Sphagnum magniporosum (Sphagnaceae, subgenus Subsecunda) a new peatmoss species from Venezuela

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We describe *Sphagnum magniporosum* sp. nov. in *Sphagnum* subgen. *Subsecunda* (Sphagnaceae) Bryophyta. The new species is described and characterized using morphological methods. The description is based on qualitative examination of morphological characters of shoots, stems, branches and leaves. The new peatmoss is known from a single locality at a tabletop (tepui) mountain in the Chimantá Massif, Canima National Park in the state Bolívar of Venezuela. The morphology of the species is compared and evaluated using keys, descriptions and illustrations of ten South American and one African *Subsecunda* species.

Keywords: biogeography, microsatellites, morphology, peatmoss, taxonomy

The peatmoss (genus *Sphagnum* L.) flora of South America is well-known for its high species diversity and many endemic taxa (Shaw et al. 2003, 2019, Costa et al. 2011). The majority of species are recorded from the Andean regions of Bolivia, Columbia, Ecuador and Peru, and the catchment area of the Amazon basin in Brazil, Columbia, Peru and Venezuela. These areas are characterized by high-humidity and precipitation. Among those countries, Brazil has the highest number of reported peatmosses (86 species, Costa et al. 2011), representing all subgenera, namely *Acutifolia*, *Cuspidata*, *Rigida*, *Sphagnum* and *Subsecunda* (Shaw et al. 2016).

Subgenus *Subsecunda* is especially species rich in South America compared to the rest of the world. Michaelis (2019) lists and circumscribes about 110 species worldwide of subgenus *Subsecunda*, and South America holds the majority of *Subsecunda* species reported. So far, less than ten of these species are also reported from outside this continent.

More than half of South American *Subsecunda* species were described between 1987 and 2002 by sphagnologist Howard Alvin Crum (1922–2002); see Buck and Anderson (2003). Most of these descriptions were based on single col-

lections made by other collectors visiting the South American continent. Crum himself points out that this is a serious weakness in the taxonomic evaluation of his described species, and he highlighted that new knowledge based on more collections and extended research are necessary to evaluate the validity of the new species. But he also wisely claimed: 'Meanwhile, it serves a practical purpose to give names to the species, to give them visibility rather than continue them in storage' (Crum 1987a). New knowledge of South American *Subsecunda* has not improved much over the two last decades, so we fully support this view.

Taxonomic classification and nomenclature of *Sphagnum* taxa have been, and still is a controversial matter, including problems related to formal inter- and intraspecific classifications (species, subspecies, varieties). However, many new species descriptions are based on evidence including both morphological examination and genetical analyses (Shaw et al. 2013, Hassel et al. 2018). Likewise, description and outline of new *Subsecunda* species are usually based on the same solid fundament with several collections from different localities and geographical areas, for example the amphi-Pacific *S. inexspectatum* Flatberg (Flatberg 2005, Shaw et al. 2014b) and *S. miyabeanum* (Shaw et al. 2014a, b). A similar approach and new knowledge are lacking for South American *Sphagnum*.

The Pantepui biogeographic region of the Guiana Highlands in Venezuela, Guyana and Brazil is characterized by about

50 isolated tabletop mountains (tepuis). Tepuis are known for their concentrations of endemic species (Huber 1988, 1992). The patterns of endemism and distribution of bryophytes of the topographic tepui islands of northern South America differ from vascular plants mainly due to higher dispersal ability of bryophytes (Désamoré et al. 2010, Costa et al. 2020). Most endemic bryophytes are assumed to originate from cold-adapted Andean ancestors dispersing to the Pantepui region (Désamoré et al. 2010). Besides the endemic species, the bryophyte flora of the Pantepui region has biogeographic elements consisting of Tropical American, Pantropical, Afro-American and globally widespread species (Costa et al. 2020). Désamoré et al. (2010) points to a relationship with the West Indian Caribbean islands whereas Robinson (1986) proposed an African or even Asian phytogeographic relationship of species in the Pantepui region. A molecular study of subgenus *Subsecunda* revealed a well-supported lineage comprising samples from Africa, South America and Australia/New Zealand (Shaw et al. 2008) corroborating close relationships between South America and Africa.

Among the 70 *Sphagnum* species reported from the South American region that includes Venezuela (Am. 4 cf. Michaelis 2019), five belong to subgenus *Subsecunda*: *Sphagnum funkiae* H.Crum, *S. gracilescens* Müll.Hal., *S. juliforme* H.Crum, *S. liesneri* H.Crum and *S. subsecundum* Nees (Michaelis 2019, GBIF 2021). Likely, the number of *Subsecunda* species in this region is higher as very little new knowledge of South American *Subsecunda* has come after the work of H. A. Crum.

After collecting *Sphagnum* specimens from tepui in the Chimantá massif, Bolívar region of Venezuela in 1985, T. Ahti finally had a chance to present the specimens in storage to K. I. Flatberg in 2017. One of these specimens was a homogenous sample of a subgenus *Subsecunda* species, not belonging to *S. juliforme*, the only *Subsecunda* species previously reported from the Chimantá Massif (GBIF 2021). Furthermore, the specimen collected has turned out to be morphologically distinct and differs from all published *Subsecunda* species as included by Michaelis (2019). Based on morphology, we describe the specimen as a new species named *Sphagnum magniporosum* (see formal description and typification below). We compare it to relevant South American subgenus *Subsecunda* species. Due to biogeographic connections between South America and Africa pointed out by Shaw et al. (2008) we also included comparisons with selected African *Subsecunda* species as outlined by Eddy (1985).

Material and methods

The specimen of *Sphagnum magniporosum* was collected at the tepui Macizo del Chimantá, Bolívar state, Venezuela in 1985. The tepui Macizo del Chimantá is part of the Pantepui biogeographic region of the Guiana Shield in the borderland between Venezuela, Guyana and Brazil (Fig. 1). Tepuis of this region consist of > 1.5 billion years old Proterozoic sandstone (Rull et al. 2019). The climate of the region is mild, with annual average temperatures around 20°C and a precipitation of about 3600 mm (Huber 1992). The rainy season is 10 months long and the tepuis are often wet and cloudy. The southeastern sections of the Chimantá Massif are characterized and often dominated by very extensive, open peat bogs (see map in Huber 1992: 163). As noted in Ahti (1992), the *Sphagnum* species are present but not a major part of the vegetation. Instead, many herbaceous or subfruticose vascular plants are the main peat-forming species, such as *Brocchinia* (Bromeliaceae), *Stegolepis* (Rapateaceae), *Psychotria* (Rubiaceae), *Baccharis* (Asteraceae) and *Syngonanthus* (Eriocaulaceae). In addition, tall lichens, primarily reindeer lichens (e.g. *Cladonia argentea*, *C. confusa*, *C. dendroides*, *C. densissima*, *C. signata*, *C. steyermarkii*, *C. subreticulata*, *Cladia globosa*) are very abundant (Ahti 1992). Several of the peatland Cladoniaceae species are endemic to the Guianas (Ahti and Sipman 2013).

The *Sphagnum* plants were investigated using morphological examination, but the ploidy level was evaluated using molecular methods. The number of microsatellites per locus has been shown to be a good method for determining ploidy levels in *Sphagnum* (Ricca et al. 2008, Kyrkjeeide et al. 2019). DNA was extracted from dried specimens using a small part of the shoot apex. Extractions were performed using the DNeasy 96 Plant Kit (Qiagen, Oslo, Norway) following the manufacture's protocol. We genotyped 15 microsatellite markers from two plants (Table 4; for methods see Kyrkjeeide et al. 2016).

Morphological examination and terminology

The description of the new species is based on morphological characteristics found in the examined type specimen. Basic morphology of the new species has been compared and evaluated with use of keys, descriptions and illustrations of South American and African *Subsecunda* species (Eddy 1985, Crum 1987a, b, 1990a, b, 1992, 1993, 1994, 1995a, b, 1997, 2001, Michaelis 2019). This published knowledge constitutes the fundament for morphological comparisons and taxonomy made here.

Studies of type collections of the compared species are not included in the present study. All the compared South American species are well described, illustrated and commented on by Crum, and summarized by Michaelis (2019). The same applies for the African species included in the study (Eddy 1985).

The *S. magniporosum* specimen was studied by preparation of semi-permanent slides mounted in glycerol. We examined branch and stem leaves, stem and branch cross sections, outer stem and branch surfaces and cross sections of branch leaves. Stems and leaves were stained with a methyl violet solution. The morphological examinations and measurements were performed using a transmission microscope, and photomicrographs were made applying the Leica Application suite LASD ver. 2.6 for stacking. Ten stem leaves and 10 branch leaves from the middle part of branches were measured for size.

The terminology used for description and characterization of leaf pores on the hyaline cell walls of *S. magniporosum*: 1) Perfect pores include circular, elliptic to more irregular perforations in the hyaline cell wall membranes. Such pores are of two types, unringed pores and ringed pores surrounded by a thickened membrane ring. Perfect pores are either free-lying from the adjacent chlorophyll cells and

Figure 1. The Pantepui ecoregion of Venezuela. <https://commons.wikimedia.org/w/index.php?curid=104644538>.

are illustrated as median pores (sometimes named luminal pores), or they lie rather tightly adjacent to the chlorophyll cells as commissural pores in ± continuous rows. 2) Imperfect pores are unringed and only with a membrane thinning, but without perforation. Such imperfect pores look paler when stained leaves are examined in microscope. 3) Pseudopores are without perforations, closely facing the chlorophyll cells, and are delimited by semi-circular, semi-elliptic to elongate-rectangular fibril bands connected to the inner walls, and sometimes have thin membranes. Pseudopores are usually confined to the concave leaf surface.

The following terminology is used for the dominating pore patterns found on the convex (dorsal) surface of the hyaline cell walls of leaves among compared species: 1) 3-seriporose cells have a mixture of commissural pores and free-lying median pores. 2) 2-seriporose cells have commissural pores without median pores. 3) 1-seriporose cells have only median pores without commissural pores. Single cell end pores are often found in addition.

Delimitation of morphologically similar species

Michaelis (2019) divides the *Subsecunda* species in six 'groups'. These groups are artificial classifications, and not based on phylogenetic or taxonomical criteria. The groups

are primarily based on 1) microscopic morphological characteristics connected to the number of stem cortical layers, 2) number of pore rows (2 or 3) on the hyaline cell walls of the leaves and 3) shape and position of the chlorophyll cells of branch leaves in cross section.

In this respect, *S. magniporosum* connects best to species group 2, characterized 'by one-layered stem cortex and more than two rows of pores on the hyaline cells'. In practical microscopy this implies that the hyaline cell walls on their convex surface of the leaves have predominantly 2-seriporose leaf cells but with a varying element of 3-seriporose cells.

This species group includes seven South American species. *Sphagnum magniporosum* shares the unicorticate stem of this group. But it deviates with predominance of 2-seriporose leaf cells, combined with an element of 1-seriporose cells or cell portions with large median pores.

Despite this pore discrepancy, we have found it most relevant to primarily compare *S. magniporosum* with the South American species aggregated in this species group of Michaelis (2019) (Table 1). In addition, we consulted the descriptions and illustrations made for species placed in Michaelis' groups 1, 3–6, but without finding species with leaf porosity similar to *S. magniporosum*.

All the seven South American species are endemic to tropical South America, and their known distributions are

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represented by herbarium collections from single localities in Brazil (five species), Colombia (one species) and Peru (one species) and none of them are recorded from Venezuela. The collections underlying the formal types are made by several collectors from 1977 to 1987 (Table 1).

No relevant new species from South America have been described since 2002 (Crum 2002). Crum's descriptions of the seven species are the basis for the treatment in Michaelis (2019) and the illustrations in Michaelis (2019) come directly from Crum's work. Three *Subsecunda* species from Brazil, viz. *S. pluriporosum* H.A. Crum (Crum 1994), *S. septatoporosum* H.A. Crum (Crum 1997) and *S. turgescens* Warnst. (Warnstorf 1895) also share the 3-seriporose cell pattern but are placed in his species group 5, with multilayered stem cortex, by Michaelis (2019). These species also differ in other morphological characters and are not further compared with *S. magniporosum*.

Among the five *Subsecunda* species from Venezuela reported by Michaelis (2019), *S. subsecundum* occurs in the Northern Hemisphere with a northern mainly amphi-Atlantic distribution. This species is well separated from *S. magniporosum* by much smaller shoots, dimorphic branch fascicles, 2-seriporose branch leaves, stem leaves much smaller than the branch leaves and without pores on their convex surface. The occurrence of *S. gracilescens* in Venezuela is uncertain. It is described with small, pale shoots, multistratose stem cortex, 2-seriporose leaves and triangular to trapezoid shape of the branch leaf chlorophyll cells in cross section. These two species are left out of further comparison with *S. magniporosum*.

Thus, we here compare *S. funkiae*, *S. juliforme* and *S. liesneri* with *S. magniporosum*. All three are described based on single herbarium collections from Venezuela (Crum 1994, 1995a). It is noticeable that none of these species are added with recent published records from Venezuela, nor are they recorded with additional collections from outside this country.

During this study we became aware that *S. magniporosum* showed morphological similarity to some African *Subsecunda* species (Eddy 1985). Eddy divide tropical/subtropical African *Subsecunda* species in two subsections, *Acrosphagnum* (C. Müll.) A. Eddy and *Subsecunda*, both are classified as sections by Michaelis (2019). The six African species belonging to subsect. *Acrosphagnum* are excluded from comparison with *S. magniporosum*, as they all possess a markedly 2–3-layered stem cortex with an enlarged surface layer with usually a large external pore and have fascicles with 2–7 branches. However, two of the species (*S. capense* Hornsch. and *S. ceylonicum* Mitt. ex Warnstorf) pos-

sess leaf cell structure approaching *S. magniporosum*, with 3-seriporose hyaline leaf cells (Eddy 1977). Eddy's subsection *Subsecunda* includes *S. truncatum* Hornsch. (including *S. bordasii* Bescher.), *S. rutenbergii* C. Müll. and *S. africanum* Wel. & Duby. The morphologically variable *S. truncatum* is distributed from southern and eastern Africa including the East African islands (Eddy 1985). *Sphagnum rutenbergii* is endemic to the East African islands (Eddy 1985), while *S. africanum* is recorded with scattered occurrences in montane regions from Angola to Malawi (Eddy 1985). According to Karlin et al. (2014), all three species belong to the *S. africanum* complex of subgen. *Subsecunda*, and is defined as the group of African and South American species referable to 'lineage D' of Shaw et al. (2008; Fig. 4). *Sphagnum africanum* shares many similar traits with *S. magniporosum*, while the two other species deviate much more in morphological details. Also, *S. rutenbergii* and *S. truncatum* have more branches in the fascicles, and they are more dimorphic and less tumid than *S. africanum*. Hence, only the latter is compared with *S. magniporosum*.

Results

Morphological comparison with South American species

Sphagnum magniporosum differs from all the compared species belonging to species group 2 of Michaelis (2019) in various morphological characteristics, both macroscopically and in microscopical details (Table 2). All compared species except for *S. subhomophyllum* and maybe *S. sonsonense* are smaller plants, and none are described with the marked orange plant colour of *S. magniporosum*.

The single branches of *S. magniporosum* is shared by *S. garysmithii* and partly by *S. luetzelburgii*, but they differ in several other morphological characteristics.

Sphagnum magniporosum has longer branch and stem leaves than the other species except for the near equal-sized stem leaves in *S. garysmithii*. As in this species, the stem leaves are large compared to the branch leaves. Stem leaf shape varies among the compared species; *S. garysmithii* deviates with its rounded leaves with obtuse apices, and *S. subhomophyllum* with its more triangular stem leaves. Differences in branch leaf shapes are less obvious.

All the compared species have stem leaf fibrillosity extending into their proximal half and usually close to the base, except for *S. cribriforme* with few fibrils or fibril stumps confined to distal leaf end part.

Table 1. Survey of the seven *Subsecunda* species known from South America circumscribed under Species group 2 in Michaelis (2019, pp. 228–230), characterized 'with one-layered stem cortex and more than two rows of pores on the hyaline cells'.

Sphagnum	Author, publication year	Type, herbarium	Collecting year	Country
cribriforme	H. A. Crum 1993	Lectotype CHR	1892	Brazil
garysmithii	H. A. Crum 1987a	Holotype MICH, isotype NY, TRH	1971	Brazil
hegewaldii	H. A. Crum 2001	Holotype MICH, isotype MO	1973	Peru
homophyllum	H. A. Crum 1992	Holotype MICH	1977	Brazil
luetzelburgii	H. Paul and H. A. Crum 2001	Holotype MICH, isotype M		
sonsonense	H. A. Crum 1995b	Holotype MICH, isotype NY, paratype MICH	1995	Colombia
subhomophyllum	H. A. Crum 1997	Holotype MICH	1987	Brazil

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Table 2. Morphological comparison of *Sphagnum magniporosum* with seven *Subsecunda* species from South America.

Sphagnum	*magniporosum*	*cribriforme*	*garysmithii*	*hegewaldii*	*homophyllum*	*luetzelburgii*	*sonsonense*	*subhomophyllum*
Plant size	medium	small	small to medium, without capitula	very small	small	small, rather loosely branched	small to medium	medium
Plant colour	yellow-orange to orange brown	pale to dark brownish brown	brown	dark redbrown above	yellowish	dark brown	light green	above bronze, below pale brown
Stem colour	dark brown	brown	dark brown	dark brown	pale	dark brown	orange-brown to dark brown	brown
Stem cortex	unicorticate	unicorticate	unicorticate	unicorticate	unicorticate	unicorticate	unicorticate	unicorticate
Stem leaves								
Shape	narrowly ovate-triangular to elliptic-ovate	ovate-triangular	rounded to elliptic	ovate	lingulate to lingulate-ovate	elliptic to elongated ovate	elongated ovate	triangular to ovate-triangular
Apex	acute to acute-obtuse, slightly truncate-erose	rounded	broadly rounded, dentate	obuse, concave	rounded	broadly rounded	obtuse	obtuse
Length (mm)	3.2–3.6	1.3–1.5	2.4–3.0	1.1–1.3	1.3	1.2–1.5	1.7–2.3	1.0–2.0
Fibrillosity	whole leaf	near apex, stumps to midleaf	whole leaf	whole leaf	whole leaf	whole leaf or near so	whole leaf	upper 1/2 to 2/3 of leaf
Leaf porosity concave surface	varying number of commissural, longitudinally rectangular to elliptic pseudopores	very few or no pores	numerous commissural, perfect, ringed pores and pseudopores in rows	scattered commissural pseudopores and few circular perfect, median pores	numerous commissural, perfect, ringed pores	several commissural, ±circular, ringed, perfect pores in apical leaf portion and scattered perfect, median pores	several commissural pseudopores in short rows, and few circular, perfect pores in cell angels	several to numerous commissural, circular to elliptic, perfect pores in loose rows, near apex with additional 2–3, circular, perfect to imperfect, median pores
Leaf porosity convex surface	2- and 3-seriporose. Numerous commissural, circular to elliptic, perfect, ±ringed pores, occupying 1/3–1/2 of cell width and usually fewer ±circular, perfect, non-ringed, median pores occupying more than half of cell width	predominantly 2-seriporose with numerous commissural, circular to elliptic, perfect, ringed pores, near leaf base 3-seriporose with larger, perfect, unringed, median pores	predominantly 2-seriporose with many small commissural, elliptic, perfect, ringed pores in dense rows, partly 3-seriporose with 3–7 fairly large, circular, unringed, perfect, median pores	predominantly 2-seriporose with numerous commissural, small, circular, perfect pores, partly 3-seriporose with scattered, small to fairly large, circular, perfect, median pores	predominantly 2-seriporose with many commissural, perfect, ringed pores, partly 3-seriporose with several perfect, median pores	predominantly 2-seriporose with numerous commissural, fairly large, ±circular, perfect and often ringed pores, partly 3-seriporose with few to several perfect, median pores, increasing in number and size in distal half of leaf	2-seriporose with numerous commissural, small, ±circular, elliptic, perfect, ringed pores, median pores unrecorded	predominantly 2-seriporose with commissural, circular to elliptic, perfect pores in loose rows, partly 3-seriporose with few, circular, perfect, perfect to imperfect, median pores
Branch fascicles	monocladous with tightly arranged, similar-sized spreading and tumid branches	with 2 short and spreading branches	monocladous, unequally long and rather short, spreading branches	with 2 short spreading branches	with 3 similar and spreading branches	with 1–2 varyingly spreading branches	with 4 branches, 2 of them spreading	with 3 branches, 2 of them spreading

(Continued)

Table 2. Continued.

Sphagnum	magniporosum	cribriforme	garysmithii	hegewaldii	homophyllum	luetzelburgii	sonsonense	subhomophyllum
Branch leaves								
Shape	widely ovate	roundish-ovate	roundish to elliptic	ovate	ovate	ovate to ovate-lanceolate	ovate-lanceolate	lanceolate to ovate
Apex	involute to narrowly rounded	rounded, often cucullate	rounded	obtuse	obtuse	obtuse	narrowly truncate	narrow, somewhat obtuse
Length (mm)	2.4–2.9	1.8–2.0	1.9–2.0	1.0–1.1	1.0–1.1	1.4–1.7	1.7–2.0	1.9–2.0
Leaf porosity concave surface	varying number of longitudinally rectangular to elliptic pseudopores, facing the commissures	mostly circular, perfect, ringed commissural pores in dense rows	numerous commissural, perfect, ringed pores and pseudopores	without pores, or in upper leaf part with some commissural, elliptic, perfect pores and pseudopores	numerous commissural, perfect, ringed pores in loose rows	without pores, or in the leaf tip with several commissural, circular to elliptic, perfect pores	several to numerous commissural pseudopores, often in short rows	numerous commissural, circular, perfect pores in rows
Leaf porosity convex surface	mainly similar to stem leaves, but median pores often fewer	predominantly 3-seriporose with many commissural, circular, perfect, ringed pores in dense rows and many median, perfect, unringed, circular pores	mainly similar to stem leaves	2-seriporose with many commissural, circular to elliptic, perfect pores, median pores unrecorded	predominantly 3-seriporose with many commissural, elliptic, perfect, ringed pores and several perfect median pores of equal size	predominantly 2-seriporose with many commissural, circular to elliptic, perfect, ringed pores in dense rows, in distal leaf portion partly 3-seriporose with few to several, perfect, median pores	predominantly 2-seriporose with many commissural, small, circular to elliptic, perfect pores in dense rows, in distal leaf portion partly 3-seriporose with 2–6 perfect, median pores of equal size	2-seriporose with numerous commissural, circular, perfect pores in rows, median pores unrecorded
Chlorophyll cells of branch leaves in cross section	elliptic to elliptic-ovate, varyingly exposed with ±thickened cell walls to both sides	elliptic, centred, on both sides narrowly exposed with thickened cell walls	rectangular, on both sides almost equally wide exposed	elliptic, on both sides narrowly exposed	narrowly elliptic, on both sides narrowly exposed with ±thickened walls	barrel-shaped to elliptic, equally exposed on both sides with thickened cell walls	inverte ovate to elliptic, broadly exposed on concave surface, narrowly exposed on convex surface	elliptic, centered, narrowly exposed on both surfaces with ±thickened walls

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All the species compared with *S. magniporosum* have 3-seriporose leaf cells present on the convex surface of the branch and/or stem leaves but with comparatively much smaller median pores. *S. hegewaldii* can also have an element of 1-seriporose leaf cells like *S. magniporosum*, and in *S. subhomophyllum* 2-seriporose leaf cells dominate except for some 3-seriporose cells in distal leaf part. But all these species lack the 1-seriporose cells or cell portions found in *S. magniporosum* with pore width equal to the hyaline cells.

The pore pattern on the concave leaf surfaces varies more. All species except *S. hegewaldii*, *S. luetzelburgii* and *S. subhomophyllum* lack median pores in the stem leaves, and *S. cribiforme* is nearly without pores. *Sphagnum magniporosum* is the only species recorded with almost exclusively pseudopores, while the other species have only perfect pores (*S. homophyllum*) or a combination of perfect pores and pseudopores (*S. garysmithii*, *S. hegewaldii*, *S. sonsonense*, *S. subhomophyllum*). The special longitudinal rectangular shape of the pseudopores found in *S. magniporosum*, is not reported in any of the species.

The elliptic shape of the chlorophyll cells reaching both surfaces with varyingly thickened walls in *S. magniporosum* is mainly shared by *S. cribriforme*, *S. hegewaldii*, *S. homophyllum* and *S. subhomophyllum*. In *S. luetzelburgii* we find elliptic to barrel shaped chlorophyll cells, and in *S. sonsonense* ovate-elliptic and more broadly exposed on the concave compared to the convex surface. *Sphagnum garysmithii* has rectangular chlorophyll cells reaching both surfaces.

The Venezuelan species included in the comparison (Table 3) have smaller and more slender shoots than *S. magniporosum*, except maybe *S. juliforme*. None of the three species have the orange colour of *S. magniporosum* . Only *S. funkiae* and *S. juliforme* are reported with stem and branch leaves approaching the length of *S. magniporosum*. *Sphagnum juliforme* is like *S. magniporosum* described having single branches and share the one-layered stem cortex. However, *S. juliforme* has very short branches, and the shape of the chlorophyll cells are rectangular (not elliptic) in cross section. *Sphagnum funkiae* has predominantly two-layered stem cortex, branch fascicles with four spreading branches and triangular stem leaves. *Sphagnum liesneri* shares the elliptic shape of the branch leaf chlorophyll cells in cross section with *S. magniporosum* but has small shoots and branch fascicles with mostly two branches. None of the compared Venezuelan species belong to species group 2 of Michaelis (2019). *Sphagnum juliforme* and *S. liesneri* belong to species group 1, with one-layered stem cortex and 2-seriporose branch leaf cells, and *S. funkiae* belongs to group 4 with multi-layered stem cortex and 3-seriporose leaf cells (Michaelis 2019). But interestingly, *S. funkiae*, *S. hegewaldii* and *S. liesneri* have an element of 1-seriporose hyaline cell portions in their stem leaves.

Comparison with *Sphagnum africanum*

Sphagnum africanum is compared with *S. magniporosum* in Table 3, both species have medium-sized shoots of rather similar colour. The two species have predominantly one-layered stem cortex, but *S. africanum* also has parts with two-layered stem cortex. *Sphagnum magniporosum* has longer leaves than *S. africanum*, but both species have longer stem than branch leaves. Moreover, the stem leaves of *S. magniporosum* are more elongate in shape. The two species share the rather widely ovate shape of the branch leaves, but *S. africanum* has markedly more rounded leaf apices. The two species share the monomorphic and tumid appearance of the branches, although *S. africanum* usually has two branches versus one in *S. magniporosum*.

The pore structure of the hyaline cells of branch leaves of *S. africanum* and *S. magniporosum* is rather similar, with abundant commissural perfect pores in ± continuous rows on the convex surface. But contrary to *S. magniporosum*, *S. africanum* also has an element of 3-seriporose cells with scattered median pores and is not illustrated with the 1-seriporose cells pattern of *S. magniporosum* (Eddy 1985; Fig. 21). The pore pattern on the concave surface of the branch leaves of the two species shows strong similarity, with common occurrence of many longitudinally rectangular pseudopores arranged along the commissures (Eddy 1985; Fig. 20). An interesting comparison lies in the cell and pore structure of the branch cortex. Both species share the morphology of elongate retort cells without or indistinct neck, and with one distal end pore. In addition, in *S. africanum* most of the ordinary cortex cells have one apical end pore, while *S. magniporosum* has many cells with 1–3, minute lateral pores (Fig. 2D). *Sphagnum africanum* and *S. magniporosum* share the basic elliptic shape of the branch leaves chlorophyll cells in cross section. Both have chlorophyll cells that reach both leaf surfaces with a varying degree of thickened walls (Eddy 1985; Fig. 20 and 21).

Ploidy level of *S. magniporosum*

Of 15 microsatellites, three had missing data for both samples, and one sample had missing data in three other markers (Table 4). This is not surprising as the specimens were collected more than 30 years ago and DNA is expected to decompose with time. The microsatellite genotyping identified one allele at each marker. For all, except one marker, the alleles are shared between the two specimens.

Discussion

The morphological examinations and comparisons of *Sphagnum magniporosum* with South American and southern African *Subsecunda* species sharing the combinations of selected morphological characters, support the distinctness of the new species. *Sphagnum magniporosum* deviates significantly from the described morphological patterns of all compared species.

The most diagnostic morphological characteristics of *S. magniporosum* are 1) the large size of the commissural and the median pores relative to breadth of the hyaline cells on the convex surface of the branch and stem leaves, and 2) the element of 1-seriporose cells or cell portions of large median pores on convex leaf surfaces. Only the Venezuelan species *S. funkiae* and *S. liesneri* among the compared species are recorded with an element of similar occurrence of 1-seriporose cells in distal portion of their stem leaves, but the median pores in these two species are illustrated much smaller than in *S. magniporum* relative to cell breadth.

Table 3. Morphological comparison of three *Subsecunda* species recorded from Venezuela, South America and *S. africanum* from Africa. Information extracted from Eddy (1985), Crum (1994, 1995a, b) and Michaelis (2019).

Sphagnum	*funkiae*	*juliforme*	*liesneri*	*africanum*
Plant size	small	short, but robust	small, slender	medium, rather lax
Plant colour	brown	brown	pale	dull green-brown to more or less completely orange-brown
Stem colour	brown	brownish	pale, yellow-brown to dark	yellow-brown to deep red-brown
Stem cortex	mostly bicorticate	unicorticate	unicorticate	unicorticate, exposed cells without pores
Stem leaves				
Shape	triangular	broadly ovate to ovate-triangular	lingulate	ovate to ovate-lingulate, not illustrated in Eddy (1985)
Apex	rounded, truncate	broadly rounded	rounded cucculate	concave and eroded
Length (mm)	1.6–2.0	2.0	0.9–1.2	1.9–2.8
Fibrillosity	upper fourth of leaf and at base	almost down to leaf base	fibrils present in upper 1/3–2/3 of leaf	whole leaf
Leaf porosity concave surface	pores lacking	pores very few to lacking	pores lacking	varying number of commissural, perfect pores and longitudinally rectangular to elliptic pseudopores
Leaf porosity convex surface	predominantly 2-seriporose with numerous commissural, large, ± circular, perfect, unringed pores, occasionally 3-seriporose with short cell median pore rows in distal leaf portion	2-seriporose with numerous commissural, ±circular, perfect, ringed pores, median pores unrecorded	mostly 2-seriporose with 6–12 commissural to sub-median, ±circular, large, pores	± similar to branch leaves (not illustrated in Eddy (1985)
Branch fascicles	4 spreading, short and similar branches	single-branched, with very short spreading branches	usually with 2 spreading branches	usually with 1–2 monomorphic and tumid branches
Branch leaves				
Shape	ovate	broadly ovate	ovate	widely ovate
Apex	narrowly rounded to obtuse, cucculate	rounded obtuse	rounded	broadly rounded, eroded and sub-cucullate
Length (mm)	1.9–2–0	1.5–1.8	0.8–1.0	(1.2–)1.4–1.9(2.1)
Leaf porosity concave surface	pores mostly lacking	with few pseudopores	pores lacking	scattered small pores and varying number of longitudinally rectangular to elliptic pseudopores along the commissures, especially in distal leaf portion
Leaf porosity convex surface	2-seriporose with numerous commissural ±circular, perfect, ringed, pores, median pores unrecorded	2-seriporose with numerous commissural, ±circular, perfect, ringed, pores, median pores unrecorded	2-seriporose with numerous commissural, circular to elliptic, perfect, ringed, pores, median pores unrecorded	predominantly 2-seriporose with numerous circular, ringed and small commissural pores occupying less than 1/3 of cell width, with an element of 3-seriporose cells with some median, circular and small ringed or unringed pores occupying less than 1/2 of cell width
Chlorophyll cells of branch leaves in cross section	rectangular to elliptic, equally exposed on both sides	rectangular, equally exposed on both surfaces	elliptic, ± equally exposed on both surfaces with ± thickened walls	elliptic, often distinctly displaced towards concave surface and with more thickened walls facing convex surface

Another deviating morphological character found in *S. magniporosum* is the 1–3 minute circular pores often present on lateral walls of the branch cortical cells (Fig. 2D). These pores occur in addition to the apical pore of the enlarged retort cells of the branch cortex (Fig. 2C). Such minute, lateral wall pores are not mentioned in Crum's descriptions nor by Eddy (1985). In fact, such pores seem unreported both at genus and subgenus/section levels (Russow 1894, Åberg 1937, Suzuki 1958, Savicz-Ljubitzkaja and Smirnova 1968, Nyholm 1969, Eddy 1977, Crum 1984, Daniels and Eddy 1990, Hill 2004, McQueen and Andrus 2007, Ander-son et al. 2009, Hölzer 2010, Lönnell et al. 2019, Lüth 2019, Michaelis 2019). However, such pores could be easily overlooked and may be revealed in further examination of *Subsecunda* species. The large leaf size with stem leaves mark-edly longer than branch leaves, distinguish *S. magniporosum* from South American species, but is a shared characteristic with *S. africanum* (Table 3). The taxonomic relationship to other *Subsecunda* species is uncertain and requires further work including molecular methods.

The descriptions and morphological characterizations of *S. magniporosum* are based on a single collection and
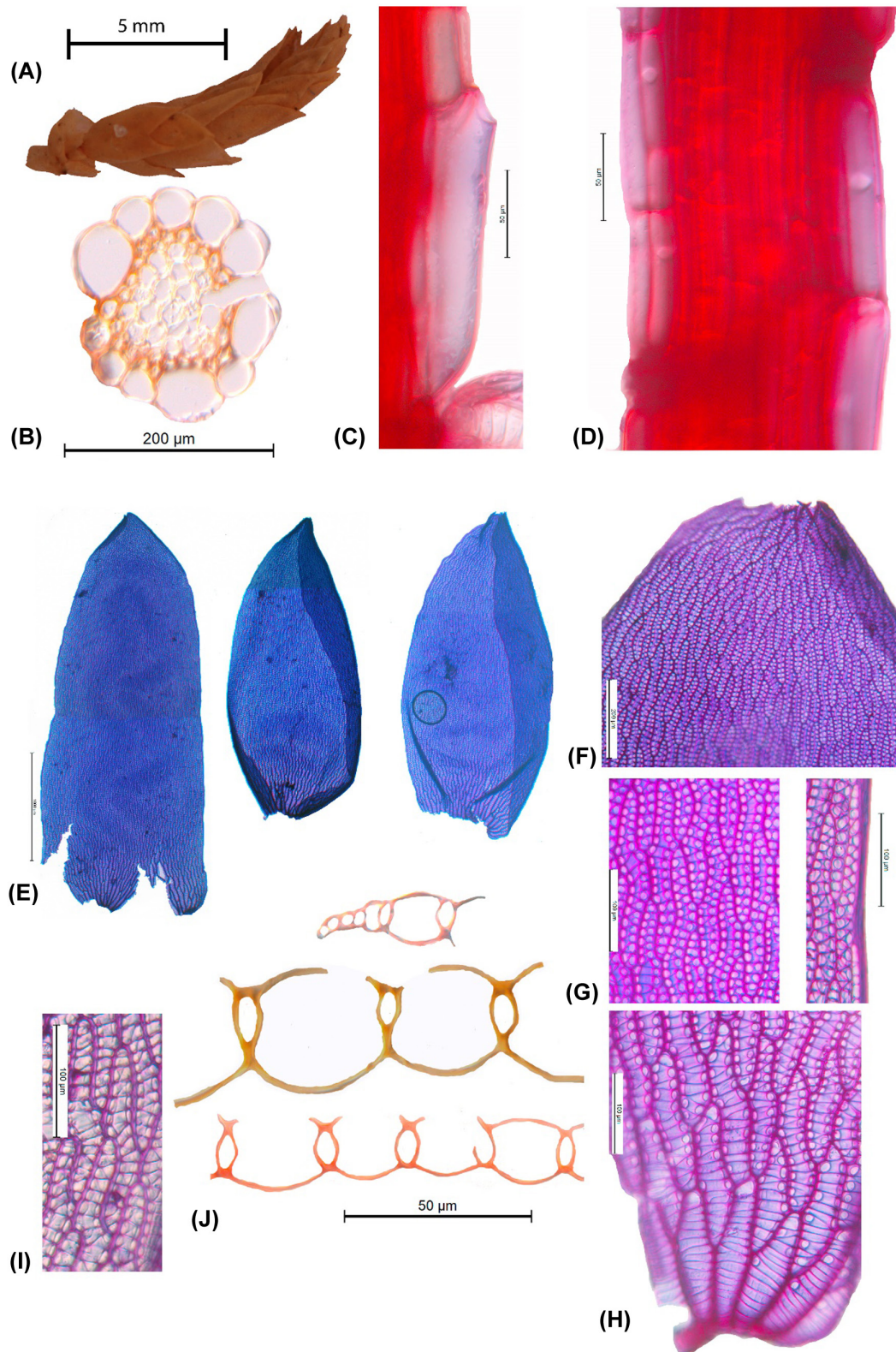
Figure 2. Microscopic pictures of different morphological characters in branch leaves of *Sphagnum magniporosum* sp. nov. (A) Branch, dry, (B) branch in transverse section, (C and D) branch cortex in superficial view, (C) retort cell, (D) ordinary branch cortex cells with lateral wall pores, (E) branch leaves from middle part of branches, (F–H) cell structure on convex surface of branch leaves, (F) distal end portion, (G) mid-median portion to left, mid-marginal portion to right, (H) proximal end portion, (I) cell structure on mid-median concave surface of branch leaves, (J) branch leaves in transverse section, convex side on the top. Material: TRH-B-104740.

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Table 4. Microsatellite markers for two samples of *S. magniporosum* show that one allele was identified for each marker, indicating a haploid ploidy level of the species. Alleles in italics had a weak genotyping signal.

Sample	Herb. ID	Microsatellite marker														
		1	7	9	12	17	19	20	22	29	30	56	65	68	78	93
1	H3239318	125	NA	NA	NA	155	258	*273*	84	204	NA	212	*181*	NA	NA	247
2	H3239318	125	NA	NA	261	155	262	*273*	84	204	NA	212	*181*	229	195	247

reflects just one particular habitat and ecological condition. Examination of more material may confirm the distinct morphology described here or reveal a broader specter of morphological variation. The comparison made with the African *Subsecunda* species *S. africanum* has similar pitfalls. Our knowledge of the phylogenetic and taxonomic significance of traits like number of stem cortex layers and leaf porosity are insufficient, but the number of stem cortical layers with thin-walled cells (predominantly one layer versus predominantly 2–3 layers) are considered of substantial taxonomic value in Northern Hemisphere taxonomic treatments of *Subsecunda* species. In the *S. subsecundum* complex identification keys are often dichotomous in this respect (McQueen and Andrus 2007). The occurrence or not of median pores on the hyaline cell walls on the convex surfaces of leaves in addition to serial commissural pores has been paid less attention in a taxonomic context. However, the documented allodiploid species *Sphagnum × triseriporum* (H.Suzuki) Shaw, endemic to Honshu Island in Japan, is diagnostically separated from closely allied Japanese species by occurrence of both commissural and median cell pores on the convex surface of the stem and branch leaves (Shaw et al. 2013). In that species the median pores are much smaller than in *S. magniporosum* relative to cell width, and the stem is multi-corticate.

The taxonomic significance of pore characteristics in South American and African *Subsecunda* species has so far been neglected. Evaluation of the taxonomic importance of the leaf pore characteristics relative to other morphological attributes of comparable species in a phylogenetic and evolutionary perspective remains. Median pores are common in the subarctic–arctic North American and Eurasian *S. inexspectatum* (Flatberg 2005) and occur even more frequently in the closely related *S. orientale* (Savicz-Ljubitzkaja and Smirnova 1968; Fig. 23). Occurrence of such pores can be a good character for morphological separation of closely related species. The allodiploid species *S. × perfoliatum* (Savicz-Ljubitzkaja and Smirnova 1968; Fig. 24) and *S. ×triseriporum* (Shaw et al. 2013), likely inherited their median pores from the parental *S. inexspectatum* and/or *S. orientale*.

The clades of joint South American and African *Subsecunda* species found by Shaw et al. (2008, Clade B and D; Fig. 4) contains both uni- and multi-layered stem cortex species, and moreover includes species with both 2-seriporose hyaline cell and 3-seriporose hyaline cells. One subclade of clade D shows close affinity between the South African species *S. africanum*, *S. bordasii* and *S. truncatum* and the Brazilian species *S. acutirameum* and *S. uleanum*. Clade B included in Shaw et al. (2008, Fig. 4) includes the African *S. capense*, *S. davidii* and *S. pycnocladum* together with species from Australia/New Zealand, and *S. sonsonense* from Colombia. The observed sister group relationships between the African and South American *Subsecunda* species suggested that recent dispersal, rather than vicariance, explains the relationship between African and South American species in clade B and D (Shaw et al. 2008; Fig. 4).

It is a striking feature that none of the South American species compared with *S. magniporosum* are reported with sexual organs in the relevant publications of Crum. As a result, information about sexuality and sporophytes of the various species is generally lacking in Michaelis (2019). Eddy (1985) does not report sporophytes in *S. africanum* and *S. rutenbergii*, while sporophytes are reported as rare in *S. truncatum*. We know that *Sphagnum* spores have the ability of long-distance dispersal by air currents even across continents (Szövényi et al. 2012, Sundberg 2013, Kyrkjee-ide et al. 2016). High dispersal ability of bryophyte spores may prevent speciation through on-going gene flow and lead to low rates of endemism (Vanderpoorten et al. 2010). However, Meleshko et al. (2021) found that genetic similarities between Northern Hemisphere peatmosses are likely due to incomplete lineage sorting and not recent gene flow. Speciation of South American peatmosses are so far not studied, but evolution of vicariant species through niche diversification and local adaptation could be an explanation for the high degree of endemism. A combination of the vicariant and dispersal hypotheses is an obvious option.

The Venezuelan Guayana region has the highest diversity and the highest rate of endemism of Venezuelan vascular plants (Duno de Stefano et al. 2009). About 42% of the vascular plants of the 50 topographic tepui islands of northern South America are endemic species and about 60% of these are single-tepui endemics. Costa et al. (2020) suggest that the proportion of endemic species in vascular plants in the Pantepui region may be three times higher than in bryophytes. Among bryophytes about one-third of the liverwort species are single-tepui endemics whereas *Sphagnum boomii* (Crum 1990b) is the only single-tepui moss species reported (Désamoré et al. 2010). Higher dispersal ability of bryophytes is assumed to explain the lower proportion of endemic bryophyte species compared to vascular plants (Désamoré et al. 2010). However, there is a possibility that also *S. magniporosum* could be a single-tepui endemic that evolved on the isolated mountain massive of Chimantá. If so, *Sphagnum* is more comparable to vascular plants with possibly many single-tepui endemics.

Until recently, *Sphagnum amazonicum* and *S. curicuriariense* were known only from their type localities, but Costa (2017) and Costa et al. (2017) reported additional sites. This demonstrates the need for field work to increase knowledge of species distributions and sexual reproduction of South American *Subsecunda* species. This is crucial for a better understanding of the observed distributional patterns, including endemism and disjunct occurrences within South America, as well as between pantropical species of South American and African.

Microsatellites indicate that *S. magniporosum* is a haploid species, as only one allele was identified for each microsatellite marker. Most of the investigated species within *Subsecunda* are monoploids recorded with haploid gametophytes (n = 19), but the subgenus includes several documented allopolyploid species (Meleshko et al. 2018, Shaw et al. 2019).

The only flora dealing with all species from the South American continent is the worldwide monograph of *Sphagnum* of Michaelis (2019). Even if his taxonomic approach is conservative and does not accept recent DNA-based works on *Sphagnum* taxonomy (Shaw et al. 2016, Hassel et al. 2018), his identification keys and circumscriptions of in total 293 species, are of value. Michaelis (2019) lists and circumscribes about 110 species of subgenus *Subsecunda* worldwide, and the South American continent is the most species rich for this subgenus.

Despite the above uncertainties, the taxonomic conclusion is still that *S. magniporosum* is morphological different from other species. It is unlikely to constitute a variant of the currently compared species. It is a strong need of research to clarify the taxonomic and phylogenetic relationships among neotropical South American species in subgenus *Subsecunda* in general, based on a combination of morphological and modern molecular methods. Ideally, extensive field work should be carried out as it would provide collections of peatmosses in their specific habitats, fresh material for genomic analyses and knowledge on distributions. Such inventories should be combined with detailed observations of sexuality, sex distributions and spore production, as well as closer examination of herbarium specimens.

Taxonomy

Sphagnum magniporosum Flatberg, Hassel & Prestø sp. nov. (Fig. 2, 3)

Sphagnum subg. *Subsecunda*

Diagnosis

Sphagnum magniporosum is recognized by medium-sized shoots with predominantly yellow-orange to brown-orange colour including the capitula. Branches single, not in fascicles, tightly arranged upward spreading, uniform in size, tumid with tightly arranged, concave leaves. In micro-morphology, it is recognized by one-layered and aporose stem cortex. Stem leaves large and narrowly ovate-lingulate to elliptic-ovate and longer than the more ovate-shaped branch leaves. Leaf hyaline cells multifibrose and 3-seriporose, on their convex (dorsal) surface with a combination of tightly arranged and predominantly circular and ringed perfect and large pores along the commissures and with a varying element of larger, predominantly circular and unringed perfect median pores (luminal pores) in separate cells or portions of cells. Rectangular-shaped pseudopores common along the commissures on the concave leaf surfaces. Elliptic shape of the chlorophyll cells of the branch leaves in cross section, slightly but varyingly enclosed on both leaf surfaces with thickened walls, more on convex than concave surface. Ploidy level of gametophyte is unknown.

Type: Venezuela, locality: Edo. (Estado) Bolívar. Distr. (Distrito) Piar: Macizo del Chimantá, sector SE. Altiplanicie levemente inclinada hacia el SSE ubicada en la sección centro-suroriental del Churí-tepui. Ecology: Vegetación predominante de arbustales enanos paramoides sobre turberas, bosquecillos ribereños y vegetación sobre rocas abiertas de arenisca. In *Bonnetia roraimae* swamp, rare, in wet hollow. 5°15′N, 61°58′W [= 5.250°N, 61.967°W], ca 2250 m a.s.l.

Leg. & det. Teuvo Ahti 44969, Otto Huber, John J. Pipoly 06-08.02.1985.

Holotype: H 3239318. Isotypes TRH B-104740 and VEN.

Etymology

The specific epithet is derived from the Latin adjective *magnus*, large, and *porosus*, porose, and alludes to the relatively large size of the leaf pores in the new species.

Belongs to *Sphagnum* subgenus *Subsecunda*.

Description

Plants (Fig. 3A) medium-sized with diameter between 0.7 and 2.0 cm in the type specimen shoots. Colour predominantly yellow-orange to orange-brown (Fig. 3A).

Capitulum (Fig. 3A) slightly convex with upwards orientated and near straight to somewhat incurved capitulum branches and indistinct terminal bud.

Stem rather weak, and dark brown except just below the capitulum, with differentiated one-layered stem cortex, occasionally with local elements of cortical duplications (Fig. 3H); cortical cells in superficial view aporose to occasionally with one obscure apical end pore (Fig. 3I); sclerodermis brownish, small-celled, 3–4 cells wide, medulla of larger, thin-walled cells.

Stem leaves (Fig. 3B) tightly arranged and lax in structure, varyingly orientated from erecto-patent, spreading to pendent-spreading along stem. Slightly widest at the middle, markedly concave with often varyingly folded portions in microscope slides, leaf border narrow with 2–4 layers of narrow, elongate cells (Fig. 3E and F to right), not expanded below. Leaf apex (Fig. 3C) acute to acute-obtuse and slightly truncate-erose. Leaf length 3.4 ± SD 0.1 (range 3.2–3.6) mm, maximum breadth 1.5 ± SD 0.1 (range 1.4–1.7) mm. Hyaline cells narrowly elongate throughout leaf, slightly S-curved to near straight, mostly non-septate except for occurrence of scattered one-septate cells towards proximal leaf ends; cells densely fibrillose throughout leaf.

On convex (dorsal) surface with 2- or 3-seriporose hyaline cells in distal 2/3 of leaf, with ca 20–40 pores in mid-median leaf portions, most pores tightly arranged along the commissures in two rows as perfect, ringed, circular to elliptic pores, mostly occupying more than 1/3 of cell width (Fig. 3D–E); in addition with a varying number of cells furnished with an element of predominantly non-ringed, perfect, circular to transversely elliptic to rectangular median pores (luminal pores) occupying most of cell width, usually found as short, series of single pores towards cell ends (Fig. 3E). Towards leaf margins with more median pores, sometimes present as 1-seriporose cells (Fig. 3E to right). In proximal part of leaf gradually less porose with fewer commissural pores and often with predominance of median pores (Fig. 3F to right), and at proximal leaf ends with only 1–3 large apical end pores (Fig. 3F to left).
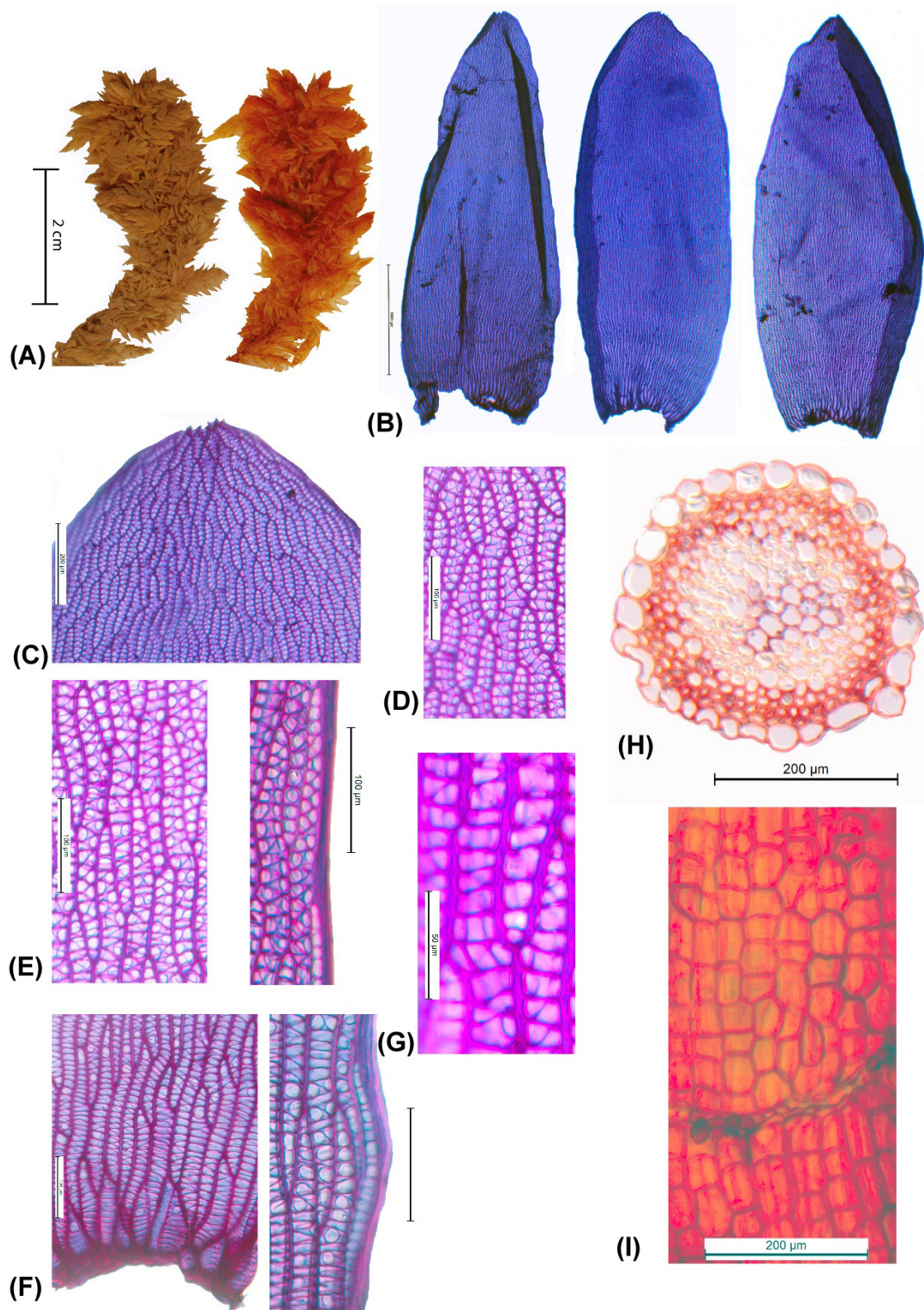
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Figure 3. Microscopic pictures of different morphological characters in stem leaves of *Sphagnum magniporosum* sp. nov. (A) Herbarium shoot, dry to left and moist to right, (B) stem leaves, (C–F) cell structure on convex surface of stem leaves, (C) distal end portion, (D) distal end, median portion, (E) mid-median portion to left, mid-median marginal portion to right, (F) cell structure on proximal end, median portion to the left, marginal to the right. 3-seriporose cells with a mixture of commissural pores and free-lying median pores are seen in the center of the photo of the marginal portion, (G) cell structure on concave mid-median portion of stem leaves, (H) stem in transverse section, (I) stem cortex in superficial view. Material: TRH-B-104740.

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On concave (ventral) surface with scattered and often obscure rectangular-shaped pseudopores along the commissures, sometimes in nearly continuous rows (Fig. 3G), sometimes with a few, small pseudopores at cell corners towards distal leaf end. Chlorophyll cells somewhat S-shaped in distal leaf portion (Fig. 3C), less so and more elongate towards proximal leaf end (Fig. 3F).

Branches (Fig. 2A) single, tightly arranged, tumid, erecto-patent, straight to somewhat upwards curved and equal-sized. Thickest at middle, bluntly tapering above, length about 6–12 mm. Branch stems pale brownish, in transverse section (Fig. 2B) with one-layered, efibrillose and partly dimorphic cortex. In superficial view (Fig. 2C) with elongate retort cells with one distal end pore with lacking or indistinct neck. Ordinary cortex cells often with 1–3 small, circular, perfect and lateral wall pores (Fig. 2D).

Branch leaves (Fig. 2E) lax in structure, densely to loosely arranged, non-ranked, straight to slightly secund at distal ends. Leaves in middle part of branches (Fig. 2E) widely ovate, widest below middle of leaf, markedly concave with loose appearance often causing involute and folded leaf portions in microscope slide preparations, involute to narrowly rounded at apex, often hidden by involute leaf margins. Leaf border narrow with 2–4 layers of elongate cells without resorption furrow (Fig. 2G to left); length 2.6 ± SD 0.2 (range 2.4–2.9) mm, breadth at widest part 1.3 ± SD 0.1 (range 1.1–1.5) mm. Hyaline cells in superficial view narrowly S-shaped-elongate (Fig. 2F and G), towards margins (Fig. 2G to right) narrower and towards proximal leaf end much longer and wider (Fig. 2H). Cells non-septate and tightly fibrillose throughout leaf, and often mixed with reticulate fibrils on concave leaf surface. On convex (dorsal) surface with ca 20–35 pores per cell in mid-median portion of leaf (Fig. 2G). The majority of pores along the commissures in 2-seriporose pattern with perfect, circular to elliptic, ringed pores mostly occupying 1/3 or more of cell width. In proximal part of leaf with wider hyaline cells, commissural pores fewer and relatively smaller, often occupying less than 1/4 of cell width, but usually with 1–3 large apical end pores (Fig. 2H). Additionally, fewer (often nearly lacking) non-ringed, perfect, circular to elliptic median pores occupying more than half of cell width are found at cell end as single pores in rows (not present in Fig. 2G to left). Such median pores are more common in cells towards leaf margins (Fig. 2G to right), while cells towards proximal leaf end have fewer or lack such pores. On concave surface most of leaf (Fig. 2I) with a varying number of longitudinally rectangular to elliptic pseudopores closely facing the commissures in more or less continuous rows, with or without some imperfect pores (Fig. 2I). Hyaline cells in transverse section with broadly elliptic shape, with equally bulging convex and concave surfaces (Fig. 2J). Chlorophyll cells in cross section (Fig. 2J) elliptic to sometimes ovate-elliptic, varyingly enclosed on both surfaces with thickened walls, but often more widely so towards concave than convex surface, without resorption furrow.

Sexual status unknown, perichaetia, perigonia and sporophytes not recorded in the examined type material. Ploidy level unknown.

Distribution and ecology

So far *S. magniporosum* is only known from the type locality in Bolívar, Venezuela (Fig. 1). Montane cloud forest and elfin woodland are common between 1600 and 2200 m a.s.l. in the Chimantá Massif. The peat is very acid, with pH 3–3.4 in the Churí-tepui, and very nutrient-deficient (Huber 1992). The high-altitude tepui parts are in the montane rain forest life zone (Ewel et al. 1968, Huber 1988). Specific habitat preferences are unknown, but the type specimen label indicates that *S. magniporosum* should be searched for in swampy, open peatlands at the tepuis (table mountains), primarily in the Bolívar area. More extensive field work combined with careful examination of collected specimens are necessary to provide additional information of its distribution and habitat preferences.

Key to differentiate *S. magniporosum* from similar South American and African *Subsecunda* species

1. Stem cortex of one cell layer, branches fascicles with 1–3 branches ……………………………………………….. 2
1. Stem cortex mostly of two cell layers, branches fascicles with 4 branches …………………………..… *S. funkiae*
2. Stem pale ……………………………………………… 3
2. Stem brown, red-brown or dark brown ……………… 4
3. Branches fascicles with 3 spreading branches …………………………………..… *S. homophyllum*
3. Branches fascicles with 2 spreading branches ………………………………………… *S. liesneri*
4. Stem leaves usually less than 2 mm …………………… 5
4. Stem leaves usually more than 2 mm ………………… 9
5. Stem laves with few or no pores on concave surface ………………………………………… 6
5. Stem laves with scattered to numerous pores on concave surface ………………………………………… 7
6. Stem leaves 0.9–1.2 mm. Branch leaves 0.8–1.0 mm and without pores on concave surface …………… *S. liesneri*
6. Stem leaves 1.3–1.5 mm. Branch leaves 1.8–2.0 mm and with circular, perfect, ringed commissural pores in dense rows on concave surface ………………… *S. cribriforme*
7. Stem leaves cell fibrils in upper 1/2–2/3 of leaf. Branches fascicles with 3 branches ……..……… *S. subhomophyllum*
7. Stem leaves cell fibrils in whole leaf. Branches fascicles with 1–2 branches ………… 8
8. Branch leaves 1.0–1.1 mm, cells on convex surface 2-seriporose with many commissural, circular to elliptic, perfect pores ……………………………..…… *S. hegewaldii*
8. Branch leaves 1.4–1.7 mm, cells on convex surface in upper part of leaf partly 3-seriporose with few to several, perfect, median pores ………………… *S. luetzelburgii*
9. Branches fascicles with 1 or 2 branches …………… 10
9. Branches fascicles with 2 hanging and 2 spreading branches ………………………………… *S. sonsonense*
10. Stem and branch leaves with several to numerous pores on the concave surface ………………….……… 11
10. Stem and branch leaves with few or completely lacks pores on the concave surface ……………… *S. juliforme*
11. Stem leaves 1.8–3.0 mm. Branch leaves 1.2–2.1 mm … 12
11. Stem leaves 3.2–3.6 mm. Branch leaves 2.4–2.9 mm …………………………………………… *S. magniporosum*

12. Stem dark brown, branch fascicles monocladous. Branch leaves on concave surface, cells with numerous commissural, perfect, ringed pores and pseudopores. Known from South America .... *S. garysmithii*

12. Stem yellow-brown to deep red-brown, branch fascicles with 1–2 branches. Branch leaves on concave surface, cells with scattered small pores and varying number of longitudinally rectangular to elliptic pseudopores along the commissures. Known from Africa. .... *S. africanum*

Data availability statement

There are no additional data for this paper.

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