ACR = Acrobolbaceae; ADE = Adelanthaceae; ARN = Arnelliaceae; BLE = Blepharidophyllaceae; GYM = Gymnomitriaceae; SOL = Solenostomataceae; SOU = Southbyaceae.

conflicting hypotheses, the relationships among species were more resolved than in the consensus considering all equally parsimonious trees obtained with equal weightings (Figs 12, 13–17, 18–21). The *Stephaniella* + *Stephaniellidium* clade was well supported (JK = 77; Fig. 12); the rest of the tree had relatively low support values (JK ≤ 64; Fig. 12), while the relationship between the clades *S. rostrata* + *S. paraphyllina* + *S. boliviensis* and *S. hamata* + *S. uncifolia* had a stronger support (JK = 97; Fig. 12), followed by the clade including *S. hamata* and *S. uncifolia* (JK = 94; Fig. 12); the relationship between *S. rostrata*, *S. paraphyllina*, and *S. boliviensis* was weakly supported (JK ≤ 64; Fig. 12).

Because these two trees are auto-consistent and optimize the fitness of the characters, we use them and their consensus to further investigate implications in character evolution and classification. Figures 13–17 shows the optimization of the characters in auto-consistent tree. The presence of paraphyllia and presence of longitudinal folds in the female bracts were synapomorphies for the *Stephaniella* + *Stephaniellidium* clade.

The presence of trigones, foliar rotund apex, and female bracts with rotund apex were the synapomorphies that excluded *Stephaniella* and *Stephaniellidium* from other families.

The Gymnomitriaceae was resolved as monophyletic and was supported by three homoplastic characters (transversal leaves, obtuse foliar apex and divided foliar apex). *Syzygiella teres* was the sister group of Gymnomitriaceae; this relationship was supported by one synapomorphy (foliar margin inflexed).

The Southbyaceae were recovered as paraphyletic; Arnelliaceae, Blepharidophyllaceae, and Acrobolbaceae were nested within them. This relationship was supported by the synapomorphy leaves opposite and united (Fig. 13–17).

Character removal

Table 3 shows the taxa retained after the character removal. The absence of 35 characters negatively affected the tree topology of the consensus, i.e., their absence collapsed the tree and therefore they were useful in recovering clades (e.g., branching-type, presence and position of stolons, presence of echlorophyllose leaves, extension on the stem of the insertion line of the alternate leaves, differentiation of the postical margin of the leaf, presence of paraphyllia on the stem, presence of longitudinal folds in the female bracts, and extent of fusion of the perianth). Other characters used for the first time in this analysis also positively contributed to tree topology (e.g., leaf shape, distance between stem leaves, leaf decurrency-type, leaf insertion-type, presence of falcate leaf apex, perianth apical cells shape, and presence of perigynium).

On the other hand, the absence of 17 characters positively affected the topology, i.e., their absence resulted in the recovering of more clades. Four additional clades were recovered when six characters were removed: arrangement of the leaf surface, ornamentation of the cell wall of the leaf, areolation-type of the leaf cells, presence of perianth, ornamentation of cells walls in female bract, presence of marsupium.

The inclusion of 29 characters was important for maintaining the *Gongylanthus*-clade. Also, it is important to note that the *Stephaniella* + *Stephaniellidium* clade was recovered in all cases, i.e., independently of the removal of either character.

Discussion

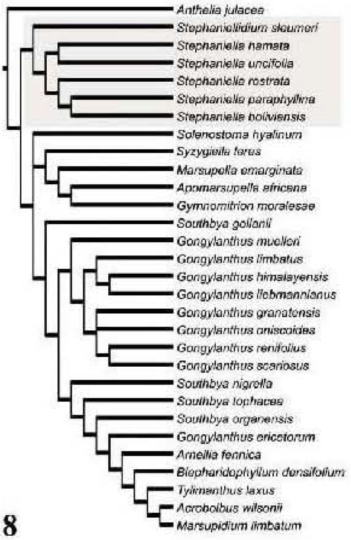
Under equal and implied weightings, the phylogenetic relationships of the Stephaniellaceae with the Gymnomitriaceae, Southbyaceae, and Arnelliaceae are inconclusive, because the consensus tree obtained with equal weightings resulted in a polytomy and also the preferred trees in both analyses (most parsimonious or with better character fit) showed all possible combinations of relationships between these groups. Nevertheless, the consensus of the auto-consistent trees is well resolved and was used to analyse the relationships of the Stephaniellaceae with other families (Figs 12, 13–17, 18–21).

It should be noted that in all analyses the Stephaniellaceae were recovered as monophyletic (Fig. 8–11, 12). Presence of paraphyllia and longitudinal folds in the female bracts were the synapomorphic characters for the family (Fig. 18–21). Schuster (2002) used these characters in the family description, so they are corroborated as diagnostic for the Stephaniellaceae.

Relationships of the Stephaniellaceae with the Gymnomitriaceae

Gradstein et al. (2001) and Schuster (1984, 2002) considered the leaf insertion line dorsally transgressing the stem midline, presence of stolons (stolons of Stephaniellaceae differ from those of Gymnomitriaceae in up to several centimetres in length, and they are sometimes longer than the main axis), leaves strongly imbricate, absence of amphigastria, rhizoids scattered as important characters to include *Stephaniella* and *Stephaniellidium* within the Gymnomitriaceae. However, in this analysis these characters were uninformative and they are not corroborated as supporting features for that purpose. This information could change with up sampling the species of Gymnomitriaceae.

Gradstein et al. (2001) cited the presence of trigones in the Gymnomitriaceae (including *Stephaniella* and *Stephaniellidium*) and Schuster (2002) did not specify their



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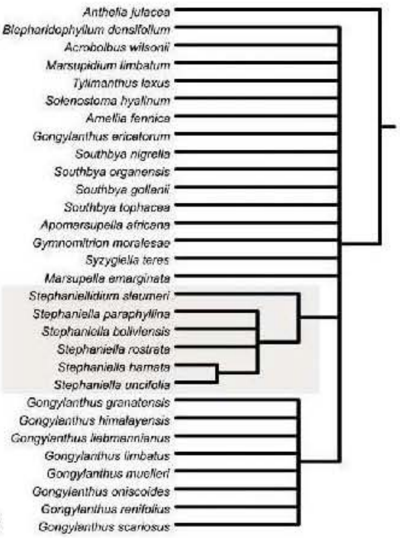

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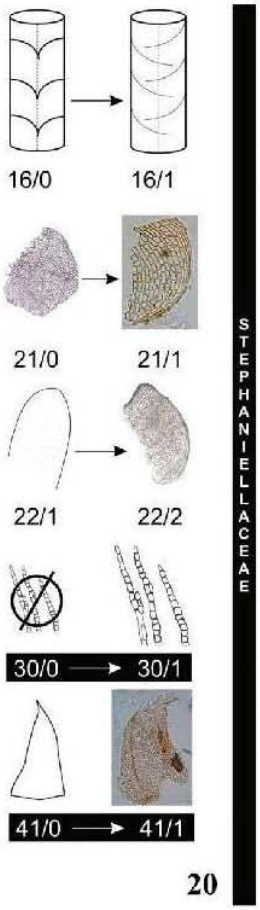

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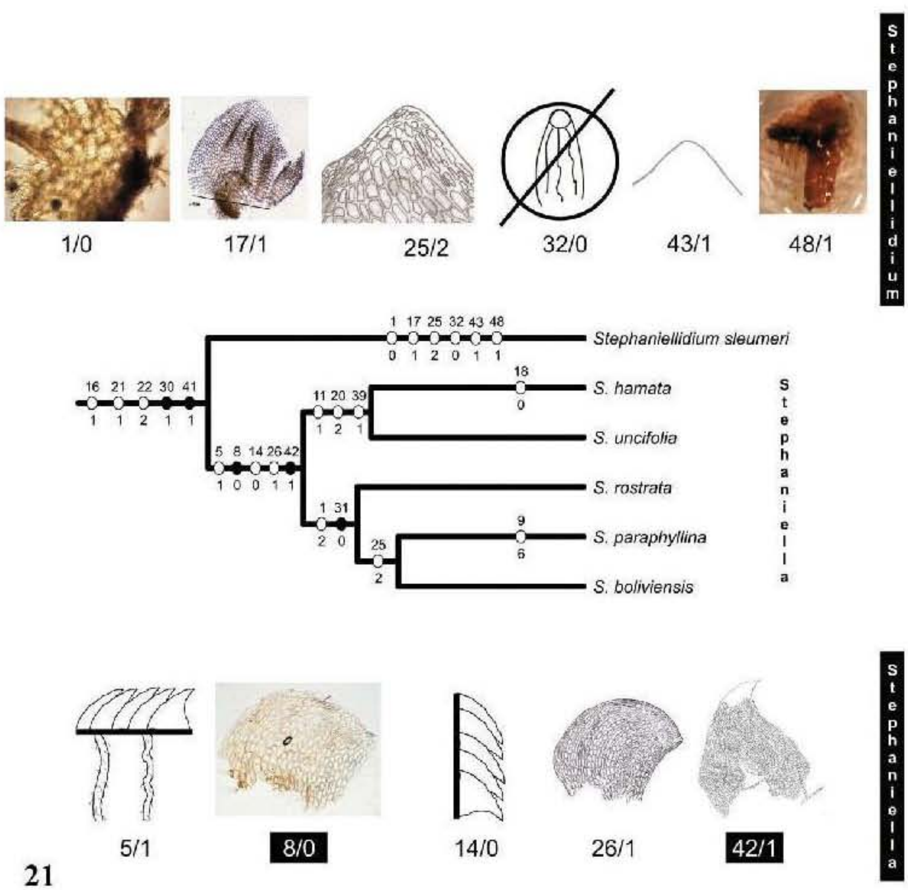

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Figs. 18–21. Stephaniellaceae clade showing synapomorphic and homoplastic characters. Position of the Stephaniellaceae in the consensus of (18) the auto-consistent trees obtained with implied weighting and (19) under equal weighting. (20) Illustration of the character transformations that support Stephaniellaceae, with the corresponding numbering according to **Appendix 2** (see supplemental material online); character transformations with black background numbering are synapomorphies, and the character transformation with white background numbering are homoplasies. 21) Character states mapped and illustrated for Stephaniellaceae. The black circles show the synapomorphies (character states) and the white circles show the homoplasies (character states).

Table 3. Taxa retained after the removal of the indicated characters.

Character removed	Taxa retained
2, 4–12, 14, 16, 19, 21, 24–27, 29–31, 33, 35, 37, 39–43, 47, 52	Stephaniellaceae
3	Stephaniellaceae Acrobolbaceae
1, 38	Stephaniellaceae *Gongylanthus*
17	Stephaniellaceae Some *Gongylanthus* spp.
50, 51	Stephaniellaceae *Acrobolbus* + *Tylimanthus*
22	Stephaniellaceae Acrobolbaceae *Gongylanthus*
45	Stephaniellaceae Acrobolbaceae Gymnomitriaceae + *Syzygiella teres*
15, 34, 36	Stephaniellaceae nested in *Gongylanthus* Acrobolbaceae Gymnomitriaceae + *Syzygiella teres*
44	Stephaniellaceae *Gongylanthus* Gymnomitriaceae without *Syzygiella teres*
13, 28, 49, 53	Stephaniellaceae *Gongylanthus* Gymnomitriaceae + *Syzygiella teres*
48	Stephaniellaceae *Acrobolbus* + *Tylimanthus* *Gongylanthus* Gymnomitriaceae + *Syzygiella teres*
23	Stephaniellaceae Acrobolbaceae *Gongylanthus* Gymnomitriaceae + *Syzygiella teres*
18, 20, 46	Stephaniellaceae Acrobolbaceae *Gongylanthus* Gymnomitriaceae + *Syzygiella teres*
32	Stephaniellaceae *Gongylanthus* Gymnomitriaceae + *Syzygiella teres* *Marsupidium* + *Solenostoma*

presence in the Stephaniellaceae. However, our observations indicate that the absence of trigones in *Stephaniella* and *Stephaniellidium* separates these genera from the other groups (Fig. 13–17).

The inflexed leaf margin of the Gymnomitriaceae distinguished it from the Stephaniellaceae (foliar margin involute; Fig. 18–21). Although the boundaries between inflexed and involute may not be clear, in Stephaniellaceae the margin is completely involute.

Relations of Stephaniellaceae with Southbyaceae and Arnelliaceae

The rounded apex of the leaf and the female bracts distinguish Southbyaceae and Stephaniellaceae from other groups. The leaf apex shape in the Stephaniellaceae easily distinguishes them from other families; however these are homoplastic characters within Stephaniellaceae (Fig. 18–21).

The phylogenetic analysis supports the proposal of Váňa et al. (2012) who considered the opposite and united leaves as a difference between Southbyaceae and Stephaniellaceae (alternate and not united leaves) (Fig. 13–17).

In this analysis, the differentiated foliar margin (Fig. 13–17) of Southbyaceae and Stephaniellaceae was hypothesized as homologous; however, this character arose independently in both groups.

Crandall-Stotler et al. (2009) cited the presence of a *Calypogeia*-type marsupium as evidence for the inclusion of *Stephaniella* within the Arnelliaceae (including *Gongylanthus* and *Southbya*). Nevertheless, our observations do not support this hypothesis; the sporophyte of *Stephaniellidium* is developed in a marsupium, while the sporophyte of *Stephaniella* is developed in a perianth (lack of marsupium) (Fig. 18–21). According to the topology obtained, the marsupium appeared independently in *S. sleumeri* and *Gongylanthus*.

The character cylindrical capsule of the sporophyte was a homoplasy between *Stephaniella*, *Stephaniellidium*, and *Gongylanthus*, and this was not corroborated as informative, as it was postulated by Crandall-Stotler et al. (2009) who considered that this character was evidence to support the relationship of *Stephaniella* and *Stephaniellidium* with members of the Arnelliaceae or Southbyaceae.

Otherwise, the 2-stratose capsule wall of the sporophyte was resolved as a plesiomorphic condition, and therefore is uninformative to establish the relationships of the Stephaniellaceae with the Arnelliaceae, Gymnomitriaceae, and Southbyaceae.

According to this phylogenetic analysis, the morphological criteria for the inclusion of *Stephaniella* and *Stephaniellidium* within the Gymnomitriaceae or Arnelliaceae (*sensu* Crandall-Stotler et al., 2009) are based on homoplasies (e.g., leaf insertion line dorsally transgressing the stem midline, strongly imbricate leaves, absence of amphigastria, foliar margin differentiated, *Calypogeia*-type marsupium, sporophyte cylindrical capsule and sporophyte wall capsule 2-stratose) (Fig. 13–17; 18–21). Therefore, we agree with Schuster (2002) in proposing the elevation of *Stephaniella* and *Stephaniellidium* to the rank of family as Stephaniellaceae. According to the topologies obtained in this analysis, the diagnostic characters of the Stephaniellaceae are: (1) presence of paraphyllia, and (2) presence of longitudinal folds in the female bracts (Fig. 18–21).

Relationships within Stephaniellaceae (Fig. 18–21)

Synapomorphies and diagnostic characters of the *Stephaniella* clade are echlorophyllose leaves and falcate apex of the female bracts (Fig. 18–21). Schmitt and Winkler (1968) and Schuster (2002) cited and illustrated these characters as diagnostic for *Stephaniella* without prior phylogenetic analysis and these conditions are here corroborated as synapomorphies for the group.

Although the presence of stolons, secund leaves, and falcate leaf apex were homoplasies for *Stephaniella*, these characters distinguish the genus from *Stephaniellidium*, where no stolons were observed, the leaves are distichous, and the apex of the female bracts is not falcate (Fig. 18–21). Schuster (2002) stressed the presence of stolons as an important character in the recognition of *Stephaniella*; however, this condition is not unique to the genus.

Schmitt and Winkler (1968) studied the relationships between the species of *Stephaniella* without phylogenetic analyses, based mainly on the features of the stem, leaf and paraphyllia shape, and arrangement of the foliar margin. Based on the above, they proposed some relationships between *S. hamata*, *S. uncifolia*, and *S. sleumeri*, species that are also characterized by foliose paraphyllia. In this analysis, the relationship between *S. hamata* and *S. uncifolia* was corroborated (Fig. 18–21). Decurrent leaves, papillose cell walls of the leaf, and oblong-sinuose apical cells of the perianth, are characters used for the first time in this analysis, which relate both species, although these characters were resolved as homoplasies.

The relationships between *S. uncifolia* and *S. sleumeri* were uncorroborated. Schmitt and Winkler (1968) described and illustrated the leaf shape of *S. hamata* and *S. sleumeri* as very similar (i.e., ovate-rotund leaf and rotund foliar apex). However, the lectotype of *S. hamata* (G-00069943, G!) was reviewed and it does not correspond with the picture or with the features illustrated by the authors. As a result, the relationships between *S. hamata* and *S. sleumeri* cannot be confirmed. The foliose paraphyllia were not informative.

Schmitt and Winkler (1968) suggested a relationship among *S. rostrata*, *S. paraphyllina*, and *S. boliviensis* by the presence of filiform paraphyllia. This relationship and the character were corroborated and supported in this analysis. The relationship between *S. paraphyllina* and *S. boliviensis* was also suggested by the presence of the foliar obtuse apex and was corroborated here. Unfortunately, we were unable to review the sexual structures of *S. boliviensis*. The type specimen was sterile and hence Stephani (1916) did not describe sexual structures in the protologue. However, these species are very similar, and are distinguished only by the leaf shape: oblate in *S. paraphyllina* and ovate in *S. boliviensis* (Fig. 18–21). Grolle (1967, on a label comment) suggested that *S. boliviensis* is a synonym of *S. paraphyllina*, a proposal that we endorse completely.

Relationships between *Stephaniellidium* and *Stephaniella*

According to the analysis, the monotypic genus *Stephaniellidium* is sister of *Stephaniella*, but this phylogenetic position opens the possibility to consider that *S. sleumeri* could be a member of *Stephaniella* (Fig. 18–21). According to Platnick (1976), 'if a single species is the sister group of a higher taxon, that taxon must be reduced to a genus in a cladistics classification' (p. 198). Although he advises against the description of monotypic genera, we consider that *S. sleumeri* lacks the synapomorphies that can be used to diagnose *Stephaniella*, having at the same time a unique combination of homoplastic characters that supports the recognition of *Stephaniellidium* as an independent genus. Following Winkler (1969), we believe that the absence of a perianth, the female bracts with obtuse apex, and the presence of a marsupium (homoplastic characters) are significant to retain *Stephaniellidium* separate from *Stephaniella* (Fig. 18–21). Molecular data may help reinforcing or rejecting this hypothesis.

Incongruences with results obtained by Shaw et al. (2015)

Regarding the familiar relationships, our results greatly differ from those obtained by Shaw et al. (2015) in the family and interspecific relationships. First, Shaw et al. (2015) assessed the relationships among species of Southbyaceae with molecular data and, unlike our results, the Southbyaceae and *Gongylanthus* and *Southbya* were monophyletic. Secondly, in Shaw et al. (2015) Blepharidophyllaceae and Acrobolbaceae were recovered as monophyletic groups and fully segregated from each other; in our analysis these families were nested within Southbyaceae

The incongruence among our results and those of Shaw et al. (2015) could be an artefact of species sampling in each analysis (e.g., type and number of species), by the use of the molecular characters, missing data, homoplasy of morphological characters but also by the number of morphological data included in both analyses. In this sense, Shaw et al. (2015) included 14 morphological characters of which only seven were used in our analysis (presence of amphigastria, interlocking merophytes, ending of the foliar apex, presence of perigynium, presence/absence of perianth, presence/absence of marsupium and sporophyte capsule shape).

Conclusions

The position of *Stephaniella* and *Stephaniellidium* and the changes in their classification are partly due to the complex morphology of their members, and lack of knowledge of sexual structures and few collections. However, as Schuster (2002), we support the elevation of *Stephaniella* and *Stephaniellidium* to the rank of family, the Stephaniellaceae. We confirm the presence of paraphyllia and the presence of longitudinal folds in the female bracts as diagnostic characters for the family.

Schuster (2002) cited that the morphology of oil bodies and the sporophyte capsule morphology are valuable characters for the taxonomy of the Stephaniellaceae. Nevertheless, the observation of these structures is very difficult. The oil bodies disintegrate rapidly after the specimens are collected; furthermore, the sporophyte capsule has rarely been observed and examined.

On the other hand, based on morphological analysis, we considered retaining the name *Stephaniellidium*, and regard it as the sister group of *Stephaniella*. The latter is well-defined by echlorophyllose leaves and female bracts with falcate apex.

We propose *S. boliviensis* to be a synonym of *S. paraphyllina.* The relationship hypothesized by Schuster (2002) between *S. rostrata–S. sleumeri* and *S. uncifolia–S. sleumeri* were not supported. The morphology of the paraphyllia is an informative character in the systematics of the group, as mentioned by Schmitt and Winkler (1968) and Schuster (2002).

Most unfortunately, the species of Stephaniellaceae were not included in the analysis of Shaw et al. (2015); therefore, their assessment of the family relationships and among the species should be evaluated with molecular data.

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Supplemental data

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Supplemental data of the Cladistic analysis of the Stephaniellaceae.

Appendix 1. Datamatrix used in the morphological analysis.

Polymorphism key A=0 1; B=1 2; C=2 3; D=3 4; E=0 3; F=1 3; G=0 2; H=2 4; I=4 5; J=1 2 3; K=3 6.

```
                              1   5   10   15   20   25   30   35   40   45   50
                              |   |    |    |    |    |    |    |    |    |    |
Anthelia julacea              120A0-11BB00C100000A0010D01210-1?11104?000C12000-2210
Blepharidophyllum densifolium 02100-01310001001002001110100 0-11110100300010100-0000
Acrobolbus wilsonii           12110-1130011100000200013013 00-0-------60021210101011
Marsupidium limbatum          10011211E101310001000101A003A0-0-------???????0100011
Tylimanthus laxus             02111201EA11110010020011000F00-0-------30021210100011
Solenostoma hyalinum          01010-1141112100A1000101100300-10111040600005000-2210
Arnellia fennica              01010-014101201-00020001100310-10010110000002101111200
Gongylanthus ericetorum       12100-013101311-A0021011100300-10010?4?30000510110200
Gongylanthus granatensis      ?00?0-113101311-10001211100200-10010????00?0??0110200
Gongylanthus himalayensis     ????0-01???1?11-?1001???100?00-10010??????????0110200
Gongylanthus liebmannianus    22000-013101311-01001211100300-10010050300102001 10200
Gongylanthus limbatus         220?0-113101311-01021211100300-10010051300005001 10200
Gongylanthus muelleri         ??0?0-113101311-00001011100300-1001????30000500110200
Gongylanthus oniscoides       ??0?0-114111311-11001211100300-1001???????????0110200
Gongylanthus renifolius       100?0-013101311-1110111A000300-10010150300 00B?0110200
Gongylanthus scariosus        ??0?0-116101311-0110121A110300-1001?????????1?0110200
Southbya nigrella             0?000-114101311-0A0G1010100300-100100G030000H00113210
Southbya organensis           B?1?0-113101311-00021011100200-100????????????0??3210
Southbya gollanii             ?20?0-1131?1?11-?10014?1100200-1001??4?3?0?0I000-3210
Southbya tophacea             120?0-113101311-?1021111100300-100101H030000H100-3210
Stephaniella paraphyllina     22011110620120010110121021030101010105031120501 0-0210
Stephaniella boliviensis      220?1110320120010110121021030 10?????????????????????0
Stephaniella hamata           12011110321120010012121031010111010103131120 3?10-0210
Stephaniella uncifolia        1201111032112001011212103101011101010313112031 10-0210
Stephaniella rostrata         220?1110320120010110121031010101010103031120301 0-0210
Stephaniellidium sleumeri     020?0-11320131011 1A012102003011 0-------3101050?1102?0
Apomarsupella africana        12011?11311031010100 0611C01300-0-------????1??00-3100
Gymnomitrion moralesae        12011111D10041010100 0301J01300-0-------3?0115000-32?0
Syzygiella teres              12011?11K1014101010003011002 10-11111041K00112000-32?0
Marsupella emarginata         22011111IA0011010100 0501201300-1001001?I00115000-3B10
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Appendix 2. Characters and character states used in the phylogenetic analyses.

1. Size proportion of epidermal and medullary cells

0 epidermal smaller than medullary cells

1 epidermal as large as the medullary cells

2 epidermal larger than medullary cells

2. Presence of differentiated cortex

In order to avoid the need for inapplicable scoring postulating at the same time the hypothesis that cortical cells are homologous independently of the wall thickening, we code this character as additive, suggesting in this way a hierarchical relationship among the character states.

0 absent

1 present with scarcely thickened

2 present with clearly thickened

3. Ornamentation of the epidermal cells of the stem

Some species of Southbyaceae have papillae on the epidermal cells of the stem. However, these are not found in species of Stephaniellaceae.

0 smooth

1 papillose

4. Branching-type

The branching-type may help to infer relationship between closely related genera (Crandall-Stotler, 1972). This was coded only in cases were the branches had leaves.

0 terminal

1 intercalary

5. Presence of stolons

Stephaniella and Gymnomitriaceae differ from *Stephaniellidium*, Arnelliaceae and Southbyaceae in the presence of stolons (Váňa et al., 2012).

0 absent

1 present

6. Positions of the stolons

Because all stolons have intercalary branching pattern, we postulate that this branching pattern preceded the formation of stolons and to depict this hypothesis we coded these characters as additive-binary.

0 lateral

1 ventral

2 basal

7. Disposition of the rhizoids on the stem

Arnelliaceae and Southbyaceae have in the same individuals both, rhizoids scattered on the stem and rhizoids in tufts (Gradstein et al., 2001; Váňa et al., 2012), while Stephaniellaceae only has rhizoids scattered on the stem.

0 scattered and in tufts

1 only scattered

8. Presence of chlorophyll in the leaves

Stephaniella is the only genus of Stephaniellaceae, Arnelliaceae, Gymnomitriaceae and Southbyaceae that do not have green leaves.

0 absent

1 present

9. Leaf shape

0 ligulate

1 oblong

2 ovate-oblong

3 ovate

4 orbicular

5 quadrate-orbicular

6 oblate

10. Separation between stem leaves

Stephaniella and *Stephaniellidium* differ from the other genera by having strongly imbricate leaves (Váňa et al., 2012). Strongly imbricate refers to leaves that are difficult to separate from each other with a needle.

0 proximal

1 closely imbricate

2 strongly imbricate

11. Leaf base

Variation in the decurrency-type was observed between the species included in the analysis.

0 not decurrent

1 decurrent

12. Leaf insertion-type

0 transverse

1 succubous

13. Angle of the leaves with respect to the stem

0 spreading-recurved

1 spreading

2 patent

3 erect

3 erect-appressed

14. Leaves distribution on the stem

Stephaniellaceae differs from other groups by having secund leaves instead of distichous (erect).

0 secund

1 distichous

15. Phyllotaxy

Unlike Arnelliaceae and Southbyaceae, Stephaniellaceae and Gymnomitriaceae have alternate leaves and they have antical leaf bases separated.

0 alternate (not united)

1 opposite (united)

16. Extension on the stem of the line of insertion of the alternate leaves

As in Gymnomitriaceae, Stephaniellaceae has leaf insertion lines dorsally transgressing the stem midline. The extension on the stem of the line of leaf insertion occurs in independently of the union of the antical leaf bases, e.g. *Haesselia*, Acrobolbaceae, Plagiochilaceae, Stephaniellaceae and Gymnomitriaceae (Gradstein et al., 2001; Schuster, 1974).

0 reaching the stem midline

1 transgressing the stem midline

17. Width of the leaf base

Differences at species level were found among the families.

0 less than 500 µm

1 more than de 500 µm

18. Arrangement of the leaf surface

Váňa et al. (2012) included this character in a taxonomic study of *Gongylanthus* and *Southbya.* Variation was found among species.

0 plane

1 concave

19. Foliar symmetry

Unlike other genera, *Stephaniella* and *Stephaniellidium* have asymmetrical leaves.

0 symmetrical

1 asymmetrical

20. Ornamentation of the cell wall of the leaf

Presence of leaf papillae has been reported in Arnelliaceae and some members of Southabyaceae and Gymnomitriaceae (Váňa et al., 2012). For the Stephaniellaceae, only *S. hamata* and *S. uncifolia* have papillae on the leaf.

0 smooth

1 punctate

2 papillose

21. Differentiation of postical margin of the leaf

All members of Southbyaceae, Stephaniellaceae have a differentiated postical margin.

0 not differentiated

1 differentiated

22. Arrangement of foliar margin

Unlike *Stephaniellidium* and Arnelliaceae, *Stephaniella* has an involute foliar margin.

This character has been widely used in the taxonomy of the genera of the Stephaniellaceae (Schmitt & Winkler, 1968; Schuster, 2002).

0 plane

1 wavy

2 involute

3 inflexed

4 recurved

5 reflexed

6 revolute

23. Areolation-type of the leaf cells

0 irregular

1 regular

24. Presence/absene of trigones

The presence or absence of trigones is an important taxonomic and phylogenetic character in leafy liverworts (Crandall-Stotler et al., 2009; Gradstein, Reiner-Drehwald, & Schneider, 2003; Schuster, 1966). Some species of Southbyaceae and Arnelliaceae have trigones, however, species of *Stephaniella* and *Stephaniellidium* lack them.

0 absent

1 present

25. Shape of the foliar apex

All members of Arnelliaceae and Southbyaceae have a rotunded apex, but in species of Stephaniellaceae and Gymnomitriaceae the apex shape is variable.

0 truncate

1 rotunde

2 obtuse

3 acute

4 acuminate

26. Presence/absence of falcate leaf apex

0 absent

1 present

27. Ending of the foliar apex

0 not divided

1 divided

28. Ornamentation of the leaf margin

All members of the Southbyaceae have an entire margin. In contrast, the members of Stephaniellaceae show variation in the ornamentation of the leaf margin.

0 ciliate

1 serrulate

2 crenulate

3 entire

29. Presence/absence of amphigastria

Stephaniellaceae and Gymnomitriaceae are characterized by the absence of amphigastria.

0 absent or rudimentary (a few cells)

1 present and well developed

30. Presence of paraphyllia on the stem

Presence of paraphyllia is an important character in the taxonomy of leafy liverworts (Gradstein et al., 2001). The Stephaniellaceae is the only family with paraphyllia of those included in this phylogenetic analysis.

0 absent

1 present

31. Dominant shape of the paraphyllia on stems

The Stephaniellaceae have filiform or/and lanceolate paraphyllia. The species of Stephaniellaceae have polymorphic shapes of the paraphyllia, but one shape was prevalent. Therefore, the ‘dominant (more common) shape of paraphyllia’ was coded.

0 filiform

1 foliose

32. Presence/absence of perianth

The perianth is considered an important taxonomic and phylogenetic character at the genus or family levels (Crandall-Stotler et al., 2009; Fulford, 1965). Members of Southbyaceae and *Stephaniella* develop the sporophyte within a perianth. In contrast, *Stephaniellidium* develops the sporophyte in a marsupium.

0 absent

1 present

33. Presence/absence of multilayer perianth

0 absent

1 present

34. Perianth exposure

Members of Southbyaceae have an immersed perianth. In contrast, *Stephaniella* has an exserted perianth.

0 immersed

1 exserted

35. Degree of fusion of the perianth

Schuster (2002) and Váňa et al. (2012) cited that *Stephaniella* has an inner pair of bracts, which are fused only at the base and that they are possibly homologous to a perianth. In this study, significant morphological differences were found between the external female bracts and the 'internal bracts' of *Stephaniella*. Thus, here it is hypothesized that the internal bracts of *Stephaniella* are homologous to the perianth. Of all genera included in the phylogenetic analysis, *Stephaniella* has a perianth fused only at the base.

0 fused only at the base

1 fused along

36. Presence/absence of longitudinal folds on the perianth

Stephaniella is the only genus included in this phylogenetic analysis that has longitudinal folds on the perianth (Schuster, 2002).

0 absent

1 present

37. Type of ornamentation on the cell walls of the perianth

This character has not been used in previous phylogenetic studies of the Southbyaceae and Stephaniellaceae.

0 smooth

1 papillose

38. Type of ornamentation at the perianth apex

This character was informative in the taxonomic and phylogenetic analyzes of Lejeuneaceae made by Gradstein et al. (2003).

0 ciliate

1 laciniate

2 dentate

3 serrulate

4 crenulate

5 entire

39. Perianth apical cells shape

Variation in the apical cells shape of the perianth was observed among some species of *Stephaniella* and in *Gongylanthus limbatus* (Herzog) Grolle & Váňa.

0 oblong

1 oblong-sinuose

40. Female bracts shape

The female bracts shape is an informative character in the taxonomy and phylogeny of leafy liverworts (Gradstein et al., 2001, 2003). This character could be useful at the generic level.

0 lingulate

1 oblong

2 ovate-oblong

3 ovate

4 quadrate-orbicular

5 orbicular

6 reniform

41. Presence/absence of longitudinal folds on the female bracts

Species of *Stephaniella* are the only ones that have plicate female bracts. Schuster (2002) considered the plicate female bracts as an important familiar character.

0 absent

1 present

42. Presence/absence of falcate female bracts apex

0 absent

1 present

43. Female bract apex shape

Generic variation was observed between *Stephaniella* and *Stephaniellidium. G. liebmannianus* is the only member of Southbyaceae that has obtuse female bracts apex.

0 rotund

1 obtuse

2 acute

3 acuminate

44. Ending of female bracts apex

Acrobolbus wilsonii Nees and *B. densifolium* are the only species included in this analysis that have divided female bracts apices. The character was included for the polarization tree.

0 not divided

1 divided

45. Ornamentation of female bracts margin

Inter specific variation was observed in the taxa included in this analysis. Schuster (2002) examined the female bracts morphology as a taxonomic character within *Stephaniella* and *Stephaniellidium.*

0 ciliate

1 laciniate

2 dentate

3 serrulate

4 crenulate

5 entire

46. Ornamentation of the cell walls on the female bracts

This character was not examined in previous taxonomic or phylogenetic studies of the Stephaniellaceae. *S. uncifolia* and some members of Arnelliaceae and Southbyaceae have papillose female bracts.

0 smooth

1 papillose

47. Presence of paraphyllia in the gynoecia

Stephaniella is the only genus included in this analysis that has paraphyllia in the gynoecia. The paraphyllia are usually longer than the stem.

0 absent

1 present

48. Presence/absence of marsupium

The marsupium has provided information at the genus and family levels in leafy liverworts (Crandall-Stotler et al., 2009; Heinrichs, Gradstein, Wilson, & Schneider, 2005; Schuster, 1966, 2002; Váňa et al., 2012). Some members of the Arnelliaceae, Southbyaceae and Stephaniellaceae have a marsupium.

0 absent

1 present

49. Marsupium-type

The marsupium-type was examined and illustrated by Schuster (1966). *Stephaniellidium* and other members of the Arnelliaceae and Southbyaceae are characterized by the presence of a *Calypogeia*-type marsupium. This character was coded as inapplicable (-) in those taxa that lack marsupium.

0 *Tylimanthus*-type

1 *Calypogeia*-type

50. Sporophyte capsule shape

The capsule shape is an informative character at the family and genus levels in leafy liverworts (Gradstein et al., 2003; Váňa et al., 2012). Only one immature capsule was observed in *S. paraphyllina.* Information on the capsule shape for the other Stephaniellaceae was obtained from the literature (Crandall-Stotler et al., 2009; Schuster, 2002; Winkler, 1969).

0 cylindrical

1 ellipsoidal

2 ovoid-globose

3 globose

51. Number of cell layers of the capsule wall

It is difficult to find sexual structures in Stephaniellaceae; we were unable to examine the capsule morphology in detail. Therefore, the information included here was obtained from the available literature (Crandall-Stotler et al., 2009; Schmitt & Winkler, 1968; Váňa et al*.*, 2012).

0 up 4-layered

1 3-layered

2 2-layered

52. Presence/absence of perigynium

0 absent

1 present

53. Shape of capsule tip

0 without acute tip rounded

1 with acute tip

CAPÍTULO 2. “TYPIFICATIONS OF SELECT SPECIES OF *STEPHANIELLA* (MARCHANTIOPHYTA: STEPHANIELLACEAE)”

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Typifications of select species of *Stephaniella* (Marchantiophyta: Stephaniellaceae)

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In a review of the literature, including a recent taxonomic revision of *Stephaniella* and *Stephaniellidium*, previous authors did not designate the nomenclatural types for three species of *Stephaniella* so that these names require lectotypification.

In the following paragraphs, I propose lectotypes for *Stephaniella boliviensis* (Stephani 1916: 182), *S. paraphyllina* (J.B. Jack 1894: 11) and *S. sleumeri* (K. Müller 1951: 177) based on materials received on loan from B, G, M and S herbaria. In designating these lectotypes the characteristics of the specimens were checked against the original description; the condition and size of the specimens were also considered for this purpose. The names of the species are listed in alphabetical order.

Stephaniella boliviensis Steph., *Bibliotheca Botanica* 87: 182, 1916.
Type:—BOLIVIA. Catena Yanakaka, ca. 4600 m, Jul 1911, *Th. Herzog 3750* (lectotype **[here designated]** M!, isolectotype G!, B!).

Note:—Stephani (1916: 182), in the original description, cited two syntypes, *Herzog 3750* and *Herzog 4794*. Váňa, in 1995, considered *3750* and *4794* at G to be isolectotype and isosyntype, respectively, but this information was not published (Váňa pers. comm.). Specimens of the remaining syntype, *Th. Herzog 4794*, were seen at G, M, and S.

Stephaniella paraphyllina J.B. Jack, *Hedwigia* 33: 11, 1894.
Type:—CORDILLERA ARGENTINO-BOLIVIANIS. Cienega, alpine region, 1873, *P.G. Lorentz s.n.* (lectotype **[here designated]** G-00120479!, isolectotype G!, M!).

Note:—From Paul G. Lorentz’s collections of 1873, Jack (1894) described the genus *Stephaniella* with *S. paraphyllina* as the type species. The type locality (Cienega in alpibus Argentino-Bolivianis, in solo glaresolutoso) was cited, but no type specimens were mentioned.

Original material of *Stephaniella paraphyllina* (G00120478, G00120479, G00115491, G; M-0182810, M), collected by Lorentz in 1873, was examined. Schmitt and Winkler (1968) considered the specimen at M to be a syntype, but it is not clear if this specimen is part of the same or different gatherings because Lorentz did not number his gatherings. Nonetheless, for nomenclatural purposes I conclude that all of the above original elements are part of a single gathering. It should be noted that the moss collection at B, which likely contained Lorentz’s best material, was destroyed (Stafleu & Cowan 1981: 157). At least one specimen in the Lorentz’s collection at G (G-00115491) was likely examined by Jack as it was stamped with his herbarium name.

Stephaniella sleumeri Müll. Frib., *Revue Bryologique et Lichénologique* 20: 177, 1951.
Type:—ARGENTINA. Prov. Tucumán: Dep. Tafí, La Cienega, Morro de las Aguadas, ca. 2,800 m, 28 Jan 1950, *H. Sleumer s.n.* (lectotype **[here designated]** S-B47665!, isolectotype B!, S!).

Note:—Müller (1951) only cited the type locality in the protologue, but did not cite a type specimen. Specimens with the same collecting data as those given in the original description are deposited at B and S and I conclude that

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these specimens represent a single gathering. No additional type information was provided when *Stephaniellidium sleumeri* (Müll.Frib.) S. Winkl. ex Grolle, *Acta Botanica Fennica* 121: 38. 1983, was proposed.

Notes

Stephaniella hamata Steph., *Bulletin de l'Herbier Boissier ser. 2*, 1: 1024, 1901.
Type:—ARGENTINA. Córdoba, *P.G. Lorentz s.n.* (lectotype [Grolle in 1967, on herbarium label] G-00069943!).

Stephani (1901) cited specimens from Argentina and Brazil in the protologue, but did not designate a type. Grolle, in 1967, designated *Lorentz s.n.* (G-00069943) as the lectotype on a label, but apparently did not publish his choice (Váňa pers. comm.). Schmitt and Winkler (1968: 126) subsequently formally proposed the lectotype.

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CAPÍTULO 3. "TAXONOMIC REVISION OF THE FAMILY STEPHANIELLACEAE (MARCHANTIOPHYTA)"

Taxonomic revision of the family Stephaniellaceae (Marchantiophyta)

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Taxonomic revision of the Stephaniellaceae

Key words: Stephaniellaceae, *Stephaniella*, *Stephaniellidium*, liverworts, paraphyllia.

Abstract – Stephaniellaceae (R.M. Schuster) R.M. Schuster is a small family that occurs in the high elevations of the Americas; recent studies confirm that it is a monophyletic group. This taxonomic revision is based on such supporting analyses and on the examination of herbarium specimens from various parts of its range, and field work of 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.

INTRODUCTION

Schuster (2002) was the first to recognize the family Stephaniellaceae, a group of small and poorly known liverworts from high elevations. A recent phylogenetic analysis by Juárez-Martínez *et al.* (2015) using morphological data supports its taxonomic status.

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.,* 2015). A phylogenetic analysis by Juárez-Martínez *et al.* (2015) and the examination of herbarium specimens concluded 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.

In addition to the species cited above, Arnell (1961) 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*., 2015). 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 author in Ajusco volcano (Distrito Federal); 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. Schuster) R.M. Schuster, 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**.

Androecium sometimes reddish tinged, male bracts poorly differentiated from vegetative leaves, antheridia 2-3(4-6) per bract, long-stalked, stalks 2-seriate (see Schuster, 2002). **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.

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.,* 2015) (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 352a,* 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.

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. **Androecium** as for the family. **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. **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.* (2015) 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.

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

Figs. 3-30

Type: Cordillera Argentino-Bolivianis. Cienega, alpine region, 1873, *Lorentz s. n.*, (lectotype G-00120479, G!, designated by Juárez-Martínez, 2014; isolectotype G!, M!).
=*Stephaniella boliviensis* Steph., Bibliotheca Botanica 87: 182, 1916, ***syn. nov.***
Type: Bolivia. Catena Yanakaka, 1911, *Herzog 3750* (lectotype, M!, designated by Juárez-Martínez, 2014; isolectotype G!, B!).

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 x 6-14 (-16) µm. Medullary cells shortly oblong to hexagonal, yellow-pale, thick-walled, but smaller than cortical cells, 10-18 (-20) µm x (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 x 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 x 10-20 µm; mid-leaf cells oblong-rectangular, rhomboid, thick- or thin-walled, (18-) 20-30 (-38) µm x (8-) 10-14 (-18) µm; postical marginal cells elongate-rectangular, thin- to thick-walled, (22-) 26-40 (-52) µm x 6-12 (-14-16) µm, L:W ratio 3-6:1. Leaf cell walls smooth. **Androecium** not seen. **Gynoecia** ~2.2 mm high. **Female bracts** 2-3 pairs, the inner ovate-falcate, 1.4 mm x 1.1 mm, with entire margin, smooth, and apex acute; basal cells rectangular, quadrate, thin-walled, 22-38 (-40) µm x 12-20 µm;

middle cells oblong, thin-walled, but thicker than basal cells, (20-) 26-38 μm x 14-20 μm; apical cells oblong, not sinuose, thick-walled, 24-30 (-36) μm x 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 x (10-) 12-18 μm; middle cells oblong, thin-walled, 22-40 μm x 14-22 μm; apical cells oblong, no sinuose, thin-walled, 34-48 (-52) μm x 10-20 μm. Cell walls of the perianth smooth. **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 4600 masl; in Brazil and Sierra Nevada in Colombia, it has been found from 2100 to 2700 masl. *S. paraphyllina* occurs in paramos and puna, and in places where larger vegetation 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 sp.* The current distribution of *S. paraphyllina* in the northern of Argentina, Brazil and South Africa suggests that it is a relictual taxon that was widely distributed in Gondwana and its populations became isolated with the break-up of Pangea, in pre-Cretaceous times. Its continental distribution may have been achived by gametophyte fragments dispersed by regional wind currents.

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, 120b* (MEXU). La Joya, extremo SW del volcán Iztaccíhuatl. 8 km al N de Paso de Cortés, 3963 m, *A. Cárdenas S. 6754b, 6756, 6757* (MEXU), *C. Juárez-Martínez 110b* (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, 352b* (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, G!), (isolectotype, G00120478, G00115491, G!), (isolectotype, M-0182810, M!). **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 24736a* (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* (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), *1020a* (NY), *S. Winkler C395* (M). S-flanke der Sierra Nevada de Santa Marta, oberhalb von San Sebastian, sparliches Bewuchsmit Ericaceen, 2700 m, *S. Winkler C206a* (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 6207a* (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 12077a* (MO). **Mérida:** Sierra de Santo Domingo, páramo de Mucuchies: Passo El Aguila an der Straβe Mérida-Valera, 3900 m, *H. Hertel 10436* (M).

The shape of the leaves of *Stephaniella paraphyllina* shows high variation (Figures 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 the stem apex or in young stems. The rotund leaves are as wide as long, or slightly wider than long (450-550 µm x 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*. 2015) (Figs. 3-17). Accordingly, the synonymy of *S. boliviensis* under *S. paraphyllina*, as proposed Grolle (1967, on a specimen label) is accepted.

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

Figs. 31-49

Type: Argentina. Córdoba, *Lorentz s. n.,* (lectotype G-00069943, G!, designated by Grolle in 1967, on herbarium label).

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 x 10-12 (-16) µm. Medullary cells shortly oblong, brown, thin-walled, 16-18 µm x (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 x 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, rhomboid, thin-walled, (18-20-) 24-34 (-38) µm x (10-) 14-18 (-20) µm; mid-leaf cells oblong-rectangular, quadrate, slightly thick-walled (14-) 20-30 (-34) µm x (10-) 12-16 (-22) µm; postical marginal cells strongly elongate, some of them linear, strongly thick-walled, 20-50 µm x 4-12 µm, L:W ratio 4-5 (-6):1. Cell walls of the leaf slightly papillose, usually near the apex. **Androecium** not seen. **Gynoecia** ~900 µm high. **Female 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 x 12-16 (-18) µm; middle cells shortly oblong, thin-walled, (22-) 26-30 (-38) µm x 10-16 µm; apical cells elongate to linear, strongly thick-walled, 20-26 (-30) µm x 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 x 14-18 (-22) µm; middle cells oblong-elongate, thin-walled, 24-32 µm x 12-18 µm; apical cells oblong-elongate, sinuose, thick-walled, (20-) 30-42 (-50) µm x 8-10 µm. Cell walls of the perianth smooth. **Sporophyte** not seen.

Distribution and ecology. *Stephaniella hamata* is only known from Argentina, Bolivia and Peru (Figure 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*. (2015) 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: Colombia, Páramo de la Rusia, and der Straβe von Duitama, 1967, *S. Winkler* C513, Herbarium S. Winkler.

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 x 8-12 (-16) µm. Medullary cells shortly oblong, yellow-pale, thin-walled, (10-) 12-16 µm x 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 x 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 leaf cells rhomboid and/or hexagonal, thin-walled, 20-26 (-32) µm x (8-) 10-14 µm; mid-leaf cells oblong, thin- or slightly thick-walled, (18-) 24-30 (-36) µm x 10-18 µm; postical marginal cells strongly elongate, thick-walled, (26-) 28-40 (-46) µm x 6-10 (-12) µm, L:W ratio 3-5 (-7). Cell walls of the leaf smooth. **Androecium** not seen. **Gynoecia** ~1 mm high. **Female bracts** 2 pairs, the inner ovate-falcate, 900-1000 µm x 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 x 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 x 10-14 µm. **Paraphyllia of the gynoecia** usually filiform, (160-) 200-300 (-370) µm long, (8-) 11-16 (-21) cells high, 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 x (12-) 14-20 µm; middle cells elongate-rectangular, thin- or thick-walled, (20-) 22-32 µm x (-6) 8-12 µm; apical cells elongate-rectangular, not sinuose, thin- or thick-walled, 34-48 (-60) µm x (6-) 8-14 (-16) µm. Cell walls of the perianth smooth. **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 where grasses grow predominately, above 3400 masl. It grows on soil, in exposed and humid sites.

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 339b, 341a* (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. Santano 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 1020b* (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 x 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). The extent of variation in these characters is also expressed in the variation of the leaf shape in this species of *Stephaniella.*

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: Argentinien, *Lorentz s. n.,* Herbar Stephani (M).

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 x 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 x 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 x (8-) 10-16 µm; mid-leaf cells oblong-rectangular or rhomboid, thick-walled, (16-) 18-28 µm x (6-) 8-14 µm; postical marginal cells strongly elongate, thick-walled, (22-) 26-46 (-58) µm x (4-) 6-10 (-12) µm; L:W ratio 3-7 (-8):1. Cell walls near leaf apex papillose, the remaining smooth. **Andrecium** not seen. **Gynoecia** ~750 µm high. **Female bracts** 2 pairs, the inner ovate-falcate, 720 µm x 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 x 10-18 µm; middle cells elongate-rectangular, elongate-rhomboid, slightly thick-walled, 30-40 µm x 10-14 µm; apical cells oblong-elongate, thick-walled, (26-) 28-42 (-44) µm x 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 x 8-12 (-14) µm. Middle cells oblong-rectangular, thin-walled, (24-) 26-40 (-44) µm x 8-12 µm. Apical cells elongate, sinuose, thick-walled, 26-46 (-54) µm x (6-) 8-10 (-12) µm. Cell walls of the perianth smooth. **Sporophyte** not seen.

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

Specimens examined. ARGENTINA. *Lorentz s. n.* (G00265372*,* G, M-0182816, M).
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 (Fig. 80-81).

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

***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 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. **Androecia** with several antheridia per bract, the latter concave, morphologically similar to stem leaves. **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. **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: Prov. Tucumán: Depto. Tafí, La Ciénega, Morro de las Aguadas, 1950, *H. Sleumer s.n.,* (lectotype B47665, S!, designated by Juárez-Martínez, 2014; isolectotype B! S!).

Plants postrate. **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 x 8-14 (-18) µm. Medullary cells oblong to isodiametric, thin-walled, hyaline, (20-) 30-40 (-50) µm x 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-) 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 x (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 x 16-36 (-46) µm; mid-leaf cells oblong-rectangular, isodiametric, thin-walled, (24-) 28-44 (-52) µm x (16-) 20-30 (-38) µm; postical marginal cells strongly elongate to linear, thin-walled, (40-) 44-90 µm x 10-20 (-24) µm, L:W ratio 3-5 (-6):1. **Oil bodies** 4-8 per cell, brown, ellipsoidal, granular. **Androecium** as for the genus. **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 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 2100 to 4420 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 110a, 112, 114* (MEXU), *A. Cárdenas S. 6754a, 6755* (MEXU). Parque Nacional Iztaccíhuatl-Popocatépetl, 3900 m, *C. Juárez-Martínez 319, 322, 323, 324, 326, 327, 332, 329, 331, 333, 334, 337, 338, 339a, 340, 341b* (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 120a* (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 gen 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, 352a* (MEXU). **ARGENTINA. Prov. Tucumán:** Depto. Tafi. La Ciénega, Morro de las Aguadas. 2800 m, *H. Sleumer s. n.* (B47665, B47664, S!) (B 30 0012078, B!). **BOLIVIA. Depto. La Paz:** Murillo, mina San Francisco, NE de Palca, 4380 m, *S. Churchill, M. Cano & J. Jiménez 24736b* (MO). **COLOMBIA.** S-flanke der Sierra Nevada de Santa Marta, oberhalb von San Sebastian, 2700 m, *S. Winkler C206b* (S). **PERU. Depto. Cajamarca:** Prov. Cajamarca. Ort. Las Lagunas, 3900 m, *P. & E. Hegewald 6207b* (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 12077b* (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*. 2015).

In some Mexican specimens of *Stephaniellidium sleumeri* (*Juárez-Martínez et al. 313, 314, 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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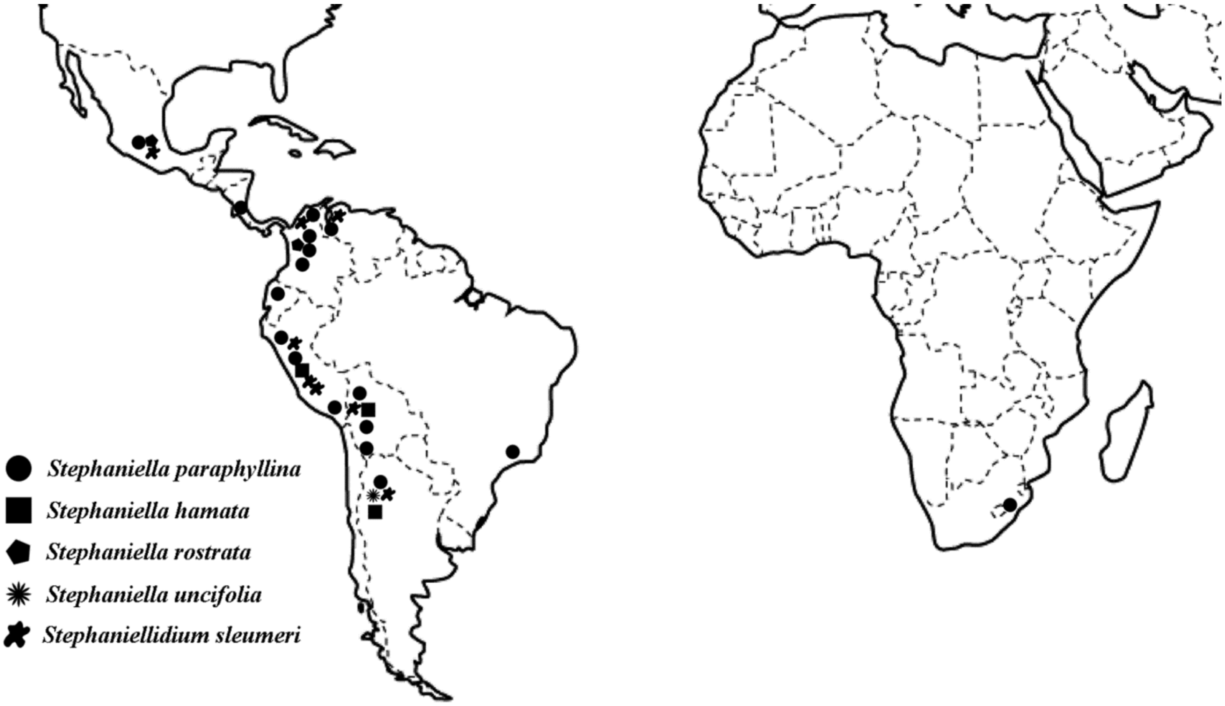

Fig. 1. Distribution map of the Stephaniellaceae and its species.

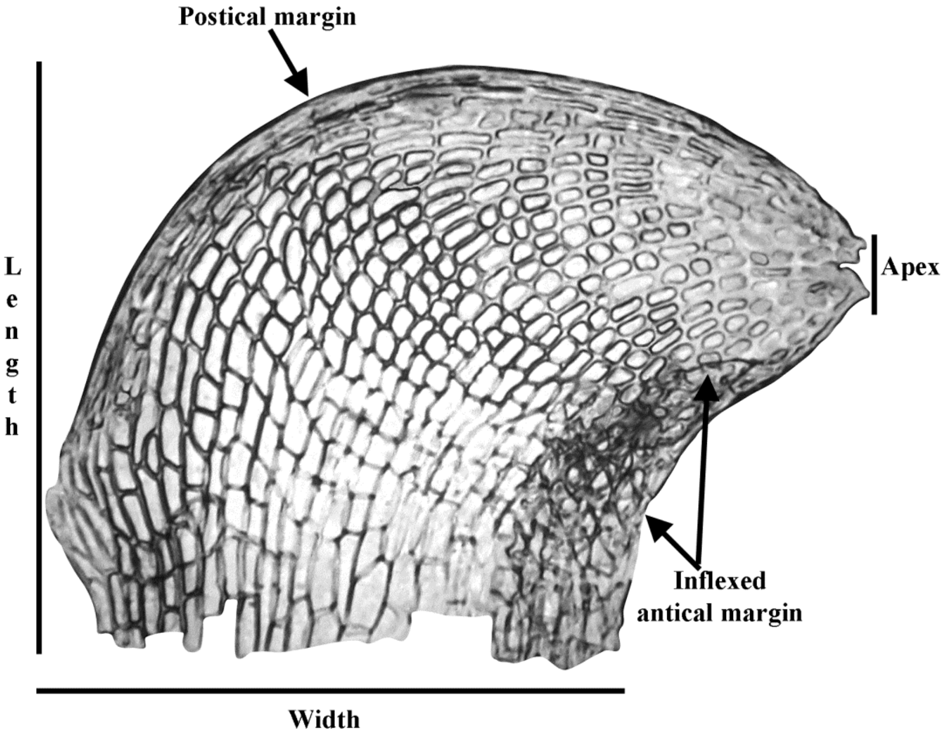

Fig. 2. Diagram of the leaf of *Stephaniella* indicating its morphology and where the measurements were obtained.

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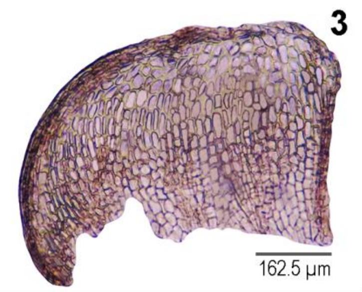

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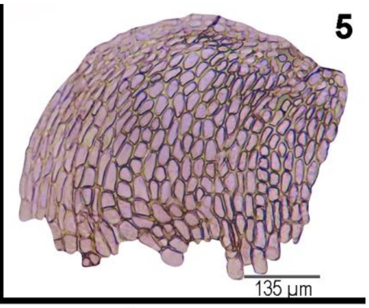

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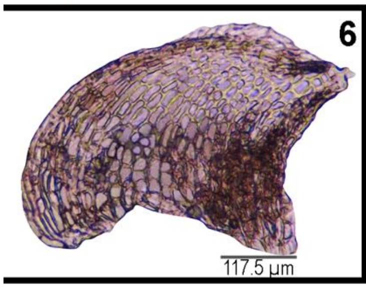

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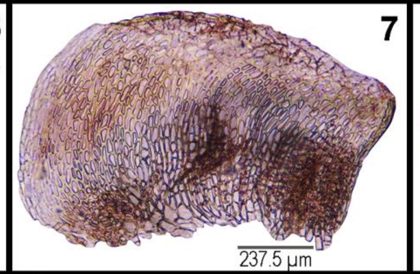

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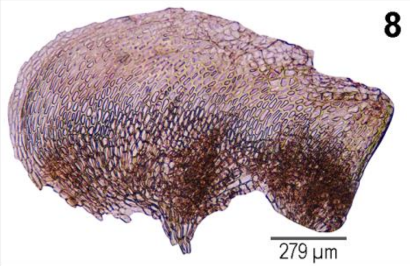

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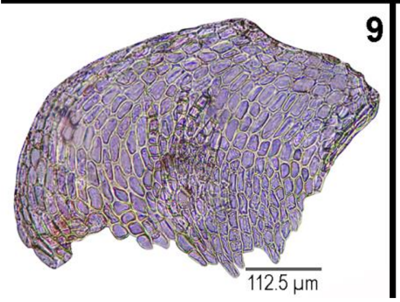

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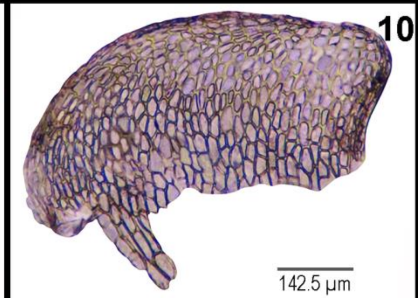

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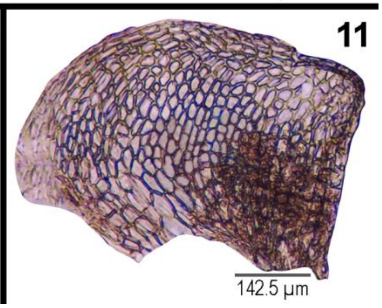

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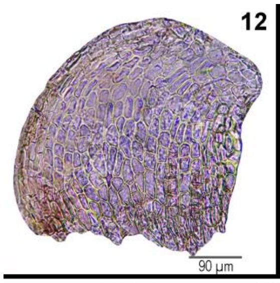

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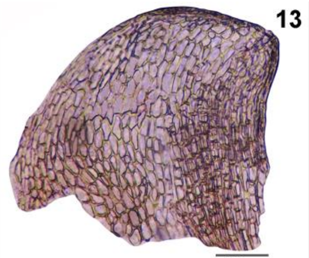

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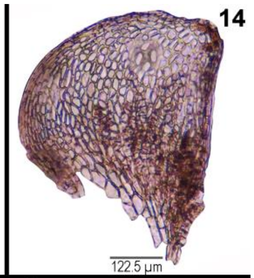

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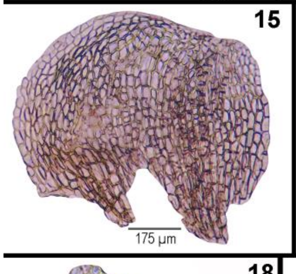

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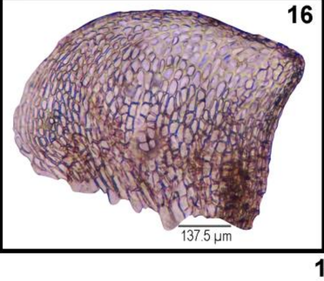

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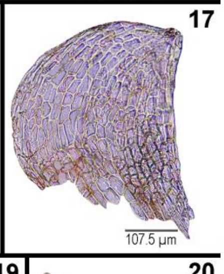

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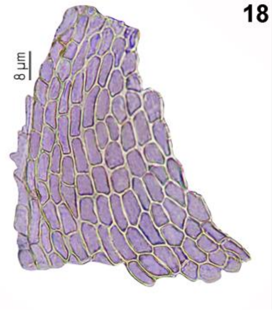

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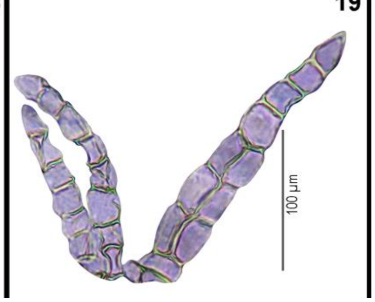

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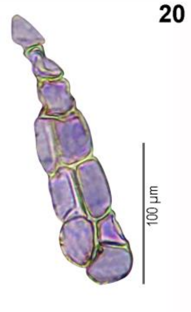

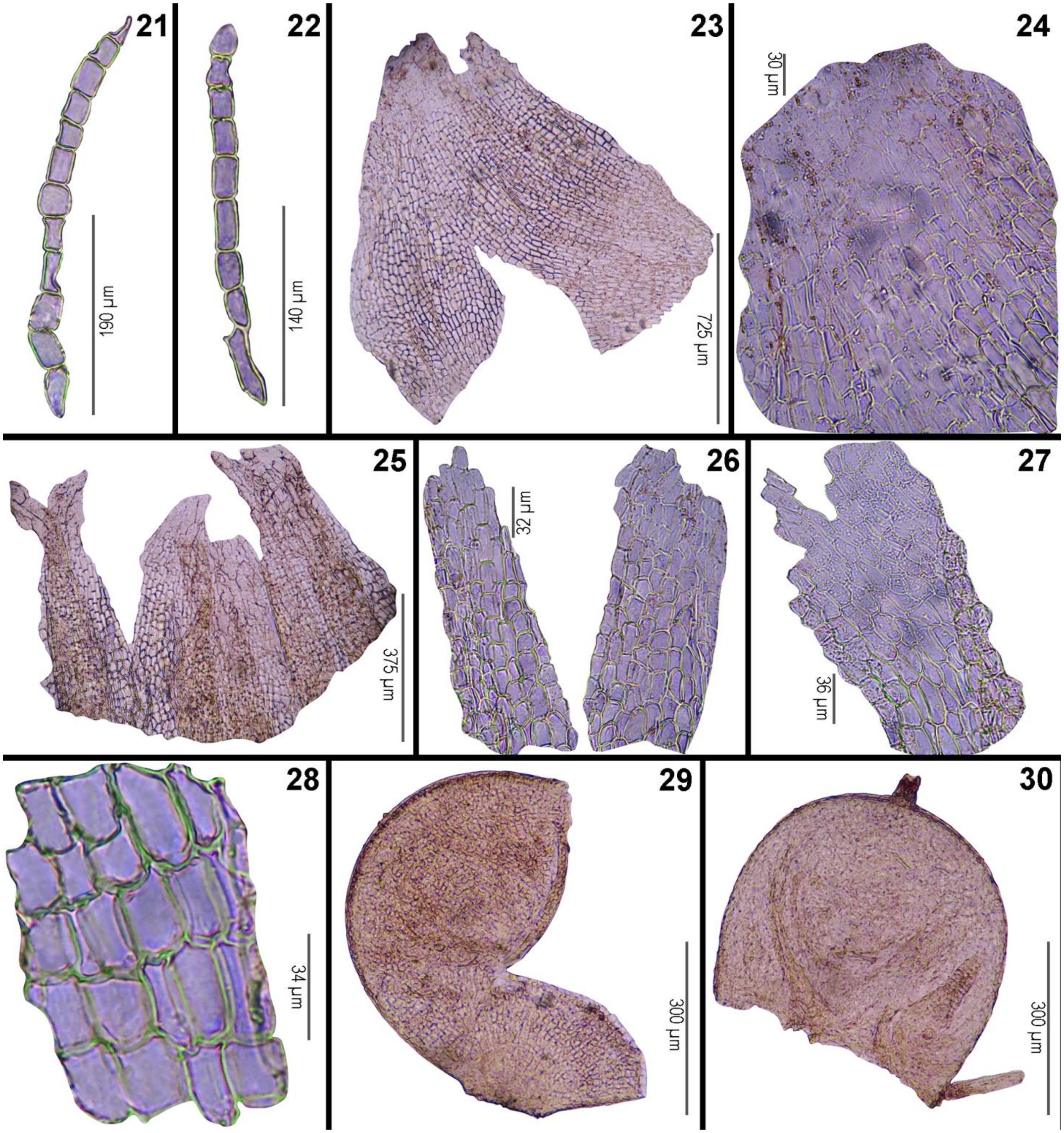

Figs. 3-30. *Stephaniella paraphyllina* J.B. Jack. **3-17.** Stem leaves. **18.** Marginal postical cells of the leaf. **19-22.** Paraphyllia of the stem. **23.** Female bract. **24.** Apical and median cells of the female bract. **25.** Perianth. **26.** Perianth apical cells. **27.** Perianth basal 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* G00115491, G).

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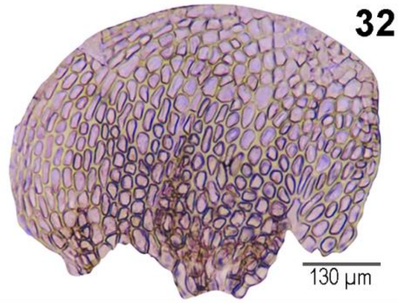

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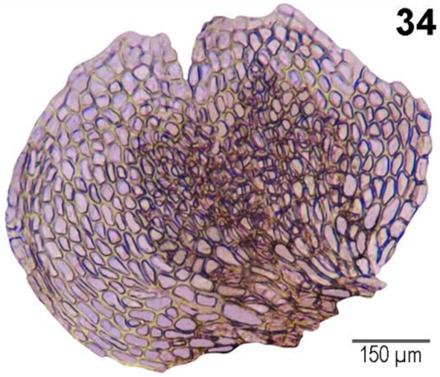

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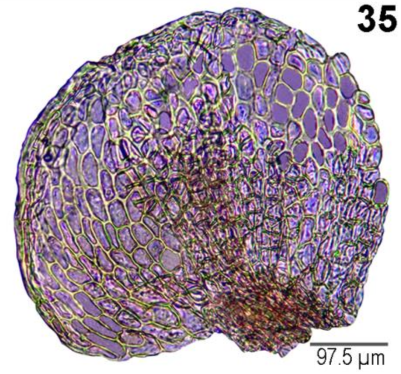

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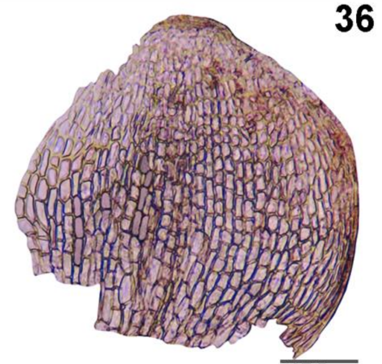

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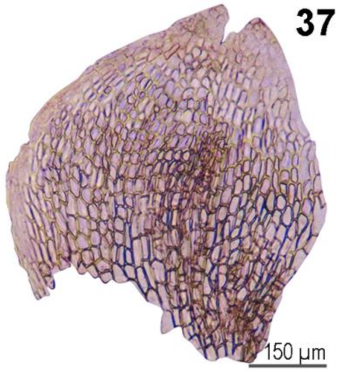

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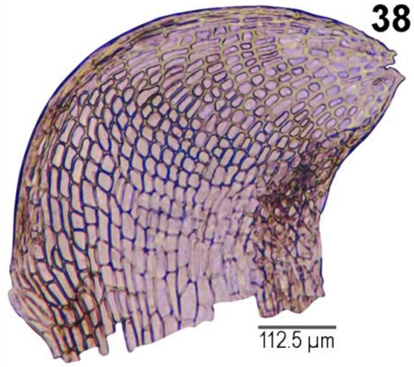

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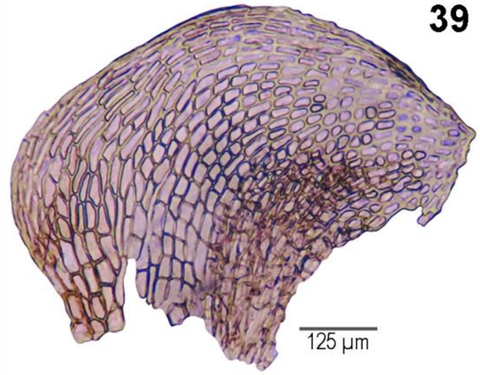

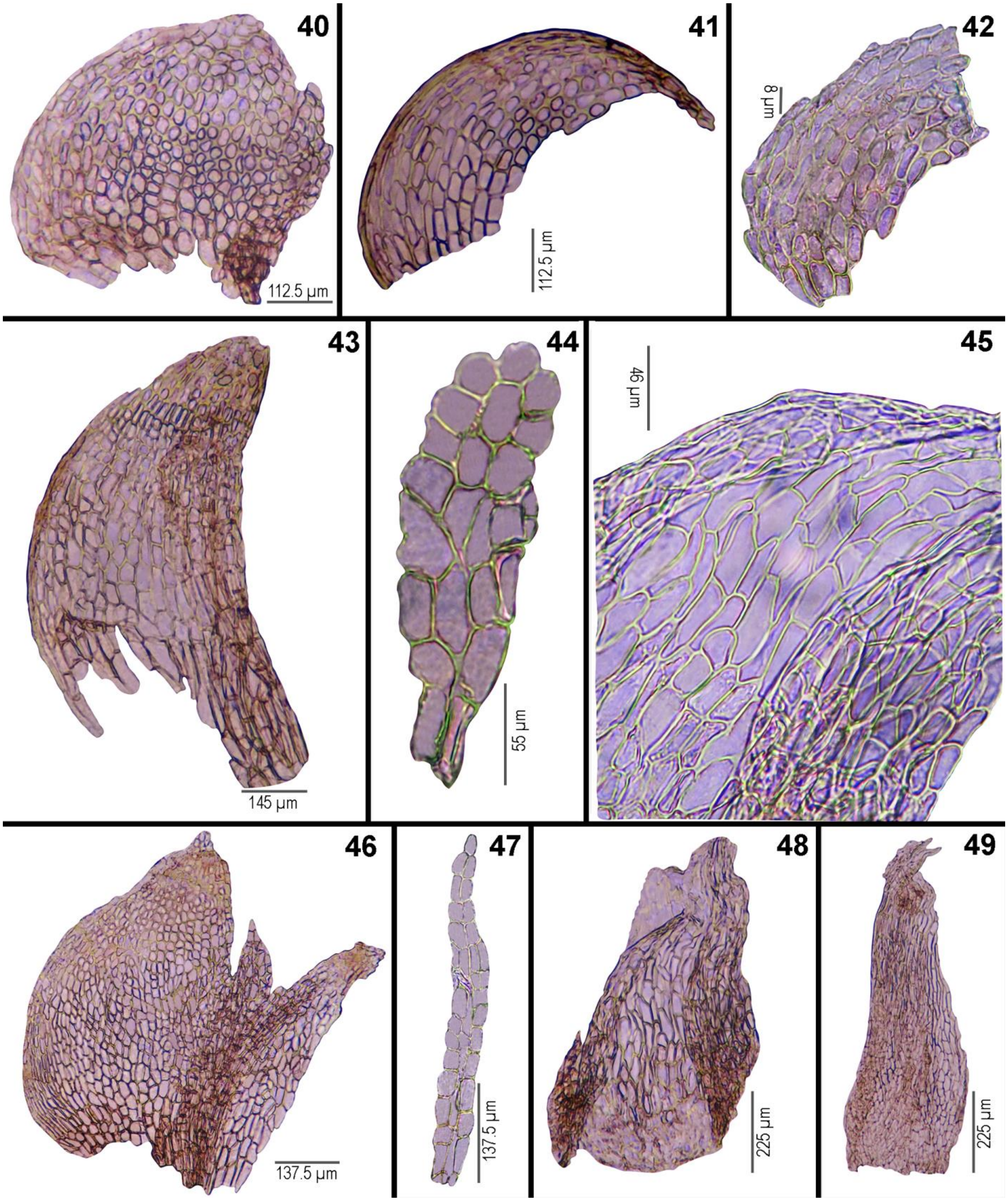

Figs. 31-49. *Stephaniella hamata* Steph. **31-40, 43.** Stem leaves. **41, 42.** Marginal postical cells of the leaf. **44.** Parahypllia of the stem. **45.** Perianth median cells. **46.** Female bract. **47.** Paraphyllia of the gynoecia. **48, 49.** Perianth. (Figs. 33, 38, 39, 41, 49, *Lorentz s.n.* G-00069943, G).

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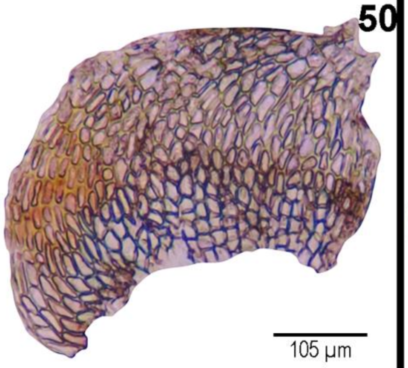

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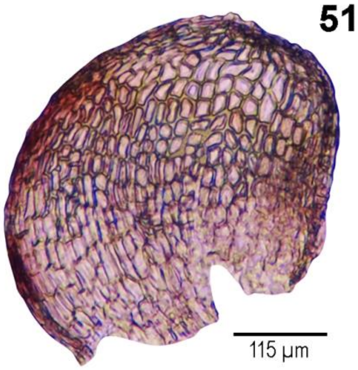

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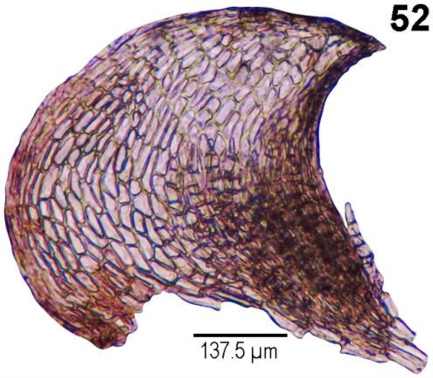

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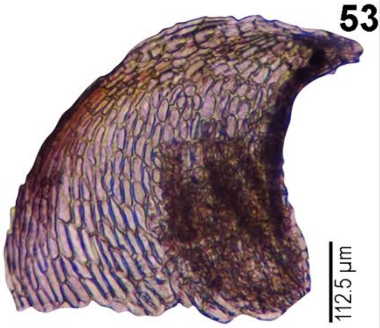

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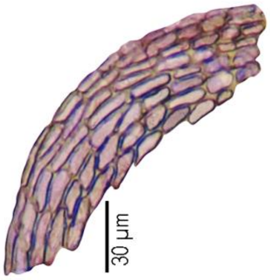

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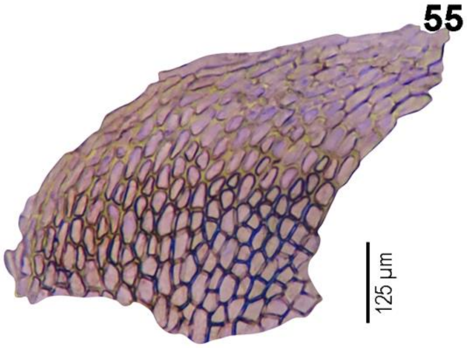

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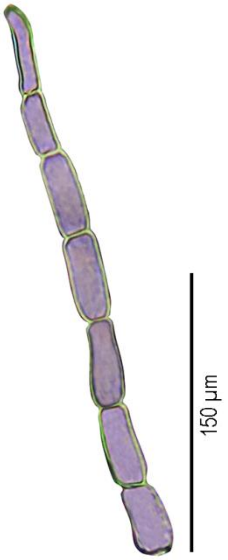

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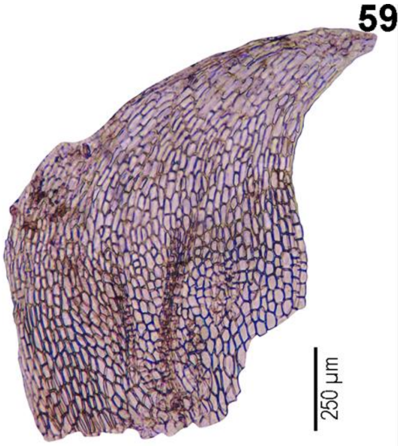

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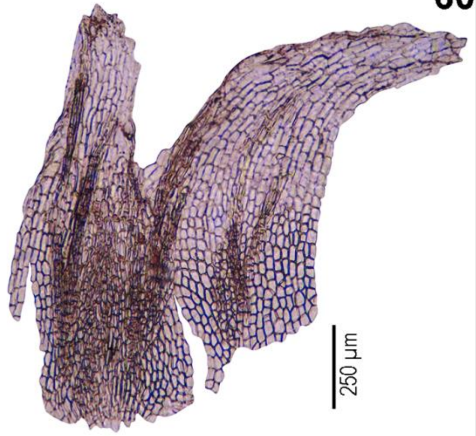

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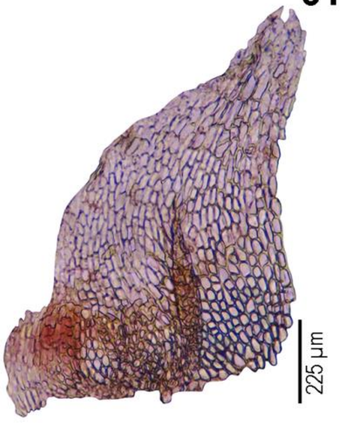

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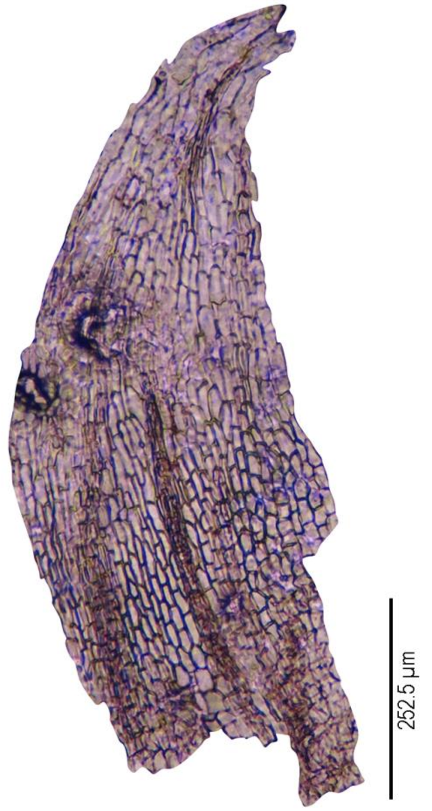

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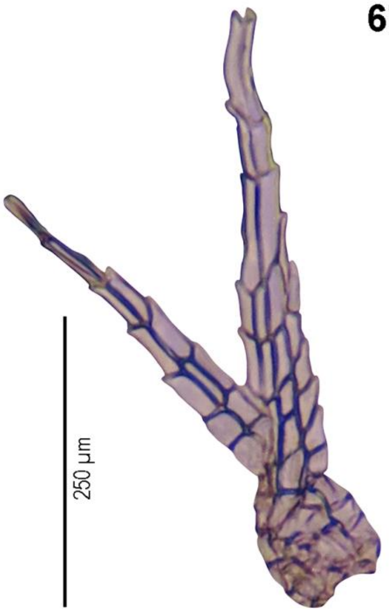

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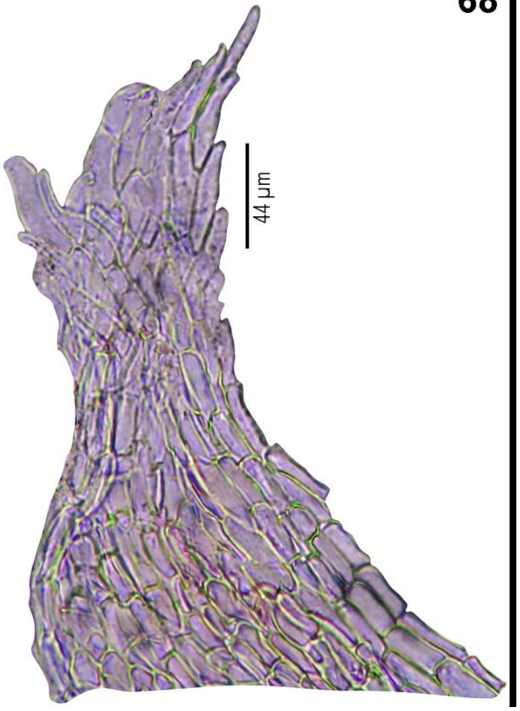

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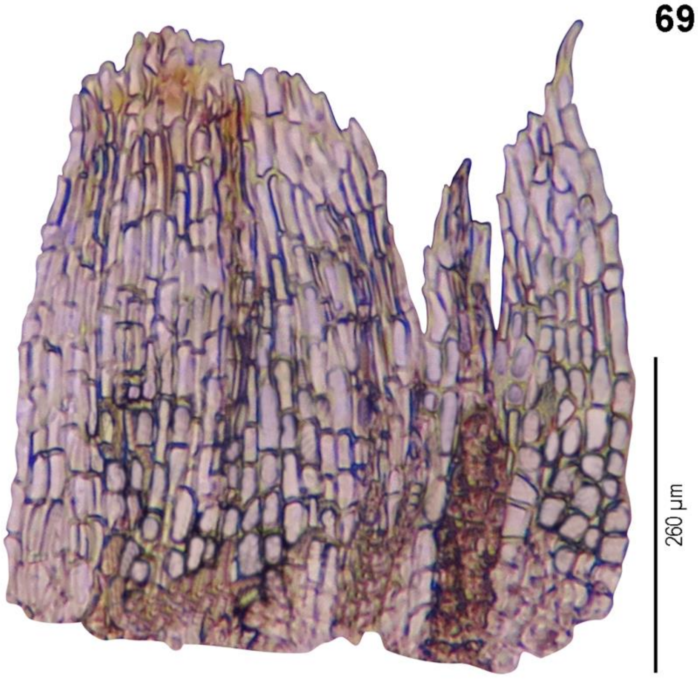

Figs. 50-69. *Stephaniella rostrata* U. Schmitt. **50-53, 55, 57, 58.** Stem leaves. **54.** Marginal postical cells of the leaf. **56.** Paraphyllia of the stem. **59-63.** Female bract. **64, 67.** Paraphyllia of the gynoecia. **65, 66.** Perianth. **68.** Perianth apical cells. **69.** Perigynium. (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, *Gradstein & Santano 4252*, B*;* Figs. 57, 58, 64, 65, 66, 68, 69, *O. Rangel & A. Cleef 1020*, NY).

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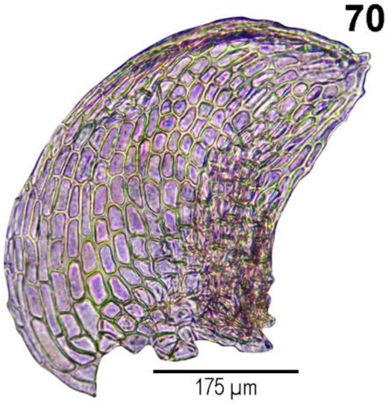

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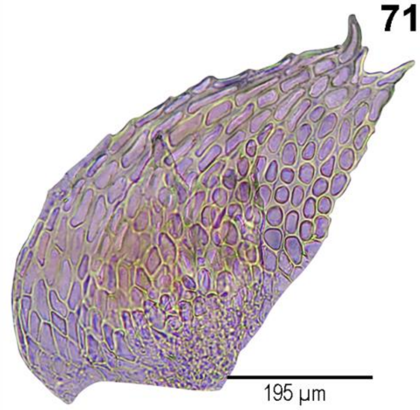

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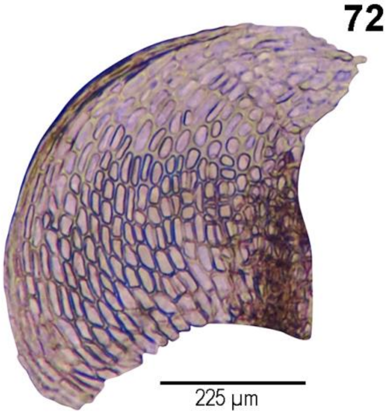

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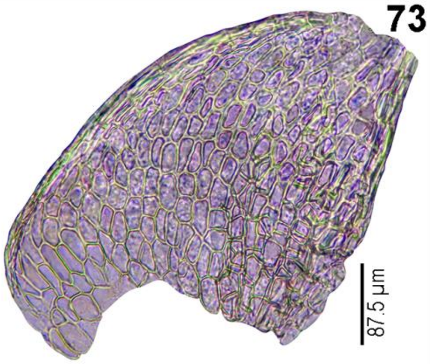

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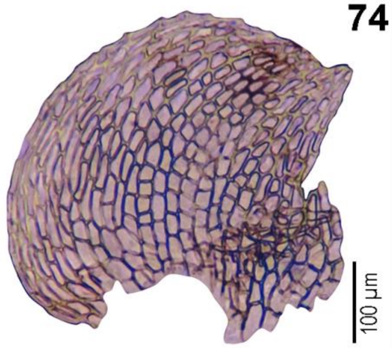

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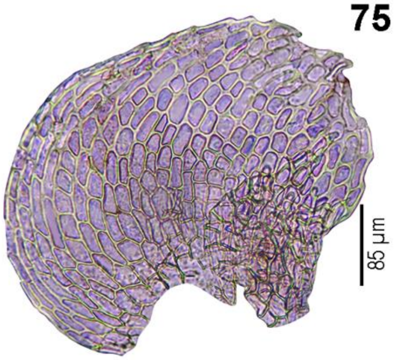

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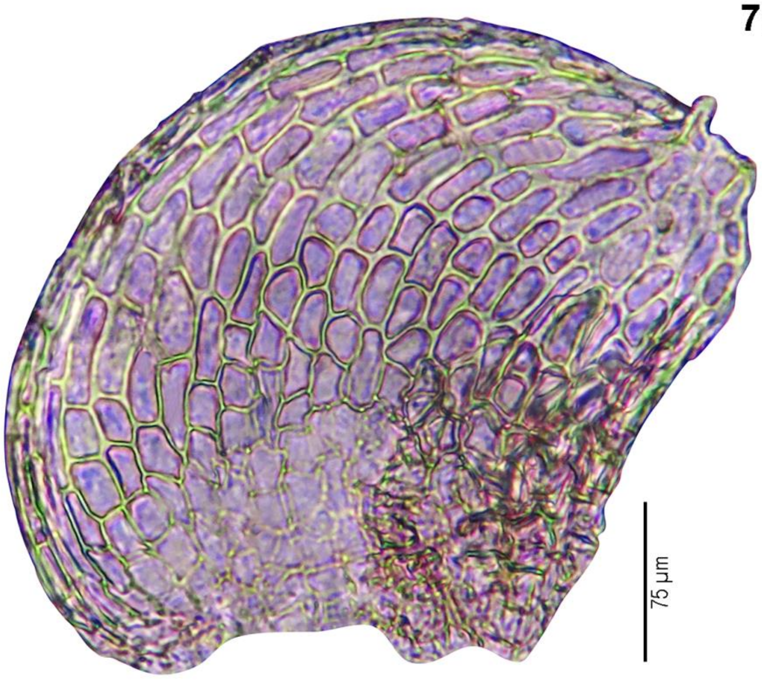

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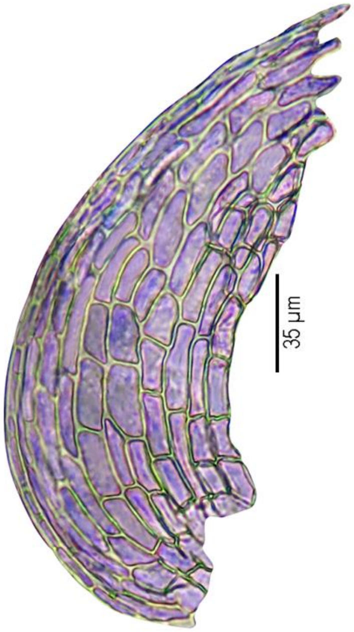

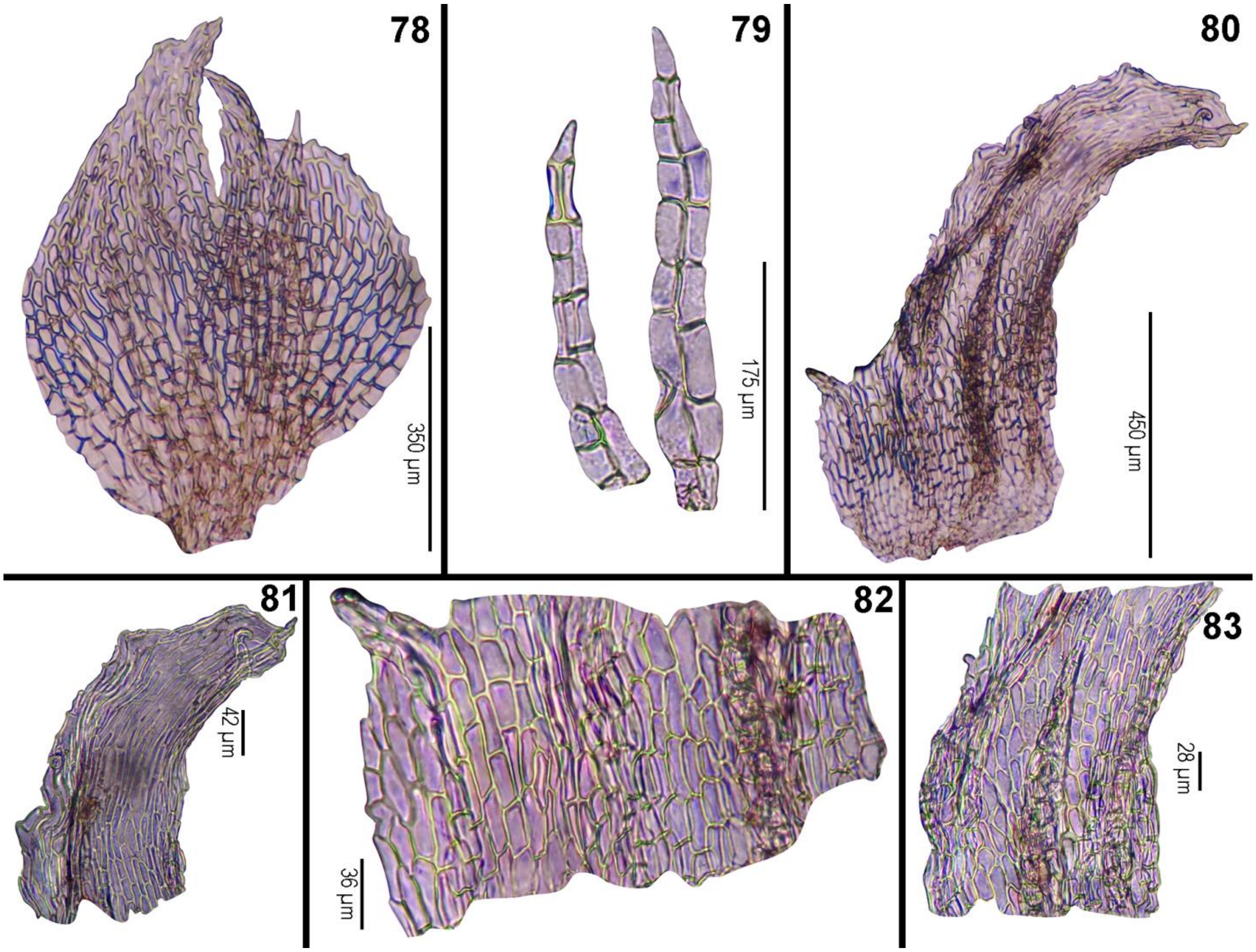

Figs. 70-83. *Stephaniella uncifolia* S. Winkler. **70-76.** Stem leaves. **77.** Marginal postical cells of the leaf. **78.** Female bract. **79.** Paraphyllia of the gynoecia. **80, 81.** Perianth. **82.** Perianth basal cells. **83.** Perianth median cells. (Figs. 73-77, *Lorentz s.n.* M-0182816, M).

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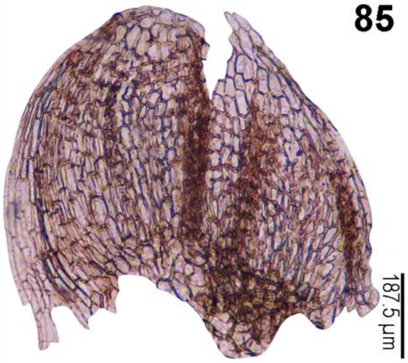

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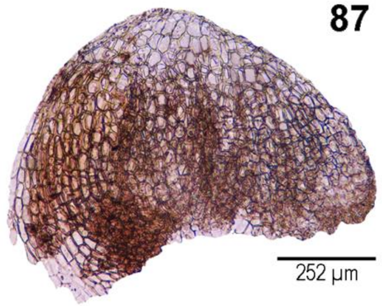

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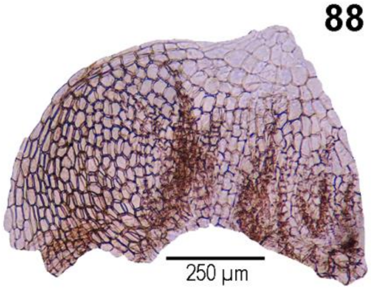

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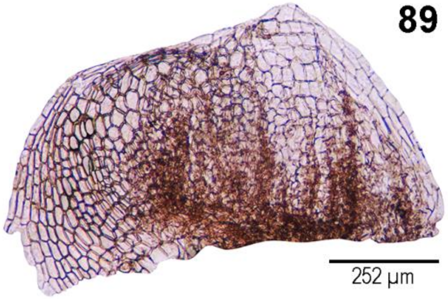

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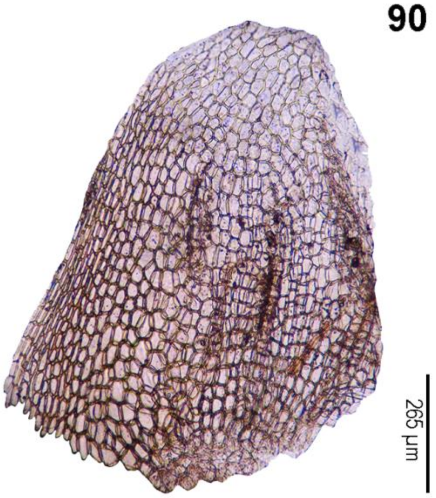

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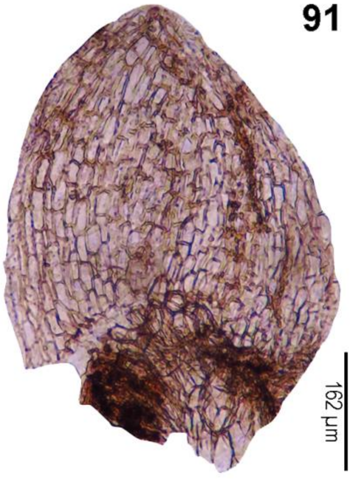

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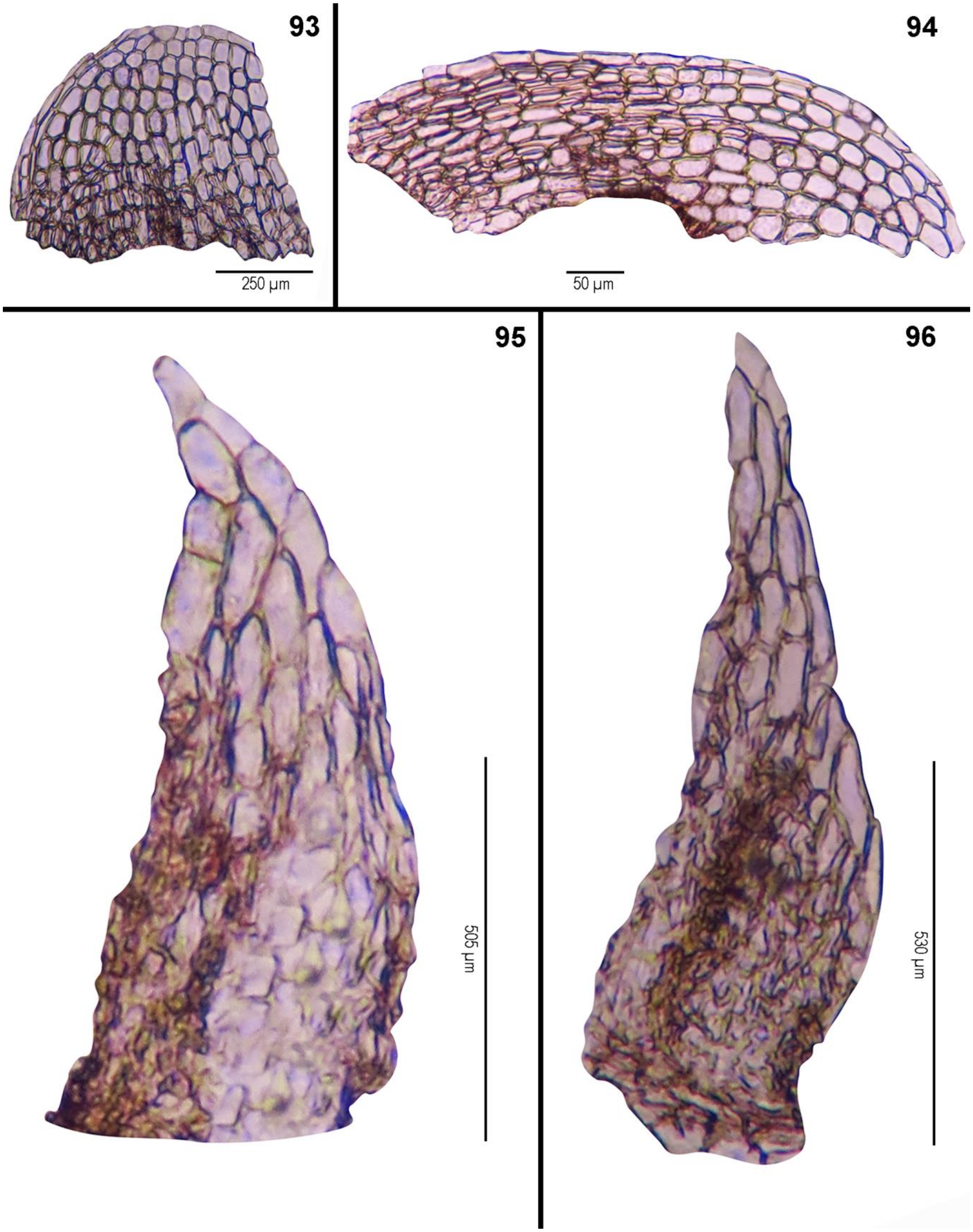

Figs. 84-96. *Stephaniellidium sleumeri* (Müll. Frib.) S. Winkler ex Grolle. **84-91.** Stem leaves. **92-94.** Marginal postical cells of the leaf. **95-96.** Paraphyllia of the stem. (Figs. 85, 91, 95, 96, *Sleumer s.n.* B-47665, S).

ANEXO 1. “BIODIVERSIDAD DE ANTHOCEROTOPHYTA Y MARCHANTIOPHYTA EN MÉXICO”

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Biodiversidad de Anthocerotophyta y Marchantiophyta en México

Biodiversity of Anthocerotophyta and Marchantiophyta in Mexico

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Resumen. No existe suficiente información florística sobre los antocerotes y las hepáticas mexicanas, pero en una evaluación preliminar se reconocen 9 especies de Anthocerotophyta, incluyendo 3 endémicas de México. Entre las Marchantiophyta mexicanas se reconocen 592 especies y variedades que incluyen 105 endémicas. Los números iniciales se modificarán substancialmente con los datos de revisiones y monografías recientes que incluyan taxa de la flora mexicana.

Palabras clave: antocerotes, diversidad briológica, hepáticas, México.

Abstract. There is insufficient floristic information on Mexican hornworts and liverworts, but a preliminary evaluation recognizes 9 species of Anthocerotophyta, including 3 Mexican endemics. There are 592 species and varieties of Mexican Marchantiophyta, including 105 endemic taxa. These preliminary numbers will certainly change with data from recent taxonomic revisions and monographs that contain information on the Mexican flora.

Key words: bryological diversity, hornworts, liverworts, Mexico.

Introducción

Las Anthocerotophyta (antocerotes) y las Marchantiophyta (hepáticas) son grupos de plantas casi desconocidos en México. En ausencia de especialistas nacionales, la mayor parte de los datos acerca de estos grupos provienen de investigaciones externas, por lo que resulta difícil determinar con certeza el número de especies en nuestra flora, sus áreas de distribución o los taxa endémicos. Además de su pequeño tamaño y escaso uso práctico o valor comercial, sin un microscopio, son plantas poco vistosas. No obstante, en muchas comunidades vegetales tienen un alto valor ecológico y con frecuencia se les considera trascendentales en la colonización de la Tierra y en la evolución de otras plantas terrestres (Vanderpoorten y Goffinet, 2009; Villarreal et al., 2010).

En sistemas de clasificación antiguos, los antocerotes y las hepáticas se clasificaban, junto con los musgos, dentro del Phylum Bryophyta (véase Watson, 1964: 22-23). En los esquemas modernos, con el apoyo de datos moleculares, se les reconoce como phyla independientes, pero sus relaciones filogenéticas todavía parecen inciertas (Goffinet, 2000). Es probable que la semejanza superficial entre los gametofitos de los antocerotes y los de formas taloides de hepáticas sea responsable de la confusión, pues aún morfológicamente,hay profundas diferencias entre estos grupos de plantas. En seguida se ofrecen datos generales sobre la identidad de cada uno.

Los antocerotes y las hepáticas tienen un ciclo de vida haplo-diplobióntico, heteromórfico, con el gametofito haploide y el esporofito diploide. Los detalles de su morfología pueden consultarse en Crum (2001), Delgadillo y Cárdenas (1990), Renzaglia et al. (2009), o en Schofield (1985), entre otros, pero se resumen en los párrafos que siguen.

El gametofito de los antocerotes es una lámina lobulada verde obscuro de unos cuantos centímetros de diámetro o de largo, dependiendo de su crecimiento como banda irregularmente lobada o como roseta, pero carece de alguna diferenciación anatómica importante. La superficie ventral lleva rizoides unicelulares lisos, mientras que en el lado dorsal se abren los arquegonios, que están embebidos en el cuerpo del gametofito, y los anteridios, en grupos o individualmente, crecen en cámaras anteridiales bajo la superficie del talo. El cuerpo del gametofito consta de varias capas de células en las que quedan algunas cámaras intercelulares que se comunican al exterior por poros ventrales; tales cámaras se llenan de mucílago y con frecuencia están ocupadas por colonias de *Nostoc*. Las células superficiales llevan 1 o varios cloroplastos grandes en los que puede haber 1 pirenoide.

En comparación con los antocerotes, el gametofito de las hepáticas es más complejo y variable en forma y estructura. Existen 2 formas de crecimiento: taloide y

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foliosa. Las formas taloides son aplanadas, con una zona meristemática distal cuya división puede producir ramificaciones dicotómicas sucesivas. Los órganos sexuales se encuentran inmersos en el cuerpo, a veces en cavidades especiales o en ramas dorsales especializadas. La superficie ventral generalmente lleva los rizoides unicelulares lisos o tuberculados y escamas que se sitúan a uno y otro lado de la línea media. La estructura anatómica puede consistir de varias capas de células parenquimatosas hasta un talo con cámaras aéreas con tejido fotosintético y un parénquima de reserva.

A diferencia de las formas taloides, las hepáticas foliosas muestran un tallo cuya estructura anatómica es muy simple; las hojas son generalmente uniestratificadas, lobadas, en 2 hileras dorsales y, a veces, una hilera ventral. Las hojas dorsales maduras tienen una inserción oblicua sobre el tallo, mientras que las hojas ventrales se insertan transversalmente. En algunos grupos (*e.g.* Frullaniaceae) las plantas presentan lóbulos foliares en forma de saco. Las hepáticas, a diferencia de los antocerotes y los musgos, presentan trígonos —engrosamientos triangulares en la pared celular— y cuerpos oleíferos —cuerpos de aceite rodeados por una membrana—. Los arquegonios pueden encontrarse en los ápices de tallos o ramas; los anteridios se encuentran solos o en grupos, en la base de hojas modificadas que se denominan brácteas perigoniales.

Los anterozoides o espermatozoides biflagelados se producen dentro de anteridios pedicelados. Los arquegonios son estructuras independientes del cuerpo, excepto en los antocerotes. La oosfera o célula femenina, después de ser fecundada por un anterozoide se divide y forma el embrión; en la madurez, éste representa al esporofito que por meiosis produce las esporas. Los esporofitos de los antocerotes son estructuras muy diferentes a los de las hepáticas; en ellos, el esporofito tiene un pie que lo une al tejido del gametofito, pero no hay seta. En su lugar se encuentra un meristemo intercalar que forma la pared de varias capas de células, una epidermis con estomas y un eje central o columela de tejido estéril. Hacia la parte distal del esporofito se forman las esporas y unos filamentos estériles o pseudoelaterios que, por la actividad del meristemo intercalar, maduran progresivamente hacia el ápice del esporofito. La apertura de la cápsula se efectúa por 2 líneas de dehiscencia que separan 2 valvas; las esporas se liberan con la participación de movimientos higroscópicos de los pseudoelaterios.

En las hepáticas, el esporofito consta de 3 partes claramente diferenciadas: el pie, la seta y la cápsula. La seta es un filamento de tamaño variable que lleva la cápsula globosa o cilíndrica en el ápice; a diferencia de los antocerotes, las hepáticas no tienen columela ni estomas; las esporas están intercaladas con elaterios altamente higroscópicos y la cápsula se abre por 4 valvas.

Diversidad

Las Anthocerotophyta son un grupo pequeño de plantas. Renzaglia et al. (2009) reconocen alrededor de 14 géneros y unas 150 especies a nivel mundial, mientras que Villarreal et al. (2010) estiman que hay 200-250 especies en el mundo. Como se mencionó en la introducción, el grupo es virtualmente desconocido en México; la información bibliográfica (Hässel, 1989, 1990) y de herbario indica que existen unas 9 especies en 3 o 4 géneros (*Anthoceros, Nothoceros* y *Phaeoceros*; Cuadro 1). La presencia de *Megaceros* no se ha confirmado y podría descartarse si se acepta su redefinición como un taxon enteramente paleotropical (Villarreal et al., 2010). De las 9 especies de Anthocerotophyta, 3 son endémicas a México. Además de establecer con claridad los límites entre taxa, se requiere un muestreo intensivo de los antocerotes pues actualmente se les ha colectado principalmente en los estados del centro del país y en Oaxaca y Chiapas, pero el número de ejemplares en herbarios locales es muy reducido.

El volumen de información sobre hepáticas es más grande que el de las Anthocerotophyta. Bischler et al. (2005) y Fulford y Sharp (1990) y revisiones taxonómicas recientes pueden considerarse como punto de partida para catalogar y evaluar la riqueza de hepáticas en México. Al catálogo preliminar preparado con la información de estas publicaciones se le deben incorporar datos taxonómicos y de nomenclatura de otras monografías. A través de esta primera aproximación podemos establecer que nuestra flora comprende alrededor de 592 especies y variedades, es decir, casi el 12% de las hepáticas del mundo (5 000; Crandall-Stotler et al., 2009). Alrededor de 105 especies son endémicas de México (casi el 18% del total). En el Cuadro 2 se muestra una lista de 11 de las 42 familias de hepáticas mexicanas con más de 10 especies. El 83% (491) de las especies conocidas se concentran en un número pequeño de familias mientras que de las 105 especies endémicas, 96 están concentradas en 9 de esas familias de hepáticas. Excepto por la familia Lejeuneaceae con 48 géneros, la mayoría de las familias restantes están representadas por 1 género y excepcionalmente hasta por 7, como en las Scapaniaceae.

Sin duda, el número y distribución de especies y variedades de antocerotes y hepáticas se modificarán significativamente con la depuración de los catálogos a través de revisiones taxonómicas y monografías modernas, especialmente si se incluye una sinonimia completa. Por las mismas razones y con trabajos de exploración y

Cuadro 1. Información florística preliminar sobre las Anthocerotophyta mexicanas

Familia	*Géneros*	*Especies*	*Especies endémicas*
Anthocerotaceae	4	9	3

Cuadro 2. Familias de Marchantiophyta de México representadas por más de 10 especies y número de especies de distribución restringida

Familia	*Géneros*	*Especies*	*Especies endémicas*
Aytoniaceae	5	18	2
Cephaloziaceae	3	13	3
Frullaniaceae	1	53	13
Lejeuneaceae	48	183	37
Lepidoziaceae	4	27	
Lophocoleaceae	4	20	5
Metzgeriaceae	1	27	
Plagiochilaceae	1	87	31
Radulaceae	1	20	2
Ricciaceae	2	22	1
Scapaniaceae	7	21	2
*Total 11/42	77/122	491/592	96/105

* Total de taxa; total en las columnas /total conocido para la flora mexicana.

recolección en México, se espera una reducción en el número de especies endémicas. El mejor conocimiento de antocerotes y hepáticas es indispensable para evaluar su importancia científica y su participación en la economía de los bosques. Aunque en algunos países ya se les considera como sujetos de conservación (Hallingbäck et al., 1996), en México, en virtud de su desconocimiento, no hay iniciativas para su protección. No obstante, antes de establecer un marco legal para proteger a especies individuales de antocerotes o hepáticas, se requiere conservar su hábitat y sus comunidades como una forma de contribuir a preservar la salud de todo el bosque.

Agradecimientos

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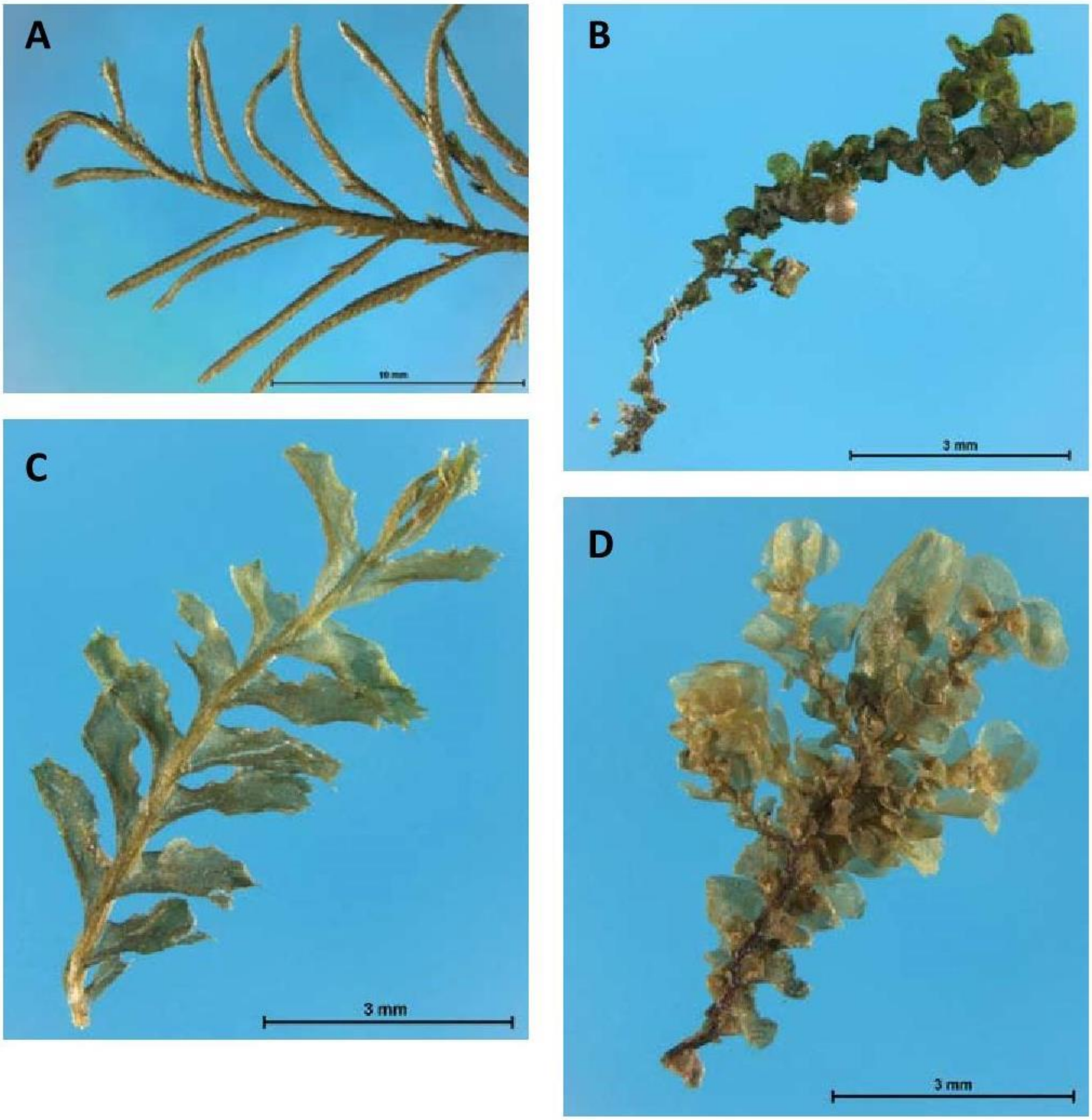

Figura 1. A, extremo distal de un tallo de la hepática foliosa *Bryopteris filicina* (Sw.) Nees. B, vista dorsal de un tallo de *Frullania pluricarinata* Gottsche. Las estructuras globosas son cápsulas de esporofitos. C, porción de un tallo de *Plagichila laetevirens* Lindenb. en vista dorsal. D, tallo de *Radula saccatiloba* Stephani en vista ventral. La estructura cilíndrica situada entre las ramas terminales es el perianto; en su interior se encuentra el esporofito.

ANEXO 2. "THE LEAFY LIVERWORTS (MARCHANTIOPHYTA) IN THE VALLEY OF MEXICO"

The leafy liverworts (Marchantiophyta) in the Valley of Mexico

Hepáticas foliosas (Marchantiophyta) del Valle de México

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ABSTRACT

The leafy liverwort flora from the Valley of Mexico has been less explored than the moss flora in the same region. There are no taxonomic, floristic and phytogeographic studies for this plant group, although in the literature there are sporadic reports. This contribution records 75 species and three varieties of leafy liverworts that ocurr in the Valley of Mexico based on the review of the literature and examination of herbarium specimens. The Lejeuneaceae (17 species) and Frullaniaceae (13 species) are the most diverse families of the region. A key and a brief description of each taxon are provided. On the other hand, 33 species recorded in the literature and/or found in herbarium collections at MEXU were not found in the field. Environmental degradation, lack of collecting in inaccessible areas, and inaccurate or incorrect data collection may account for their current absence.

Keywords: leafy liverworts, Valley of Mexico, Lejeuneaceae.

RESUMEN

La flora de hepáticas de la Cuenca de México ha sido poco estudiada en comparación con la flora de musgos de la misma región. No hay trabajos taxonómicos, florísticos y fitogeográficos de hepáticas foliosas para la región, aunque la literatura cita esporádicamente algunos ejemplares. En este estudio, con base en la revisión de la literatura, de ejemplares de herbario y de colectas recientes, se registraron 75 especies y tres variedades de hepáticas foliosas. Las Lejeuneaceae (17 especies) y las Frullaniaceae (13 especies) son las familias más diversas de la región. Esta contribución incluye una clave para la identificación y una breve descripción para cada taxón. Por otro lado, 33 especies registradas en la literatura y/o encontradas en los acervos de MEXU no fueron halladas en el campo. Es probable que la contaminación ambiental, la falta de colecta en zonas inaccesibles o los datos históricos de colecta inexactos o incorrectos expliquen su ausencia actual.

Palabras clave: hepáticas foliosas, Cuenca de México, Lejeuneaceae.

INTRODUCTION

The so-called Valley of Mexico (or more properly named, the Basin of Mexico) is located in the central-eastern region of the Neovolcanic Belt, in the zone of contact between the Neartic and Neotropical floristic regions (Delgadillo, 1992; Romero and Velázquez, 1999; Rzedowski and Rzedowski, 2005). It comprises the entire surface of Federal District, the fourth part of the State of Mexico, about 7% of Hidalgo, and small areas of the states of Tlaxcala, Puebla and Morelos (Rzedowski and Rzedowski, 2005).

The bryophyte flora of the Valley of Mexico is one of the best known areas in Mexico. Cárdenas and Delgadillo (2009) listed and illustrated ~367 species and varieties of mosses, but there are only fragmentary records for its leafy liverwort flora. Parker (1954) recognized several genera and species of leafy liverworts from the Valley of Mexico (*Lophocolea bidentata* (L.) Dumortier, *Plagiochila* sp., *Porella platyphylla* (L.) Pfeiffer, *Dicranolejeunea incongrua* (L. & G.) St., *Microlejeunea* sp. and *Strepsilejeunea* sp.). Taxonomic, floristic, and phytogeographic studies on leafy liverworts are nonexistent, so that the contribution of Parker (1954) is the only study for the leafy liverworts of the region, although in the bryological literature specimens from the Valley of Mexico are sporadically cited.

This contribution provides an artificial key and a brief description of the leafy liverwort species from the Valley of Mexico.

MATERIAL AND METHODS

Based on reviewed literature and examination of herbarium specimens in the Bryophyte Collection in the National Herbarium (MEXU), a preliminary list of 80 species of leafy liverworts from Valley of Mexico was obtained. The list was depurated, i.e., the names in synonymy or invalid were deleted, and then the list included 66 species names.

A total of 307 specimens of leafy liverworts were collected in various types of vegetation from March 2009 to April 2010, in the following localities from Valley of Mexico: Los Dinamos, Ajusco volcano, Desierto de los Leones, Reserva Ecológica del Pedregal de San Ángel, from Distrito Federal; Huixquilucan, Llano Grande, Parque Nacional Izta-Popo, Tlalmanalco, San Rafael, Cerro Gordo, Presa Iturbide, Villa del Carbón, Sierra de Alcaparrosa, from Estado de México and Parque Nacional El Chico from Hidalgo. In some localities from Federal District (e.g., Milpa Alta, Parque Tezozomoc, Bosque de Chapultepec, Bosque de Tlalpan and Xochimilco) non specimen of leafy liverworts was found. The specimens collected were deposited in MEXU.

Based on the preliminary list and the collected specimens, an artificial key of the species from Valley of Mexico as well as a brief description for each species are provided.

RESULTS

The leafy liverwort flora from the Valley of Mexico comprises 75 species and three varieties included in ca. 25 families; 10 species are new records for the area, and three from Mexico: *Cephaloziella verrucosa, Frullania decidua* and *Stephaniella rostrata.*

The Lejeuneaceae is the family with the largest number of species (17 species), followed by Frullaniaceae (13 species). The Anastrophyllaceae, Cephaloziaceae, and Plagiochilaceae had three to six species each. The remaining families are represented by less than three species each.

Thirty-three species have been recorded in the literature but they were not found in the Valley of Mexico.

Key to the species of leafy liverworts from the Valley of Mexico

1. Leaf base 2-3 layers of cells thick. Antheridia and archegonia on abaxial surface of stem. **2**

1. Leaf base one layer of cells thick. Antheridia axillary, archegonia terminal or on the branches ………………………………………………………………………………..... **3**

2. Stem with large tubercles; reddish rhizoids. Plicate leaves, shortly rectangular with rounded angles, slightly longer than wide ...………………..…… **19. *Fossombronia lamellata***

2. Stem without tubercles; brown rhizoids. No plicate leaves, semicircular, wider than long ……..……………………………………………………………… **55. *Noteroclada confluens***

3. Leaf apex deeply divided into several filiform segments, leaf segments1-7 cells at base ... …………………………………………………………………………………...……… **4**

3. Leaf apex undivided or divided into several not filiform segments, leaf segments 7 or more cells at base ....…………………………………………………………………. **8**

4. Leaves succubous, with bisbifid apex, leaf segments with opposite or verticillate cilia. Leaf cells striate-papillose ...…………...……………………… **77. *Trichocolea floccosa***

4. Leaves incubous or transverse, apex tridentate or deeply divided almost from the base into 2-4 segments without cilia. Leaf cells striate-papillose, verruculose or smooth **5**

5. Leaves with tridentate apex, leaf segments 3-7 cells wide at base ……....………………
…………………………...……………………...……………….. **9. *Bazzania stolonifera***

5. Leaves with divided apex deeply divided almost from the base, leaf segments 1-4 cells wide at base ...……..……………………………………………………………..… **6**

6. Leaves inserted transversely. Leaf segments 1-2 cells at base. Trigones lacking. Leaf cells striate-papillose or verruculose. Amphigastria and leaves similar …….………….. **7**

6. Leaves incubous. Leaf segments 2-4 cells at base. Trigones weakly differentiated. Leaf cell smooth. Amphigastria quadrifids ………….……...………..….. **46. *Lepidozia reptans***

7. Leaf apex divided into 4 segments. Leaf cells strongly verruculose. Perianth with 3 keels.
……………………………………………………..…..………... **38. *Kurzia capillaris***

7. Leaf apex divided into 3-4 segments. Leaf cells strongly striate-papillose. Perianth without keels ...…………………………..………….... **12. *Blepharostoma trichophyllum***

8. Leaves differentiated into lobe and lobule ...………………………...………….. **Key 1**

8. Leaves not differentiated into lobe and lobule ...……………………..……………….. **9**

9. Leaf apex undivided ...…………………………...……………………………… **Key 2**

9. Leaf apex divided into 2-3 segments ...……………….…………………………. **Key 3**

Key 1. Leaves differentiated into lobe and lobule

1. Amphigastria absent. Lobule plane, broadly attached to stem. Gemmae present on antical margin of the leaf, discoid ...…………………………………............ **64.** ***Radula quadrata***

1. Amphigastria present. Lobule plane or sac-like, narrowly or broadly attached to stem. Gemmae absent on antical margin of the leaf ...………………………...………………. **2**

2. Lobule broadly attached to lobe through a long keel ..…………………………………….. **3**

2. Lobule narrowly attached to lobe through a short keel ...…………………..………….. **20**

3. Amphigastria undivided ...……..…………………………………..………………………….. **4**

3. Amphigastria divided or subtruncate ………………………………..……….……….. **10**

4. Perianth ciliate or laciniate. Ventral merophyte 2-4 cells wide ...……………………...….. **5**

4. Perianth without cilia or lacinia. Ventral merophyte 4-11 cells wide …...………………… **7**

5. Perianth with 3 keels, two lateral dentate or ciliate and one postical broadly rounded, entire or with a little teeth or cilia, without antical keel. Perianth with two innovations. Leaves ovate or orbicular ...………………………………………………….……………….. **6**

5. Perianth with 4 keels, two laterals and two postical, sometimes one antical; all keels dentate-ciliate. Innovations lacking. Leaves ovate-oblong ...... **50.** ***Lopholejeunea nigricans***

6. Leaves orbicular. Lobule ca. ½-⅔ lobe length, sometimes smaller than lobe; first lobule tooth 3-6 cells long. Postical keel of perianth without cilia ...…...... **2.** ***Acanthocoleus juddii***

6. Leaves ovate. Lobule ca. ¼ lobe length; first lobule tooth 2 cells long. Postical keel of perianth with a little cilia ..………………………… **1.** ***Acanthocoleus aberrans*** **var.** ***laevis***

7. Leaves ovate, erecto-patent. Ventral merophyte 4-5 cells wide. Perianth inflated 3-4 keels, the keels entire and rounded. Amphigastria insertion line arched ...………….……… **8**

7. Leaves ovate-oblong, spreading. Ventral merophyte 6-11 cells wide. Perianth strongly flattened dorsoventrally, without keels. Amphigastria insertion line strongly arched ………..…………………………………...……………………….… **51. *Marchesinia brachiata***

8. Perianth with 4 keels, two laterals and two postical. Lobule free margin with three teeth. Paraphyllia on the abaxial surface of the stem, lamellate ..… **13. *Brachiolejeunea laxifolia***

8. Perianth with 8 keels, two laterals and one postical. Lobule free margin with two teeth. Paraphyllia on the stem lacking ……………………………….……………………………….. **9**

9. Lobule free margin with teeth spaced from each other by 3-4 marginal cells longer than median cells ...……………………………………..….. **10. *Blepharolejeunea incongrua***

9. Lobule free margin with teeth spaced from each other by 3-5 marginal cells as large as the median cells ...…………………………………….. **11. *Blepharolejeunea securifolia***

10. Leaf apex obtuse to acute or rarely shortly apiculate ...…………………………...….. **11**

10. Leaf apex rounded ...…………………………………………………………….. **15**

11. Amphigastria distant from each other, apex subtruncated, segments of the amphigastria divergent. Trigones poorly developed ..………………………... **36. *Harpalejeunea molleri***

11. Amphigastria distant to contiguous from each other, apex clearly bifid, segments of the amphigastria not divergent. Trigones well-developed ...……………………………...….. **12**

12. Hyaline papilla distal. Leaf apex obtuse to acute. Leaf lobules well-developed, inflated. …………………………………………………………………………………..... **13**

12. Hyaline papilla proximal. Leaf apex acute to shortly apiculate. Leaf lobules obsolete ..... ……………………………………………………………………………………...**14**

13. Amphigastria ovate ...……………………………………………… ***Strepsilejeunea sp.***

13. Amphigastria obcuneate ...…………………….………….. **73. *Strepsilejeunea obtusistipula***

14. Leaves distant to contiguous. Leaf apex acute to rarely acuminate. Amphigastria $^{2}/_{5}$ -½-bifid ………………...………………………..…………….. **40. *Lejeunea cordistipula***

14. Leaves imbricate. Leaf apex acute to shortly apiculate. Amphigastria ⅓-bifid ………….
……………………………………………………………………. **41. *Lejeunea flaccida***

15. Leaf cells papillose ..………...………………………….……………………… **16**

15. Leaf cells smooth ..………...………………………………………………..……. **17**

16. Amphigastria ovate-rhomboid, lateral margins angled at mid-blade. Perianth keels simple, not bicarinate ..………………………………..………. **42. *Lejeunea laetevirens***

16. Amphigastria oval, lateral margins rounded to shortly spread at mid-blade. Perianth keels bicarinate ..………………………..……………................ **43. *Lejeunea lepida***

17. Leaf lobule vestigial, its base formed by 5-7 cells and a filiform tooth (5-) 6-10 cells long and 1-2 (-3) cells wide. Amphigastria distant from each other …………………………
…………………………………………………………….….… **45. *Lejeunea trinitensis***

17. Leaf lobule well-developed, inflated, its base formed by more than 8 cells, with a small tooth 1-2 cells long. Amphigastria distant to contiguous from each other ……………… **18**

18. Leaves oblong. Amphigastria ½-bifid ……………..…………….. **44. *Lejeunea seriata***

18. Leaves ovate. Amphigastria $^{1}/_{6}$-bifid ……………...………………………………… **19**

19. Ocelli 1 (-3) only in some leaves. Lobules reaching ½ the leaf length. Amphigastria segments 2-3 cells wide at base ..……………….……………… **54. *Microlejeunea bullata***

19. Ocelli lacking. Lobules reaching less than ½ the leaf length. Amphigastria segments 5-8 cells wide at base ..………………..…………………..………… **39. *Lejeunea capensis***

20. Postical leaf margin entire, slightly undulate. Leaf lobule flat (laminated). Stem paraphyllia ciliate. Amphigastria undivided. Perianth campanulate ..… **63. *Porella leiboldii***

20. Postical leaf margin entire, not undulate. Leaf lobule inflated, sac-like. Stem paraphyllia lacking. Amphigastria divided. Perianth not campanulate ...………………...………… **21**

21. Leaf lobules cylindrical or clavate ...……………..……………………………… **22**

21. Leaf lobules galeate or cucullate ...……...……………………………………….. **24**

22. Lobules clavate, distant from the stem. Leaves ovate, without basal appendages. Trigones triangular …...…………………..…………………… **23. *Frullania caulisequa***

22. Lobules cylindrical, very close to the stem. Leaves ovate or obovate-oblong, with auricles at base. Trigones cordate and sometimes sinuous ....……………...………. **23**

23. Leaves obovate-oblong, apex acute to mucronate, incurved. Postical leaf margin reflexed. Amphigastria semicircular, sometimes orbicular ……….. **32. *Frullania triquetra***

23. Leaves ovate, apex apiculate, not incurved. Leaf margin reflexed throughout. Amphigastria broadly ovate …………………………...…………... **22. *Frullania atrata***

24. Perianth with 8-12 keels ...…………………………..…………………………… **25**

24. Perianth with 3-4 keels ...……...……………………………………………………… **26**

25. Laminar portion of lobule narrowly triangular, not undulate, not extending beyond the postical leaf margin so the keel is short. Amphigastria obovate-oblong, basal appendages short. Margin of the inner female bracts entire, apex obtuse …. **29. *Frullania pluricarinata***

25. Laminar portion of lobule oblong-ligulate, strongly undulate, extending beyond the postical leaf margin so the keel is long. Amphigastria broadly reniform, basal appendages long. Margin of the inner female bracts with 5-10 teeth, apex acute .....…………………….. ……………………………………………………..….. **20. *Frullania arecae* var. *arecae***

26. Amphigastria obovate-oblong ...……………………………… **31. *Frullania tetraptera***

26. Amphigastria ovate, orbicular or reniform ...……………………………………. **27**

27. Laminar portion of lobule extending beyond the postical leaf margin. Inner female bracteole connate more than ½ of its length with the lobules of the female bracts ...………..
……………………..…………………………………..…. **30. *Frullania riojaneirensis***

27. Laminar portion of lobule not extending beyond the postical leaf margin. Inner female bracteole connate less than ½ of its length or almost free with the lobules of the female bracts ...…………………………………………………………………………… **28**

28. Leaves squarrose ...……………………………………………………...………. **29**

28. Leaves not squarrose ....……………………………………………………..…. **30**

29. Stylus filiform. Amphigastria ovate-orbicular, not auriculated at base. Intermediate thickenings abundant throughout the leaf …………………….…… **26. *Frullania ericoides***

29. Stylus foliose. Amphigastria reniform, auriculate at base. Intermediate thickenings scarce only at leaf base .....…………………..……………………… **27. *Frullania gibbosa***

30. Laminar portion of lobule triangular ...……………..…………….. **21. *Frullania arsenii***

30. Laminar portion of lobule with other forms ...…………………………………...… **31**

31. Amphigastria narrowly or broadly ovate, ⅓-½-bifid ……………..….....…………..... **32**

31. Amphigastria orbicular or almost orbicular, $^{1}/_{5}$-¼-bifid ……………..……………………
……………………....…………………………………………. **25. *Frullania decidua***

32. Perianth pyriform or obovate. Amphigastria narrowly ovate .... **28. *Frullania inflata***

32. Perianth oblong-elliptical. Amphigastria broadly ovate ..…..... **24. *Frullania cuencensis***

Key 2. Leaf apex undivided

1. Leaf margins slightly or strongly dentate ...……………………………………………... **2**

1. Leaf margins entire …………………………………………………………………….. **7**

2. Antical leaf margin plane, recurved or reflexed. Trigones confluent; vitta weakly developed in the basal and mid-leaf ...……….………………………………………………… **3**

2. Antical leaf margin plane or incurved. Trigones not confluent; vitta lacking ...…..……. **4**

3. Ventral-type branches. Leaves ovate-orbicular. Leaf insertion transverse ……………….. ………………………………...………………………… **4. *Adelanthus lindenbergianus***

3. Lateral-type branches. Leaves ovate to ovate-oblong. Leaf insertion succubous ...………. ……………………………………………………………… **58. *Plagiochila bifaria***

4. Abaxial leaf surface with numerous propagules ...……………………………………... **5**

4. Abaxial leaf surface without propagules ...……………………………………………… **6**

5. Leaves widespread. Teeth present on the apex and on the postical leaf margin ...……….. ………………………………………...…………………….. **61. *Plagiochila patula***

5. Leaves narrowly spread. Teeth present only at leaf apex ...…. **62. *Plagiochila xalapensis***

6. Leaves ovate-orbicular; margins finely dentate. Trigones cordate. Stem with 1-3 cell layers thick in section ....……………………………………… **57. *Plagiochila asplenioides***

6. Leaves ovate-oblong; margins strongly dentate. Trigones triangular. Stem with 3-4 cell layers thick in section ……………………………………..... **60. *Plagiochila diversifolia***

7. Leaves succubous, opposite ...…………………………...…………………………… **8**

7. Leaves succubous, alternate ...………………………………………………………… **10**

8. Antical leaf margins connate, plane. Postical leaf margin not connate, undulate, with elongate cells. Leaf apex rounded. Leaf cells smooth ...……....………………………... **9**

8. Antical and postical leaf margins connate. Antical margin revolute, the postical margin slightly undulate, cells not elongate. Leaf apex subacute to slightly bifid. Leaf cells finely papillose ...…..…....………………………………...…………… **74. *Syzygiella anomala***

9. Leaves concave ...……………………………………… **34. *Gongylanthus liebmannianus***

9. Leaves plane or almost plane ...…………………….....……. **35. *Gongylanthus muelleri***

10. Leaves lingulate. Cells of the postical leaf margin strongly elongate ...……………... **11**

10. Leaves variable in shape, but not ligulate. Cells of the postical leaf margin not or slightly elongate .....…………………………………………………………..….. **12**

11. Sporophyte developing within the perianth. Leaf cells smooth ……..…………..……….

…………………………………………………….… **66. *Solenostoma amplexifolium***

11. Sporophyte developing within the marsupium. Leaf cells strongly papillose ...…………

………………………………………………………… **47. *Lethocolea glossophylla***

12. Leaves closely imbricate. Plants with axillary paraphyllia ………………………….. **13**

12. Leaves distant, contiguous, or sometimes imbricate. Plants without paraphyllia ..…... **15**

13. Leaves longitudinally plicate. Stolons lacking. Paraphyllia lanceolate ...………………..

……………………………………………………..….. **72. *Stephaniellidium sleumeri***

13. Leaves plicate lacking. Stolons present. Paraphyllia filiform or biseriate ...…………. **14**

14. Leaves oblate or ovate, wider than long or as wide as long. Leaf apex obtuse, entire ......

………………………………………...…………….. **70. *Stephaniella paraphyllina***

14. Leaves largely ovate, longer than wide, sometimes as long as wide. Leaf apex acute, prolonged, slightly serrulate or prorulose ...…………………….... **71. *Stephaniella rostrata***

15. Leaf cells papillose ...………..…………………………………………………... **16**

15. Leaf cells smooth ...………..……………………………………………………….. **17**

16. Leaves spreading. Postical marginal cells slightly elongate ...…………………………...

…………………………………………………..... **69. *Solenostoma sphaerocarpum***

16. Leaves appressed. Postical marginal cells shortly rectangular …………………………..

…………………………………………………………….... **75. *Syzygiella autumnalis***

17. Rhizoids originating from the stem epidermal cells ...……..… **68. *Solenostoma decolor***

17. Rhizoids originating from the leaf base ..…………………..…. **67. *Solenostoma callithrix***

Key 3. Leaf apex divided into two or more segments

1. Amphigastria present, conspicuous or formed by a few cells ..…………………………. **2**

1. Amphigastria lacking ..……………………………………………………………. **9**

2. Leaves succubous, incubous or inserted almost longitudinally ..…………………………. **3**

2. Leaves inserted transversely or almost transversely ....………………………………. **6**

3. Leaves incubous. Leaf apex usually trifid; leaf cells papillose ...………..………………...

………………..………………………………………. **76. *Triandrophyllum subtrifidum***

3. Leaves succubous. Leaf apex bifid, rarely trifid toward the stem base; leaf cells smooth ..

…...…………………………………………….……………………………………… **4**

4. Leaves usually with one tooth on the postical margin; antical margin incurved. Leaves ½-⅓-bifid. Amphigastria formed by a few cells …………….... **59. *Plagiochila corniculata***

4. Leaves without tooth on the postical margin; antical margin not incurved. Leaves ⅓-^{1}/₄-bifid. Amphigastria well-differentiated, deeply bifid ………...…………………………. **5**

5. Leaves ¼-bifid. Amphigastria with a long filament on the lateral margins ....

…………….……………………….….....……...…………. **48. *Lophocolea bidentata***

5. Leaves ⅓-bifid. Amphigastria without a filament on the lateral margins …………………

…………….………………………………………………………. **49. *Lophocolea parca***

6. Plants less than 0.5 mm wide. Leaves ½-bifid, segments triangular, obtuse or acute. Vitta lacking ……………...………………………………………………………………… **7**

6. Plants more than 5 mm wide. Leaves ⅔-bifid, segments largely acuminate. Vitta bifurcated near of the leaf base ……...…..… **37. *Herbertus juniperoideus* ssp. *acanthelius***

7. Leaves without teeth on the lateral margins. Leaf cells smooth to weakly verruculose. Amphigastria formed by more than 8 cells, lanceolate, only present in some branches …....

……..…………………………………......…………..… **16. *Cephaloziella divaricata***

7. Leaves sometimes with 1-2 teeth on the lateral margins. Leaf cells smooth to strongly papillose. Amphigastria formed by less than 8 cells, lanceolate to asymmetrically bifid, present in all branches ..………..……………..……………..……………………… **8**

8. Marginal leaf cells protruding; leaf segments green, without reddish-magenta tinged. Leaf cells smooth .....………………………..……………………..… ***Cephaloziella sp.***

8. Marginal leaf cells protruding, with 1-2 teeth on the lateral margins; leaf segments reddish-magenta tinged. Leaf cells strongly papillose ..….....… **17. *Cephaloziella verrucosa***

9. Stem with hyalodermis ...…...…………………………………………………….. **10**

9. Stem without hyalodermis ...……………………………………………….....…. **13**

10. Leaves inserted transversely or almost transversely, ½-bifid …………….....………. **11**

10. Leaves succubous, $^{2}/_{5}$-$^{1}/_{2}$-bifid ……………....…………………………………………. **12**

11. Postical margin of the leaf forming an inflated sac. Leaf segments largely triangular, 5-8 cells at base, leaf ending in 4-7 apical cells …………...………… **56. *Nowellia curvifolia***

11. Postical margin of the leaf not forming an inflated sac. Leaf segments short and narrowly triangular, 3-4 cells at base, leaf ending in 1-3 apical cells .. **15. *Cephalozia dussii***

12. Stem cross section with 11-12 cortical cells in one layer and 12 medullary cells. Leaves ½-bifid. Leaf cells smooth ……………..…………..……….…. **14. *Cephalozia bicuspidata***

12. Stem cross section with 10-11 cortical cells in one layer and 14-15 medullary cells. Leaves $^{2}/_{5}$-bifid. Leaf cells finely verruculose ……….. **33. *Fuscocephaloziopsis catenulata***

13. Antical margin of the leaf inserted transversely, postical margin oblique ...…………. **14**

13. Leaves succubous or transverse ...……………………………………………………. **18**

14. Leaf segments ovate-lanceolate ...………………………... **5. *Anastrophyllum auritum***

14. Leaf segments triangular ...……………………………………………...………. **15**

15. Plants less than 0.5 mm wide. Leaves symmetrically bifid. Gemmae on adaxial surface of the leaf, almost cubical, red, one-celled. Leaf cells smooth or finely verruculose ..……..
………………………………………….……………..... **6. *Anastrophyllum hellerianum***

15. Plants more than 0.5 mm wide. Leaves asymmetrically bifid, antical segment smaller or narrower than the postical segment. Gemmae present or lacking. Leaf cells papillose **16**

16. Leaves ovate to broadly ovate. Trigones confluent. Gemmae not seen ..…………..… **17**

16. Leaves ovate, sometimes quadrate. Trigones triangular. Gemmae angled, red, multicellular (2-4-celled) ...…………………...……..……….. **7. *Anastrophyllum minutum***

17. Antical and postical margins of the leaf incurved ...……..... **5. *Anastrophyllum auritum***

17. Postical margin of the leaf plane, antical margin slightly recurved ...……………………
………………………………………………………… **8. *Anastrophyllum tubulosum***

18. Leaves transversely inserted ………………………………………………………. **19**

18. Leaves succubous ...…………………………………………………………...… **20**

19. Leaves strongly imbricate, ovate, $^{1}/_{5}$-⅓-bifid. Leaf segments slightly longer than wide or as long as wide ………………...…………………………….…. **53. *Marsupella miniata***

19. Leaves contiguous to imbricate, ovate-orbicular, bifid less than $^{1}/_{5}$ their length. Leaf segments wider than long ...………………………………...….. **52. *Marsupella emarginata***

20. Leaf cells smooth ...…………..……………………………...……………………… **21**

20. Leaf cells papillose ...………..……………………….....…………………………… **22**

21. Plants less than 0.7 mm wide. Leaves distant to contiguous, bifid; apex of segments obtuse. Leaf cells without trigones. Gemmae not seen ...…….. **18. *Cylindrocolea rhizantha***

21. Plants more than 0.7 mm wide. Leaves imbricate, bifid to quadrifid; apex of segments apiculate, ending in one long tooth one-celled. Leaf cells with tiny trigones. Gemmae uni- or bicellular, angled ...………...…………………………….…. **65. *Schistochilopsis incisa***

22. Leaves asymmetrically bifid to trifid, to $^{1}/_{10}$ their length. Apex of segments acute-acuminate. Gemmae red, bicellular, ovoid, clustered on the stem tip ...…………………..….…………………………………………………………………… **78. *Tritomaria exsecta***

22. Leaves asymmetrically bifid, to ⅓ their length. Apex of segments obtuse-acute. Gemmae not seen ...………………………………………………… **3. *Acrobolbus wilsonii***

Distinctive characters of the species of leafy liverworts from the Valley of Mexico

The following descriptions contain only the diagnostic gametophytic characters. The sporophytic characters are not included because the sporophytes are rare in the leafy liverworts. The characters of taxonomic importance are: insertion and leaf shape, cell shape, presence or absence trigones, ocelli and vitta; presence or absence of amphigastria and their shape; rhizoid color. In most groups the shape and ornamentation of the gynoecium are useful features for taxonomic identification. In Lejeuneaceae and Cephaloziaceae the morphology of hyalodermis and the medulla of the stem are meaningful.

The descriptions of *Bazzania stolonifera* and *Frullania inflata* were taken from Fulford (1963) and Clark and Svihla (1944), respectively.

An * indicates new records for the Valley of Mexico; ** correspond to new records for Mexico, and *** species recorded in the literature and found in MEXU herbarium, but not in recent collections. The remaining species are those reported in the literature and that were also found in this study.

1. *Acanthocoleus aberrans* var. *laevis* Gradst.

Leaves ovate. Mid-leaf cells shortly elongate. Ventral merophyte 2-4 (-6) cells wide. Inner female bracteole with margin plane, entire, apex rounded. Perianth with two lateral dentate or ciliate keels and one postical rounded with a few tooth or cilia only in the distal section.

2. ***Acanthocoleus juddii* Kruijt *****

Leaves broad, orbicular. Leaf lobules large, rectangular, with a conspicuous tooth. Ventral merophyte two cells wide. Perianth with two lateral keels winged in the distal section and one ventral keel rounded, without cilia.

3. *Acrobolbus wilsonii* Nees

Leaves asymmetrically and deeply bifid, antical segment of the leaf narrower than the postical segment; leaf segments obtuse to acute. Leaves usually with one tooth on the antical and postical margins. Trigones triangular, small. Leaf cells papillose.

4. *Adelanthus lindenbergianus* (Lehm.) Mitt. ***

Branches ventral-intercalar type (cf. Crandall-Stotler, 1972). Antical margin of the leaf reflexed, entire; antical and postical margins dentate. Trigones large, confluent, vitta weakly developed in mid-leaf. Leaf cells smooth.

5. *Anastrophyllum auritum* (Lehm.) Steph. ***

Leaves asymmetrically bifid up to ¼ their length or less, antical segment narrower than the postical segment, antical and postical margins incurved. Trigones large, confluent. Leaf cells thickened and papillose. Perianth mouth hyaline. Gemmae not seen.

6. *Anastrophyllum hellerianum* (Nees) R.M. Schust. ***

Plant filiform, ~0.5 mm wide. Leaves deeply and symmetrically bifid. Leaf cells smooth to scarcely verruculose. Gemmae one-celled, almost cubical, red tinged on the adaxial surface of the leaf.

7. *Anastrophyllum minutum* (Schreb.) R.M. Schust. ***

Leaves asymmetrically bifid up to ¼-$^{2}/_{5}$ their length, leaf segments triangular. Leaf cells papillose. Gemmae angled, 2-5-celled, red tinged, on the adaxial surface of the leaf.

8. *Anastrophyllum tubulosum* (Nees) Grolle ***

Leaves broadly ovate, asymmetrically bifid up to ¼-$^{2}/_{5}$ their length; leaf segments broadly triangular with apex and sinus acute. Trigones large, confluent, with convex sides. Leaf cells papillose. Gemmae not seen.

9. *Bazzania stolonifera* (Sw.) Trevis. ***

Leaves broadly spreading, imbricate, asymmetrically ovate. Leaf apex tridentate; teeth acute to obtuse, mostly unequal, 3-7 cells long, 3-7 cells wide at base, the sinuses broad. Leaf margins straight to undulate. Sporophyte capsule ovoid-cylindrical, the wall with 4-5 cell layers.

10. *Blepharolejeunea incongrua* (Lindenb. & Gottsche) van Slageren & Kruijt

Leaves imbricate. Leaf apex rounded to apiculate, incurved. Ventral merophyte (-2) 4 cells wide. Inner female bracts obovate, apex rounded, incurved to apiculate, the margins entire. *B. incongrua* is characterized by marginal cells of the lobule longer than the inner cells of the lobule.

11. *Blepharolejeunea securifolia* (Steph.) R.M. Schust.

Leaves imbricate. Leaf apex rounded, incurved. Ventral merophyte 4 cells wide. Inner female bracts ovate, apex rounded, incurved, the margins entire. Spores rectangular. *B. securifolia* may be confused with *B. incongrua*, but in the former species the marginal cells of the lobule are the same size as the inner cells of the lobule.

12. *Blepharostoma trichophyllum* (L.) Dumort. ***

Leaf apex divided 3-4 filiform segments, each segment with one cell at base; cells of segments rectangular. Leaf cells strongly striate-papillose. Perianth long, cylindrical, without keels.

13. *Brachiolejeunea laxifolia* (Taylor) Schiffn.

Lobule margin with three teeth (two in *B. incongrua* and *B. securifolia*). Lamellate paraphyllia on the abaxial surface of the stem (lacking in *Blepharolejeunea*). Perianth with four keels (two laterals and two postical; in *Blepharolejeunea* only three keels, two laterals and one postical).

14. *Cephalozia bicuspidata* (L.) Dumort.

Hyalodermis with 12 medullary cells and 11-12 cortical cells. Leaves succubous, distant, ½-bifid, ovate to almost rectangular; leaf segments with 4-8 cells at base and ending in 1-2 cells at the tip. Trigones lacking. Leaf cell walls thin and smooth. Perianth long, cylindrical, mouth crenulate.

15. *Cephalozia dussii* Fulford *

Stem cross section with 6 medullary cells and 6-7 cortical cells. Leaves oblique almost transversal, distant, ½-bifid, ovate; leaf base segment with 3-4 cells and ending in 1-3 cells at the tip. Cells of the segments and the sinus quadrate. Trigones lacking. Leaf cell walls thin and smooth.

16. *Cephaloziella divaricata* (Sm.) Schiffn. *

Leaves transversally inserted, sometimes oblique, ½-bifid. Leaf apex acute to obtuse, base of segments 9-10 cells. Trigones lacking. Leaf cells smooth to weakly verruculose. Amphigastria in some branches, lanceolate. Gemmae not seen.

17. *Cephaloziella verrucosa* Steph. **

Leaves distant, ½-bifid or more, some leaves with 1-2 teeth on the lateral margins. Leaf segments red-magenta tinged, acute-obtuse, 7-10 cells at base. Leaf cells strongly papillose. Amphigastria lanceolate, sometimes asymmetrically bifid. Gemmae two-celled, ovoid and reddish, clustered on the stem tip.

18. *Cylindrocolea rhizantha* (Mont.) R.M. Schust. ***

Stem without hyalodermis. Leaves distant to contiguous, ½-bifid, ovate; segments triangular, apex obtuse. Trigones lacking. Leaf cell walls thin and smooth. Amphigastria lacking.

19. *Fossombronia lamellata* Steph.

Leaves plicate, two or more cell layers thick, shortly rectangular, with long tubercles and reddish rhizoids scattered. Mid-leaf cells oblong. Leaf cells thin and smooth. Trigones lacking. Rhizoids of the adaxial surface reddish.

20. *Frullania arecae* (Spreng.) Gottsche var. *arecae* ***

Lobules galeate, laminar section of the lobule extending beyond of the postical leaf margin, entire, strongly undulate. Trigones large, nodulose, with occasional intermediate thickenings. Amphigastria large, broadly reniform with basal appendages large, sometimes their margins undulate. Inner female bracteole highly connate with the bracts on both sides. Perianth with 8-10 keels.

21. *Frullania arsenii* Steph. *

Leaf base large with basal appendages. Distal margins of the leaf strongly incurved. Trigones small, triangular, weakly sinuose, intermediate thickenings scarce. Lobules galeate, laminar portion broadly triangular. Amphigastria 3-4 times the width of the stem, almost orbicular, distant from each other, 1/5-1/4-bifid. Perianth with 4 keels.

22. *Frullania atrata* (Sw.) Dumort. ***

Leaf base with one auricle. Leaf margins completely reflexed, apex undivided, apiculate. Trigones sinuose, intermediate thickenings, abundant at leaf base. Lobules cylindrical. First branch amphigastrium with margin entire, apex undivided and recurved. Amphigastria broadly ovate, margins strongly recurved, base with two auricles pronounced.

23. *Frullania caulisequa* (Nees) Nees *

Leaves ovate, apex incurved, rounded, leaf base without basal appendages. Trigones of the leaf base nodulose, and larger than the trigones of the leaf apex, intermediate thickenings scarce. First branch amphigastrium bifid, ovate, plane. Unlike other species of *Frullania, F. caulisequa* has lobules distant from the stem, obovate. Amphigastria plane, ovate, loosely imbricate, apex obtuse.

24. *Frullania cuencensis* Taylor

Leaves imbricate to loosely imbricate, ovate to orbicular; distal margins strongly incurved. Trigones large. Basal appendages of the leaf large. Laminar portion of the lobule narrowly triangular. Amphigastria distant from each other, almost orbicular, 3-4 times the width of the stem; $^{1}/_{5}$-$^{1}/_{4}$-bifid.

25. *Frullania decidua* Spruce **

Leaves contiguous to slightly imbricate, ovate; distal margins slightly incurved. Laminar portion of the lobule narrowly triangular. Amphigastria distant from each other, orbicular, as long as wide, $^{1}/_{5}$-$^{1}/_{4}$-bifid.

26. *Frullania ericoides* (Nees) Mont.

Leaves squarrose (dry and wet), broadly ovate, imbricate, basal appendages strongly auriculate. Trigones sinuose, intermediate thickenings abundant throughout leaf, asymmetrical, strongly nodulose. Stylus filiform. Amphigastria ovate to orbicular, plane, imbricate, not auriculate at base. Female bracteole usually connate with one of the lateral margins only (sometimes with both lateral margins).

27. *Frullania gibbosa* Nees ***

Leaves squarrose when wet and appressed when dry, almost imbricate, basal appendages semirotund. Trigones nodulose, intermediate thickenings scarce. Stylus foliose.

Amphigastria reniform to orbicular, imbricate, auriculate at base. Female bracteole connate with the bracts on both lateral margins.

28. *Frullania inflata* Gottsche ***

Leaves ovate to suborbicular; leaf apex obtuse to rounded, leaf base appendiculate. Leaf lobule galeate. Stylus triangular to ovate, 2 cells wide at base, 2-8 (-9) cells long. Amphigastria flat, ovate, narrowed toward base, 1/3-1/2-bifid. Female bracteole either free or connate with one or both bracts, bidentate, margins entire or with 1 or 2 small teeth near base. Perianth ¾ exserted, inflated when mature, pyriform or obovate, abruptly narrowed into a short beak.

29. *Frullania pluricarinata* Gottsche

Leaves contiguous to imbricate, ovate, basal appendages semirotund. Trigones well-diferentiated, intermediate thickenings lacking at the mid-leaf, present at the leaf base. Amphigastria obovate to oblong, distant to contiguous from each other. Laminar portion of the lobule not prolonged beyond the postical leaf margin. Inner female bracteole shortly bifid, highly connate with the bracts on both lateral margins. Perianth with 8-12 keels.

30. *Frullania riojaneirensis* (Raddi) Spruce

Leaves ovate, imbricate, distal margins slightly incurved. Trigones nodulose, intermediate thickenings frequent. Laminar portion of the lobule prolonged beyond of the postical leaf margin. Amphigastria orbicular, cordate at base, distant to contiguous from each other. Inner female bracteole highly connate with the female bracts. Perianth with 4 keels.

31. *Frullania tetraptera* Nees & Mont.

Leaves ovate, imbricate, distal margins incurved, basal appendages semirotund. Trigones triangular, intermediate thickenings scarce at leaf base. Amphigastria obovate to oblong, contiguous to distant from each other, $^{1}/_{6}$-$^{1}/_{5}$-bifid. Perianth with 4 keels.

32. *Frullania triquetra* Lindenb. & Gottsche *

Leaf base with one auricle, postical leaf margin reflexed, apex incurved, acute to mucronate. Trigones cordate, large. Lobules cylindrical. Amphigastria semirotund, sometimes orbicular, margins recurved, base auriculate. First branch amphigastrium entire, ovate and revolute.

33. *Fuscocephaloziopsis catenulata* (Huebener) Váňa & L. Söderstr. ***

Hyalodermis with 14-15 medullary cells and 10-11 cortical cells. Leaves succubous, contiguous to imbricate, $^{2}/_{5}$-bifid, ovate; leaf segment connivent, with 3-5 cells at base and ending in 1-2 cells at the tip. Trigones lacking. Leaf cells thin and smooth to finely verruculose.

34. *Gongylanthus liebmannianus* (Lindenb. & Gottsche) Steph.

Leaves opossite, concave, imbricate. Antical margin of the leaf connate, postical margins not connate. Cells of the postical leaf margin strongly elongated, sometimes red tinged. Trigones lacking or small. Leaf cells smooth. Rhizoids numerous, brown.

35. *Gongylanthus muelleri* (Gottsche) Steph.

Leaf opposite, imbricate. Antical margin of the leaf connate, postical margin not connate. Cells of the postical leaf margin elongated, sometimes red tinged. Trigones lacking or small. Leaf cells thin and smooth. Rhizoids numerous, brown. *G. muelleri* may be confused with *G. liebmannianus,* but *G muelleri* has plane leaves.

36. *Harpalejeunea molleri* (Steph.) Grolle *

Leaves ovate, concave, imbricate, falcate when wet. Leaf apex obtuse to acute, incurved. Trigones inconspicuous. Lobule inflated with one tooth, free margin strongly involute. Ventral merophyte 2 cells wide. Amphigastria distant from each other, apex subtruncate, segments divergent, 4-6 cells at base.

37. *Herbertus juniperoideus* subsp. *acanthelius* (Spruce) K. Feldberg & Heinrichs ***

Leaves ⅔-bifid, falcate; leaf segments largely acuminate, ending in 3-10 cells. Vitta bifurcating near leaf base. Trigones and intermediate thickenings well-differentiated, knob-like. Leaf cells papillose. Amphigastria slightly smaller than the leaves.

38. *Kurzia capillaris* (Sw.) Grolle ***

Leaves transversally inserted, divided in 4 segments of 1-2 cells at base; segment cells shortly rectangular. Leaf cells thickened and verruculose. Amphigastria trifid to quadrifid. Perianth with 3 keels.

39. *Lejeunea capensis* Gottsche

Stem cross section with 5-8 layers of cortical cells and 7 medullary cells. Ventral merophyte two cells wide. Leaves ovate, plane. Trigones and intermediate thickenings lacking. Leaf cells papillose. Amphigastria distant to contiguous from each other, 2-4 times the width of the stem, $^{1}/_{3}$-$^{2}/_{5}$-bifid. Gynoecia with one innovation. Perianth inflated, without keels, emerging among the bracts up to $^{1}/_{3}$-$^{1}/_{4}$ its length.

40. *Lejeunea cordistipula* Lindenb. & Gottsche ***

Leaves distant to contiguous, ovate. Leaf apex acute or rarely acuminate, ending in 1-2 cells. Trigones with three convex sides, intermediate thickenings present. Leaf lobule inconspicuous formed by 5-8 cells. Amphigastria distant from each other, ovate, $^{2}/_{5}$-$^{1}/_{2}$-bifid; segments long, triangular.

41. *Lejeunea flaccida* Lindenb. & Gottsche***

Leaves imbricate, ovate-cordate, flaccid; leaf apex acute to shortly apiculate. Ventral merophyte 2 cells wide. Amphigastria ovate-cordate, ⅓-bifid. Perianth pyriform.

42. *Lejeunea laetevirens* Nees & Mont.

Stem cross section 7-8 cortical cells and 3 medullary cells. Ventral merophyte 3 cells wide. Leaves ovate, plane, distant to contiguous; leaf apex rounded. Leaf cells papillose. Hyaline papilla proximal. Amphigastria ovate-rhomboid, distant from each other, angled at mid-blade. Perianth with not bicarinate keels.

43. *Lejeunea lepida* Lindenb. & Gottsche ***

Stem cross section 7 cortical cells and 5-6 medullary cells. Ventral merophyte 2 cells wide. Leaves ovate, plane, distant to contiguous; leaf apex rounded. Leaf cells papillose. Hyaline papilla proximal. Unlike *L. laetevirens, L. lepida* has the keels of the perianth bicarinate and the lateral margins of the amphigastria rounded or a little spread at mid-blade, but not angled.

44. *Lejeunea seriata* Lindenb. & Gottsche ***

Leaves imbricate, oblong, apex rounded, entire; postical margin suberect. Lobule small, cucullate. Amphigastria ½-bifid, distant from each other, small, rotund, lateral margins not angled. Perianth oblong-obovate.

45. *Lejeunea trinitensis* Lindenb. *

Leaves ovate, contiguous to loosely imbricate; leaf apex broadly rounded. Ventral merophyte 2 cells wide.

L. trinitensis distinguished from other species of *Lejeunea* by vestigial lobules with 5-7 cells long, 1-2 (-3) cells wide and 5-7 cells at base; the lobule not exceed the half of the length of the leaf. Hyaline papilla apical.

46. *Lepidozia reptans* (L.) Dumort. ***

Leaves inccubous, contiguous; leaf apex divided in 3-4 segments; the segments 2-4 cells at base, quadrate-hexagonal; apex of the segments acute. Leaf cells thin and smooth. Amphigastria quadrifid, 2-3 cells at base.

47. *Lethocolea glossophylla* (Spruce) Grolle *

Marginal cells of the leaf forming a conspicuous border that is evident with polarized light; in leaf cross section the marginal cell is thicker and rounded than the other leaf cells. Leaf cells papillose. Sporophyte is developed within marsupium.

48. *Lophocolea bidentata* (L.) Dumort.

Leaves succubous, almost longitudinal, ovate, contiguous, plane, broadly spread, ¼-bifid, sometimes trifid toward the stem base. Trigones lacking. Leaf cells thin and smooth. Amphigastria deeply bifid with a long filament on each side of the blade.

49. *Lophocolea parca* (Gottsche) Fulford & Sharp ***

Leaves succubous almost longitudinal, ovate to quadrate, ⅓-bifid. Amphigastria ovate, distant from each other, deeply bifid, without filaments on the blade margins.

50. *Lopholejeunea nigricans* (Lindenb.) Schiffn. ***

Ventral merophyte 4 cells wide. Leaf apex plane or incurved, margins entire, occasionally distally dentate. Trigones small to medium, intermediate thickenings present. Leaf lobule with a one-celled tooth. Amphigastria ovate to suborbicular, insertion curved or arched. Perianth with 4-5 keels dentate-ciliate, two laterals, two postical teeth, and sometimes one antical tooth.

51. *Marchesinia brachiata* (Sw.) Schiffn. ***

Ventral merophyte 6-11 cells wide. Amphigastria broadly obovate-orbicular, entire, margins plane or recurved, the base strongly decurrent, insertion line strongly arched.

Gynoecia with two innovations. Perianth strongly flattened dorsoventrally, lateral margins entire.

52. *Marsupella emarginata* (Ehrh.) Dumort.

Plants with stolons. Leaves transversally inserted, ovate-orbicular, contiguous to imbricate, less than $^{1}/_{5}$-bifid; segments wider than long, the apex rounded to acute, sometimes discolored.

53. *Marsupella miniata* (Lindenb. & Gottsche) Grolle

Plants with stolons. Leaves transversally inserted, ovate, densely imbricate, $^{1}/_{5}$-$^{1}/_{3}$-bifid; segments slightly longer than wide or as long as wide. Apex of the segments, usually, discolored, ending in one or two cells. Leaf cells with trigones large and confluent.

54. *Microlejeunea bullata* (Taylor) Steph.

Plants small, less than 0.5 mm wide. Leaf lobules large, reaching up to ½ its length, globose, with entire keel. Ocelli sometimes present at base and mid-leaf. Amphigastria deeply ½-⅔-bifid; the segments suberect, rarely connivent, base of segment 2-3 cells wide. Lateral margins of the inner female bracts weakly crenulate. Perianth with 4 keels.

55. *Noteroclada confluens* Taylor

Plants large, ca. 1 cm wide. Leaves with 2-3 cells layers, wider than long. Trigones lacking. Leaf cells thin and smooth. Rhizoids brown. Antheridia and archegonia on the abaxial surface of the stem.

56. *Nowellia curvifolia* (Dicks.) Mitt. ***

Postical leaf margin forming an inflated sac up to ½ the length of the leaf, globose necklace-like. Leaf segments largely triangular, cells quadrate to shortly rectangular. Amphigastria lacking.

57. *Plagiochila asplenioides* (L.) Dumort.

Stem cross section with 1-3 layers of cortical cells, thicker and smaller than medullary cells. Leaves ovate-orbicular, contiguous to imbricate; the margins finely dentate, teeth 1-3 cells long and 1-2 cells at base, sometimes lacking. Trigones triangular to cordate. Postical leaf margin not or little decurrent along stem, antical margin decurrent. Propagules lacking.

58. *Plagiochila bifaria* (Sw.) Lindenb. ***

Stem cross section with 2-5 layers of cortical cells. Leaves postically secund, ovate to ovate-oblong. Leaf apex broadly rounded or truncate. Unlike other species of *Plagiochila, P. bifaria* has a vitta formed by elongated cells from near leaf base to mid-leaf. Trigones of the vitta nodulose, or elongated and confluent. Asexual reproduction through fragments of deciduous leaves of flagelliform branches, rarely by propagules on the abaxial surface of the leaves.

59. *Plagiochila corniculata* Dumort.

Leaves distant, ½-⅓-bifid, usually with one tooth on the postical leaf margin. Leaf apex acute. Antical leaf margin incurved. Leaf cells smooth. Amphigastria inconspicuous formed by a few cells. Asexual reproduction through deciduous leaves; propagules lacking.

60. *Plagiochila diversifolia* Lindenb. & Gottsche ***

Leaves ovate-oblong; upper half of the postical margin and apex with teeth 1-5 cells wide and 1-4 cells at base; apical teeth slightly larger than others. Cells of the leaf base slightly elongated. Amphigastria inconspicuous a few cells. Propagules not seen.

61. *Plagiochila patula* (Sw.) Lindenb.

Abaxial surface of the leaf with numerous propagules. Leaves ovate to elongated. This species may be confused with *P. xalapensis,* but its leaves are widespread and the teeth are at the apex and postical margin of the leaf.

62. *Plagiochila xalapensis* Gottsche

Leaves ovate to elongated, narrowly spread, teeth present only at leaf apex. Abaxial surface of the leaf with numerous propagules.

63. *Porella leiboldii* (Lehm. & Lindenb.) Trevis.

Leaves inccubous, ovate-oblong, widespread; apex rounded. Postical leaf margin plane to undulate. Amphigastria wider than the stem, ovate. Leaf lobule oblong-ovate. Bases of the lobules and amphigastria apendiculates and ciliate. Perianth campanulate.

64. *Radula quadrata* Gottsche

Leaves broadly ovate to concave, imbricate; leaf margins weakly undulate. Leaf cells thin and smooth. Trigones small. Leaf lobules flattened, quadrate to shortly rectangular, broadly attached to the stem. Amphigastria lacking. Discoidal gemmae on the antical margin of the leaf.

65. *Schistochilopsis incisa* (Schrad.) Konstant.

Leaves plicate, bifid to quadrifid; segments polymorphic, apex of the segments apiculate, ending in one long tooth, some segments with obtuse apex. Amphigastria lacking. Gemmae one- or two-celled, angled.

66. *Solenostoma amplexifolium* (Hampe) Váňa & Schäf.-Verw. ***

This species and *Lethocolea glossophylla* have lingulate leaves and the cells of the postical leaf margin are strongly elongated. However, *L. amplexifolia* has leaf cells smooth and the sporophyte is developed within perianth. In contrast, *L. glossophylla* has a leaf cells strongly papillose and the sporophyte is developed within marsupium.

67. *Solenostoma callithrix* (Lindenb. & Gottsche) Steph.

Leaves ovate to orbicular, contiguous, distant toward the base. Trigones triangular, sometimes cordate. Leaf cells smooth to scarcely papillose. This is distinguished by its rhizoids that originate from the leaf base.

68. *Solenostoma decolor* (Schiffn.) R.M. Schuster ex Váňa, Hentschel & Heinrichs

Leaves ovate to orbicular, distant to contiguous. Leaf cells smooth. This species may be confused with *J. callithrix,* but differs in that *S. decolor* have rhizoids originating in the epidermal cells of the stem.

69. *Solenostoma sphaerocarpum* (Hook.) Steph. ***

Leaves ovate to orbicular, spread; leaf apex rounded, sometimes emarginated. Cells of the postical margin of the leaf slightly elongated. Leaf cells papillose. Rhizoids scattered, reddish.

70. *Stephaniella paraphyllina* J.B. Jack

Plants strongly adhered to the substrate. Leaves strongly imbricate, not longitudinally plicate, oblate to ovate, hyaline. Leaf apex obtuse, entire. Axillary paraphyllia usually filiform.

71. *Stephaniella rostrata* U. Schmitt **

Plants strongly adhered to the substrate. Leaves loosely imbricate, not longitudinally plicate, ovate, hyaline. Leaf apex acute, slightly serrulate or prorulose. Axillary paraphyllia usually filiform.

72. *Stephaniellidium sleumeri* (Müll. Frib.) S. Winkl. ex Grolle

Plants strongly adhered to the substrate. Leaves strongly imbricate, longitudinally plicate, broadly ovate to reniform, green. Leaf apex rounded-obtuse to rounded, entire. Axillary paraphyllia always foliose.

73. *Strepsilejeunea obtusistipula* Steph. ***

Leaves distant; leaf apex acute to obtuse. Leaf lobule oblique to oblong. Amphigastria broadly obcuneate, three times the width of the stem; apex emarginated, segments slightly divergent. Inner female bracts oblong-elliptic. Inner female bracteole obovate. Perianth pyriform.

74. *Syzygiella anomala* (Lindenb. & Gottsche) Steph. ***

Antical and postical margins of the leaves connate; antical margins revolute, postical margins slightly undulate; leaf apex subacute to slightly bifid. Trigones large with three convex sides, intermediate thickenings scarce. Leaf cells finely papillose. Amphigastria small, vestigial or lacking.

75. *Syzygiella autumnalis* (DC) K. Feldberg, Váňa, Hentschel & Heinrichs. ***

Leaves ovate to orbicular, appressed, apex rounded to emarginated. Cells of the leaf margin quadrate to shortly rectangular forming a border. Trigones triangular. Leaf cells papillose. Amphigastria lacking.

76. *Triandrophyllum subtrifidum* (Hook. & Taylor) Fulford & Hatcher *

Leaves concave; leaf apex trifid, sometimes ⅓-$^{2}/_{5}$-bifid, apex of the segments obtuse, sometimes acute; basal cells of the segments quadrate to shortly rectangular. Leaf base sometimes with short filiform appendages. Trigones small. Leaf cells thin and papillose.

77. *Trichocolea floccosa* Herzog & Hatcher ***

Leaves bisbifid almost from the base, leaf segments narrowly triangular with long cilia on the margins, opposite or verticillate. Leaf cells striate-papillose. Amphigastria small, quadrifid to ¾-bisbifid.

78. *Tritomaria exsecta* (Schmidel) Schiffn. ex Loeske *

Leaves concave, asymmetrically bifid to trifid to $^{1}/_{10}$ their length; antical segment smaller than postical segment. Leaf apex acute-acuminate. Trigones triangular, those of the base larger than those of the mid-leaf. Leaf cells strongly papillose. Rhizoids abundant, hyaline to brown. This species is characterized by numerous reddish tinged, 2-celled gemmae, ovoid at apex of the leaf segments.

Excluded species

Cephaloziella dentata (Raddi) Müll. Frib., *Cryptolophocolea connata* (Sw.) L. Söderstr. & Váňa, *Jungermannia gracillima* Sm., and *Porella platyphylla* (L.) Pfeiff. are excluded because they were not collected in the Valley of Mexico or were not available at MEXU, and have doubtful historical records.

DISCUSSION

The number of leafy liverworts in the Valley of Mexico is low for the size of the area. In addition to the apparent paucity in exploration, other factors are worthy of consideration to explain current numbers in this flora. The following should be mentioned:

1. Environmental degradation. The Valley of Mexico is one of the most populated and polluted regions of the world. Population growth has affected in several forms the biota of the region. Zambrano et al. (2000) reported the local extinction and the decline in abundance of lichens in Desierto de los Leones, attributing it, partly, to the open structure of the forest and the air pollution. Also, Delgadillo and Cárdenas (2000) reported the presumed extinction of moss species in Mexico City. Durán and Rivera (1982) and Durán (1993) evaluated the effect of certain pollutans on epiphytic mosses in Mexico City; the latter author showed a decline in moss frequency in this urban area. In Canada and Europe, the effects of environmental degradation has been well documented (see Davies et al.,

2007; Gignac and Dale, 2005; Hodgetts, 1996; Larsen et al., 2007; Nelson and Halpern, 2005). Adams and Preston (1992) indicated that the decline in abundance and extinction of some species of bryophytes (e.g., *Frullania dilatata, Radula complanata,* and *Porella platyphylla*) are the result of high concentrations of air pollutants, mostly, sulfur dioxide. Hence, the potential extinction of leafy liverwort due to various human activities in the Valley of Mexico may not be ignored.

2. Inaccessible areas. Some historical records and species not found in this study (e.g., *Anastrophyllum minutum, A. auritum* and *Frullania arecae*) were reported for Popocatépetl volcano, which remains closed to the public due to volcanic activity.

3. Inaccurate or incorrect data collection. Authors unfamiliar with local geography have mistakenly cited localities for various specimens. For example, Gradstein (1994) recorded *Dicranolejeunea axillaris* (Nees & Mont.) Schiff. from the Valley of Mexico with a specimen collected from Valle de Bravo; therefore, the species was not included in this study.

4. Although the vascular flora of the Valley of Mexico is very diverse, the dryland scrubby vegetation of the lower elevations and the coniferous forests of the upper elevations are not expected to yield substantial increase in the number of leafy liverworts species. This is particularly true of the epiphytic taxa.

Despite the numbers cited, it is expected that further exploration in specific sites will add to our knowledge of this group of plants in the Valley of Mexico.

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CONCLUSIÓN GENERAL

La familia Stephaniellaceae es un grupo monofilético de acuerdo con las sinapomorfías presencia de parafilios y presencia de pliegues longitudinales en las brácteas femeninas. Algunas estructuras como la morfología de los cuerpos oleíferos y de la cápsula del esporofito son importantes en la taxonomía del grupo. Sin embargo, la observación de tales estructuras es difícil; los cuerpos oleíferos se desintegran rápidamente después de que los ejemplares son colectados; además, la cápsula del esporofito ha sido observada en pocas ocasiones. Como consecuencia de lo anterior, en este estudio se evaluaron los caracteres ya identificados por otros, pero haciendo un esfuerzo especial por encontrar otros rasgos que apoyen el reconocimiento formal de los taxa.

Las relaciones de Stephaniellaceae con Gymnomitriaceae, Southbyaceae y Arnelliaceae permanecen inconclusas y desafortunadamente, Shaw et al. (2015) no incluyeron a las Stephaniellaceae en su análisis molecular. Evidentemente, esta es una línea complementaria de investigación para mejorar la comprensión de la taxonomía y la biología de este grupo de hepáticas.

Stephaniellidium es un género independiente y es el grupo hermano de *Stephaniella.* Se caracteriza por la presencia de hojas clorofilosas y plegadas longitudinalmente, y por la presencia de marsupio. Por su parte, *Stephaniella* se caracteriza por tener hojas clorofilosas y brácteas femeninas con ápice falcado. Las relaciones entre las especies de *Stephaniella* fueron aclaradas en este estudio. *Stephaniella boliviensis* se corroboró como sinónimo de *S. paraphyllina,* con base en la morfología de la hoja y de los parafilios.

El gametofito de las especies de Stephaniellaceae es poco variable. Por ejemplo, en *Stephaniella,* la forma de los parafilios no es exclusiva de una especie, es decir, los parafilios filiformes y lanceolados pueden estar presentes en una o varias especies. Sin embargo, una sola forma es la dominante en cada especie. Por otro lado, aunque Schmitt y Winkler (1968) ilustraron la forma y el ápice de la hoja con límites morfológicos bien marcados entre las especies, la revisión del material tipo muestra que puede haber sobreposición de formas entre las especies. En este sentido, Schuster (2002) sugiere que la escasa diferenciación entre especies de *Stephaniella* indica que la especiación en el género ocurrió recientemente en áreas que son comparativamente jóvenes como el ambiente del páramo o el alpino. A pesar de lo anterior, el hallazgo de caracteres útiles para la identificación de especies (distancia entre las hojas del tallo, decurrencia de la hoja y forma de las células apicales de la hoja) indica que las Stephaniellaceae son un grupo plástico con potencial de variación y especiación todavía sin determinar.

En conclusión, la morfología tuvo poca utilidad en la resolución de las relaciones a nivel de familia. Por lo tanto, las relaciones entre familias o las interespecíficas estudiadas aquí, deberán ser evaluadas y corroboradas con datos moleculares.

Finalmente, aunque la flora de hepáticas de México es menos diversa que la de musgos y plantas vasculares, se espera que en estudios posteriores el número de especies conocidas para el país aumente como resultado de la mayor exploración de zonas particulares. La presencia de taxa de briofitas de diversas afinidades geográficas refleja la relación de la flora con la de otras partes del mundo. Los eventos geológicos como la separación de los continentes, así como la formación de los sistemas montañosos, son importantes en el establecimiento de los patrones de distribución de las briofitas.

La recolección de ejemplares, preparación de claves, catálogos y estudios filogenéticos con datos morfológicos y moleculares de hepáticas, contribuirán al estudio taxonómico, sistemático, florístico y fitogeográfico de este grupo de plantas en México. Esta información puede contribuir al conocimiento de su origen, edad y al reconocimiento de las vías de migración, a aumentar el conocimiento, manejo y conservación integral de la biodiversidad.

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