Research article

Acta Botanica Mexicana

Taxonomy of *Hedwigia filiformis* (Bryopsida: Hedwigiaceae), with the clarification of the confounded identity of its synonym *Hedwigia integrifolia*

Taxonomía de *Hedwigia filiformis* (Bryopsida: Hedwigiaceae), con la clarificación de la identidad confundida de su sinónimo *Hedwigia integrifolia*

Efraín De Luna[1, 2]

Abstract:

Background and Aims: *Hedwigia integrifolia* is still conflated with *Hedwigidium imberbe*, despite previous distinction of these two species. This paper offers clarification of the taxonomic status of *Hedwigia integrifolia*, as a synonym of *H. filiformis*. The latter name is re-established only for the species characterized by filamentous pseudoparaphyllia, leaf cells with peltate papillae, and perichaetial leaves ciliate.

Methods: Protologues, specimens of *Hedwigia* worldwide from several herbaria, and personal collections were studied to evaluate the taxonomic and nomenclatural status of *H. integrifolia*, along with the similar species *Hedwigia filiformis*. Anatomical observations were recorded of pseudoparaphyllia, leaf cell papillae, and capsule neck stomata.

Key results: My examination of numerous *Hedwigia* specimens worldwide led to the conclusion that *Hedwigia integrifolia* is a heterotypic synonym of *Hedwigia filiformis*. For the correct identification of *Hedwigia filiformis*, a morphological description and illustrations are provided for this species, so far known to occur in Canada, the USA, Mexico, Italy, Japan and South Korea.

Conclusions: *Hedwigia filiformis* differs from other species in *Hedwigia* mostly by its slender sympodial branches, short ovate leaves with revolute margins, the very short hyaline leaf acumina, and the short elliptical apical cell.

Key words: *Braunia*, *Hedwigia*, *Hedwigiales*, *Hedwigidium*, nomenclature, taxonomy.

Resumen:

Antecedentes y Objetivos: *Hedwigia integrifolia* todavía es confundida con *Hedwigidium imberbe*, a pesar de aclaración previa. En este trabajo se clarifica el estado taxonómico de *Hedwigia integrifolia* como un sinónimo de *H. filiformis*. Este último nombre es re-establecido únicamente para la especie caracterizada por los pseudoparafilios filamentosos y papilosos, las células foliares con papilas ramificadas y las hojas periqueciales ciliadas.

Métodos: Se estudiaron los protólogos, especímenes de *Hedwigia* en varios herbarios y colecciones personales para evaluar la taxonomía y nomenclatura de *H. integrifolia* y la especie similar *Hedwigia filiformis*. Las cápsulas y tallos con hojas se estudiaron anatómicamente para observar los pseudoparafilios, las papilas de las células foliares y los estomas de las cápsulas.

Resultados clave: El examen de numerosos especímenes de *Hedwigia* lleva a la conclusión que *Hedwigia integrifolia* es un sinónimo heterotípico de *Hedwigia filiformis*. Para la identificación correcta de *Hedwigia filiformis*, se proveen una descripción e ilustraciones de esta especie, por ahora conocida de Canadá, los Estados Unidos de América, México, Italia, Japón y Corea del Sur.

Conclusiones: *Hedwigia filiformis* difiere de otras especies de *Hedwigia* más notablemente por las ramas simpodiales delgadas, las hojas ovaladas cortas con márgenes revolutos, los ápices foliares hialinos muy cortos y la célula apical elíptica.

Palabras clave: *Braunia*, *Hedwigia*, Hedwigiales, *Hedwigidium*, nomenclatura, taxonomía.

[1]Instituto de Ecología, A.C., Red de Biodiversidad y Sistemática, Carretera Antigua a Coatepec 351, El Haya, 91070 Xalapa, México.
[2]Author for correspondence: efrain.deluna@inecol.mx

Received: May 24, 2022.
Reviewed: June 15, 2022.
Accepted by Marie-Stéphanie Samain: September 14, 2022.
Published Online first: September 30, 2022.
Published: Acta Botanica Mexicana 129 (2022).

To cite as: De Luna, E. 2022. Taxonomy of *Hedwigia filiformis* (Bryopsida: Hedwigiaceae), with the clarification of the confounded identity of its synonym *Hedwigia integrifolia*. Acta Botanica Mexicana 129: e2080. DOI: https://doi.org/10.21829/abm129.2022.2080

e-ISSN: 2448-7589

Introduction

The genus *Hedwigia* P. Beauv. (Bryopsida: Hedwigiaceae) is characterized by filamentous, papillose pseudoparaphyllia, hyaline leaf apex, upper leaf cells with tall branched papillae, ciliate perichaetial leaves, very short setae, eperistomate and urceolate capsules, and a flat umbellate operculum (De Luna, 1995). There are 12 species of *Hedwigia*, mainly distributed in the cold and temperate regions around the world (Hedenäs, 1994; Buck and Norris, 1996; Biasuso, 2007; Ignatova, et al., 2016, 2017). In the United States of America (USA), until now six species have been recorded: *Hedwigia ciliata* (Hedw.) P. Beauv., *Hedwigia detonsa* (M. Howe) W.R. Buck & D.H. Norris, *Hedwigia stellata* Hedenäs (Eckel, 2015), *Hedwigia integrifolia* P. Beauv. (Dalton et al., 2012), *Hedwigia filiformis* (Michx.) P. Beauv. (Palisot de Beauvois, 1805), and *Hedwigia nemoralis* Ignatova, Ignatov & Fedosov (Ignatova et al., 2016). Among these, the taxonomic concepts of *Hedwigia integrifolia* and *H. filiformis* are reviewed here for the first time.

Michaux (1803) described *Anictangium filiforme* Michx. with two of his specimens from Eastern North America. Soon after, Palisot de Beauvois (1805) described *Hedwigia integrifolia* from one of his specimens collected also somewhere in Eastern North America. In the same publication, Palisot de Beauvois (1805) transferred *Anictangium filiforme* to *Hedwigia*, although later, Sprengel (1820) treated this species as *Gymnostomum filiforme* (Michx.) Spreng. Both taxa have been classified in genus *Hedwigia* because of the ciliate perichaetial leaves, the hyaline leaf apices, and the immersed eperistomate capsules. However, the taxonomic distinction of these two Eastern North American species was obscured very soon after their description. One reason was that *H. filiformis* and *H. integrifolia* were considered synonyms of *Hedwigia ciliata* (Bridel-Brideri, 1806, under *Anictangium ciliatum*; Weber and Mohr, 1807; Arnott, 1825; Müller, 1851; Jaeger, 1876; Rabenhorst, 1890; Jones, 1933). A second reason the identity of *H. integrifolia* remained concealed is because it was later wrongly synonymized with *Hedwigidium imberbe* (Sm.) Bruch & Schimper by Hooker and Taylor (1818, 1827) and Steudel (1824, as *Schistidium imberbe* (Sm.) Nees & Hornsch.).

For a long time, the name *Hedwigia integrifolia* was wrongly linked with the different species characterized by leaves with green apices, multiple low papillae on leaf cells, and entire perichaetial leaves (Nyholm, 1960; Scott and Stone, 1976; Smith, 1978; Cortini-Pedrotti, 2001). These morphological features identify *Hedwigidium imberbe* (Allen, 2010; Dalton et al., 2012, as *Braunia imberbis* (Sm.) N. Dalton & D.G. Long; De Luna, 2021). Available clarifications have already shown that *H. integrifolia* and *Hedwigidium imberbe* are two different species, not synonyms (Allen, 2010; Dalton et al., 2012, as *B. imberbis*; De Luna, 2021). However, few details have been provided on the taxonomy of *H. integrifolia*. Allen (2010) discussed the possible synonymy of *H. integrifolia* with *Hedwigia ciliata*, and Dalton et al. (2012) concluded that "further study is needed to determine the exact status of this taxon, so it is provisionally left as a species of *Hedwigia*". After acknowledging the explanations by Allen (2010) and Dalton et al. (2012), Eckel (2015) concluded: "Presently the application of the name *H. integrifolia* is awaiting further study".

The goal of this paper is to highlight morphological details that clarify the identity of *Hedwigia integrifolia*, as originally described for the Eastern North American species (Palisot de Beauvois, 1805). The name *Hedwigia integrifolia* applies only to specimens showing the filamentous pseudoparaphyllia, hyaline leaf apex, upper leaf cells with tall branched papillae, and perichaetial leaves ciliate. Early on, Palisot de Beauvois (1805) noticed the very close relationship between *Hedwigia filiformis* and *Hedwigia integrifolia*. Hedenäs (1994, p. 155) also suggested a similarity of *Hedwigia filiformis* with *H. integrifolia*. Therefore, this study compared the taxonomic concepts of both species. As a result of this taxonomic research, *H. integrifolia* is proposed here as a synonym of the older *Hedwigia filiformis*.

Materials and Methods

Specimens

In total, 124 specimens of *Hedwigia* were examined. Among these, 39 specimens of *Hedwigia filiformis* from Canada, the United States of America (USA), Mexico, Japan, and South Korea, and some personal collections in the USA and Mexico, were studied to document morphological features of this species. To evaluate the taxonomic and nomenclatural status of this taxon, comparisons were undertaken with representative specimens worldwide of other species of *Hedwigia*,

including *H. ciliata*, *H. detonsa*, *H. nivalis* (Müll. Hal) Mitt., and *H. stellata*. Specimens from the following herbaria were examined: AAU, B, BM, BR, DUKE, F, JE, MEXU, MICH, MO, NSW, NY, QCA, S, US, and XAL (Thiers, 2022).

Anatomy

Portions of stems of plants representative of *H. filiformis* were prepared for anatomical studies to examine details of pseudoparaphyllia, leaf cell papillae, and stomata on capsule necks (voucher specimens: USA, North Carolina, *E. De Luna 1751* (DUKE, XAL), *E. De Luna 1752* (DUKE, XAL). Features of pseudoparaphyllia, leaf cell papillae, and stomata are helpful in the generic distinction between *Hedwigia* and *Hedwigidium* Bruch & Schimper (De Luna, 1995, 2021). Therefore, to observe anatomical details of pseudoparaphyllia, leaf cell papillae, and stomata, capsules and portions of stems with the leaves attached were fixed in a FAA solution (Formaldehyde 10%, Alcohol 50%, Acetic Acid 5% and water 35%), dehydrated in a tertiary butyl alcohol (TBA) series, and embedded in paraffin (Johansen, 1940). Dehydration proceeded by transferring the capsules and stems to three different solutions of water, ethanol, and TBA. The first solution was prepared with 50% ethanol, 40% water, and 10% TBA. The second solution consisted of 30% TBA, 60% ethanol, and 10% water. The final solution contained only ethanol (60%) and TBA (40%). Time in each stage was only 2-3 hours. Separately, capsules and stems embedded in paraffin were transversely and longitudinally sectioned using a rotary microtome (Brunel YDA, Wiltshire, UK). The thickness of the sections ranged from 6 to 10 µm. Capsules and stem sections were stained with fast green, safranin, and Heidenhain´s haematoxylin. Permanent mounts were prepared with a synthetic resin. Observations under a compound microscope (K7, Zeiss, Jena, Germany) were recorded with digital photographs (D-SLR Canon 60D, Tokyo, Japan).

Results

Generic classification

Hedwigia filiformis presents morphological features that undoubtedly place the species in the genus *Hedwigia*, such as filamentous pseudoparaphyllia (Fig. 1), the leaf cells with branched papillae (Fig. 2A, B), and cryptopore stomata in capsule necks (Fig. 2C). The anatomical details show pseudoparaphyllia are filamentous and papillose (Fig. 1), as in other species of *Hedwigia*. The leaf cross sections reveal 1-2 branched papillae per cell, on both sides (Fig. 2A, B). The longitudinal sections of the capsule neck document the sunken stomata (Fig. 2C), as described for other species in *Hedwigia*. Moreover, the perichaetial leaves are ciliate, although in the upper margins only.

Taxonomic treatment

Hedwigia filiformis (Michx.) P. Beauv., Prodr. Aethéogam.: 60. 1805. Figs. 1, 2, 3.

≡ *Anictangium filiforme* Michx. Fl. Bor. -Amer. 2: 287. 1803.

≡ *Hedwigia filiformis* (Michx.) P. Beauv., Prodr. l'Aethéogamie 60: 1805.

≡ *Anictangium ciliatum* var. *filiforme* (Michx.) Brid., Muscol. Recent. Suppl. 1: 23. 1806.

≡ *Gymnostomum filiforme* (Michx.) Spreng. Neue Entdeck. Pflanzenk. 1: 233. 1820.

≡ *Anoectangium filiforme* (Michx.) Steud. Nomenclator Botanicus 2: 58. 1824.

≡ *Anictangium ciliatum* var. *nigroviride* Arn., Disp. Méth. Mousses: 11. 1825. (nom. illeg. incl. var. prior. *A. ciliatum* var. *filiforme* (Michx.) Brid. 1806).

≡ *Anictangium ciliatum* var. *concolor* De Not. Musc. Ital. Spicilegium: 19. 1837. (nom. illeg. incl var. prior. *Anictangium ciliatum* a. *filiforme* (Michx.) Brid. 1806).

≡ *Schistidium ciliatum* var. *concolor* De Not., Syllab. Musc.: 278. 1838. (nom. illeg. incl. var. prior. *Anictangium ciliatum* var. *filiforme* (Michx.) Brid. 1806).

≡ *Schistidium ciliatum* var. *filiforme* (Michx.) Hampe, Linnaea 13: 43. 1839.

≡ *Hedwigia ciliata* var. *concolor* De Not., Atti Reale Univ. Genova 1: 717.1869. (nom. illeg. incl. var. prior. *Anictangium ciliatum* var. *filiforme* (Michx.) Brid. 1806).

Type citation: "In rupibus Carolinae et Canadae". SYNTYPES: (UNITED STATES OF AMERICA. *Michaux s.n.*, the specimen labelled as "*Hedwigia filiformis*, *integrifolia* P. Beauv." (possible syntype, Muhlenberg herbarium in PH, barcode PH00079823). CANADA. *Michaux s.n.* (not located).

= *Hedwigia integrifolia* P.Beauv., Prodr. Aethéogam. 60. 1805.

≡ *Anoectangium integrifolium* (P. Beauv.) Schwägr. Sp. Musc., Frond., Suppl. 1: 38. 1811.

≡ *Hedwigia beauvoisii* Bach. Pyl. in Lam. Encycl., Suppl. 3:10-11. 1813. (nom. illeg. incl. sp. prior).

≡ *Hedwigidium integrifolium* (P. Beauv.) Dixon ex C.E.O. Jensen. Skand. Bladmossfl.: 369. 1939. Type citation: "Je l'ai rapportée de l´Amérique septentrionale." TYPE: UNITED STATES OF AMERICA. États-Unis, *A. M. F. J. Palisot de Beauvois s.n.* (Lectotype designated here: P! PC0719797; isolectotype: E).

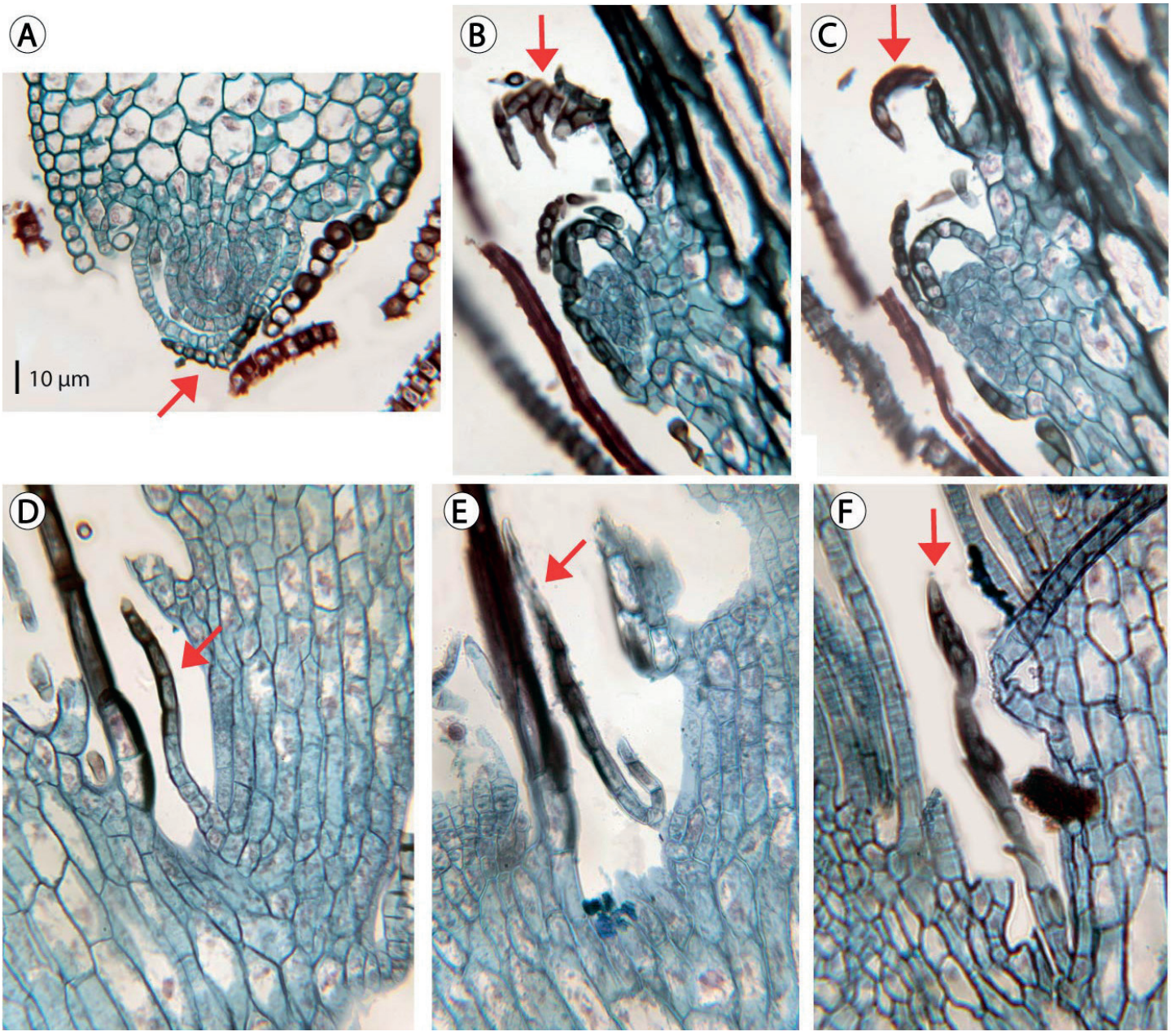

Figure 1: Anatomical features of pseudoparaphyllia in *Hedwigia filiformis* (Michx.) P. Beauv. A-C. pseudoparaphyllia at the base of a branch bud (arrows). A. branch bud in transverse section with small developing leaves covered by the pseudoparaphyllia; B. longitudinal section of a branch bud showing a filamentous pseudoparaphyllium distally branched (arrow); C. the same branch bud as in B, but here the contiguous longitudinal section shows the same pseudoparaphyllium in the next focusing plane; D-F. pseudoparaphyllia at the base of a fully developed branch. The left side is the main stem, and the branch is at the right side of the bifurcation. The pseudoparaphyllia are at the base of the newer branch (arrows); D. longitudinal section of the branching point with a filamentous pseudoparaphyllium; E. the same pseudoparaphyllium as in D, but now this is the next longitudinal section showing a different focusing plane; F. longitudinal section of the branching point with a filamentous pseudoparaphyllium.

Diagnostic character states in italics.

Plants grayish, green at the upper branches, small to medium sized, 1.2-2.8 cm long; sympodial stems slender, not stoloniferous; pseudoparaphyllia filamentous, simple or sometimes bifurcate from 1-2 basal cells, distal cells papillose; stem leaves erect, appressed; leaves imbricate when dry, spreading when moist, 1.3-1.9 mm long, 0.9-1.3 mm wide, flat, short ovate, upper half of leaf somewhat triangular, *acute to short acuminate, acumen channeled, leaf margin narrowly recurved, reflexed up to the acumen*; leaf apex slightly scarious, not spinulose, *hyaline leaf tip only about 3-8% of leaf length*, leaf apex ending in only three or four elliptical cells, *apical cell short, elliptical*; upper and median leaf cells subquadrate to short-oblong, 8-11 × 7-8 µm, with 1-2 simple or branched papillae on adaxial and abaxial surfaces, most papillae with 2 short branches, some papillae with 3 short branches; basal median cells long rectangular, porose, with few simple papillae, or without papillae; basal marginal cells quadrate in several rows, smooth; autoicous; perichaetial leaves narrow lanceolate, 2.1-2.5 × 0.7-0.9 mm, slenderly acuminate, cilia scarce, only along upper margins; setae very short, 0.2-0.3 mm; capsules wide urceolate, 1.0-1.2 × 1.2-1.5 mm, mouth wider than urn middle width, exothecial cells quadrate, short rectangular, becoming oblate at mouth border; capsule neck with stomata phaneropore; operculum plano-convex; spores 20-30 µm; calyptra very small, conic-mitrate, entire at the base, hairy.

Distribution: **North America:** Canada, United States of America, Mexico. **Europe:** Italy (as *Hedwigia ciliata* var. *concolor*, Erbar. Crittogam. Ital., no. 1017, *fide* De Notaris, 1869, p. 717-718). **Asia:** Japan, South Korea.

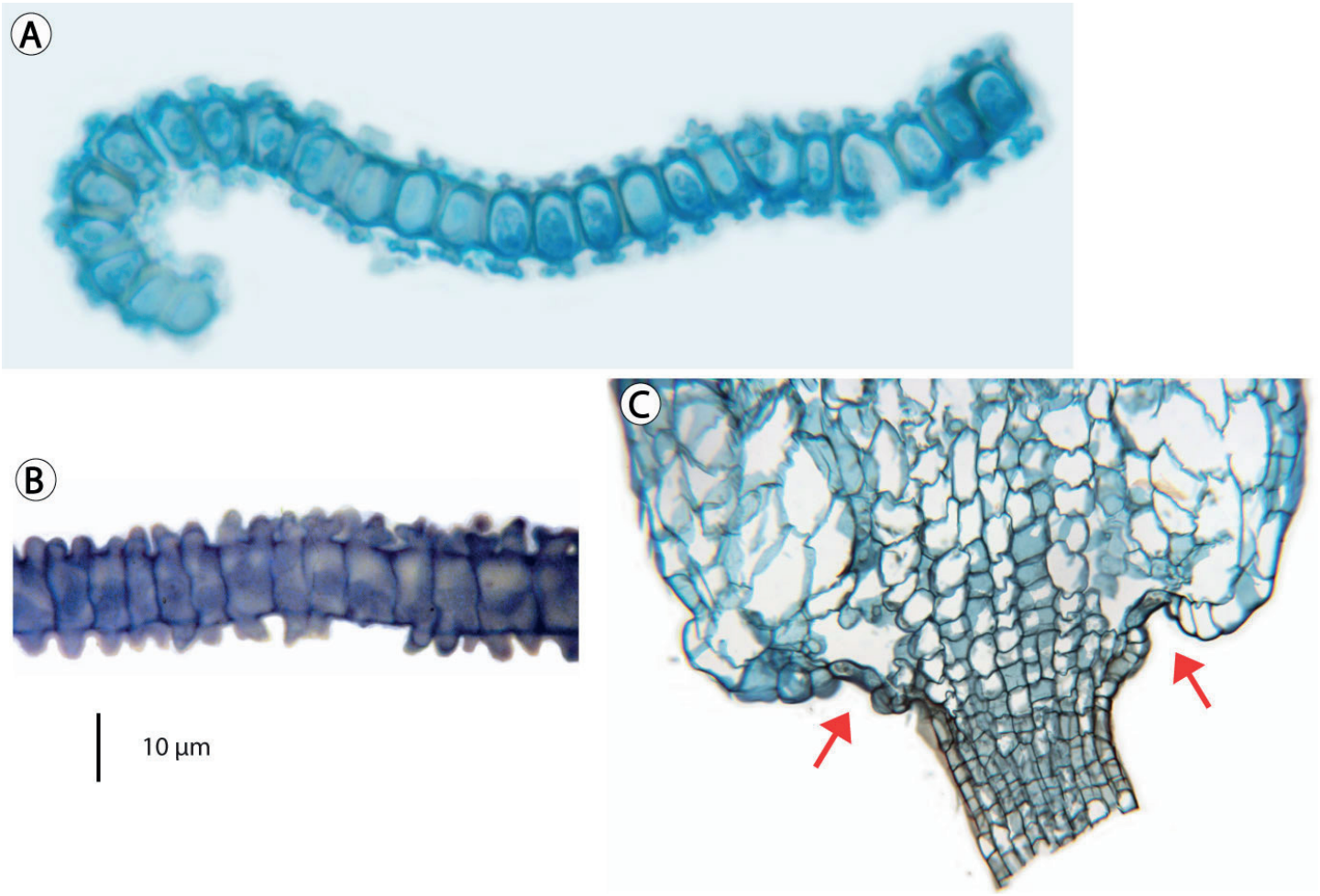

Figure 2: Anatomical features of leaf cell papillae and stomata in *Hedwigia filiformis* (Michx.) P. Beauv. A. cross section of a leaf showing the recurved margin and the peltate papillae over leaf cells, on both sides; B. cross section showing 1-2 branched papillae on both sides of the leaf; C. longitudinal section of a mature capsule showing two cryptopore stomata (arrows) at the base of the urn.

Specimens examined: NORTH AMERICA: CANADA. Ontario, Brighton, 9.V. 1875, *J. Macoun s.n.* (Canadian Musci 168) (DUKE); 15.V.1885, *J. Macoun s.n.* (Canadian Musci 297) (DUKE, F); loc. cit., 4.X.1888, *J. Macoun s.n.* (DUKE); on boulders in woods, Brighton, 16.X.1893, *J. Macoun s.n.* (Canadian Musci 297e), (as *H. ciliata* var. *subnuda*, DUKE, FH); loc. cit.,16.X.1893, *J. Macoun s.n.* (Canadian Musci 615), (as *H. ciliata* var. *subnuda*, FH); on boulders at Ottawa, *J. Macoun s.n.* (Canadian Musci 108) (as *H. ciliata* var. *viridis*, DUKE, FH); on boulders, Hastings, 28.IV.1889, *C. J. Macoun s.n.* (Canadian Musci 297) (FH); Muskoka, Foot's Bay Ca 9 km S of along Moon River, *R. Ireland 23943* (DUKE); mouth of McKenzie river, Thunder Bay, *R. F. Cain 2807* (DUKE). **MEXICO**. San Luis Potosí, *M. P. Maury 7666* (*fide* Bescherelle, 1901, as *Hedwigia subrevoluta*). Veracruz, Malpais de la Joya, *C. J. W. Schiede s.n*. (*fide* Müller, 1851); cerca de Teocelo, orillas del río Magueyitos, *E. De Luna 2516* (XAL). **UNITED STATES OF AMERICA**. Arizona, Sta. Rita Mts, *J. Haskell 3408* (DUKE, as *H. ciliata* f. *viridis*). District of Columbia, Rockbreek, 1893, *J. M. Holzinger s.n.* (Musci Americae Septentrionalis exsiccati 172) (DUKE, FH). Georgia, Savannah, *fide* Hampe (1839, p. 43); Georgiae superioris, (Northern Georgia), Musci Boreali-Americani, 1865, Edition 2 #225 (PH); Dade Co., Sitton Gulf Creek, N of Cloudland Canyon State Park, *E. De Luna 1804* (DUKE). Kansas, Great Plains, Woodoon, *S. Churchill 9469* (DUKE). Illinois, La Salle, Upper Illinois Canyon, Starved Rock State Park, *P. D. Voth and D. Richards 962* (DUKE). Maryland, Plumneis Island, 7.V.1905, *E. B. Chamberlain 2571b* (DUKE, FH), *3910* (DUKE, FH). Minnesota, Chippewa Co., Cedar Lake, near Cedar Lake, Montevideo, 18.VI.1901, *J. M. Holzinger s.n.* (Musci Acrocarpi Boreali-Americani 37) (DUKE); Chipewa Co., Cedar Lakes, small ponds in the valley of the Minnesota River, VII.1901, *J. M. Holzinger s.n.* (FH). New Hampshire, Sullivan Co., North Newport, IX. 1918, *C. S. Wilson s.n.* (DUKE, FH). New York, fide Torrey (1819); loc. cit., *L. E. Anderson 20616* (DUKE). North Carolina, Piedmont, *L. E. Anderson 2403* (DUKE); Graham Co., Slickrock Creek, Unicoi Mtns, near of Tapoco, *E. De Luna 1749* (DUKE); Graham Co., Santellah Creek, Unicoi Mtns, near of Tapoco, *E. De Luna 1750* (DUKE); Orange Co., Duke Forest, near Eno River, *E. De Luna 1751* (DUKE), *1752* (voucher for anatomical study here) (DUKE, XAL); Piedmont, 17.VIII.1892, *J. K. Small s.n.* (DUKE, as *H. ciliata* var. *viridis*). Pennsylvania, *fide* Dillenius (1742, LXXXIII, 5e). Vermont, Orleans Co., Willoughby, 19.VI. 1897, *G. G. Kennedy s.n.* (DUKE, FH); Chittenden Co., Newfane, s.f., *A. J. Grout 84* (XAL); Burlington, 21.VIII. 1896, *A. J. Grout s.n.* (DUKE, FH). Virginia, Fauquier Co., Western slope of Bull Run Mountains, *H. A. Allard 10332* (DUKE, FH).

Specimens examined: Asia. JAPAN. Shikoku, Kochi Pref., Kochi-shi, Kochi Castle, *M. Higuchi 1333* (BR); Honshu, 1955, *H. Ochi s.n.* (DUKE); Honshu, Kyushu (*fide* Suzuki, 2016, as *Hedwigia ciliata* var. *viridis*). **SOUTH KOREA.** Hongno, 1909, *Taquet s.n.* (S) (*fide* Kim et al., 2020, as *Hedwigia albicans* var. *microcarpa*, and also as *Hedwigia ciliata* var. *viridis*); Kang-Ouen-To, *M. I. Faurie 51* (*fide* Cardot, 1904, as *Hedwigia ciliata* var. *viridis*); Syou-Ouen, *M. I. Faurie 114* (*fide* Cardot, 1904, as *Hedwigia ciliata* var. *viridis*); Fusan, *M. I. Faurie 79* (*fide* Cardot, 1904, type of *Hedwigia ciliata* var. *microcarpa*).

Additional specimens examined for other *Hedwigia* species

Specimens examined of *Hedwigia ciliata*: **BOLIVIA.** Departamento La Paz, Prov. Inquisivi, along the Rio Ckanchu, ca. 4 km SW of Quime, *M. Lewis 87273* (NY). **BRASIL.** Santa Catarina, Serra Geral, I.1890, *E. Ule s.n*. (Bryotheca Brasiliensis 78) (H, JE, 2NY, SP). **CANADA.** British Columbia, Fraser River, *W. Schofield 25601* (DUKE). *Manitoba, near Ontario boundary, C. H. Hand 1072* (DUKE); Wabowden, *H. A. Crum and L. E. Anderson 7700* (DUKE). **DENMARK.** Greenland, Godthåb, *J. Lewinsky 73545 (DUKE).* **ECUADOR.** Andes Quitensis, in monte Pichincha, *R. Spruce 1292* (BM). Pichincha, camino al volcán Pululahua, cerca de San Antonio, 40 km al N de Quito, *E. De Luna 1882* (DUKE, XAL). **MEXICO.** Tlaxcala, cerca de Villareal, cañada al N de Villareal, *E. De Luna 2721* (XAL). Veracruz, Cofre de Perote, cerca de El Conejo, *E. De Luna 1748* (XAL); Las Vigas, entre Perote y Xalapa, *E. De Luna 1802* (DUKE, XAL). **UNITED STATES OF AMERICA.** New York, *A. J. Grout 123* (DUKE). North Carolina, Swain Co., Smoky Mountains, *L. E. Anderson 3312* (DUKE).

Specimens examined of *Hedwigia detonsa*: **UNITED STATES OF AMERICA.** California, North of Yreka, *W. B. Schofield 23034* (DUKE).

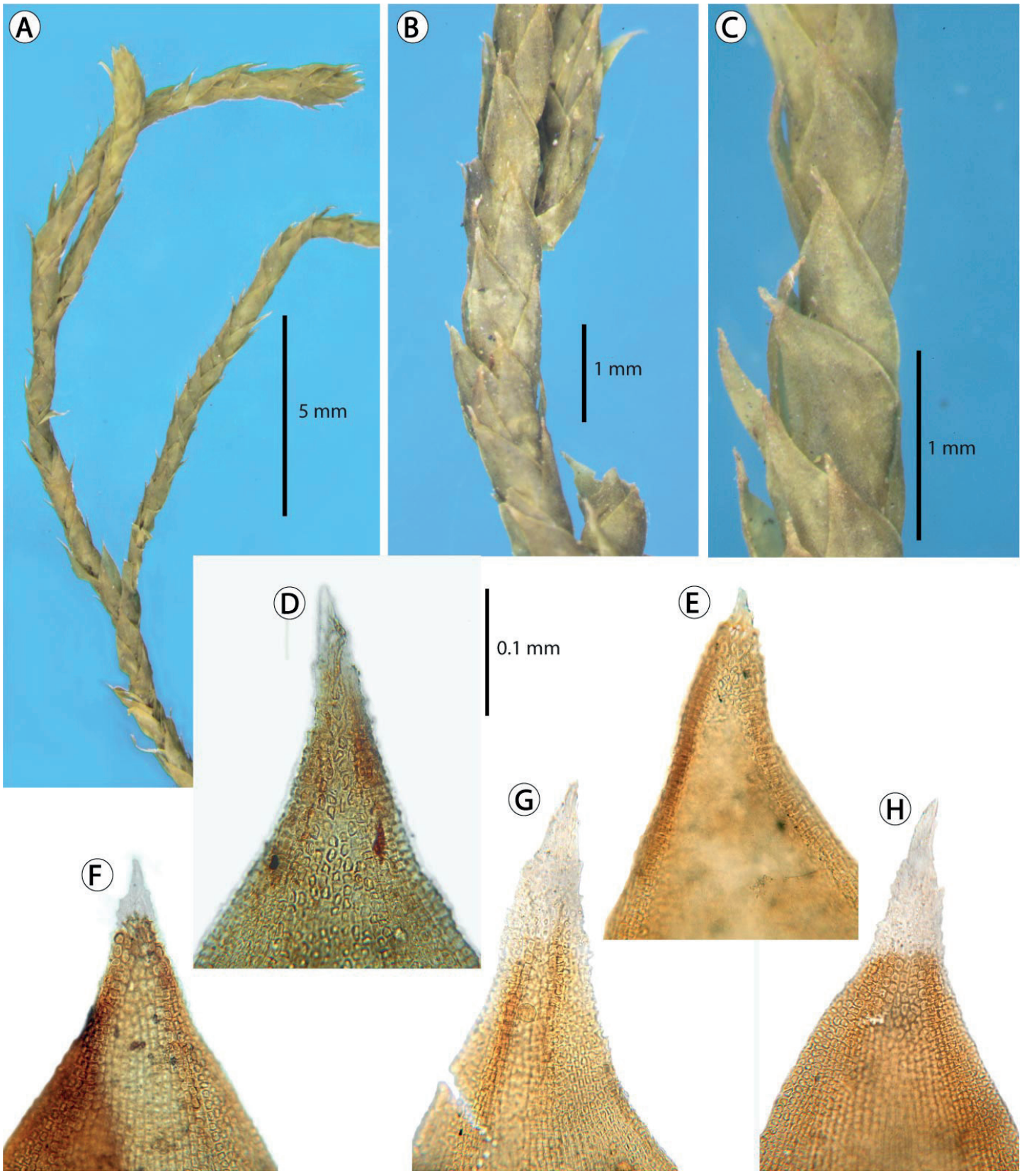

Figure 3: Morphological features of *Hedwigia filiformis* (Michx.) P. Beauv. A. slender sympodial stems and branches; B. leaves appressed when dry; C. detail of leaves showing the hyaline part very short. (A-C, from *De Luna 2516,* Mexico, Veracruz (XAL)); D-H. leaf apices acute to short acuminate, with a very short hyaline part. The upper leaf cells are subquadrate, and the apical cell is short elliptic. (D, from *Macoun s.n.*, 1893, Canada, Ontario, "Canadian Musci 615" (FH); E, from *Small s.n.,* 1892, USA, North Carolina (DUKE); F, from *Anderson 2403,* USA, North Carolina (DUKE); G, from *Churchill 9469,* USA, Kansas (DUKE); H, from *Anderson 20616,* USA, New York (DUKE).

Specimens examined of *Hedwigia nivalis*: **COLOMBIA.** New Granada, 1863, *A. Lindig s.n*. (NY). **DOMINICAN REPUBLIC**. La Vega, *W. C. Steere 23105* (DUKE). **ECUADOR**. Cajas, *M. Lewis 78-3139* (QCA). **MEXICO**. Chihuahua, Sierra Chinatú, *D. S. Correll and H. S. Gentry 22960* (DUKE). Hidalgo, Tepeapulco, *A. Cárdenas 3423* (DUKE, MEXU). Veracruz, Sierra de Chiconquiaco, cerca de Alto Lucero, al SW del poblado Monte Verde, *E. De Luna 2724* (XAL); laderas del Cofre de Perote, cerca de Tembladeras, *E. De Luna 2710* (XAL). Tlaxcala, cerca de Villareal, al N de Huamantla, *E. De Luna 2645* (XAL). **VENEZUELA**. Sin loc., *J. J. Linden s.n*. (BM); Trujillo, *D. Griffin III and C. López PV1227* (DUKE).

Specimens examined of *Hedwigia stellata*: **SWEDEN**. Småland, 1917, *H. Müller s.n.* (DUKE). **UNITED STATES OF AMERICA.** Arizona, Santa Rita Mountains, V.1881, *C. G. Pringle s.n.* (DUKE). Kentucky, Lechter, Co., *A. C. Risk 862* (DUKE).

Nomenclature and syntypes of *H. filiformis*

The original description of *Anictangium filiforme* (Michaux, 1803) stated: "*A. caulibusgracili-filiformibus: foliis arcte imbricatis, ovalibus, in acumen concolore denticulatis; perigonialibus apice ciliosis: operculo subconoideo: calyptra subvillosa*". Furthermore, Michaux (1803, p. 287) compared *A. filiforme* to *H. ciliata*: "*Affine A. ciliato; minus et multo gracilius, apice foliorum non scarioso*". He cited two specimens in the original description of *A. filiforme*: "*Hab. in rupibus Carolinae et Canadae*". These two Michaux specimens were available to Bridel-Brideri (1806), who noticed about the leaves in *Anictangium filiforme*: "*in acumine concolore denticulatis*". He commented: "*Nihil aliud est quam Anictangii nostri varietas. nam quamuis auctor separet, quod statura minus longeque gracilius fit et folia apice scariosa habeat. Ego autem in speciminibus e Carolina mecum communicatis specificum discrimen deprehendere non potui*", which translates: *"It is nothing else than our Anictangium variety for although the author pulls apart, it becomes less and far slenderer in stature and leaves scarious at the apex. Shared specimens from Carolina with me I was unable to detect a difference*". Palisot de Beauvois (1805) transferred *Anictangium filiforme* to the genus *Hedwigia*. The distinguishing features of this species as compared to *H. ciliata* were the very slender stems and the very short hyaline leaf apex.

Torrey (1819) presumably added a third specimen of *Hedwigia filiformis* when he cited this moss (as *Anictangium filiforme*) growing in the area nearby New York city; Sprengel (1820) possibly cited the same specimen as "*habitat ad rupes Nov. Eborac. Eddy*". The word "*Eboraci*" means "*Place at the water*", it is the Latin form of the name of the City of York in England. The locality "*Nov. Eborac*" is likely in New York, USA. In the same publication, Sprengel (1820) compared *Gymnostomum filiforme* (Michx.) Spreng. with *H. ciliata*, stating: "*simile G. ciliato (Hedwigia ciliata Hedw) sed huius folia magis patula apice diaphana*"; that is "but the leaves of this diaphanous tip are more widely spread". Greville and Arnott (1824, p. 60) examined the Michaux specimens and added one more collected by B. D. Greene in Boston. Hampe (1839, p. 43) added a fifth specimen from "Savannah" for *Schistidium ciliatum* var. *filiforme* and observed it was a "*forma vix piligera*" (barely hairy form). Russell (1844, p. 174, as *Anictangium filiforme*) also examined the specimen collected by Greene and listed another collection by A. L. Rusell, on Taghannoe Mountain, Shefield. These collections by Michaux´s, by Eddy from New York, by Greene from Boston, by Rusell in Massachusetts, and one more from "Savannah" are the only six specimens originally identified as *H. filiformis*. Since then, this name has no longer been used. The current herbarium location of these historical specimens is unknown, including the two Michaux syntypes.

Several historical investigations have been undertaken to gain insight in the localities for the many type specimens collected by Michaux (Sargent, 1889; Uttal, 1984; Weakly, 2004). However, I could not find any mention of *Anictangium filiforme* in these examinations of the field notes of André Michaux. As for the location of the syntypes, the bryophyte collections by Michaux are mostly at the Museum d´Histoire Naturelle in Paris (PC). An online internet search for specimens collected by Michaux in Paris (PC) returned no records for *Anictangium filiforme* or under *Hedwigia*. There are several Michaux type specimens in the herbaria BM, BR, JE, P, and S, but for other moss species. Michaux is listed as one of the important collectors in the Herbarium of the Academy of Natural Sciences, Philadel-

phia, USA (PH); one specimen stored there as *H. filiformis* although without collector data, might be a syntype (JSTOR, 2022). The specimen is at the top of the image. These plants consist of slender stems with appressed leaves, the hyaline part very short, and they are certainly *H. filiformis*. The herbarium packet is at the bottom of the image online; it has a printed label from the Muhlenberg herbarium, and is annotated as "*Hedwigia filiformis*, *integrifolia* P. Beauv." (barcode PH00079823). I am suggesting this specimen as a possible syntype only. According to Pennell (1942, 1950), Andre Michaux (1746-1802) made the American Philosophical Society one of his headquarters. Since 1785 onwards, Henry Muhlenberg did receive North American collections from Michaux. This specimen originally identified as *Hedwigia filiformis* is part of the Muhlenberg herbarium, which much later in 1898 was gifted to PH (Mears, 1978). In conclusion, ideally this name would be lectotypified here; however, this is not possible based on the material I have seen.

There is an even older specimen collected very likely by Dillenius in Pennsylvania, although originally identified as *Hedwigia ciliata* (Dillenius, 1742, as "*Sphagnum nodosum hirsutum & incanum*"). The sheet of the Dillenius herbarium at Oxford (OXF) for *Hedwigia ciliata* (LXXXIII, 5) contains a row of three specimens (Fig. 4); the rightmost specimen is labelled "e Pensylvania". About this specimen "5e", Druce et al. (1907, p. 203) informed: "Garney labels it *H. ciliata*, var *secunda*, Br. & Schimp." This label is indeed visible at the left of the row of the three specimens (Fig. 4). The corresponding illustrations in Table XXXII by Dillenius (1742) show two different plants: "5. A" looks most likely as *Hedwigia ciliata*, but "5. B." shows small plants, slender stems, and imbricated leaves, certainly suggesting *H. filifomis*.

Discussion

Generic classification

Since Allen (2010) and Dalton et al. (2012) had warned of the wrong use of the name *Hedwigia integrifolia*, specimens were studied in anatomical details to corroborate if this species is correctly placed in genus *Hedwigia*. In *Hedwigidium*, pseudoparaphyllia are broad and foliose (De Luna, 1995, 2021), while they are filamentous in *Hedwigia* (De Luna, 1995; Biasuso, 2007). Stomata are phaneropore in capsule necks in *Hedwigidium* (De Luna, 1995, 2021; Allen, 2010), while they are cryptopore in *Hedwigia* (De Luna, 1995; Allen, 2010). Variation in leaf cell papillae has been useful in the comparison and distinction of species within *Hedwigia* (Hedenäs, 1994; Biasuso, 2007; Ignatova et al., 2016). Features such as the filamentous pseudoparaphyllia, the leaf cells with branched papillae, and the cryptopore stomata in capsule necks undoubtedly confirm the species in *Hedwigia* (Figs. 1, 2, 3).

However, the name *Hedwigia integrifolia* is still widely used for the species characterized by multiple low papillae on leaf cells, short setae, inmersed capsules, and perichaetial leaves entire, originally described as *Gymnostomum imberbe* Sm. (Smith, 1811). A search in databases available online (CNABH, 2022) for current information on specimens and pictures of *Hedwigia integrifolia* returns worldwide records of *Hedwigidium imberbe*, which is wrong. Records available online of specimens collected in several localities in Europe are erroneously identified as *Hedwigia integrifolia*. In the GBIF database, *Hedwigia integrifolia* is used for pictures and records of plants whose correct identity is *Hedwigidium imberbe* (GBIF Secretariat, 2021a, species 7403134, GBIF Secretariat, 2021b). In the "Taxonomy" page of *Braunia imberbis* for the plants database of France *Hedwigidium integrifolium* (P. Beauv.) Dixon is listed wrongly as synonym of *Hedwigia integrifolia* (MNHN and OFB, 2003-2022, name 5075). The same taxonomic confusion is still present in the UK online database which considers *H. integrifolia* as the accepted name, including *Hedwigia imberbis* as well as *Hedwigidium integrifolium* as synonyms (NBN Atlas, 2022, UK species NBNSYS0000036725). There are many more cases in which the correct identity of European records in herbaria and online databases should be *Hedwigidium imberbe*, not *Hedwigia integrifolia*. This confusion between *H. integrifolia* and *Hedwigidium imberbe* has remained despite the clarifications provided by Allen (2010) and Dalton et al. (2012), and the morphological details for the correct identification of *Hedwigidium imberbe* (De Luna, 2021). The morphological details provided should help to clarify the taxonomic identity of *Hedwigia integrifolia*, proposed here as a synonym of *H. filiformis*.

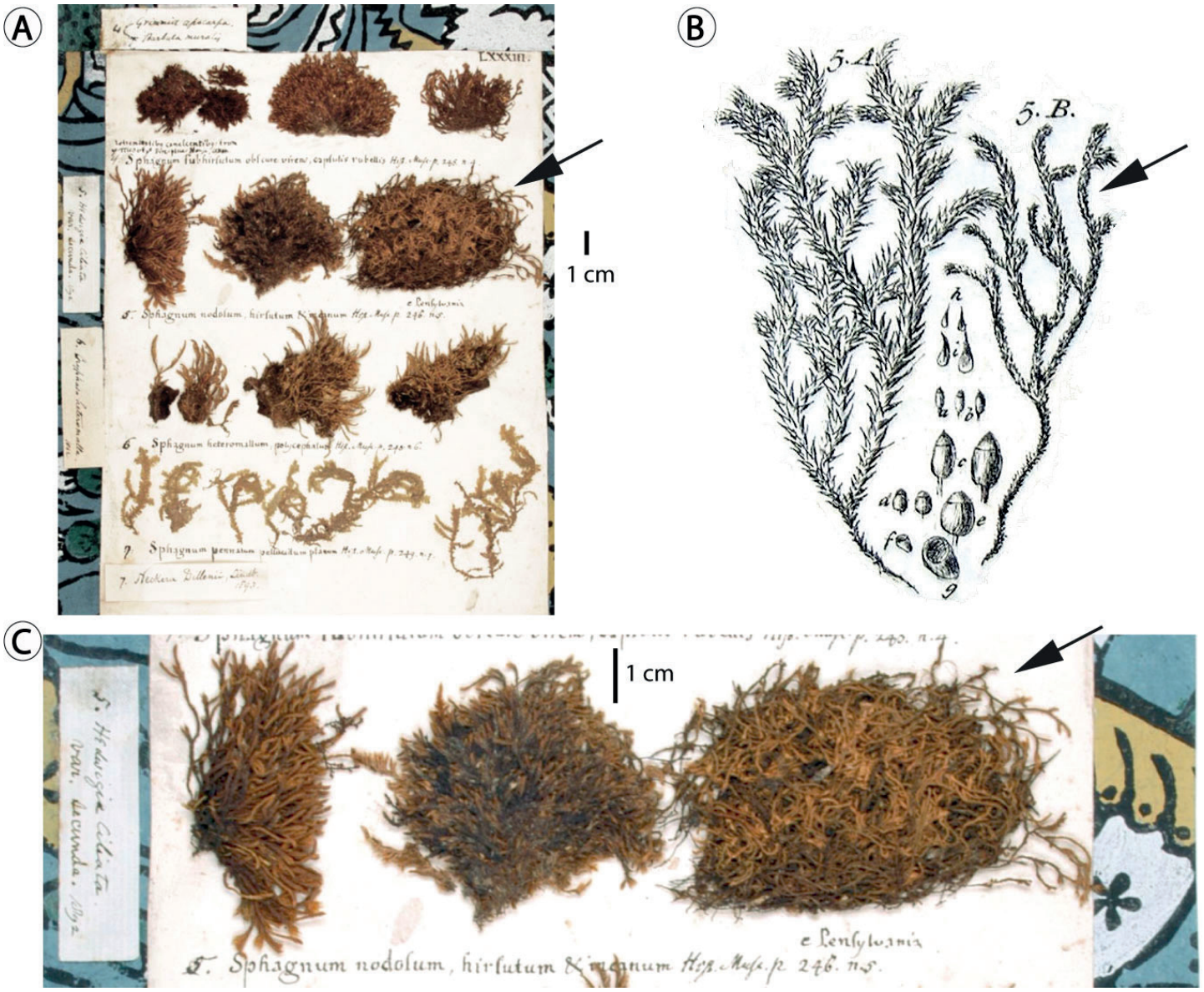

Figure 4: Specimen of *Hedwigia filiformis* (Michx.) P. Beauv. in the Dillenius herbarium sheet LXXXIII in OXF. A. the second row in the sheet contains three specimens, which together are labelled as "5. *Sphagnum nodosum hirsutum & incanum*"; the third specimen in this row is labelled as "e Pensylvania" (arrow). The identity of this specimen is *H. filiformis*; B. detail of the drawings in Table XXXII (Dillenius, 1742) showing two plants. 5. A is *Hedwigia ciliata* (Hedw.) Ehrh. ex P. Beauv.; 5. B shows a plant with slender stems and appressed leaves (arrow); this is a drawing based on the specimen "e. Pensylvania"; C. detail of the third specimen in the row, labelled "e Pensylvania" (arrow).

Synonyms of *Hedwigia filiformis*

In the original description, Palisot de Beauvois (1805) clearly characterized *H. integrifolia* by the short hyaline leaf apex, the ciliated perichaetial leaves, and tall branched papillae on upper leaf cells. At the same time, Palisot de Beauvois (1805) noticed the very close relationship of *Hedwigia filiformis* and *Hedwigia integrifolia*. *Hedwigia filiformis* was listed before *H. integrifolia*, on the same page 60, and he commented on *H. integrifolia*: "Je la soupçonne être la même, ou une variété de l'espèce précèdente". In modern times, Hedenäs (1994, p. 155) also suggested a similarity of *Hedwigia filiformis* with *H. integrifolia*. Hedenäs did not see the original description of *A. filiforme*, but he referred to the second edition of Michaux's flora (Michaux, 1820), where it is stated that

Anictangium filiforme lacks a hair-point in the leaves. Thus, Hedenäs (1994) concluded that *Hedwigia integrifolia* rather than any taxon of the *H. ciliata* complex was suggested by the description. The original description of *A. filiforme* (Michaux, 1803, p. 287), reads: "*A. caulibus gracili-filiformibus: foliis arcte imbricatis, ovalibus, in acumine concolore denticulatis; perigonialibus apice ciliosis: operculo subconoideo: calyptra subvillosa*". Indeed, specimens I examined from Eastern Canada and Eastern USA cannot be subdivided in two groups; all share the small ovate leaves, a very short hyaline acumen, and the few cilia only in the upper portion of the perichaetial leaves. The taxonomic concepts of *H. integrifolia* and *H. filiformis* are so similar, as previously suggested (Palisot de Beauvois, 1805; Hedenäs, 1994), that now these two should be treated as synonymous.

In Index Muscorum (Wijk et al., 1969, p. 673), the name *H. beauvoisii* is attributed to A. J. M. Bachelot de la Pylaie dating back to Steudel (1824). Following this, Hedenäs (1994, p. 149) listed "*Hedwigia beauvoisii* Pyl. in Steud., Nomencl. Bot. 2: 196. 1824. nom. nud. in synon. = *H. ciliata* (Hedw.) P. Beauv." among the synonyms of *Hedwigia ciliata*. However, the name *H. beauvoisii* was actually published in the "Encyclopédie Méthodique. Botanique. Supplement 3" by Lamarck (1813) with a description, which reads: "8. HEDWIGIE de Beauvois. Hedwigia Beauvoisii. (N.) Hedwigia caule ramofo, nodofo; foliis ovato-lanceolatis, ftride imbricatis, concavis, acutis; perichatialibus ciliatis. Hedwigia integrifolia. Pal.-Beauv. Æth. p. 60". The final note compares this new species with *H. ciliata*: "Elle m'a été communiquée par M. de Beauvois, qui l'a recueillie dans l'Amérique septentrionale". This appears in an entry for the genus *Hedwigia* that was authored by "B. de la Pylaie". The direct reference to *H. integrifolia* and very likely the same Beauvois type specimen certainly suggests *H. beauvoisii* Bach. Pyl. is a superfluous name for *H. integrifolia*.

Taxonomic distinction of *H. filiformis*

Hedwigia filiformis differs from other species in *Hedwigia* mainly by its very slender sympodial branches, short widely ovate leaves, recurved leaf margins, and very short hyaline leaf acumina (Fig. 3). Most species in *Hedwigia*, for example, *H. ciliata*, *H. detonsa*, *H. nivalis*, and *H. stellata*, have narrowly lanceolate leaves with much larger hyaline leaf apices, the upper leaf cells are strongly papillose, the acumen is spinulose, and the apical cell is narrow and long. In *H. filiformis* the hyaline part consists of few cells and the apical cell is elliptical and short.

Hedwigia filiformis is very similar to *H. brevipilifera* Biasuso described from Argentina in the ovate lanceolate leaves, the short hyaline leaf tip, and the absence of spines in the leaf apex (Biasuso, 2007). The main differences are found in the leaf margin and in the leaf cell papillae. In *H. brevipilifera* the leaf margin is reflexed, only in the basal third of the leaf, and the papillae have 3-4 short branches. In *H. filiformis* the leaf margin is recurved up two thirds of leaf length, and the leaf cell papillae have 1-2 branches only, on both leaf sides. The European *H. nemoralis*, recently described as new species (Ignatova et al., 2016), is also morphologically similar to *H. filiformis*. In *H. nemoralis* the plants are small, the leaves are ovate, canaliculate and short acuminate, the apical cell short, and the perichaetial leaves are weakly ciliate. Besides European Southern Russia and China, this species is known only from three specimens from North America. The excellent illustrations and the detailed morphological description of *H. nemoralis* provided by Ignatova et al. (2016) offer convincing indication of the similarity between *H. filiformis* and *H. nemoralis*. Presently, I could not find anything to separate *H. nemoralis* from *H. filiformis* morphologically, which suggests that *H. nemoralis* might be a synonym of *H. filiformis*.

Several varieties or subspecies within *Hedwigia ciliata* share some morphological features with *H. filiformis*, particularly the slender stems and the leaf apex. All the original descriptions of *Hedwigia cilata* var. *viridis* Bruch & Schimp., *Hedwigia ciliata* var. *secunda* Bruch & Schimp., *Hedwigia subrevoluta* (Müll. Hal.) Mitt., *Hedwigia ciliata* subsp. *subnuda* Kindb., and *Hedwigia ciliata* var. *microcarpa* Cardot highlight the very short hyaline acumina (Bruch and Schimper, 1846; Müller, 1851; Macoun, 1892; Cardot, 1904). All these names should be considered as possible synonyms of *H. filiformis*. In the case of *Hedwigia ciliata* var. *viridis* Bruch & Schimp., the description with an illustration in Bruch and Schimper (1846) reads: "*foliis undique patentibus vel subsecundis, minus confertis, intense viridibus, apice vix diaphanis (tab 11, delta)*". However, no explicit collector or locality are given in the original description. Later, Husnot (1887,

p. 143) listed this taxon in France with "Feuilles vertes, Trés briévement décolorées á la pointe". In North America, Lesquereaux and James (1884) and Limpricht (1889) stated that this variety has stems slender, with leaves green or scarcely discolored at tip. Macoun (1892) stated this variety was very common in Ontario (Canada). For the USA, Jones (1933) described his "*Hedwigia ciliata* forma *viridis*" with the "stems slender; leaves imbricated or spreading, bright green, scarcely at all hyaline".

Moreover, the North American *Hedwigia ciliata* subsp. *subnuda* is very similar to *H. filiformis* in the leaf apex. The description of this subspecies in Macoun (1892) reads: "Leaves nearly hairless, the greater number broadly ovate, borders reflexed; cells larger, subquadrate". This was originally described with two collections by Macoun from Canada (Macoun, 1892). The type citation reads: "On rocks in McKay´s Woods at Ottawa; also on boulders, in woods, near Wooler, Ont. Oct 6th, 1888 (Macoun)". Later, Barnes (1896) cited these two specimens for *H. cilata* subsp. *subnuda* Kindb. as: "Mac Cat. 78, on rocks in woods: Ottawa; also near Wooler, Ont". In this case "Mac Cat. 78" referred to "Macoun, Catalogue of Canadian Plants, Part VI, Musci", as explained by Barnes (1896) in his introduction. I studied seven Macoun specimens (DUKE, FH) and the morphological features are congruent with the concept of *Hedwigia filiformis*. However, since none of these Macoun specimens have the label information exactly as in the two syntypes, possible synonymy can only be suggested for now.

Notes on worldwide distribution of *H. filiformis*

The currently known distribution of *Hedwigia filiformis* includes Eastern Canada, the United States of America, Eastern Mexico, Italy, Japan and South Korea, and it seems rare where it occurs. However, I believe that most bryologists make a quick identification as *Hedwigia ciliata* and other locations may have been missed. For example, taxonomic treatments for Eastern North America provide indication that at least some specimens of *Hedwigia ciliata* may belong to *H. filiformis*. Ireland (1982) described the plants of *Hedwigia* collected in the Maritime provinces of Canada as having leaves with recurved margins below, leaf apex acute or acuminate, a short hyaline tip, and leaf cells with 1-2, rarely more, simple or branched papillae on both sides (Ireland, 1982; illustrated in Plate 233, p. 410). Also, Crum (1976, p. 130) observed that the length of the hyaline leaf points was highly variable in specimens collected in the area of the Great Lakes forests (USA). Similarly, Crum and Anderson (1981) made the same observation that the length of the hyaline leaf tips was highly variable. Some specimens from Eastern North America indeed have the hyaline part in some leaves reduced to only very few apical cells (Fig. 3F-H). My collections from Georgia and North Carolina (USA) sampled plants with very short hyaline acumina, which I originally interpreted as part of the variation of *H. ciliata*. I used some of these plants as vouchers for my studies of protonema development (De Luna, 1990a) and for anatomical studies of the branching patterns (De Luna, 1990b). Now I consider the correct identification of the vouchers for those studies should be *H. filiformis*. This contribution will highlight the presence of *H. filiformis* and encourage a search into the many *Hedwigia* collections already in herbaria.

In Europe, *H. filiformis* was originally recorded in Italy as *Anictangium ciliatum* var. *concolor* in (De Notaris, 1837) and as *Hedwigia ciliata* var. *concolor* (Erbar. Crittogam. Ital., no. 1017, De Notaris, 1869, p. 717-718). De Notaris (1837) observed in *Anictangium ciliatum* var. *concolor* that the leaf apex was barely greyish "foliis siccitate appressis, apice vix canescentibus". Later, De Notaris (1869) again noticed about *Hedwigia ciliata* var. *concolor* in Italy the leaves were: "vel vix canescentia" (or barely gray hairs). Other historical records of several varieties of *Hedwigia ciliata* so similar with *Hedwigia filiformis* hint to the need of searching for specimens with slender stems and short hyaline apices among the many specimens collected in Europe. For example, Bruch and Schimper (1846) described two taxa from Europe, *H. ciliata* var. *viridis* and *H. ciliata* var. *secunda*, although without precise localities. These plants were described as "having the leaves with a diaphanous tip that disappears almost completely", according to the translation from "Les feulies sont plus ou moins espacees et prennent uue coleur brunt-vert en meme temps que la pointe diaphane disparait presque totalment". Next, in France, Husnot (1887) observed about *H. cilata* var. *viridis* that the leaves were "very briefly discolored at the tip" ("Feuilles vertes, tres brievement decolorees a la pointe"). Also, Limpricht (1889) listed two varieties as: *H. albicans* var.

secunda, and *H. albicans* var. *viridis*. Among specimens cited (Limpricht, 1889, p. 820) he listed "Rabenhorst, Bryoth. Eur. No 678" as *H. albicans* var *viridis*. In England, Dixon and Jameson (1896, p. 161) noted that in *H. ciliata* var. *viridis* the leaves were imbricate when dry, bright green, tip hardly hyaline. They added: "Another form described by Schimper as var. *secunda* is also found". In the review of European mosses, Roth (1904, p. 453) also reported the same two varieties. The morphological features of the small ovate leaves with a very short hyaline apex, noticed by Bruch and Schimper (1846), De Notaris (1837, 1869), Husnot (1887), Limpricht (1889), and Dixon and Jameson (1896), suggest a similarity with *H. filiformis* and *H. nemoralis*.

In Japan and South Korea, *H. filiformis* might not be as rare as it appears now. Previous records of *Hedwigia ciliata* var. *viridis* from Japan (Honshu, Kyushu), as reported by Suzuki (2016), and specimens collected in South Korea recently identified as *Hedwigia albicans* var. *microcarpa* (Cardot) Sasaoka, and also as *Hedwigia ciliata* var. *viridis* (Kim et al., 2020, p. 388), need reexamination. For example, *H. ciliata* var. *microcarpa* was originally described as having the capsules very constricted below the mouth and the leaves with a short hair point (Cardot, 1904). This suggests possible synonymy of *H. ciliata* var. *microcarpa* with *H. filiformis*. The specimens I studied from South Korea and Japan indeed have the hyaline hair-points in vegetative leaves (when not worn off), extending less than 1/8 the leaf length; the perichaetial leaves have only few and weakly crisped cilia in the upper margin; and most medial and upper leaf cells have 1-2 abaxial small papillae, usually bifurcated.

Conclusions

This study offers morphological details to document the taxonomic status of *Hedwigia integrifolia*. This name refers to a species characterized by leaf cells with peltate papillae and perichaetial leaves ciliate, originally described from Eastern North America. The species has remained poorly understood for a long time, first because it was placed under synonymy of *Hedwigia ciliata*, and later, because of a failure to see the difference between *H. integrifolia* and *Hedwigidium imberbe*. A wide examination of herbarium specimens and protologues of other similar species of *Hedwigia* worldwide revealed that *H. integrifolia* is a heterotypic synonym of the earlier name *H. filiformis*.

The re-establishment of *Hedwigia filiformis* is another example of the recent reevaluation of the morphological variation within the genus, considered monotypic for a long time. The genus *Hedwigia* has certainly turned out to be taxonomically diverse, first with the morphological identifications of more than one species in Europe (Hedenäs, 1994), later in western North America (Buck and Norris, 1996), and the morphological recognition of a new species *H. brevipilifera*, from Argentina (Biasuso, 2007). First, Buchbender et al. (2014) in Europe, and recently Ignatova et al. (2016, 2017) in Russia, discovered well-defined molecular lineages worthy of the rank of species. These morphological and molecular studies within *Hedwigia* have helped in our interpretation of the morphological variation of this genus found in other areas of the world. Likewise, I propose here that the morphologically well-defined *H. filiformis* should be reestablished at the species level. Identification of morphological groups ranked as species within *Hedwigia* will serve as a guide for the sampling design in the next round of molecular phylogenetic studies in order to test if they represent well defined lineages, or not.

Author contributions

EDL conceived and designed the study, carried out the nomenclatural, taxonomic, and anatomical studies, wrote the manuscript, reviewed, and approved the final version.

Funding

The author thanks the Instituto de Ecología, A.C. (INECOL), Consejo Nacional de Ciencia y Tecnología (CONACYT), Mexico, for the continued support. Field trips and visits to herbaria for his research were funded in part by a grant from the USA National Science Foundation (BSR-8914704).

Acknowledgments

I am grateful to curators of herbaria for loans of specimens (AAU, B, BM, BR, DUKE, F, JE, MEXU, MICH, MO, NSW, NY, QCA, S, US, and XAL). I appreciate very much the help from Chelsea R. Smith (Collections Manager, PH, Botany Department, Academy of Natural Sciences of Drexel University, Philadelphia, USA) for support in obtaining the image of a speci-

men of *Hedwigia filiformis*, and references for the history of the Muhlenberg herbarium. I am grateful for the help of two reviewers in correcting important nomenclatural details for this published version. The careful revision of the editorial team and Marie-Stéphanie Samain is deeply appreciated.

Literature cited

Allen, B. 2010. Moss flora of Central America, Part 3: Anomodontaceae - Symphyodontaceae. Missouri Botanical Garden. St Louis, USA. Pp. 16-30.

Arnott, G. A. W. 1825. Nouvelle Disposition Méthodique des Espèces de Mousses. J. Tastu. Paris, France. Pp. 72.

Barnes, C. R. 1896. Analytic keys to the genera and species of North American mosses. Bulletin of the University of Wisconsin, Science series 1(5): 157-368.

Bescherelle, M. E. 1901. Les récoltes bryologiques de Paul Maury au Mexique. Journal de Botanique (Morot) 15(11): 380-388.

Biasuso, B. 2007. The genus *Hedwigia* (Hedwigiaceae, Bryophyta) in Argentina. Lindbergia 32(1): 5-17. https://www.jstor.org/stable/20150227 (consulted January, 2022).

Bridel-Brideri, S. E. 1806. Muscologiae Recentiorum Supplementum, Pars 1, Apud C. G. Ettingerum. Gotha, Germany. Pp. 271. DOI: https://doi.org/10.5962/bhl.title.20

Bruch, P. and W. P. Schimper. 1846. Hedwigiaceae. In: Bruch, P., W. P. Schimper and W. V. T. Gümbel (eds.). Bryologia Europaea, seu Genera Muscorum Europaeorum monographice illustrate, Vol. III. E. Scheizerbart. Stuttgart, Germany. Pp. 272-275.

Buchbender, V., H. Hespanhol, M. Krug, C. Sérgio, A. Séneca, K. Maul, L. Hedenäs and D. Quandt. 2014. Phylogenetic reconstructions of the Hedwigiaceae reveal cryptic speciation and hybridisation in *Hedwigia.* Bryophyte Diversity and Evolution 36(1): 1-21. DOI: https://doi.org/10.11646/bde.36.1.1

Buck, W. R. and D. H. Norris. 1996. *Hedwigia stellata* and *H. detonsa* (Hedwigiaceae) in North America. Nova Hedwigia 62(3): 361-370.

Cardot, J. 1904. Première contribution à la flore bryologique de la Corée. Mit 27 Abbildungen im Text. Beihefte zum Botanischen Centralblatt 17: 1-44.

CNABH. 2022. Consortium of North American Bryophyte Herbaria. https://bryophyteportal.org/portal/ (consulted January, 2022).

Cortini-Pedrotti, C. 2001. Flora dei muschi d'Italia, parte I. Antonio Delfino Editore. Roma, Italia. Pp. 817.

Crum, H. A. 1976. Mosses of the Great Lakes Forest. Contributions from the University of Michigan Herbarium 10: 1-404.

Crum, H. A. and L. E. Anderson. 1981. Mosses of Eastern North America, Vol. 2. Columbia University Press. New York, USA. Pp. 665-1328.

Dalton, N., E. M. Kungu and D. G. Long. 2012. The misapplication of *Hedwigia integrifolia* P. Beauv. and identity of *Gymnostomum imberbe* Sm. (Hedwigiaceae, Bryopsida). Journal of Bryology 34(1): 59-61. DOI: https://doi.org/10.1179/1743282011Y.0000000041

De Luna, E. 1990a. Protonemal development in the Hedwigiaceae (Musci), and its systematic significance. Systematic Botany 15(2): 192-204. DOI: https://doi.org/10.2307/2419173

De Luna, E. 1990b. Developmental evidence of acrocarpy in *Hedwigia ciliata* (Musci: Hedwigiaceae). Tropical Bryology 2(1): 53 60. DOI: https://doi.org/10.11646/BDE.2.1.5

De Luna, E. 1995. The circumscription and phylogenetic relationships of the Hedwigiaceae (Musci). Systematic Botany 20(3): 347-373. DOI: https://doi.org/10.2307/2419500

De Luna, E. 2021. Seta length variation and the refutation of *Hedwigidium* = *Braunia* (Hedwigiaceae, Bryopsida). Acta Botanica Mexicana 128: e1810. DOI: https://doi.org/10.21829/abm128.2021.1810

De Notaris, G. 1837. Muscologiae Italicae Spicilegium. Mediolani, Ex typis F. Rusconi. Italy. Pp. 26.

De Notaris, G. 1869. Epilogo della briologia Italiana. Atti Reale Università di Genova, Italy. Pp. 781.

Dillenius, J. J. 1742. Historia muscorum in qua circiter sexcentae species veteres et novae ad sua genera relatae describuntur et iconibus genuinis illustrantur: cum appendice et indice synonymorum. E Theatro Sheldoniano (1741) Oxonii. London, UK. Pp. 576.

Dixon, H. N. and H. G. Jameson. 1896. The student's handbook of British mosses. V. T. Sumfield. Eastbourne, UK. 696 pp.

Druce, G. C., S. H. Vines and J. J. Dillenius. 1907. The Dillenian herbaria: an account of the Dillenian collections in the herbarium of the University of Oxford, together with a biographical sketch of Dillenius, selections from his correspondence, notes, &c. The Clarendon Press. Oxford, UK. Pp. 258.

Eckel, P. M. 2015. Hedwigiaceae. In: Flora of North America Editorial Committee (eds.). Flora of North America North of Mexico: Bryophyta, part 2, Vol. 28. New York, USA. Pp. 83-89.

GBIF Secretariat. 2021a. GBIF Backbone Taxonomy. *Hedwigia integrifolia* P. Beauv in Checklist dataset. DOI: https://doi.org/10.15468/39omei

GBIF Secretariat. 2021b. Species 7403134. GBIF Backbone Taxonomy. https://www.gbif.org/species/7403134 (consulted January, 2022).

Greville, R. K. and G. A. W. Arnott. 1824. Memoir IV: Tentamen methodi muscorum; or, a new arrangement of the genera of mosses, with characters, and observations on their distribution, history, and structurre. Memoirs of the Wernerian Natural History Society 5: 42-89.

Hampe, G. E. L. 1839. Relation über die von dem Reisenden C. Beyrich auf seiner letzten Reise in Nordamerika gesammelten Laubmoose. Linnaea 13: 39-48.

Hedenäs, L. 1994. The *Hedwigia ciliata* complex in Sweden, with notes on the occurrence of the taxa in Fennoscandia. Journal of Bryology 18(1): 139-157. DOI: https://doi.org/10.1179/jbr.1994.18.1.139

Hooker, W. J. and T. Taylor. 1818. Muscologia Britannica; containing the mosses of Great Britain and Ireland, systematically arranged and described with plates illustrative of the characters of the genera and species. Longman, Hurst, Rees, Orme, and Brown. London, UK. Pp. 152.

Hooker, W. J. and T. Taylor. 1827. Muscologia Britannica; containing the mosses of Great Britain and Ireland, systematically arranged and described with plates illustrative of the characters of the genera and species. 2nd ed, Corrected and Enlarged. Longman, Rees, Orme, Brown and Green. London, UK. Pp. 272.

Husnot, P. T. 1887. Muscologia gallica: descriptions & figures des mousses de France et des contrées voisines. T. Husnot/F. Savy. Caen. Paris, France. Pp. 458.

Ignatova, E. A., O. I. Kuznetsova and M. S. Ignatov. 2017. Further comments on the genus *Hedwigia* (Hedwigiaceae, Bryophyta) in Russia. Arctoa 26: 132-143. DOI: https://doi.org/10.15298/arctoa.26.13

Ignatova, E. A., O. I. Kuznetsova, V. E. Fedosov and M. S. Ignatov. 2016. On the genus *Hedwigia* (Hedwigiaceae, Bryophyta) in Russia. Arctoa 25: 241-277. DOI: https://doi.org/10.15298/arctoa.25.20

Ireland, R. R. 1982. Moss flora of the Maritime Provinces. National Museum of Natural Sciences Publications in Botany, No. 13. National Museums of Canada. Ottawa, Canada. Pp. 738.

Jaeger, A. 1876. Genera et species muscorum systematice disposita seu Adumbratio florae muscorum totius orbis terrarium (continuatio), Part 6. Berich über die Thätigkeit der St. Gallischen Naturwissenschaftlichen Gesellschaft. S Gallen, Helvetii. Pp. 85-188.

Johansen, D. A. 1940. Plant microtechnique. Mac Graw-Hill. New York, USA. Pp. 523.

Jones, G. N. 1933. Grimmiaceae. In: Grout, A. J. (ed.). Moss flora of North America, North of Mexico, Vol. 2, Part 1. Newfane, USA. Pp. 65.

JSTOR. 2022. JSTOR Global Plants. https://plants.jstor.org/stable/10.5555/al.ap.specimen.ph00079823 (consulted January, 2022).

Kim, W., M. Higuchi and T. Yamaguchi. 2020. An updated list of mosses of Korea. Journal of Species Research 9(4): 377-412. DOI: https://doi.org/10.12651/JSR.2020.9.4.377

Lamarck, M. 1813. Encyclopédie Méthodique. Botanique. Continuée par J. L. M. Poiret. Supplément, 3. H. Agasse. Paris, France. Pp. 780.

Lesquereaux L. and T. P. James 1884. Manual of the mosses of North America. S. E. Cassino and Company. Boston, USA. Pp. 447.

Limpricht, K. G. 1889. Die Laubmoose Deutschlands, Oesterreichs und der Schweiz, Part 1: Abtheilung: Sphagnaceae, Andreaeaceae, Archidiaceae, Bryineae (Cleistocarpae, Stegocarpae, Acrocarpae). Lieferung XIII. Eduard Kummer. Leipzig, Germany. Pp. 769-836.

Macoun, J. 1892. Catalogue of Canadian Plants, Part VI, Musci. William Foster Brown and Co. Montreal, Canada. Pp. 295.

Mears, J. A. 1978. Some Sources of the Herbarium of Henry Muhlenberg (1753-1815). Proceedings of the American Philosophical Society 122(3): 155-174. https://www.jstor.org/stable/986550 (consulted January, 2022).

Michaux, A. 1803. Flora Boreali-Americana, sistens caracteres plantarum quas in America septentrionali collegit et detexit, Tomus secundus. Levrault, Parisiis & Argentorati. Parisiis, France. Pp. 340.

Michaux, A. 1820. Flora Boreali-Americana, sistens caracteres plantorum quas in America septentrionali collegit et detexit. Aeditio nova, Tomus secundus. Bibliopola Jouanaux Junior. Parisiis, France. Pp. 340.

MNHN and OFB (ed.). 2003-2022. Name 5075, sheet of *Hedwigia integrifolia* P. Beauv., 1805. Inventaire national du patrimoine naturel (INPN). https://inpn.mnhn.fr/espece/cd_nom/5075/tab/taxo (consulted January, 2022).

Müller, C. 1851. Synopsis muscorum frondosorum omnium hucusque cognitorum II. Sumptibus Alb. Foerstner. Berolini, Germania. Pp. 105.

NBN Atlas. 2022. The National Biodiversity Network. Species *Hedwigia integrifolia* Overview. https://species.nbnatlas.org/species/NBNSYS0000036725#names (consulted January, 2022).

Nyholm, E. C. 1960. Illustrated Moss Flora of Fennoscandia, II. Musci-Fasc. 4. Swedish Natural Science Research Council, C. W. K. Gleerup Publs. Stockholm, Norway. Pp. 408.

Palisot de Beauvois, A. M. F. J. 1805. Prodrome des Cinquième et Sixième Familles de l'Aethéogamie. Les Mousses. Les Lycopodes. Fournier fils, Marais. Paris, France. Pp. 114.

Pennell, F. W. 1942. Botanical collectors of the Philadelphia local area. Bartonia 21: 38-64.

Pennell, F. W. 1950. Historic botanical collections of the American Philosophical Society and the Academy of Natural Sciences of Philadelphia. Proceedings of the American Philosophical Society 94(2): 137-151. https://www.jstor.org/stable/3143214 (consulted January, 2022).

Rabenhorst, L. 1890. Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Österreich und der Schweiz. Vol. 4, part 1. E. Kummer. Leipzig, Germany. Pp. 826.

Roth, G. 1904. Die Europäischen Laubmoose. Beschrieben und gezeichnet. Erster Band, kleistokarpische und akrokarpische Moose bis zu den Bryaceen. Verlag von Wilhelm Engelmann. Leipzig, Germany. Pp. 556.

Russell, J. L. 1844. Art. XII, Musci of Eastern Massachussetts. Boston Journal of Natural History 5: 172-189.

Sargent, C. S. 1889. Portions of the journal of André Michaux, botanist, written during his travels in the United States and Canada. 1785-1796. With an introduction and explanatory notes by C. S. Sargent. Proceedings of the American Philosophical Society 26(129): 1-145. https://www.jstor.org/stable/982940 (consulted January, 2022).

Scott, G. A. M. and I. G. Stone. 1976. The Mosses of Southern Australia. Academic Press. London, UK. Pp. 495.

Smith, J. E. 1811. English Botany, Vol 32. R. Taylor and Co. London, UK. Pp. 2237.

Smith, A. J. E. 1978. The Moss Flora of Britain and Ireland. Cambridge University Press. Cambridge, UK. Pp. 706.

Sprengel, K. 1820. Neue Entdeckungen im Ganzen Umfang der Pflanzenkunde 1. Mit 3 Kupfertafeln. Friedrich Fleischer. Leipzig, Germany. Pp 452.

Steudel, E. G. 1824. Nomenclator botanicus enumerans ordine alphabetico nomina atque synonyma tum generica tum specifica, et a Linnaeo et recentioribus de re botanica scriptoribus, Plantis cryptogamis imposita, Vol. 2. Sumtibus J. G. Cottae. Stuttgardtiae et Tubingae. Stuttgart. Germany. Pp. 450. DOI: https://doi.org/10.5962/bhl.title.544

Suzuki, T. 2016. A Revised New Catalog of the Mosses of Japan. Hattoria 7: 9-223.

Thiers, B. 2022. Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium. New York, USA. http://sweetgum.nybg.org/science/ih/ (consulted January, 2022).

Torrey, J. 1819. A catalogue of plants growing spontaneously within thirty miles of the city of New-York. Websters and Skinners. Albany, USA. Pp. 100.

Uttal, L. J. 1984. The type localities of the Flora Boreali-Americana of André Michaux. Rhodora 86: 1-65.

Weakly, A. 2004. In the footsteps of André Michaux? Report from the Herbarium. The North Carolina Botanical Garden Newsletter 2: 9.

Weber, F. and D. M. H. Mohr. 1807. Botanisches Taschenbuch auf das Jahr 1807. Deutschlands kryptogamische Gewächse. Erste Abtheilung. Filices, Musci frondosi et hepatici. In der akademischen Buchhandlung. Kiel, Germany. Pp. 509.

Wijk, R. van der, W. D. Margadant and P. A. Florschütz. 1969. Index Muscorum, Vol. V (T-Z, Appendix). Regnum Vegetabile 65: I-XII, 1-922.