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Assessment of historical *Andreaea* names from northwestern Argentina clarifies the taxonomy of ecostate *Andreaea* species in the Central Andes

Evaluación de nombres históricos de *Andreaea* del noroeste argentino clarifica la taxonomía de las especies ecostadas de *Andreaea* en los Andes centrales

Guillermo M. Suárez[1,2*], Juan Larraín[3] & Denilson Fernandes Peralta[4]

Summary: The genus *Andreaea* Hedw. remains poorly understood in the Andean region of South America, where species delimitation has historically been based on highly variable morphological characters. In this study, the type material of *Andreaea arachnoidea*, *A. lorentziana*, *A. fragilis*, and *A. semisquarrosa*, all described by Müller from northwestern Argentina based on collections made by Lorentz during the nineteenth century, was critically revised. Examination of specimens preserved at JE demonstrated that these names do not represent distinct taxa, but correspond respectively to *A. rupestris*, *A. mutabilis*, or *A. acutifolia*. Morphological variation observed among the studied specimens mainly involves habit, branching pattern, leaf orientation, and leaf acumination, characters strongly influenced by environmental conditions in high-Andean habitats. The reinterpretation of *A. arachnoidea* further demonstrated that the arachnoid structures mentioned in the protologue correspond to fungal hyphae associated with the gametophores rather than to intrinsic morphological features of the moss. The synonyms proposed here contribute to the taxonomic clarification of *Andreaea* in South America and reinforce the floristic affinities between the Central Andes and austral-temperate bryophyte floras. We designate lectotypes for all the studied names.

Key words: Andreaeaceae, bryophytes, nomenclature, taxonomy, typification.

Resumen: El género *Andreaea* Hedw. permanece escasamente conocido en la región andina de Sudamérica, donde la delimitación de especies se ha basado históricamente en caracteres morfológicos altamente variables. En este trabajo se revisó críticamente el material tipo de *Andreaea arachnoidea*, *A. lorentziana*, *A. fragilis* y *A. semisquarrosa*, descriptos por Müller para el noroeste argentino a partir de colecciones realizadas por Lorentz durante el siglo XIX. El estudio de los ejemplares conservados en JE demostró que estos nombres no representan taxones distintos, sino que corresponden respectivamente a *A. rupestris*, *A. mutabilis* y *A. acutifolia*. La variación morfológica observada entre los ejemplares estudiados involucra principalmente el hábito, el patrón de ramificación, la orientación foliar y el grado de acuminación de las hojas, caracteres fuertemente influenciados por las condiciones ambientales de los ecosistemas altoandinos. La reinterpretación de *A. arachnoidea* mostró además que las estructuras aracnoideas mencionadas en el protólogo corresponden a hifas fúngicas asociadas a los gametofitos y no a caracteres intrínsecos del musgo. Las sinonimias propuestas contribuyen a clarificar la taxonomía de *Andreaea* en Sudamérica y refuerzan las afinidades florísticas entre los Andes centrales y las floras briológicas austro-templadas. Se designan lectotipos para todos los nombres estudiados.

Palabras clave: Andreaeaceae, briófitas, nomenclatura, taxonomía, tipificación.

[1] Facultad de Ciencias Naturales e IML, Miguel Lillo 205, Universidad Nacional de Tucumán (UNT), San Miguel de Tucumán T4000JFE, Argentina.
[2] Unidad Ejecutora Lillo (CONICET-Fundación Miguel Lillo), Miguel Lillo 251, San Miguel de Tucumán T4000JFD, Argentina. *E-mail: guillermosuarez@conicet.gov.ar
[3] Centro de Investigación en Recursos Naturales y Sustentabilidad (CIRENYS), Universidad Bernardo O'Higgins, Santiago, Chile.
[4] Instituto de Pesquisas Ambientais, Av. Miguel Stéfano, 3687 - CEP 04301902 - São Paulo, SP. Brazil

Introduction

The genus *Andreaea* Hedw. (Andreaeaceae, Bryophyta) is one of the most readily recognizable moss genera due to its distinctive sporophyte, which lacks a seta, stomata, annulus, operculum, and peristome, with the capsule elevated on a pseudopodium and dehiscing through longitudinal slits (Murray, 1988a; Frey & Stech, 2009). Despite the ease of generic identification, species delimitation within *Andreaea* remains poorly understood, particularly in the Andean region of South America, where many names were established during the nineteenth century based on limited material and have not been critically reassessed since their original publication.

Taxonomic treatments of *Andreaea* have traditionally relied on gametophytic characters such as leaf shape, the degree of leaf vagination, basal marginal cell structure, laminal cell papillosity, costa development, and sexual condition (Murray, 1988a). However, several of these traits exhibit considerable morphological variation, often complicating the interpretation of Andean populations. This problem is especially evident in high-elevation environments, where plants frequently exhibit compact growth forms and reduced sporophyte production as a consequence of extreme climatic conditions (Schiavone & Suárez, 2009; Suárez & Schiavone, 2011).

Comparative studies by Vitt (1980) demonstrated that characters previously regarded as diagnostic within ecostate species of *Andreaea*, including *A. rupestris* Hedw., *A. mutabilis* Hook. f. & Wilson, and *A. acutifolia* Hook. f. & Wilson, may vary substantially among populations. Likewise, recent taxonomic revisions in Brazil by Peralta (2020) showed that several names previously treated as endemic represent morphological variants of widespread species of *Andreaea*, reinforcing the need for critical reassessment of historical South American taxa.

Botanical exploration of northwestern Argentina during the second half of the nineteenth century played a fundamental role in documenting the flora of the Central Andes and adjacent montane regions. Among the most important explorers of this period was Paul Günther Lorentz, who conducted extensive botanical expeditions in the provinces of Tucumán and Salta between 1870 and 1874 (Suárez *et al*., 2013). According to Novara (1983), Lorentz explored several remote mountain areas, including the high-elevation grasslands and rocky slopes between Tafí del Valle, Siambón, and the Cuesta de la Caldería, collecting numerous vascular plants and bryophytes under difficult geographic and climatic conditions. The collections obtained during these expeditions were later studied by Carl Müller (1879), who described four species of *Andreaea* from northwestern Argentina: *A. arachnoidea* Müll. Hal., *A. lorentziana* Müll. Hal., *A. fragilis* Müll. Hal., and *A. semisquarrosa* Müll. Hal. These names were based on specimens collected in alpine environments of the provinces of Tucumán and Salta and represent some of the earliest records of the genus in the Central Andes of Argentina. Despite the historical importance of these collections, their taxonomic identity remained largely unassessed after their original publication, and the names persisted in the literature as insufficiently known taxa (Crosby *et al*., 1999).

The present study reassesses the taxonomic identity of the historical *Andreaea* species described by Müller from northwestern Argentina through examination of the original type material preserved at the Herbarium Haussknecht (JE). The results clarify the occurrence of *A. acutifolia*, *A. rupestris*, and *A. mutabilis* in the Central Andes and provide new insights into the taxonomy and biogeography of ecostate species of *Andreaea* in South America.

Materials and Methods

Type specimens of *A. arachnoidea*, *A. lorentziana*, *A. fragilis*, and *A. semisquarrosa* housed in the Herbarium Haussknecht (JE), Friedrich Schiller University Jena, were examined morphologically using conventional bryological techniques. These specimens may represent some of the few extant original

materials of these names, as a large part of the Herbarium Berolinense (B), including Müller's collections, was destroyed during World War II, although duplicate material may still exist in other herbaria (Suárez *et al.*, 2013). The specimens examined at JE belong to the original herbarium of P.G. Lorentz and correspond to the collections available to C. Müller when preparing the descriptions of the new species published in 1879. Consequently, they constitute original material sensu the International Code of Nomenclature (Turland *et al*., 2025) and provide the basis for the lectotypifications proposed herein.

Leaves and sporophytic structures (when present) were mounted in Hoyer's solution following Anderson (1954) and studied under light microscopy.

Species circumscriptions and diagnostic characters were evaluated through comparison with original descriptions and modern taxonomic treatments of the genus, particularly Vitt (1980), Murray (1988a, 2006), and Peralta (2020). Particular attention was paid to leaf shape, degree of leaf vagination, basal marginal cell structure, laminal cell papillosity, and other characters considered diagnostic in the revision of Vitt (1980).

Results

Key to the ecostate species of *Andreaea* occurring in northwestern Argentina

1. Leaves narrow-lanceolate to panduriform, slightly constricted above the base; basal marginal cells predominantly rectangular to elongate. .... *A. acutifolia*
1'. Leaves ovate to narrow-lanceolate, not panduriform, not constricted above the base; basal marginal cells predominantly rounded quadrate to short-rectangular. 2
2. Leaves broadly ovate-lanceolate, strongly concave, with a distinctly vaginate base; plants usually robust, densely foliate. ..... *A. rupestris*
2'. Leaves narrowly lanceolate, usually secund and often falcate, lacking a distinctly vaginate base; plants lax. …..... *A. mutabilis*

Andreaea rupestris Hedw., Spec. Musc. Frond. 47, pl. 7: f. 2: g-p. 1801. *Typus*: *In rupibus Sueciae, Angliae, Bructeri (negant Ehrhart et Schrader) et Saxoniae superioris abunde ad saxa Bielberg Annaemontani* (?) [*lectotypus* G-hb Hedwig, designated by Vitt (1980)]. Fig. 1.

= *Andreaea arachnoidea* Müll. Hal., Linnaea 42: 220. 1879. Protologue: *Argentinia subtropica, regio alpina in montibus prope Tafi, Martio c. fr. immaturis*. *Typus*: [ARGENTINA] subtropica, montes inter Tafi et Siambon, *P. G. Lorentz s. n.* (*lectotypus* JE04000681!, designated here). *Syn. nov.*

= *Andreaea lorentziana* Müll. Hal., Linnaea 42: 221. 1879. Protologue: *Argentinia subtropica alpina, Cuesta de la Calderia, 27. Majo 1873. Typus*: [ARGENTINA] subtropica. Cuesta de la Calderia, *P. G. Lorentz s. n.* (*lectotypus* JE04004368!, designated here). *Syn. nov.*

= *Andreaea arachnoidea* var. *gracilis* Broth., Bibliotheca Botanica 87: 8. 1916. *Nom. nud.* Based on: BOLIVIA. "An Felsen im obersten Montehuaikotal, ca. 3800 m", Jul 1911, *T. Herzog 3756* (JE).

Plants forming dense tufts, blackish to dark reddish-brown. Stems erect, sparingly branched. Leaves ovate-lanceolate, concave, distinctly vaginate at base, gradually acuminate; margins crenulate due to projecting mammillose cells; costa absent. Laminal cells thick-walled, median and distal cells subisodiametric and mammillose, basal laminal cells short- to long-rectangular, marginal cells rounded-quadrate to short-rectangular. Perichaetial leaves differentiated, larger, obovate, with obtuse to cucullate apices. Capsules cylindrical, elevated on pseudopodia, dehiscing by four longitudinal valves; peristome absent.

Distribution and ecology: *A. rupestris* is a widespread species occurring in Europe, Asia, North America, Greenland, Iceland, and Australasia (Murray, 2006; Vitt, 1980). In South America, this species has been recorded from Colombia (Churchill & Linares, 1995; Peralta, 2020), Bolivia (Churchill *et al*., 2009), Chile (Müller, 2009), Argentina (Matteri & Schiavone, 2002), and montane regions of Brazil (Peralta, 2020).

In northwestern Argentina, the species

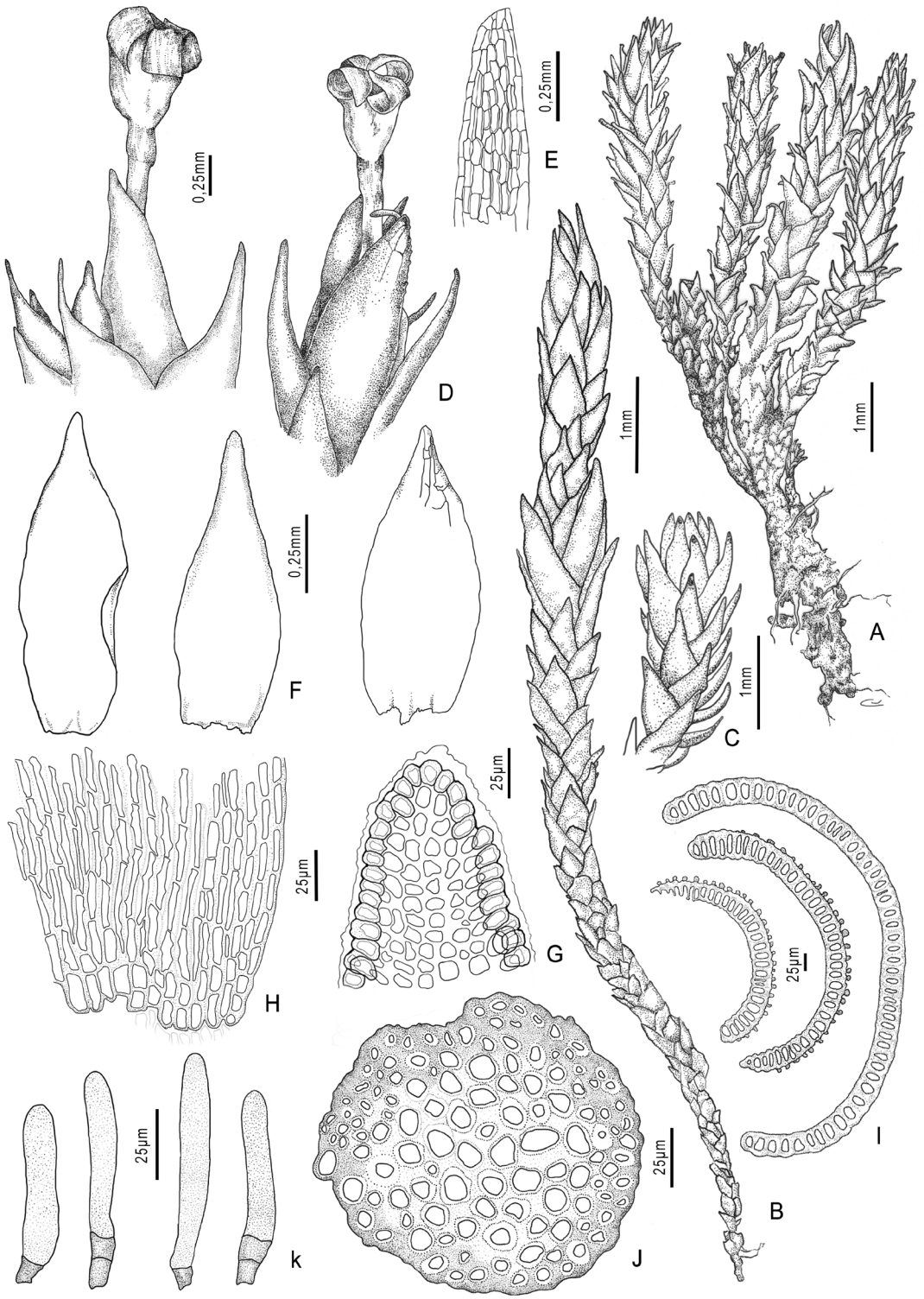


Fig. 1. *Andreaea rupestris* Hedw. A: Habit. B-C: Stems with leaves. D: Sporophytes. E: Exothecial cells. F: Leaves. G: Leaf apex. H: Basal laminal cells. I: Transverse sections of leaves. J: Transverse section of stem. K: Axillary hairs. Drawn from *Lorentz s.n.* (lectotype of *A. arachnoidea*, JE).

occurs in high-altitude grasslands. These surroundings correspond to the Andean alpine systems locally known as "pastizales de altura" (Suárez *et al*., 2013; Jimenez *et al*., 2015; Flores *et al*., 2017), a vegetation complex widely distributed above the montane forests in the Sierras of Tucumán and Salta. These alpine environments constitute distinctive phytogeographical units characterized by harsh climatic conditions and a vascular flora dominated by Andean endemic species.

Additional specimens examined: Bolivia. An Felsen beim Huaillattanisee (Quimzacruz-Cordillere), ca. 4900 m, *Herzog 2961* (JE) as *A. arachnoidea*; mehrfach im Hochtal Viloco (Quimzacruzcord.), 4400-4700 m, *Herzog 3155* (JE) as *A. arachnoidea*; an Schieferfelsen des Cerro Tunari, ca. 5000 m, *Herzog 4771* forma sine filis (JE) as *A. arachnoidea*.

Notes: Examination of the lectotypes designated here for *A. arachnoidea* and *A. lorentziana* supports their inclusion within the morphological concept of *A. rupestris* proposed by Vitt (1980). Both specimens possess broadly lanceolate, strongly concave ecostate leaves with predominantly rounded-quadrate to short-rectangular basal marginal cells, characters that closely match the circumscription of *A. rupestris*. In addition, they share the differentiated perichaetial leaves and cylindrical capsules typical of the species.

The epithet *arachnoidea* appears to have been based on the presence of delicate filamentous structures covering portions of the gametophyte, described by Müller in the protologue as *arachnoideo-reticulata*. Microscopic examination revealed that these structures correspond to septate hyphae from a fungus growing on the leaf surface rather than to intrinsic gametophytic features of the moss. Similar fungal colonization was also observed in Bolivian material identified as *A. arachnoidea*, a condition already documented and illustrated by Herzog (1916, Fig. 1A). The presence of these hyphae probably contributed to the historical interpretation of this morphotype as taxonomically distinct.

In the commentary following the protologue of *A. lorentziana*, Müller (1879) separated the species from *A. arachnoidea* primarily on gametophytic features such as plant habit, branching pattern, and leaf orientation in dry and moist conditions. These are variable characters in *Andreaea*, and we consider them part of the morphological variation of *A. rupestris*.

Andreaea mutabilis Hook. f. & Wilson, London Journal of Botany 3: 536. 1844. *Typus*: AUCKLAND IS., *J. D. Hooker* (*lectotypus* BM [herbaria Wilson], designated by Dale H. Vitt 1980; *isolectotypi* BM, FH). Campbell Is., *J. D. Hooker s. n.* (*syntypi* BM, FH). Fig. 2.

= *Andreaea fragilis* Müll. Hal., Linnaea 42: 223. 1879. Protologue: *Argentinia subtropica alpina, Cuesta de Pinos, 27. Majo 1873, sterilis, inter Grimmiam cespitulum unicum inveni. Typus*: [ARGENTINA] subtropica. Cuesta de Pinos, in alpinis, *P. G. Lorentz s. n.* (*lectotypus* JE04000667!, designated here). *Syn. nov.*

Plants forming loose to compact tufts, blackish to dark reddish-brown. Stems erect, sparingly branched. Leaves lanceolate to ovate-lanceolate, widest near base, straight to falcate and frequently secund; apex narrowly acute to acuminate, incurved; margins incurved, entire or occasionally weakly crenulate due to projecting papillae; costa absent; leaf base not distinctly vaginate. Laminal cells thick-walled and heterogeneous, distal cells papillose and mostly unistratose, proximal cells elongate to subrectangular, marginal basal cells quadrate. Perichaetial leaves differentiated, convolute and sheathing. Sporophytes not observed.

Distribution and ecology: *A. mutabilis* is a widely distributed bipolar species with scattered populations in mountain areas in the Tropics, occurring in South America, Europe, eastern Asia, Australia, New Zealand, subantarctic islands, and several Pacific islands (Murray, 2006), generally growing on exposed acidic or siliceous rocks in cold and humid habitats. In South America, the species has been recorded from Argentina (Matteri, 2003), Chile (Müller, 2009) and Ecuador (Murray, 1988b).

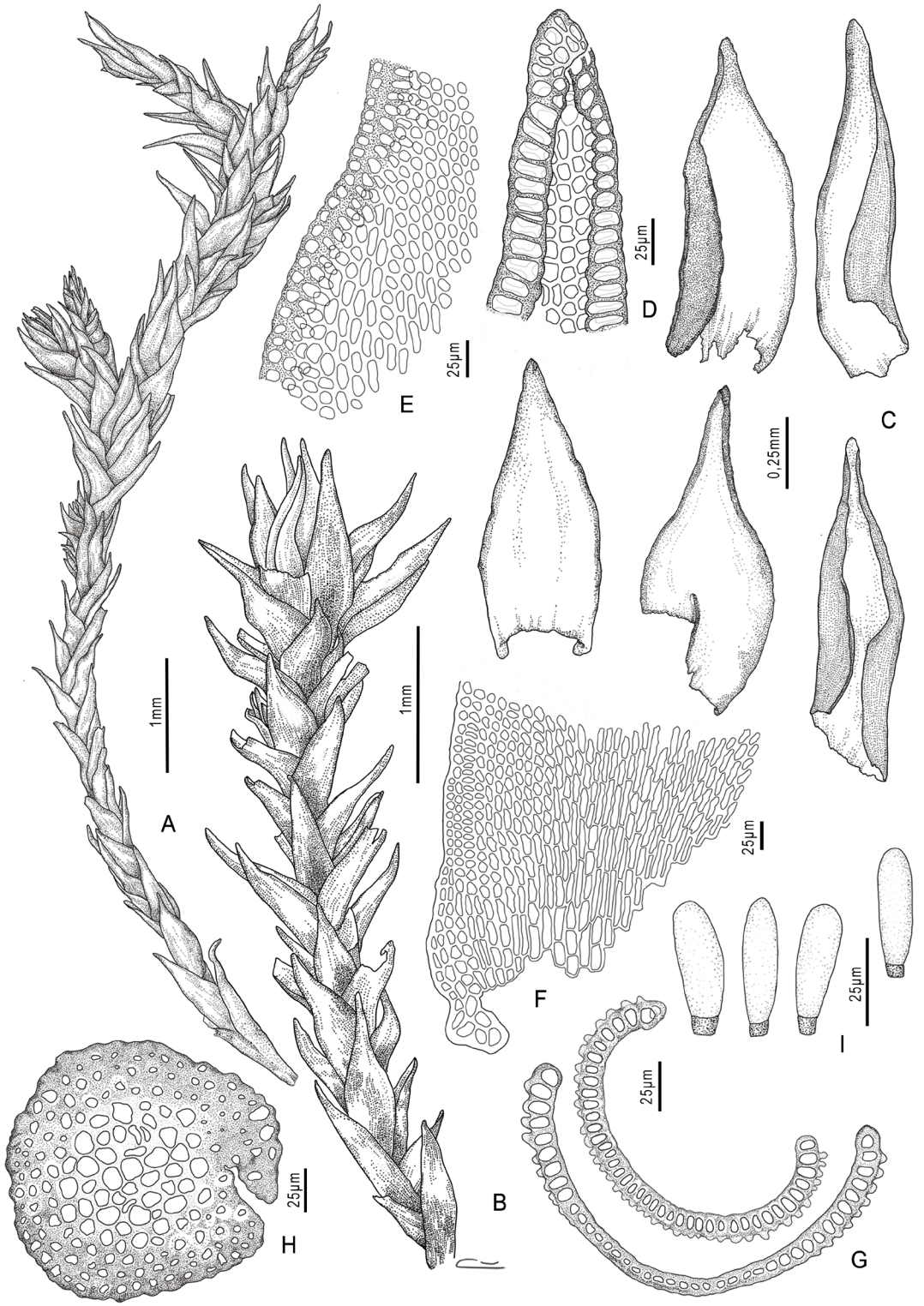


Fig. 2. *Andreaea mutabilis* Hook. f. & Wilson. A-B: Habit. C: Leaves. D: Leaf apex. E: Apical laminal cells. F: Basal laminal cells. G: Transverse sections of leaves. H: Transverse section of stem. I: Axillary hairs. Drawn from *Lorentz s. n.* (lectotype of *A. fragilis*, JE).

Notes: Examination of the lectotype designated here for *A. fragilis* supports its inclusion within the concept of *A. mutabilis* proposed by Vitt (1980). The type specimen possesses narrowly lanceolate leaves lacking a distinct vaginate base, with blades straight to slightly falcate and basal marginal cells predominantly isodiametric, closely matching the diagnostic characters described and illustrated by Vitt for *A. mutabilis*. The heterogeneous laminal areolation, ecostate leaves, and overall lax habit further support this interpretation. No morphological characters were observed that justify recognition of *A. fragilis* as a distinct species.

The epithet *fragilis* refers to the brittle and delicate appearance of the gametophytes emphasized by Müller (1879) in the protologue, where the plants are described as forming *laxissime intertextis* cushions composed of densely interwoven slender branches. Müller also highlighted the rigidity and brittleness ("Starrheit und Brüchigkeit") observed in Scandinavian specimens, characters probably associated with desiccated gametophytes growing under exposed alpine conditions. These features, however, fall within the broad morphological variation currently accepted for *A. mutabilis*.

The comparison established by Müller (1879) with *A. sparsifolia* J.E. Zetterst. & Björnstr. (currently treated as a synonym of *A. rupestris*) further suggests that species delimitation was originally based mainly on habit and branching architecture, characters now considered highly variable within the genus.

Andreaea acutifolia Hook. f. & Wilson, London Journal of Botany 3: 535. 1844. *Typus*: HERMITE IS. [CHILE]. Cape Horn, *J. D. Hooker 106B* (*lectotypus* BM [Herbaria Wilson], designated by Vitt (1980); *isolectotypi* BM [Herbaria Hooker], BM [Herbaria Wilson], NY [Herbaria Mitten as Wilson 107B]). Falkland Is., 1839-1843, *J. D. Hooker* (*syntypi* BM, FH); Auckland Is., 1839-1843, *J. D. Hooker s. n.* (*syntypus*); Campbell Is., 1839-1843, *J. D. Hooker s. n.* (*syntypi* BM, FH, NY). Fig. 3.

= *Andreaea semisquarrosa* Müll. Hal., Linnaea 42: 222. 1879. Protologue: *Argentinia subtropica alpina, Nevado de Castillo prope Salta, 1873; inter Grimmias crescens*. *Typus*: [ARGENTINA] subtropica. Nevado de Castillo prope Salta, in alpinis, *P. G. Lorentz s. n.* (*lectotypus* JE04000664!, designated here). *Syn. nov.*

Plants forming dense blackish to dark reddish-brown tufts. Stems erect, sparingly branched. Leaves panduriform to long-lanceolate, widest near base or equally wide at base and mid-leaf, usually falcate and secund; apex narrowly acute to acuminate, frequently reflexed, often abruptly contracted into a long acumen; margins incurved, proximally crenulate to toothed due to projecting papillae; costa absent; leaf base distinctly vaginate. Laminal cells heterogeneous, distal cells papillose and unistratose, proximal marginal cells rectangular and frequently oblique. Sporophyte not observed.

Distribution and ecology: *A. acutifolia* is an austral montane and subantarctic species distributed in southern South America, Australia, New Zealand, and several subantarctic islands (Murray, 2006). In South America, the species has been recorded from Bolivia (Churchill *et al*., 2009), Argentina (Matteri, 2003), Brazil (Peralta, 2020), and southern Chile (Müller 2009), occurring mainly in high-elevation Andean environments and cold, humid austral regions. In northwestern Argentina, *A. acutifolia* grows in alpine systems.

Notes: Examination of the lectotype designated here for *A. semisquarrosa* supports its inclusion within the concept of *A. acutifolia* proposed by Vitt (1980). The type specimen exhibits panduriform leaves with a distinctly sheathing base and predominantly rectangular to oblique basal marginal cells, characters that closely correspond to the circumscription of *A. acutifolia*. The secund leaves, differentiated perichaetial bracts, and overall leaf morphology further support this interpretation. No characters were found that justify recognition of *A. semisquarrosa* as a distinct species.

The epithet *semisquarrosa* refers to the distinctly reflexed lower leaves emphasized by

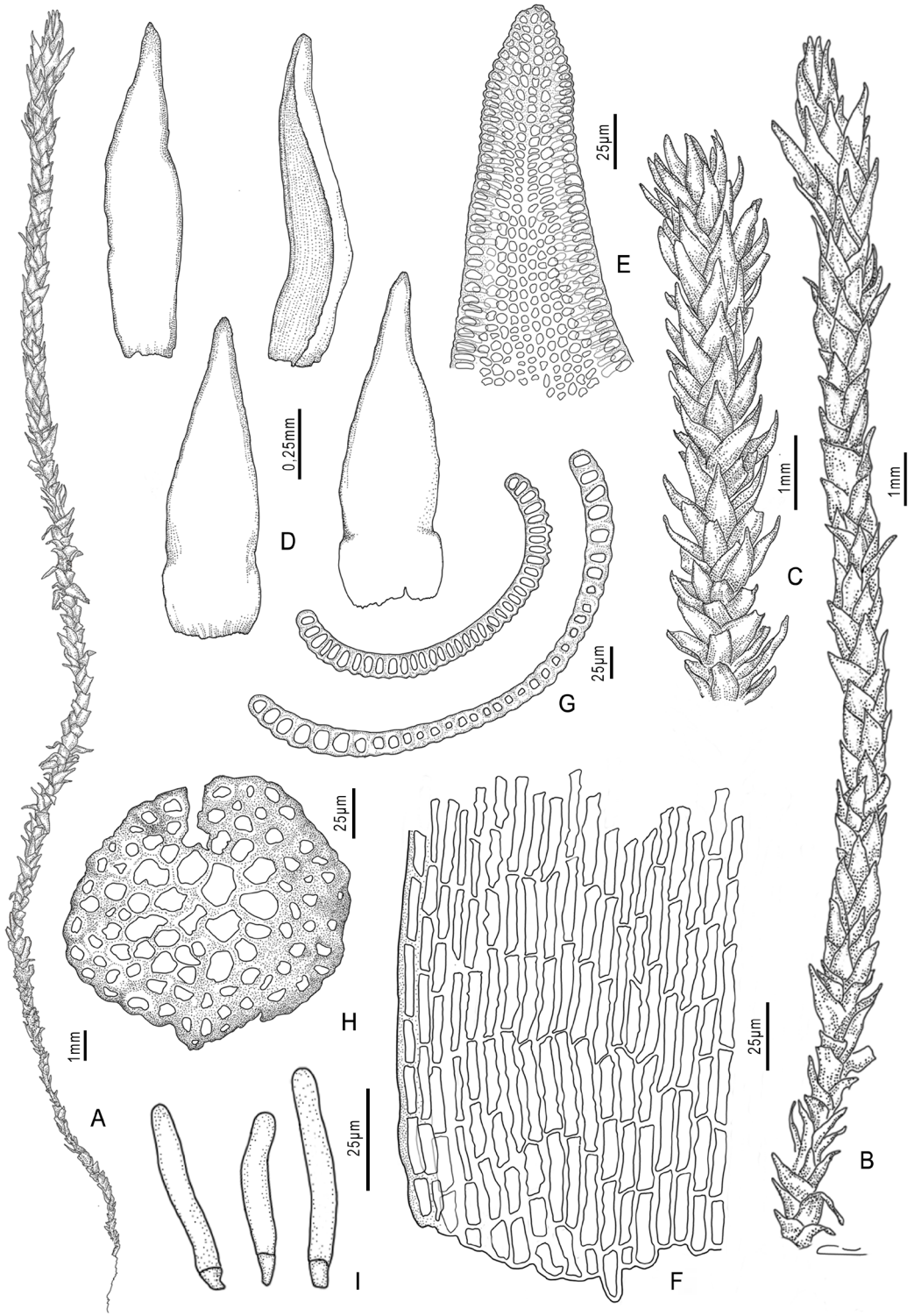


Fig. 3. *Andreaea acutifolia* Hook. f. & Wilson. A-C: Habit. D: Leaves. E: Leaf apex. F: Basal laminal cells. G: Transverse sections of leaves. H: Transverse section of stem. I: Axillary hairs. Drawn from *Lorentz s.n.* (lectotype of *A. semisquarrosa*, JE).

Müller (1879) in the protologue (*propter folia inferiora distincte reflexa*), a feature that gives the plants a partially squarrose appearance when dry. Müller (1879) further noted that the species appeared "different at first sight from all congeners" (*ab omni congeneribus primo adspectu diversa*), highlighting the unusual habit of the plants.

Discussion

The present study clarifies the taxonomic identity of the species of *Andreaea* described by Müller (1879) from northwestern Argentina based on collections made by Lorentz during the nineteenth century. Examination of the type material preserved in JE demonstrates that the names *A. arachnoidea*, *A. lorentziana*, *A. fragilis*, and *A. semisquarrosa* do not represent distinct taxa, but fall within the morphological variation currently accepted for *A. rupestris*, *A. mutabilis*, and *A. acutifolia*, respectively, following the species concepts proposed by Vitt (1980) and later treatments by Murray (2006) and Peralta (2020).

The species described by Müller (1879) were mainly differentiated by variations in habit, leaf orientation, branching pattern, and degree of leaf acumination. However, these characters appear to be highly variable in populations growing under exposed alpine conditions, as already suggested for the genus by Vitt (1980) and Murray (2006). High-elevation Andean environments are characterized by intense solar radiation, strong thermal amplitude, periodic desiccation, and persistent winds, factors that commonly produce dwarfism, compact growth forms, modified leaf orientation, and frequent reduction or absence of sporophyte production in bryophytes. Such environmentally induced variation probably contributed to the historical overestimation of species diversity in Andean representatives of *Andreaea*.

The reinterpretation of the historical names proposed by Müller (1879) further demonstrates that several characters traditionally used to distinguish Andean species of *Andreaea*, including habit, branching pattern, and leaf orientation, are strongly influenced by environmental conditions. In particular, the arachnoid structures observed in *A. arachnoidea* correspond to fungal hyphae associated with the gametophytes rather than to taxonomically informative gametophytic features. The presence of these hyphae probably contributed to the historical interpretation of this morphotype as taxonomically distinct.

The present study also highlights the importance of historical herbarium collections for the interpretation of Andean bryophyte diversity. Most original Müller collections were destroyed during the Second World War, making the surviving material preserved in JE especially valuable for taxonomic reassessment. The Lorentz collections constitute an important historical record of the bryoflora of northwestern Argentina and provide a unique opportunity to re-evaluate nineteenth-century taxonomic concepts using modern species circumscriptions.

From a biogeographical perspective, the confirmed occurrence of *A. rupestris*, *A. mutabilis*, and *A. acutifolia* in northwestern Argentina reinforces the floristic affinities between the Central Andes and the austral-temperate and subantarctic regions of southern South America. The distribution patterns observed in these species agree with previous interpretations of austral and Andean bryophyte affinities proposed by Matteri & Schiavone (2002), Murray (2006), and Müller (2009), and support the hypothesis that high-elevation Andean systems may function as dispersal corridors and refugia for cold-adapted bryophytes across the Southern Hemisphere.

Additional studies integrating molecular, ecological, and morphological evidence will be necessary to better understand species limits and patterns of variation in Andean populations of *Andreaea*. In particular, broadly distributed taxa such as *A. rupestris* warrant further study to evaluate whether they comprise genetically differentiated lineages across their extensive geographic ranges. The reduction of four historical names to synonymy further suggests that species diversity within the ecostate *Andreaea* complex may have been overestimated in some regions. This observation is consistent with the need for a comprehensive reassessment of closely related ecostate taxa, including *A. regularis* Müll. Hal., as well as other Andean species known from few collections, such as *A. clavata* Broth. and *A. vilocensis* Broth. (Suárez,

2024; Suárez & Hentschel, 2024). Although these taxa are currently maintained as distinct, their distribution in the Central Andes and the presence of partially overlapping morphological characters highlight the need for an integrative revision combining morphology, type studies, and molecular evidence. The present study demonstrates the importance of critical revision of historical type material for understanding the true diversity and distribution of Andean bryophytes, particularly in morphologically variable genera such as *Andreaea*.

Author contributions

GMS designed and conducted the research, examined the type material, analyzed and interpreted the morphological data, and prepared the manuscript. JL and DFP contributed to the analysis and interpretation of the data. All authors contributed to the final preparation and revision of the manuscript and approved the final version.

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