



Acta botánica mexicana

ISSN: 0187-7151

ISSN: 2448-7589

Instituto de Ecología A.C., Centro Regional del Bajío

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Acta botánica mexicana, no. 128, e1810, 2021

Instituto de Ecología A.C., Centro Regional del Bajío

DOI: <https://doi.org/10.21829/abm128.2021.1810>

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Seta length variation and the refutation of *Hedwigidium* = *Braunia* (Hedwigiaceae, Bryopsida)

Variación de la longitud de la seta y la refutación de *Hedwigidium* = *Braunia* (Hedwigiaceae, Bryopsida)

Efraín De Luna¹ 

Abstract:

Background and Aims: Traditionally regarded as a monotypic genus, *Hedwigidium* was recently proposed to be identical to *Braunia*, because "... some *Braunia* species have a seta as short as that of *Hedwigidium*". This paper offers data and analyses for a refutation of the taxonomic hypothesis that *Hedwigidium* = *Braunia*.

Methods: Seta length measurements (n=682) were sampled in 20 species of the four genera of Hedwigiaceae to compare variation between *Hedwigia* (n=10), *Hedwigidium* (n=40), *Braunia* (n=614), and *Pseudobraunia* (n=18). Measurements were subjected to analyses of variance and multiple comparison tests, to reveal if some *Braunia* species have a seta as short as that of *Hedwigidium*, or not.

Key results: Analyses of variance followed by Mann-Whitney pairwise tests reveal that the average seta length in *Hedwigidium imberbe* (0.7 mm, sd=0.21) is different from the average seta length in each of the seven *Braunia* species with short setae, all in the range of 2.0-2.3 mm. For the first time, the geographical distribution of *Hedwigidium* is documented and mapped. Literature records are verified for Europe (United Kingdom, Norway, France, Italy, and Spain), Africa (Cameroon, DR Congo, Malawi, Tanzania, Uganda, Zimbabwe, South Africa, Reunion Island, Kenya), and Southeast Asia (India, Sri Lanka, Indonesia). In the New World, *Hedwigidium* is confirmed for Mexico, Guatemala, El Salvador, Honduras, Costa Rica, Dominican Republic, and South America (Venezuela, Colombia, Ecuador, Peru, Bolivia, Chile, Argentina, and Brazil).

Conclusions: The data and statistical analyses presented here refute the taxonomic conclusion proposing *Hedwigidium* is synonymous with *Braunia*. None of the *Braunia* species has a seta as short as that of *Hedwigidium*. Therefore, still surviving unrefuted is the alternative hypothesis that *Hedwigidium* is a separate genus. Taxonomic characters important in distinguishing this genus from other genera in the Hedwigiaceae are discussed.

Key words: *Braunia*, *Hedwigia*, Hedwigiales, morphometrics, refutation.

Resumen:

Antecedentes y Objetivos: Tradicionalmente considerado monotípico, *Hedwigidium* fue recientemente propuesto idéntico a *Braunia*, porque "... some *Braunia* species have a seta as short as that of *Hedwigidium*". Este trabajo ofrece datos y análisis para refutar la hipótesis taxonómica *Hedwigidium* = *Braunia*.

Métodos: Se midió la longitud de la seta (n=682) en 20 especies de los cuatro géneros de Hedwigiaceae para comparar la variación entre *Hedwigia* (n=10), *Hedwigidium* (n=40), *Braunia* (n=614) y *Pseudobraunia* (n=18). Las mediciones se sometieron a análisis de varianza y comparaciones múltiples para revelar si algunas especies de *Braunia* tienen setas tan cortas como las de *Hedwigidium*, o no.

Resultados clave: Los análisis de varianza seguidos de comparaciones pareadas de Mann-Whitney revelaron que el promedio de la seta en *Hedwigidium imberbe* (0.7 mm, sd=0.21) es diferente del promedio de la longitud de la seta en cada una de las siete especies de *Braunia* con setas cortas, todas en el rango de 2.0-2.3 mm. Por primera vez, se documenta y se mapea la distribución geográfica de *Hedwigidium*. Se verifican los registros para Europa (Reino Unido, Noruega, Francia, Italia, España), África (Camerún, RD Congo, Malawi, Tanzania, Uganda, Zimbabwe, Sudáfrica, Isla Reunión, Kenia) y el Sureste de Asia (India, Sri Lanka, Indonesia). En el Nuevo Mundo, *Hedwigidium* se confirma para México, Guatemala, El Salvador, Honduras, Costa Rica, República Dominicana, y América del Sur (Venezuela, Colombia, Ecuador, Perú, Bolivia, Chile, Argentina, Brasil).

Conclusiones: Los datos y análisis estadísticos presentados aquí refutan la conclusión taxonómica que *Hedwigidium* es idéntico a *Braunia*. Ninguna de las especies de *Braunia* tienen setas tan cortas como las de *Hedwigidium*. Por lo tanto, aun sobrevive sin refutar la hipótesis alternativa de que *Hedwigidium* es un género separado. Se discuten caracteres taxonómicos adicionales importantes en la distinción de este género de otros géneros en las Hedwigiaceae.

Palabras clave: *Braunia*, *Hedwigia*, Hedwigiales, morfometría, refutación.

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Received: October 29, 2020.

Reviewed: January 5, 2021.

Accepted by Marie-Stéphanie Samain: January 22, 2021.

Published Online first: February 8, 2021.

Published: Acta Botanica Mexicana 128 (2021).



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To cite as: 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>

e-ISSN: 2448-7589

Introduction

In the moss family Hedwigiaceae, there is only one species with a combination of immersed capsules, green leaf tips, low leaf cell papillae, and broad undulate perichaetial leaves (Fig. 1). This unique blend of features has been conventionally regarded to justify the generic rank for this taxon as *Hedwigidium* Bruch & Schimp. As exposed by Allen (2010), the correct identity and nomenclature for the only species in the genus must be *Hedwigidium imberbe* (Sm.) Bruch & Schimp. Allen (2010) examined morphological differences and pointed out that the northeastern North American *Hedwigia integrifolia* P. Beauv. is not a synonym of *Hedwigidium imberbe*, originally described from Ireland. Therefore, Allen (2010) aptly discovered that the well-known name *Hedwigidium integrifolium* (P. Beauv.) Dixon was widely misapplied in the literature and herbarium specimens. Later, Dalton et al. (2012) also acknowledged that *Hedwigia integrifolia* differs from *Hedwigidium imberbe* in several important characters, supporting their taxonomic

separation from *Hedwigia* P. Beauv. They examined the type for *Hedwigia integrifolia* and corroborated that it belongs in *Hedwigia*. The type specimen has leaves with a hyaline acumen, the leaf cells have branched papillae, and the perichaetial leaves are ciliate, as in *Hedwigia ciliata* (Hedw.) P. Beauv. In this case, Dalton et al. (2012) resolved prudently: “further study is needed to determine the exact status of this taxon, so it is provisionally left as a species of *Hedwigia*”. Notably, Dalton et al. (2012) recognized *Hedwigia* and *Hedwigidium* as different genera, despite both taxa having identical seta lengths (<1 mm) and similar capsule shapes (globose, urceolate).

In contrast, in the same paper, Dalton et al. (2012) moved *Hedwigidium imberbe* (Fig. 1) to *Braunia* Bruch & Schimp. The genus *Braunia* is characterized by thick-walled, sinuose leaf cells with pluri-papillose longitudinal walls, exerted capsules, usually cylindrical urns, and a cucullate calyptra (Bruch and Schimper, 1846; Brothorus, 1909; Biasuso, 1992; De Luna, 1992, 2016). Dalton et al. (2012)

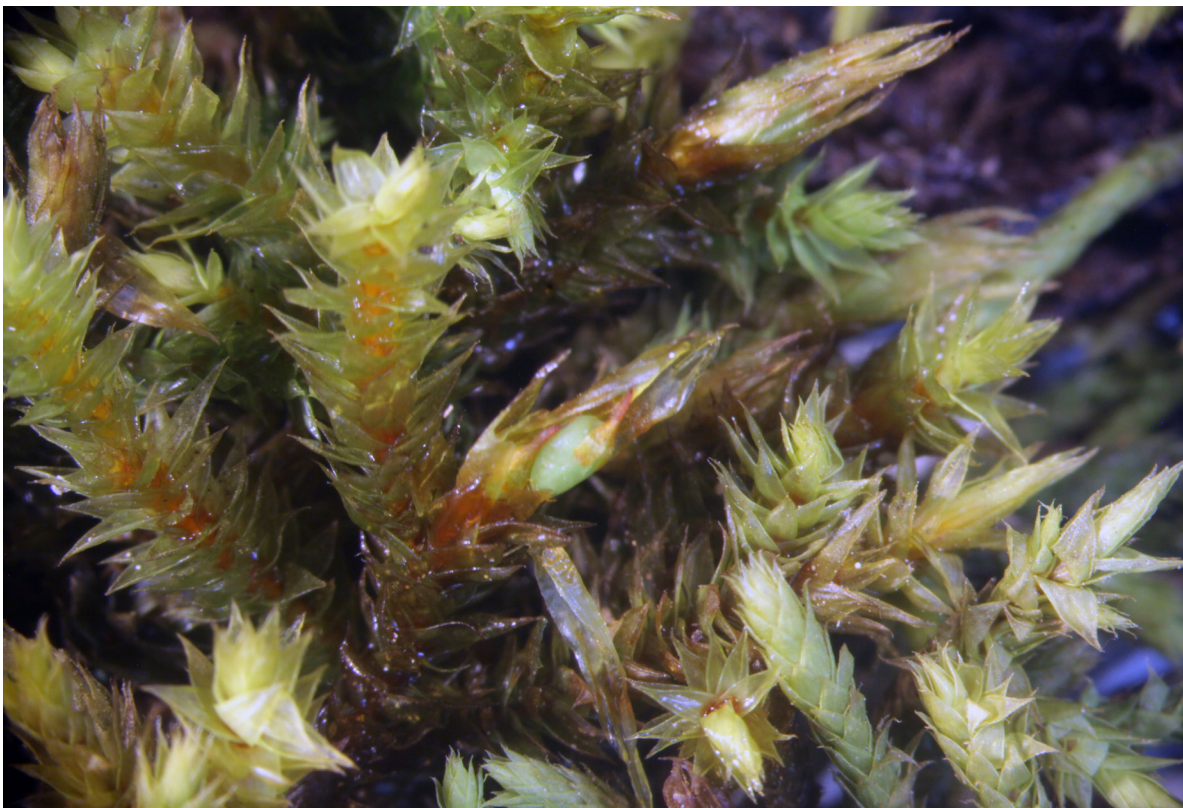


Figure 1: *Hedwigidium imberbe* (Sm.) Bruch and Schimp. A plant showing several branches with sporophytes covered by long perichaetial leaves. One cluster of perichaetial leaves has been dissected to show the immersed urn with the operculum covered by the small calyptra still in place (from specimen De Luna 2717 (XAL), growing on rock; near Villareal, Tlaxcala, Mexico).

made the new combination *Braunia imberbis* (Sm.) N. Dalton & D.G. Long, consequently synonymizing *Hedwigidium* with *Braunia*. As justification for this hypothesis, Dalton et al. (2012) asserted "... some *Braunia* species have a seta as short as that of *Hedwigidium* – in *B. reflexifolia* (Müll. Hal.) E.B. Bartram seta length is 2 mm or less". They argued: "Seta length cannot therefore be used as a clear-cut generic character". Dalton et al. (2012) concluded: "For these reasons, the new combination *Braunia imberbis* is made below, and thus *Hedwigidium* is synonymized with *Braunia*". However, their taxonomic inference was based on untested premises about seta length variation.

The assertion by Dalton et al. (2012) "... some *Braunia* species have a seta as short as that of *Hedwigidium*" is a type of empirical statement that can be scrutinized in the context of the current standards of the science of biological systematics. Anyone applying the relevant technique can test empirical statements (Popper, 1992: 99) under refutationist and verificationist philosophies (Wiley, 1975; De Luna, 1995a; Kluge, 1997). The taxonomic hypothesis of *Hedwigidium* being identical to *Braunia* was presented without evidence and without any formal analysis (statistical, phenetic or phylogenetic) of actual measurement data. Therefore, this paper is intended as a simple exercise in Popperian refutation of the two competing hypotheses: *Hedwigidium* = *Braunia* and the alternative *Hedwigidium* ≠ *Braunia*. The goal of this research was to provide measurement data and statistical analyses required to appropriately test the taxonomic utility of seta length in the Hedwigiaceae. Seta length measurements were sampled to test the Dalton et al. (2012) assertion that some *Braunia* species have a seta as short as that of *Hedwigidium*. Measurements of seta length in numerous specimens worldwide were subjected to analysis of variance to compare variation in *Hedwigidium imberbe* with 17 species of *Braunia*, *Pseudobraunia californica* (Lesq.) Broth. and *Hedwigia ciliata*. This study appropriately tests the taxonomic utility of seta length in the Hedwigiaceae and refutes the hypothesis that *Hedwigidium* is identical to *Braunia*. Therefore, the alternative hypothesis which traditionally considers *Hedwigidium* as a monotypic genus cannot be rejected for now.

Material and Methods

Specimens

The specimens studied of *Hedwigia*, *Hedwigidium*, *Braunia* and *Pseudobraunia* (Lesq. & James) Broth. (Hedwigiaceae) belong to several herbaria (AAU, B, BM, BR, DUKE, F, JE, MEXU, MICH, MO, NSW, NY, QCA, S, US, and XAL). A list of the 20 species of Hedwigiaceae sampled and the number of specimens for each species examined are provided in Table 1.

Distribution map

The geographic distribution of *Hedwigidium* was reviewed and verified with herbarium specimens from each country previously recorded in the literature (except Europe where the genus is already well-documented). The list of representative specimens for this review of the distribution of *Hedwigidium* is presented below in the section "Specimens examined".

Digital images and seta length data

Prepared semi-permanent slides were used for photographs with a digital camera (D-SLR Canon 60D) attached to the C tube of a stereoscopic microscope (Zeiss, Stemi SV11, Jena, Germany). Digital images of complete sporophytes were obtained from specimens of the four genera in the Hedwigiaceae (Table 1). Images were used to record quantitative data for statistical analyses of seta length variation. Measurements of seta length were obtained with software ImageJ v. 1.53a (Schneider et al., 2012) and scaled in millimeters.

Morphometric analyses

This paper reports measurement data and an application of analyses of variance, a standard and well-known test procedure that uses sample measurements to decide between competing hypotheses for the equality of sample means (Zar, 1996). Statistical analyses of seta length variation were implemented with PAST v. 3.20 (Hammer et al., 2001) for MacOS (v. 10.13.6). Analyses of variance were designed at two grouping levels (PAST menu "Univariate>ANOVA etc. (several samples) >several sample tests"). First, all observations (n=682) were classified

Table 1: List of twenty species studied and summary statistics for seta length variation in *Hedwigidium* Bruch & Schimp., *Braunia* Bruch & Schimp., *Pseudobraunia* (Lesq. & James) Broth., and *Hedwigia* P. Beauv. (Hedwigiaceae). Species names are followed by the number of specimens sampled (n), sample mean, and standard deviation (sd) values of seta length, and the observed range of measurements (min, max). The eight species marked with an asterisk are the species included in the second analysis of variance and multiple comparison tests, as explained in the Material and Methods section and illustrated in Figure 2.

	Species	n	mean	sd	min	max
1	<i>Hedwigidium imberbe</i> (Sm.) Bruch and Schimp.*	40	0.7	0.21	0.2	1
2	<i>B. reflexifolia</i> (Müll. Hal.) E.B. Bartram *	29	2.0	0.31	1.3	2.6
3	<i>B. exserta</i> Müll. Hal. *	61	2.1	0.44	1.5	4
4	<i>B. tucumanensis</i> Biasuso *	28	2.3	0.32	1.5	3.1
5	<i>B. squarrulosa</i> (Hampe) Müll. Hal. *	32	4.1	1.34	3	10
6	<i>B. subincana</i> Broth. *	46	6.8	1.62	3	10
7	<i>B. incana</i> Müll. Hal.	2	6.5	0.70	6	7
8	<i>B. alopecura</i> (Brid.) Limpr. *	23	7.4	2.27	4	12
9	<i>B. subplicata</i> E. Britton *	19	7.8	2.54	4	11
10	<i>B. nephelogenes</i> De Luna & W.R. Buck	24	8.4	2.16	5	13
11	<i>B. cirrhifolia</i> (Mitt.) A. Jaeger	58	8.5	2.61	4	14
12	<i>B. rupestris</i> (Mitt.) A. Jaeger	22	8.8	1.59	5	11
13	<i>B. argentinica</i> Müll. Hal.	20	9.3	1.17	7	12
14	<i>B. canescens</i> Schimp. ex E. Britton	22	9.8	1.69	7	12
15	<i>B. andrieuxii</i> Lorentz	69	10.1	2.12	6	15
16	<i>B. plicata</i> (Mitt.) A. Jaeger	64	10.1	2.89	5	21
17	<i>B. attenuata</i> (Mitt.) A. Jaeger	24	11.0	2.71	7	16
18	<i>B. secunda</i> (Hook.) Bruch & Schimp.	71	12.0	3.36	7	22
	<i>Braunia</i> (17 spp.)	614	7.8	3.94	1.3	22
19	<i>Pseudobraunia californica</i> (Lesquereux) Brotherus	18	6.8	2.33	4	12
20	<i>Hedwigia ciliata</i> (Hedw.) P. Beauv.	10	0.5	0.29	0.2	1

into four *a priori* groups to compare variation among *Hedwigia* (n=10), *Hedwigidium* (n=40), *Braunia* (n=614), and *Pseudobraunia* (n=18). Second, a subsample of only seven *Braunia* species with seta length average values lower than 8 mm were included to compare with *Hedwigidium*, so that the number of multiple comparisons remained within reasonable limits. In this case, measurements of seta length (n=278) were classified by species into eight *a priori* groups for analysis of variance and pairwise post-hoc comparison tests. In this analysis, the Mann-Whitney pairwise test available in PAST software was employed with the Bonferroni corrected *p* values. Besides *Hedwigidium imberbe* (n=40), the seven *Braunia* species included were: *Braunia exserta* Müll. Hal. (n=61), *B. tucumanensis* Biasuso

(n=28), *B. reflexifolia* (n=29), *B. squarrulosa* (Hampe) Müll. Hal. (n=32), *B. alopecura* (Brid.) Limpr. (n=23), *B. subplicata* E. Britton (n=19), and *B. subincana* Broth. (n=46). The geographical amplitude of this subsample of seven species of *Braunia* with short setae covers South America, Mexico, Central America, and Europe. All other species of *Braunia* present in Africa and India have seta length averages well above 8 mm (Table 1).

Data availability

The datasets generated and analyzed during the current study are available from the author on request. A user and password will be sent to access files in the following URL: http://www.filogenetica.org/data_files/index.php?

Results

Summary statistics of seta length variation in the Hedwigiaceae are presented in Table 1. The first analysis of variance comparing four genera revealed that seta length is very variable in the 17 species of *Braunia* sampled (Table 1). Unquestionably the sample mean in *Braunia* (7.8 mm, $sd=3.9$) differs from the value recorded for *Hedwigidium* (0.7 mm, $sd=0.21$). However, as expected, the average seta length in *Hedwigidium* is not different from the sample mean in *Hedwigia* (0.5 mm, $sd=0.29$).

The second analysis of variance shows there is no overlap in measurements between *Hedwigidium* and the subsample of seven species of *Braunia* with short seta lengths (Fig. 2). The average seta length in *B. exserta*, *B. tucumanensis*, and *B. reflexifolia* is in the range of 2.0-2.3 mm. These values might seem very close to the values in *Hedwigidium*, but the Mann-Whitney pairwise test

assessed the difference, and it is significant between sample means. This *a posteriori* test reveals that measurements of the seta in *Hedwigidium* are different from the seven *Braunia* species in all pairwise comparisons. The average seta length in *B. squarrulosa* is 4.1 mm ($sd=1.34$), in *B. subincana* it is 6.8 mm ($sd=1.62$), in *B. alopecura* it is 7.4 mm ($sd=2.27$) and in *B. subplicata* it is 7.8 mm ($sd=2.54$). All other species of *Braunia* not included in the second analysis have seta lengths longer than 8 mm (Table 1).

Discussion

This numerical exercise corroborates the intuitively perceived differences in seta length between *Hedwigidium* and *Braunia*. The two analyses of variance presented here reject the hypothesis of equal sample means. None of the *Braunia* species has a seta as short as that of *Hedwigidium*, as Dalton et al. (2012) asserted. Their declaration: "some

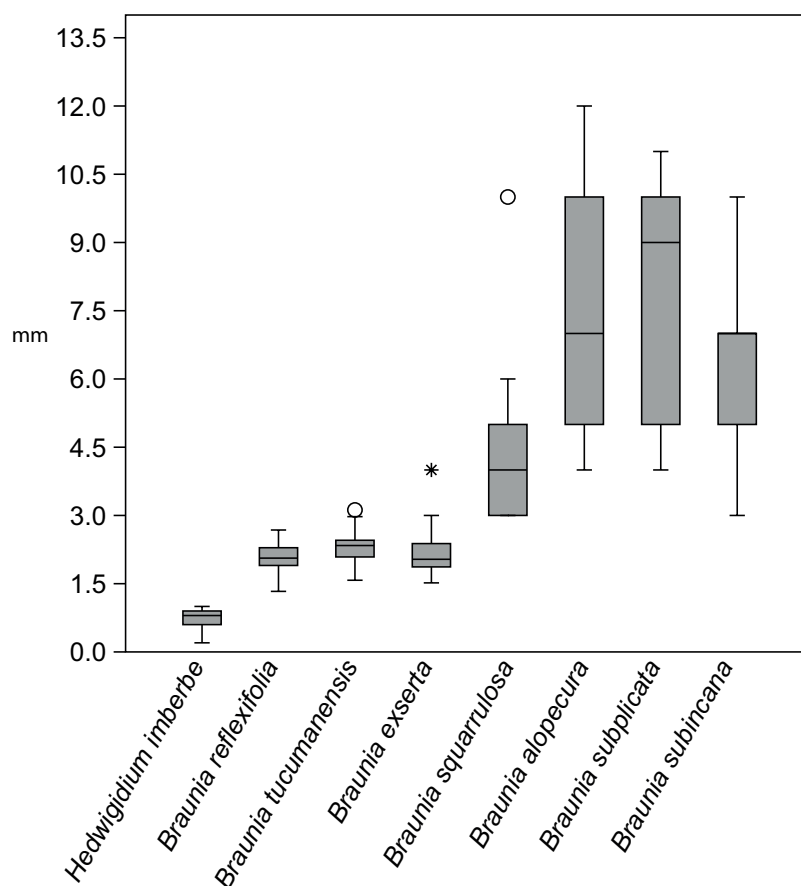


Figure 2: Variation in seta length in *Hedwigidium* Bruch & Schimp. and *Braunia* Bruch & Schimp. Comparing distributions of measurements from 278 specimens sampled for *Hedwigidium imberbe* (Sm.) Bruch and Schimp. and seven species of *Braunia* Bruch & Schimp. with short setae. Box and whisker plots for each species illustrate estimated median value, quartiles, and the range of seta length measurements. Outliers are identified with symbols.

Braunia species have a seta as short as that of *Hedwigidium* – in *B. reflexifolia* (Mull. Hall) E.B. Bartram seta length is 2 mm or less” does not hold as true when the assessment is based on actual data and on formal statistical analyses. The data and results of analyses presented here refute the taxonomic conclusion by Dalton et al. (2012) on the synonymy of *Hedwigidium* with *Braunia*.

This quantitative example illustrates a simple exercise in Popperian refutation to test a very specific hypothesis on the nature of seta length variation. If as a result of the test, the hypothesis of *Hedwigidium* as a separate genus survives, this does not imply the use seta length variation as a classical ‘key character’, indicating generic differences. Neither this analysis advocates a proposal of a new taxonomic group nor a change in phylogenetic structure within the family. It must be clear that the central result is the refutation of the hypothesis *Hedwigidium* = *Braunia* and the failure to refute the hypothesis *Hedwigidium* ≠ *Braunia*. The surviving hypothesis of *Hedwigidium* as a different genus from *Braunia*, as originally proposed by Bruch and Schimper (1846), cannot be rejected on the basis of current data. *Hedwigidium* can still be used as an alternative to the taxonomic change proposed by Dalton et al. (2012).

Notwithstanding, the taxonomic hypothesis *Hedwigidium* = *Braunia* (Dalton et al., 2012) has been accepted by some. Buchbender et al. (2014) and Ignatova et al. (2016) used this generic taxonomy by labelling three terminals as *B. imberbis* in their phylogenetic analyses of several species of *Hedwigia*. However, Fife (2014), De Luna (2016) and Wigginton et al. (2020) did not accept such taxonomic hypothesis and the nomenclatural implications. Synapomorphic characters justifying *Hedwigidium* had already been uncovered in a preliminary phylogenetic morphological analysis of the Hedwigiaceae by De Luna (1995b), namely, broad perichaetial leaves with undulate margins, a short seta, ribbed capsules, a conical operculum, and a small calyptra with a subtubulose base. Therefore, De Luna (2016) excluded *B. imberbis* from his key and list of 23 species of *Braunia* worldwide, highlighting the need for combined morphological and molecular phylogenetic analyses for the grouping and generic classification in the Hedwigiaceae.

In the context of available phylogenetic information, variation in seta length is congruent with other morphological and molecular data in the Hedwigiaceae. In separate morphological and molecular phylogenetic analyses, one clade includes *Hedwigia* and *Pseudobraunia* as sister taxa (De Luna, 1995b; Cox et al., 2010), and this clade is sister to another clade that includes *Braunia* and *Hedwigidium* (De Luna, 1995b; Cox et al., 2010). The same basic topology ((*Braunia*, *Hedwigidium*) (*Pseudobraunia*, *Hedwigia*)) was suggested in recent phylogenetic analyses of molecular sequence data (Ignatova et al., 2016: fig. 1; Liu et al., 2019: fig. 1). Variation in seta length is congruent with this molecular sequence phylogenies. The seta is uniformly very long in the Rhacocarpaceae (Frahm, 1996), the sister group of the Hedwigiaceae (Cox et al., 2010). Sporophytes with long setae and exserted capsules are also present in *Braunia* and *Pseudobraunia*, whereas sporophytes with very short setae and immersed capsules are known in *Hedwigia* and *Hedwigidium*. Therefore, character optimization over the backbone tree topology within the Hedwigiaceae suggests two independent changes from long to very short seta in *Pseudobraunia* to *Hedwigia* and *Braunia* to *Hedwigidium*.

Obviously, seta length as a single morphological character can hardly be used as an argument for a certain taxonomic ranking. As Allen (2010) had already discussed, “if setae length is disregarded one might consider merging all four genera”. Merging two pairs of genera would also be an option for a ranking compatible with the backbone phylogeny, in which *Hedwigia* includes *Pseudobraunia*, and *Hedwigidium* is merged with *Braunia*. Still one more ranking option consists of just merging one sister pair, *Pseudobraunia* with *Hedwigia*, and leaving the other two genera separate. However, we still do not know how many species there are in *Hedwigidium* and if all species in *Braunia* belong to a monophyletic or a paraphyletic group. A combined morphological and molecular phylogenetic analysis of the relationships of species and genera within the Hedwigiaceae is still missing. Meanwhile, I prefer a ranking system of four genera.

In summary, it was premature to consider *Hedwigidium* as synonym of *Braunia* given the paucity of data and lack of detailed taxonomic and phylogenetic analyses. The proposition that Dalton et al. (2012)

presented for the generic classification and for the name of this species, as *Braunia imberbis*, was unsupported and flawed. Their taxonomic inferences were undermined, because they did not report data and formal analysis of seta length to test the generic status of this species in *Hedwigidium* or as a species in *Braunia*. When assessing *Hedwigidium* and *Braunia*, they disregarded differences in seta length. The data and analyses presented here overturn the proposed synonymy of *Hedwigidium* and *Braunia* in favor of conserving the original hypothesis of *Hedwigidium* as a separate genus.

Generic taxonomic characters

There are a number of morphological features that distinguish *Hedwigidium* from the other three genera in Hedwigiaceae. Originally, Bruch and Schimper (1846)

distinguished *Hedwigidium* by the less-branched stems, the frequent stoloniform branches, the plicate leaves, the conical operculum, and the cucullate calyptra, as compared to other genera in the Hedwigiaceae. The detailed description by Müller (1851, as *Neckera imberbis* (Sm.) Müll. Hal.), provided additional important character states which circumscribed this taxon: “densifolia ferruginea, apicibus viridibus obtusis; folia caulina ... anguste ovato-acuminata, margine lato revoluta, ... perich. longius vaginanti-lanceolato-acuminata, plicata inferne anguste elongate, basi laxe, apice incrassate quadrata reticulata; ... operc. brevi conico oblique, calyptra parva cucullata, saepius fissa”. These morphological features were illustrated in the early literature of the genus (Figs. 3A-K).

Among the important characters that distinguish *Hedwigidium* from the other three genera in the family

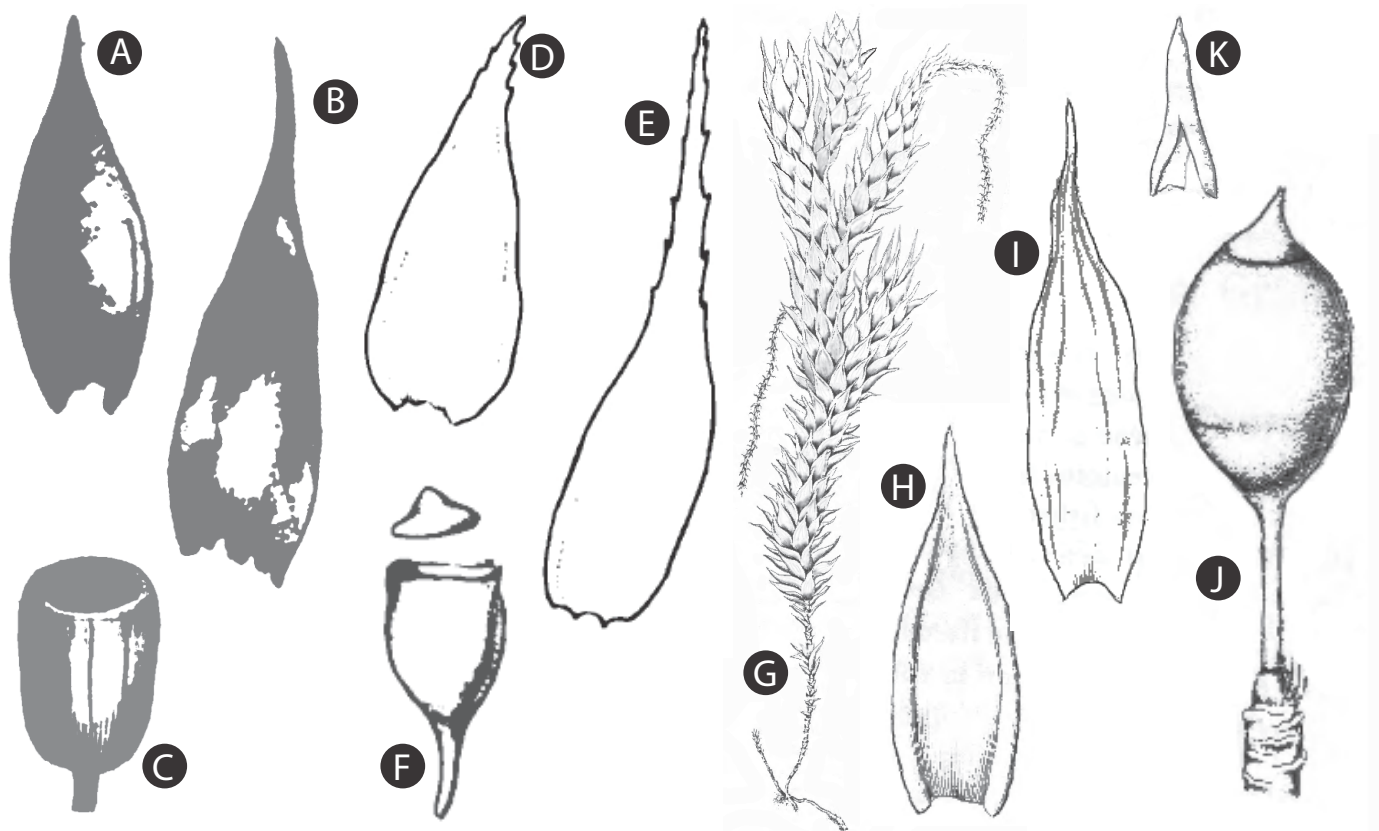


Figure 3: Historical illustrations of the morphological characters in the diagnoses of genus *Hedwigidium* Bruch & Schimp. A-C. leaf, perichaetial leaf, and capsule (redrawn from Smith (1811), as *Gymnostomum imberbe* Sm.); D-F. leaf, perichaetial leaf, capsule, and operculum (redrawn from Hooker and Taylor (1827), as *Anictangium imberbe* (Sm.) Hook. and Taylor); G-K. stem, leaf, perichaetial leaf, capsule, operculum, and calyptra (redrawn from Bruch and Schimper (1846), as *Hedwigidium imberbe* (Sm.) Bruch and Schimp.).

are the very broad perichaetial leaves with undulate margins. The size of the perichaetial leaves is variable from twice or more the length of the vegetative leaves (Figs. 4C-D, H). There are some species in *Braunia* with large perichaetial leaves, but these are narrowly lanceolate and never undulate at the margins. Besides the broad perichaetial leaves, other features are found in the immersed sporophytes. Synapomorphic characters justifying *Hedwigidium* are a short seta, ribbed capsules, a

conical operculum, and a small calyptra with a subtubulose base (De Luna, 1995b). The very short seta, (0.5-)0.7-0.9(-1.1) mm, distinguishes *Hedwigidium* from *Pseudobraunia* and all species of *Braunia*. There are some species in *Braunia* with short setae, such as *B. exserta* (2-3 mm), *B. reflexifolia*, (2-3 mm), and *B. tucumanensis* (2.-3.5 mm); however, the capsules in these *Braunia* species are always fully exserted and the operculum is conic-rostrate (Biasuso, 1992). Moreover, the urn in *Hedwigidium* is broadly urceo-

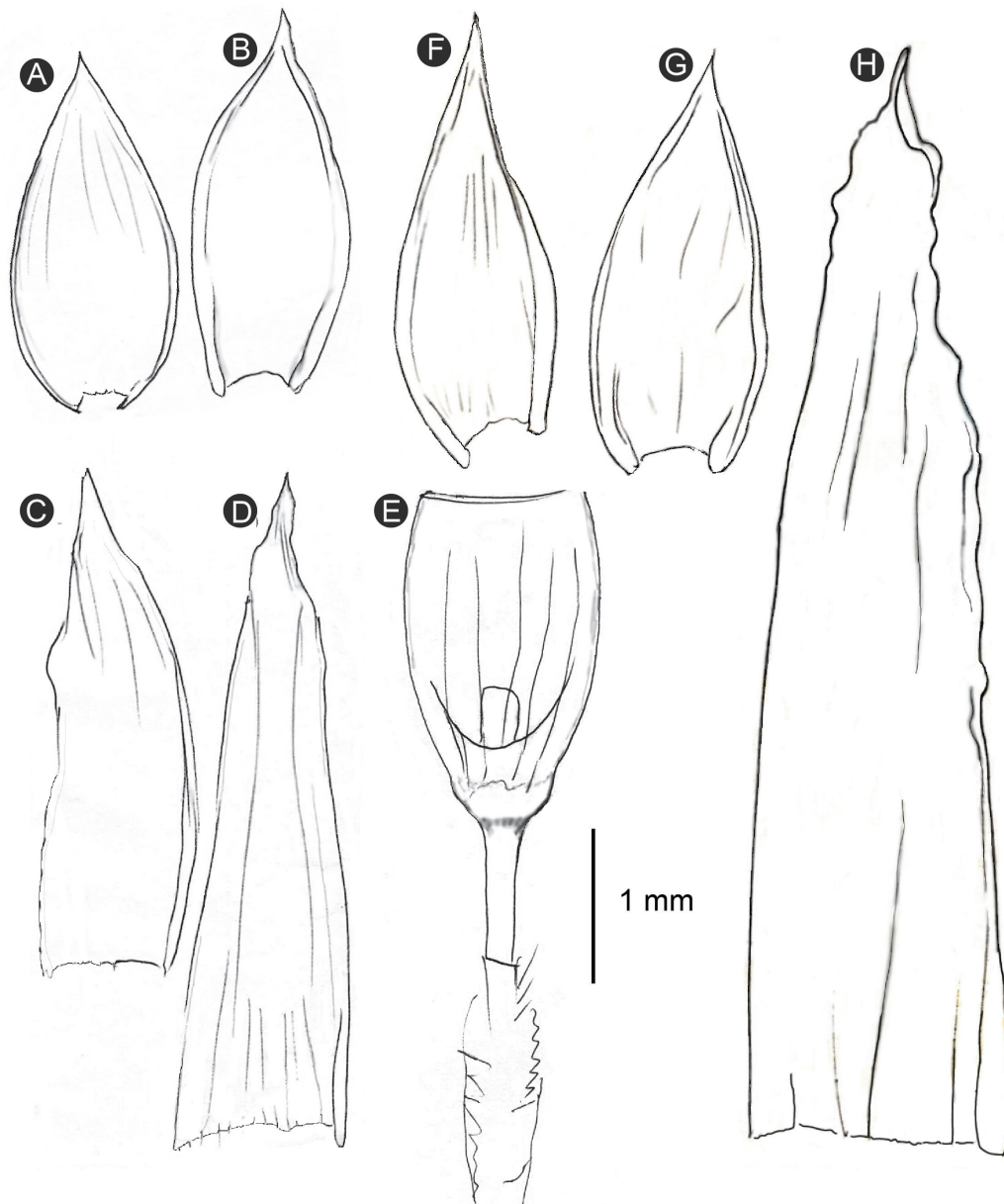


Figure 4: Morphological features of *Hedwigidium* Bruch & Schimp. A-B. leaves; C-D. perichaetial leaves; E. sporophyte (A-E, from *Sharp 5449* (DUKE), Guatemala); F-G. leaves; H. perichaetial leaf (F-H, from *Adams s.n.* (BM), Cameroon).

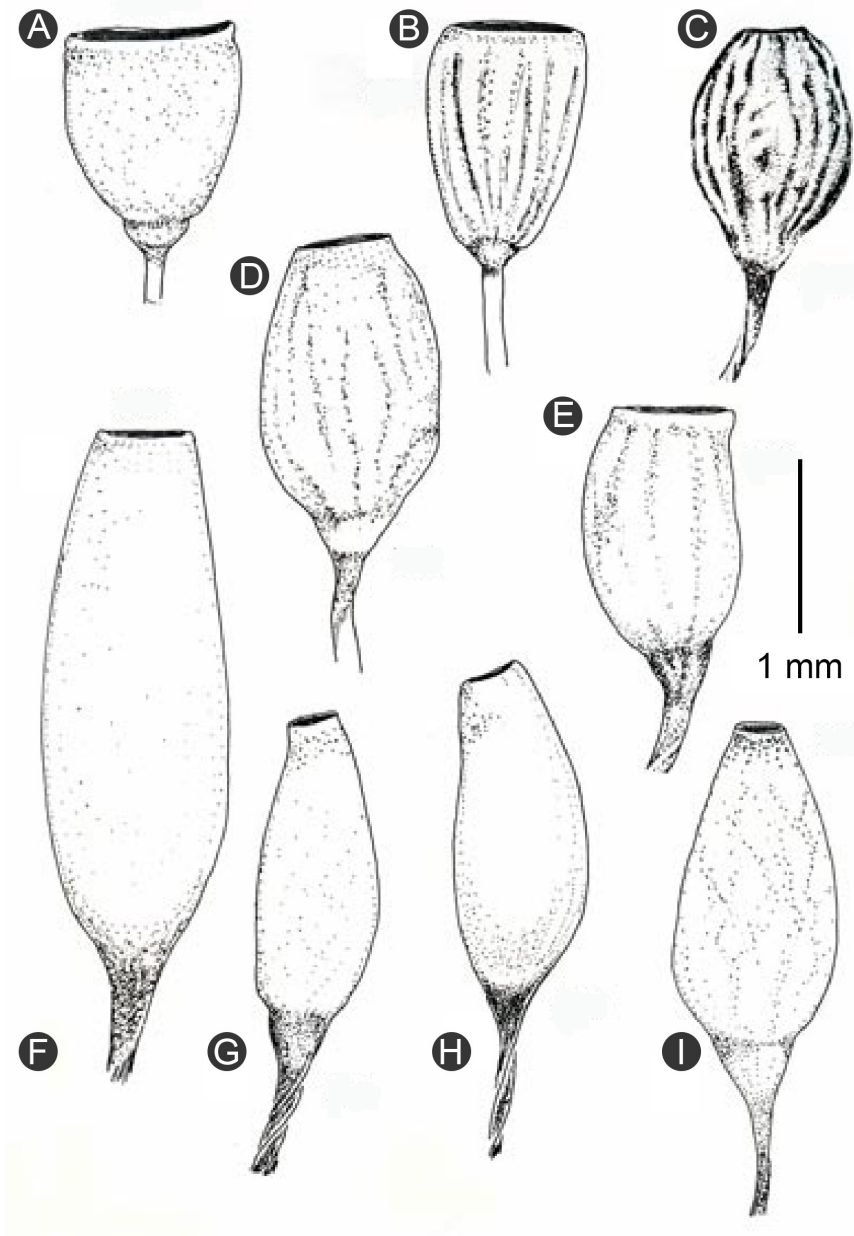


Figure 5: Capsule shape in *Hedwigidium* Bruch & Schimp. compared with variation in other genera of the Hedwigiaceae. A. *Hedwigia ciliata* (Hedw.) P. Beauv.; B. *Hedwigidium imberbe* (Sm.) Bruch and Schimp.; C. *Braunia nephelogenes* De Luna & W.R. Buck; D. *Braunia subincana* Broth.; E. *Braunia exserta* Müll. Hal.; F. *Braunia schimperi* Bruch & Schimp.; G. *Braunia plicata* (Mitt.) A. Jaeger; H. *Braunia alopecura* (Brid.) Limpr.; I. *Braunia secunda* (Hook.) Bruch & Schimp.

late or cyathiform and deeply furrowed or ribbed (Fig. 5B). In some species of *Braunia* the urn is broad, and sulcate, such as in *B. nephelogenes* DeLuna & W.R. Buck and in *B. subincana* (Figs. 5C-D). However, most species in *Braunia* have sporophytes with a cylindrical or ellipsoidal urn with a narrow capsule mouth (Figs. 5E-I). The low conical, shortly rostrate operculum, and a small cucullate calyptra, with

a subtubulose base also distinguish *Hedwigidium* (Figs. 6D-G). The calyptra in all species of *Braunia* is large and cucullate (Figs. 6H-K), and the operculum in all species of *Braunia* is conical with a high rostrum (Figs. 6L-O).

Hedwigidium is further distinguished from *Hedwigia* and *Pseudobraunia* in the flagelliform-stoloniferous branches emerging from the stems. Moreover, the papillose

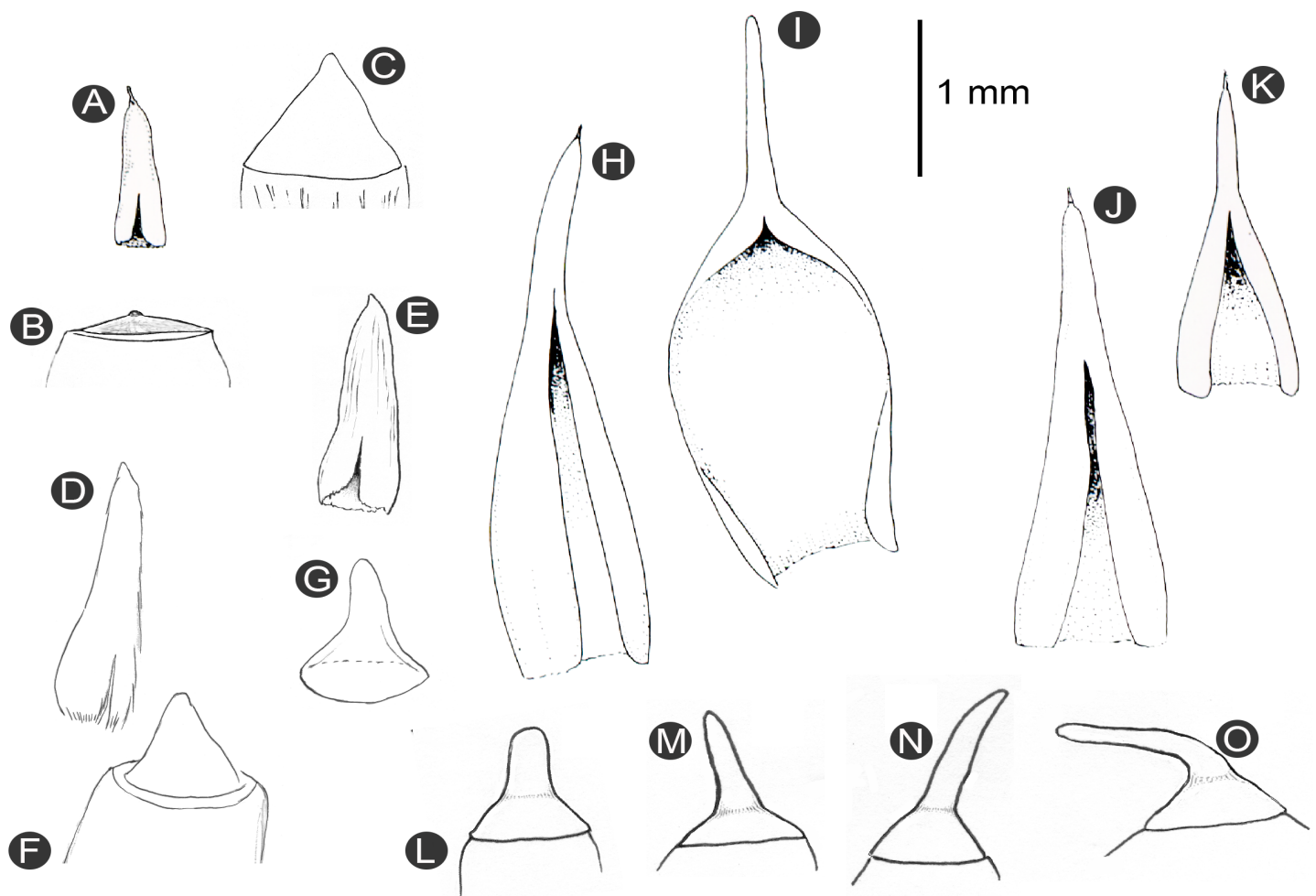


Figure 6: Calyptrae and operculum in *Hedwigidium* Bruch & Schimp. compared with variation in other genera of the Hedwigiaceae. A-B. *Hedwigia cilata* (Hedw.) P. Beauv.; C. *Pseudobraunia californica* (Lesquereux) Brotherus.; D-G. *Hedwigidium imberbe* (Sm.) Bruch and Schimp.; H. *Braunia argentinica* Müll. Hal. I. *Braunia rupestris* (Mitt.) A. Jaeger; J. *Braunia exserta* Müll. Hal.; K. *Braunia cirrhifolia* (Mitt.) A. Jaeger; L. *Braunia alopecura* (Brid.) Limpr.; M. *Braunia schimperii* Bruch & Schimp.; N. *Braunia secunda* (Hook.) Bruch & Schimp.; O. *Braunia squarrulosa* (Hampe) Müll. Hal.

pseudoparaphyllia in *Hedwigidium* are broad and short, similar to those in *Braunia*, while the pseudoparaphyllia are filamentous in *Pseudobraunia* and *Hedwigia*. The leaves in *Hedwigidium* are ovate-lanceolate, plicate, with strongly recurved margins, and have concolorous short-acuminate apices; whereas in *Hedwigia* and *Pseudobraunia* the leaves are narrowly lanceolate and have hyaline apices (Figs. 7A-P). The upper leaf cell papillae in *Hedwigidium* are low, unbranched, and scattered over the cell lumina, rather than tall and centered over the cell lumina as in *Pseudobraunia*, or tall and branched as in *Hedwigia*. The upper leaf cells in *Hedwigidium* and some species in *Braunia* are similarly rectangular, sinuose, and pluripapillose. There are very nice SEM pictures in the paper by Dalton et al. (2012, Figs.

1A, C), showing the similar leaf cell papillae in *Hedwigidium imberbe* and *Braunia attenuata* (Mitt.) A. Jaeger. Previously, Sharp et al. (1978) had shown also the similar leaf cell papilla in *B. secunda* (Hook.) Bruch & Schimp., *B. squarrulosa* and *Hedwigidium imberbe*.

In the absence of sporophytes, *Hedwigidium* is indeed hard to distinguish from some species of *Braunia*, but this happens only in some regions. In Mexico, *Hedwigidium* is difficult to distinguish from *Braunia secunda* because of the similar ovate-lanceolate leaves, with recurved leaf margins and concolorous leaf apices. In South America the same similarities in the lanceolate leaves mask the identity of *B. subplicata* and *Hedwigidium*. Likewise, in Africa it is difficult to separate *Hedwigidium* from *B. entodonticarpa*

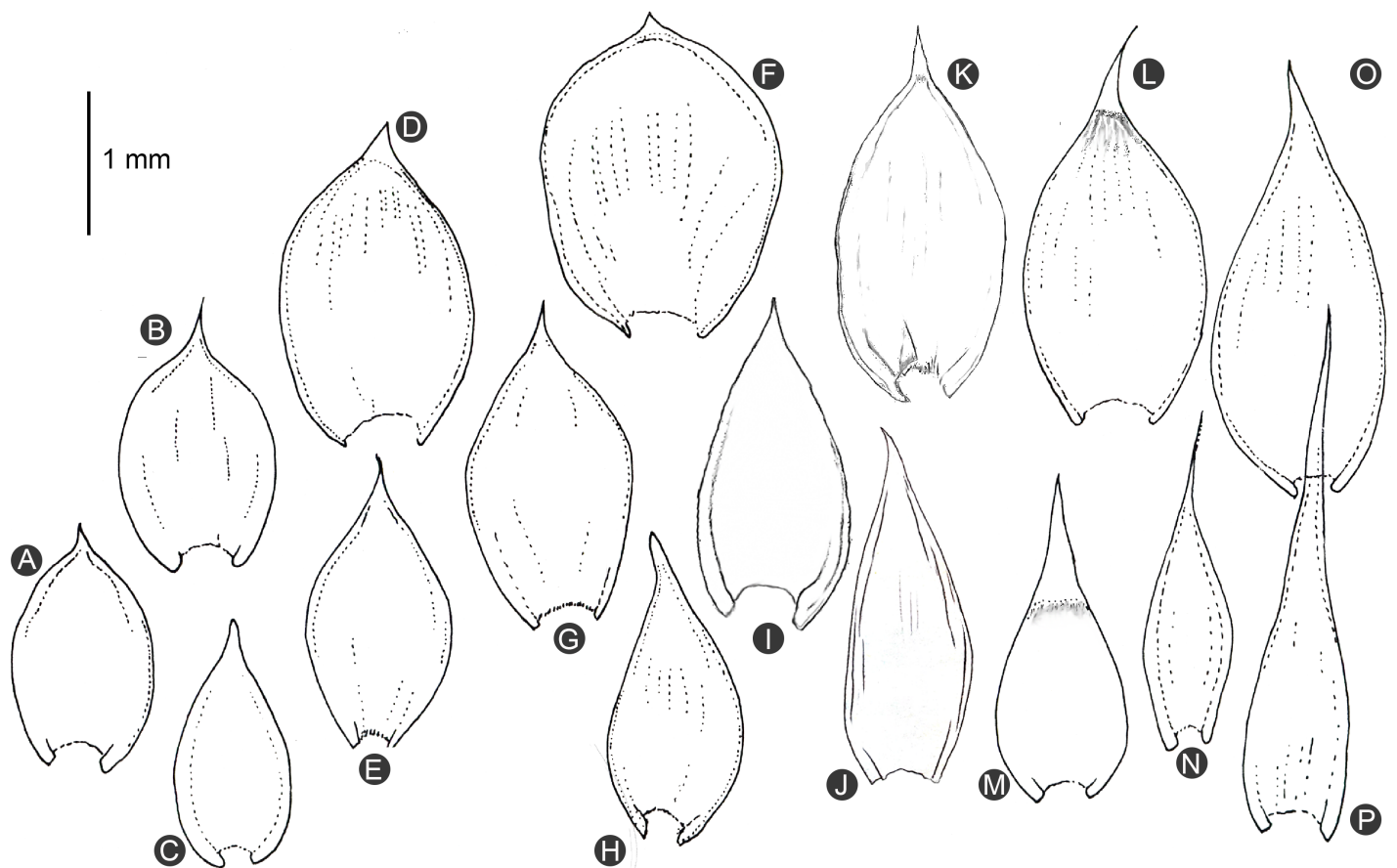


Figure 7: Leaf shape in *Hedwigidium* Bruch & Schimp. compared with variation in other genera of the Hedwigiaceae. A. *Braunia diaphana* (Müll. Hal.) A. Jaeger; B. *B. subincana* Broth.; C. *Braunia alopecura* (Brid.) Limpr.; D. *Braunia camptoclada* P. de la Varde & Thér.; E. *Braunia exserta* Müll. Hal.; F. *Braunia schimperi* Bruch & Schimp.; G. *Braunia squarulosa* (Hampe) Müll. Hal.; H. *Braunia secunda* (Hook.) Bruch & Schimp.; I-J. *Hedwigidium imberbe* (Sm.) Bruch and Schimp.; K. *Braunia canescens* Schimp. ex E. Britton; L. *Braunia arbuscula* (Welw. & Duby) A. Gepp.; M. *Hedwigia ciliata* (Hedw.) P. Beauv.; N. *Braunia attenuata* (Mitt.) A. Jaeger; O. *B. cirrhifolia* (Mitt.) A. Jaeger; P. *Braunia nephelogenes* De Luna & W.R. Buck.

Müll. Hal. and *B. rupestris* (Mitt.) A. Jaeger, because of the ovate-lanceolate leaves with recurved margins in these species. The leaves in all other species of *Braunia* in Mexico, South America and Africa are different from *Hedwigidium* (Figs. 7A-P). For example, only species of *Braunia* will have hyaline leaf apices. This feature will distinguish *B. plicata* (Mitt.) A. Jaeger in Mexico. In South America the hyaline apices separate *B. canescens* Schimp. ex E. Britton (Fig. 7K) and *B. incana* Müll. Hal. Similarly, in Africa the green leaf apices differentiate *Hedwigidium* from *B. diaphana* (Müll. Hal.) A. Jaeger (Fig. 7A) and *B. arbuscula* (Welw. & Duby) A. Gepp. (Fig. 7L). In Africa there are three species of *Braunia* with concolorous leaf acumen: *B. entodontocarpa*, *B. camptoclada* P. de la Varde & Thér. (Fig. 7D), and *B. schimperi* Bruch & Schimp. (Fig. 7F). However, these spe-

cies can be distinguished from *Hedwigidium*, even without sporophytes. The leaves in these species are widely ovate, oblong, and orbiculate, with a sharply differentiated mucronate or cuspidate leaf apex. In *Hedwigidium* the leaves are ovate-lanceolate with a gradually acuminate apex (Figs. 7I-J).

Taxonomic treatment

Hedwigidium Bruch & Schimp., Bryol. Eur. 3: 155. 1846.

TYPE: *Hedwigidium imberbe* (Sm.) Bruch & Schimp.

Hedwigia sect. *Hedwigidium* (Bruch & Schimp.) Mitt. J. Proc. Linn. Soc., Bot. 7: 160. 1863.

Harrisonia subg. *Hedwigidium* (Bruch & Schimp.) Hampe. Verh. Zool.-Bot. Ges. Wien 21: 386. 1871.

Hedwigia subg. *Hedwigidium* (Bruch & Schimp.) Lindb. Musci Scand. 40. 1879.

Braunia sect. *Hedwigidium* (Bruch & Schimp.) Müll. Hal. Linnaea 42: 378. 1879.

Plants medium or robust (2-3 cm), in loose or dense tufts or mats, dark green or red-brown; stems sympodially branched, plagiotropic, tips ascending; branches short, terete and blunt, some stoloniform; pseudoparaphyllia foliose, base much wider than long, lobed-dentate, cells papillose; leaves imbricate, spreading, concave, weakly plicate, short-ovate, ovate-lanceolate to narrowly lanceolate, apiculate, or gradually acuminate, ecostate; leaf apex concolorous, entire, erose, crenulate or serrulate; leaf margins revolute or narrowly recurved up to the base of the acumen; leaf cells thick-walled, sinuose, medial and upper cells with 3-4 low, rounded, unbranched papillae, marginal, bending over lumen; apical cells short- to long-elliptical; upper cells long-rectangular to subquadrate or oblate; basal median cells long-rectangular, yellow; basal marginal cells shortly rectangular, quadrate, or oblate, smooth, dark reddish brown; autoicous; perigonia terminal on short sympodia, alternating with sympodia terminated with perichaetia; perichaetial leaves erect, elongate, overtopping the capsules, margins entire, undulate; paraphyses short, or as long as the perichaetial leaves; setae short, neck very short ampullaceous, capsules immersed, erect, symmetric, broadly urceolate, subglobose, to cyathiform, furrowed when wet or dry, red brown, macrostomus, exothecial cells subquadrate, isodiametric to oblong, stomata few, superficial, only at neck, operculum base conic, umbonate, rounded or small rostellate; calyptra cucullate, small, or conic-mitrate, 1.5 mm long, 2-4-lobed, covering only the operculum; spores 20(24-27)-33 µm, vermiculate-papillose.

The number of species in *Hedwigidium* is unknown. Since Bruch and Schimper (1846) established *Hedwigidium*, a few more species were classified in the genus. Jaeger (1876), besides *H. imberbe*, listed *H. emersum* (Müll. Hal. & Hampe) A. Jaeger from New Zealand, and *H. drummondii* (Taylor) A. Jaeger from western Australia. A few years later he added *H. rhabdocarpum* (Hampe) A. Jaeger from Colombia and *H. glyphocarpum* (Hampe) A. Jaeger from Bra-

zil (Jaeger, 1880). Two more species were included in the genus when Paris (1896) first listed *H. teres* (Müll. Hal.) Paris from central Africa (Mount Kilimanjaro); from South Africa he added *H. erosum* (Müll. Hal.) Paris. The last two species to be included in the genus were *H. macrocalyx* (Müll. Hal.) Paris and *H. serrae* (Müll. Hal.) Paris, both from southwestern Brazil (Paris, 1900). Brotherus (1925: 70) considered the genus to have two species; however, Magill and van Rooy (1998) placed the South African *H. erosum* as a synonym of *H. imberbe*. Eventually, all nine species were considered synonyms under *H. imberbe*. Taxonomic work in progress evaluating type specimens and worldwide morphological variation might reveal several species. Meanwhile the genus is here considered monotypic. Valid names are listed as synonyms of *H. imberbe*, some of which need lectotypification.

Hedwigidium imberbe (Sm.) Bruch & Schimp. Bryol. Eur. 3 (fasc. 29-30): 157. 1846.

≡ *Gymnostomum imberbe* Sm., Engl. Bot. 32: 2237. 1811 ≡ *Anictangium imberbe* (Sm.) Hook. & Taylor, Muscol. Brit. 14. 1818 ≡ *Schistidium imberbe* (Sm.) Nees & Hornsch., Bryol. Germ. 1: 99. 1823 ≡ *Anictangium ciliatum* var. *rufescens* Arnott, Mém. Soc. Linn. Paris 5: 226. 1827 ≡ *Schistidium ciliatum* var. *imberbe* (Sm.) Huebener, Muscologia Germanica 30. 1833 ≡ *Hedwigia imberbis* (Sm.) Spruce, Musci Pyren. 263. 1847 ≡ *Neckera imberbis* (Sm.) Müll. Hal., Syn. Musc. Frond. 2: 105. 1851 ≡ *Braunia imberbis* (Sm.) N. Dalton & D.G. Long, J. Bryol. 34(1): 60. 2012. Type citation: "Discovered on dry rocks upon mountains in the west of Ireland by Miss Hutchins, who in 1809 sent specimens to Mr. Turner, which he has kindly communicated to us". TYPE: UNITED KINGDOM. Ireland, Glengariff, 1810, *Miss (Ellen) Hutchins. Mr. Turner s.n.* (holotype: LINN, isotype: BM).

= *Schistidium drummondii* Taylor, London J. Bot. 5: 57. 1846. (*Schistidium australe* Wilson. London Journal of Botany 5: 58. 1846, invalid) ≡ *Neckera drummondii* (Taylor) Müll. Hal., Syn. Musc. Frond. 2: 106. 1851 ≡ *Hedwigia imberbis* var. *drummondii* (Taylor) Wilson, Flora Tasmaniae 2: 179. 1859 ≡ *Hedwigidium drummondii* (Taylor) A. Jaeger. Ber. Thätigkeit St. Gall. Naturwiss. Gesell. 1874-1875: 173 (Gen. Sp. Musc. 2: 89). 1876 ≡ *Hedwigia drummondii*

(Taylor) Kindb., Enumeratio Bryinearum Exoticarum 15. 1888. Type citation: “*S. australe*, Wils. Mss. et Herb. Hook. n. 3658 (fide G. J. Lyon). -Swan River, *Mr. James Drummond*”. TYPE: PATRIA NOVA-HOLLANDIA, ad Swanriver, *J. Drummond 3658* (Herb. Lyon-BM000986156, Herb. Lyon-BM000986155, Herb. Wilson-BM000986150, Herb. Wilson-BM000986151, Herb. Wilson-BM000986152, Herb. Wilson-BM000986154, Herb. Wilson-BM000986149, Herb. Wilson-BM000986148).

= *Neckera emersa* Müll. Hal. & Hampe, Linnaea 26: 502. 1855 ≡ *Hedwigidium emersum* (Müll. Hal. & Hampe) A. Jaeger, Ber. Thätigkeit St. Gall. Naturwiss. Gesell. 1874-75: 173. 1876. Type citation: “Nova-Hollandia austr., sine loco indicato”. TYPE: *F. J. H. von Müller s.n.* (Herb. Hampe-BM000986141, Herb. Hampe-BM000986142, Herb. Hampe-BM000986143, BM000986165).

= *Harrisonia rhabdocarpa* Hampe, Linnaea 32: 148. 1863 ≡ *Braunia rhabdocarpa* (Hampe) Müll. Hal, Linnaea 42: 378. 1879 ≡ *Hedwigidium rhabdocarpum* (Hampe) A. Jaeger, Ber. Thätigkeit St. Gall. Naturwiss. Gesell. 1877-78: 508 (Gen. Sp. Musc. 2: 772). 1880 ≡ *Hedwigia rhabdocarpa* (Hampe) Kindb., Enumeratio Bryinearum Exoticarum 15. 1888. Type citation: “(*Lindig*) 2005. Hab. Bogota Chapinero ad saxa riparia, 2700 metr., October”. TYPE: NOVA GRANADA. Bogota Chapinero, alt. 2700 metr, ad saxa riparia, X.1859, *Lindig 2005* (Herb. Hampe-BM000960783).

= *Harrisonia glyphocarpa* Hampe, Vidensk. Meddel. Dansk Naturhist. For. Kjøbenhavn, ser. 3, 10: 263. 1878 ≡ *Hedwigidium glyphocarpum* (Hampe) A. Jaeger, Ber. Thätigkeit St. Gall. Naturwiss. Gesell. 1877-1878: 508 (Gen. Sp. Musc. 2: 772). 1880 ≡ *Hedwigia glyphocarpa* (Hampe) Kindb., Enumeratio Bryinearum Exoticarum 15. 1888. Type citation: (Brazil), “Rio Preto; (*Glaziou*) nr. 9070”. TYPE: BRASIL. Rio de Janeiro, *Glaziou 9070* (Herb. Hampe-BM000986128, Herb. Bescherelle-BM000986129, BM000986132, NY).

= *Braunia teres* Müll. Hal., Flora 71: 415. 1888 ≡ *Hedwigidium teres* (Müll. Hal.) Paris, Index Bryol. 555. 1896. Type citation: “(*H. Meyer*), Monte Kilimandscharo, ad finem sylvestrem superiorem inter 3000-4000 m”. TYPE: Monte Kilimandscharo, *Dr. Hans Meyer* (n.v.).

= *Braunia novae-seelandiae* Müll. Hal. in Beckett, Trans. Proc. New Zealand Inst. 26: 275. 1894. Type citation:

“Selwyn Gorge, Canterbury, September 1892; No. 417; T. W. N. B. (named by Dr K. Müller)”. TYPE: NEW ZEALAND. Canterbury, Selwyn Gorge, on dry rock, IX.1892, *T.W.N. Beckett 417* (NSW).

= *Braunia macrocalyx* Müll. Hal., Bull. Herb. Boissier 6: 110. 1898 ≡ *Hedwigidium macrocalyx* (Müll. Hal.) Paris, Index Bryol. Suppl. 1: 179. 1900 ≡ *Hedwigidium imberbe* var. *macrocalyx* (Müll. Hal.) Herzog, Biblioth. Bot. 87: 104. 1916. Type citation: (Brazil), “Brasilia, Serra Itatiaia, in rupibus alt. 2100 et 220 m., Febr. 1894: *E. Ule*, Coll. No. 1848, 1849; Agulhas Negras, in rupibus, 2300 m.: *idem* No. 1850, 1854”. TYPE: (n.v.).

= *Braunia serrae* Müll. Hal., Bull. Herb. Boissier 6: 111. 1898 ≡ *Hedwigidium serrae* (Müll. Hal.) Paris, Index Bryol. Suppl. 1 180. 1900. Type citation: “(Brazil), Brasilia, Sa Catharina, Serra do Oratorio, ad cataractam rivuli Pelotas, Aprili 1889: *E. Ule*, Coll. No. 536; Serra Geral, ad rupes, Januario 1890: *idem*, Coll.”. TYPE: BRAZIL. Prov. Santa Catharina, Serra Geral, I.1890, *Ule 536*, *Ule 79* (JE-04008589, PC, US).

= *Braunia macowaniana* Müll. Hal., Hedwigia 38(2): 123. 1899. Type citation: “Prom, bonae spei, Mte. Boschberg prope Somerset East, in fissuris irrigates rupium basalticarum, 1877: *Prof. Mac Owan*, misit 1878 sterilem; Natal, Jammerlappen: *J. Dittrich* (1898), Ig. Hb. Arboreti Zoeschen-Diek”. TYPE: SOUTH AFRICA. Somerset East, monte Boschberg, in rupibus basalticus, 1877, *Mac Owan 41* (Hb. C. Müller, Vereinigte Hb, JE); *Mac Owan s.n.* (JE_04008596); SOUTH AFRICA. Jammerlappen, Natal, 1898, *J. Dittrich s.n.* (JE_04008593).

= *Braunia erosa* Müll. Hal., Hedwigia 38: 124. 1899 ≡ *Hedwigidium erosum* (Müll. Hal.) Paris, Index Bryol. Suppl. 1 179. 1900. Type citation: (South Africa), “Prom. bonae spei, Capetown, ad rupes prope Rondebosch, 1875: *Dr. A. Rehmann*”. TYPE: 1875, *Rehmann s.n.* (n.v.).

= *Hedwigidium imberbe* var. *andesiticum* M. Fleisch., Hedwigia 44: 315. 1905. Type citation: “Exsiccata: M. Fleischer, Musci Archip. Ind. No. 314 (1904). An Andesitfelsblöcken. Ost_Java: am Ardjoeno im Hochgebirge auf waldfreien bei Lalidjiwa 2500-2800 m im Mai 1901 vom Verfasser entdeckt”. TYPE: JAVA. Ost-Java, Am Ardjoenogebirge bei lali Djiwa an Andesitfelsen, 2500-2700 m, 10.V.1901, *Fleischer 314* (BM000986130, JE, NY).

Not: *Hedwigidium integrifolium* (P. Beauv.) C.E.O. Jensen, Skand. Bladmossfl., 369. 1939 (= *Hedwigia integrifolia* P. Beauv., Prodr. Aethéogam, 60. 1805).

Illustrations

Bartram (1949: fig. 105 H-J); Beckett (1894: plate xxvi, 1-6 as *Braunia novae-seelandiae* Müll. Hal.); Bruch and Schimper (1846); Catcheside (1980: fig. 178, as *Hedwigia integrifolia*); Churchill and Linares (1995: fig. 101 a-, as *Hedwigidium integrifolium*); Crum (1994: fig. 496); Dixon and Jameson (1896: plate XXIV, J, as *Hedwigia imberbis*); Fleischer (1906: fig. 135, as *Hedwigidium imberbe* var. *andesiticum*); Fife (2014: plate 1, I-M, as *Hedwigidium integrifolium*); Husnot (1890: plate XLI, as *Hedwigia imberbis*); Meagher and Fuhrer (2003: plate 61, as *Hedwigia integrifolia*); Scott and Stone (1976: plate 68, as *Hedwigia integrifolia*); Seppelt et al. (2013: plate 10).

Distribution

Europe: United Kingdom, Norway, France, Italy, and Spain. **Africa:** Cameroon, DR Congo, Malawi, Tanzania, Uganda, Zimbabwe, Reunion Island, Kenya, South Africa. **Asia:** India, Sri Lanka, Indonesia. Australia, New Zealand. **Central America:** Mexico, Guatemala, El Salvador, Honduras, Costa Rica, Dominican Republic. **South America:** Venezuela, Colombia, Ecuador, Peru, Bolivia, Chile, Argentina, Brazil.

Specimens examined. The records for most countries are documented with herbarium specimens. Countries are grouped by continent. Literature references are also included after the specimens.

EUROPE

UNITED KINGDOM. Ireland, Glengarriff, 1810, *Hutchins* (Mr. Turner) s.n. (BM). Bruch and Schimper (1846), Wilson (1841), Smith (1978, as *Hedwigia integrifolia*). **NORWAY.** Bruch and Schimper (1846), Nyholm (1960, as *Hedwigia integrifolia*). **FRANCE.** Müller (1851), Ros et al. (2013), Hugonnot (2015); Le Bail (2015, as *Braunia imberbis*). **SPAIN.** Ros et al. (2013, as *Braunia imberbis*). **ITALY.** Ros et al. (2013, as *Braunia imberbis*); Frahm (1976, as *Hedwigidium integrifolium*).

AFRICA

CAMEROON. West Africa, III.1898, *Bornmüller s.n.* (B), as *Hedwigidium montis-deorum*; Cameroon Mt, 2.IV.1952, No collector given, *M45* (BM) as *B. rupestris*; Mt. Cameroon, 2.IV.1952, *Adams s.n.* (BM). O'Shea (2006). **DEMOCRATIC REPUBLIC OF CONGO** (formerly Zaire). Virunga, flanc nord du Kirisimbi, mixed with *Braunia arbuscula*, *De Sloover 13090 b* (DUKE); Virunga, *De Sloover 13092* (DUKE); Ruwenzori, *Bequaert 4579* (BR). O'Shea (2006). **KENYA.** Bizot et al. (1978), Kis (1985), O'Shea (2006). **MALAWI.** Mt. Mulanje, rio Muloza, *Hodgetts 7227* (BM); Mt. Mulanje, Sapitwa, *Hodgetts 7735* (BM); Mt. Mulanje, Chisongoli, *Porley 16* (BM); Mt. Mulanje, Chinzama Hut, *Wigginton M1302* (BM). Wigginton et al., (2020, as *H. integrifolium*). **REUNION ISLAND.** Crosby 8421 (DUKE), 8429 (DUKE). Ah-Peng and J. Bardat (2005). O'Shea (2006). **RWANDA.** O'Shea (2006). **SOUTH AFRICA.** Natal, Jammerlapen, 1898, *Ditrich s.n.* (JE); Somerset East monte Boschberg, *MacOwan 41* (JE); Mt. Boschberg, 1887, *MacOwan s.n.* (JE); Natal, Royal National Park, *Magill 6730* (MO), as *Braunia secunda*; *van Rooy 1203* (MO). Magill and van Rooy (1998), O'Shea (2006). **TANZANIA.** Kilimanjaro Mt., *De Sloover B-478* (BR); Kilimanjaro Mt., *Pócs 6994/I* (F); Kilimanjaro Mt. Philipia, *Pócs 6720/M* (NY). Bizot et al. (1978), Kis (1985), O'Shea (2006). **UGANDA.** Mt. Kineti Imatong Mts, *Thomas 1846* (BM), as *Braunia schimperiana*; Kigezi, *Hedberg 2069* (DUKE), 2093 (DUKE). Kis (1985), O'Shea (2006). **ZIMBABWE.** *Magill 10213* (MO). O'Shea (2006).

ASIA

INDIA. Chopra (1975), Vashistha (1998), Daniels (2010). All as *Hedwigidium integrifolium*. **SRI LANKA** (formerly Ceylon). Au deu Sipfelfshen des Kirigalpota, II.1906, *Herzog s.n.* (JE), 2320 (DUKE). **INDONESIA.** 10.V.1901, *Fleischer s.n.* (JE, NY); Ost-Java, Am Ardjoenogebirge bei lali Djiwa an Andesitfelsen, 10.V.1901, *Fleischer s.n.* (BM, JE, NY), 314 (BM, JE, NY), as *Hedwigidium andesiticum*. **AUSTRALIA.** Western Australia, Swan River, *Drummond 3658* (BM); Müller s.n. (BM); *Streimann 35662* (DUKE); Tasmania, *Watts s.n.* (NSW), as *H. campbellii*. Sainsbury (1955), Scott and Stone (1976), Catcheside (1980) as *Hedwigia integrifolia*.

NEW ZEALAND. Selwyn Gorge, Canterbury, *Beckett* 417 (NSW), as *B. novae-sealandiae*; Selwyn Gorge, *Becket s.n.*, (BM). [Fife \(2014\)](#).

CENTRAL AMERICA AND THE CARIBBEAN

MEXICO. Ciudad de México, *Cárdenas* 3741 (MEXU, XAL); Cuajimalpa, *Vivas* 337 (MEXU, XAL). Chiapas, Motozintla, *Delgadillo* 4780 (DUKE). Durango, near Buenos Aires, *Breedlove* 69168 (DUKE). Estado de México, Nevado de Toluca, *De Luna* 1754 (DUKE, MEXU), 1755 (DUKE, MEXU), 1759 (DUKE, MEXU). Hidalgo, *Cárdenas* 3429 (DUKE, MEXU); Parque Nacional El Chico, *De Luna* 1798 (XAL). Jalisco, Nevado de Colima, *De Luna* 45 (DUKE, MEXU), 548 (DUKE, MEXU). Michoacán, volcán Paricutín, cerca de San Lorenzo, *De Luna* 1778 (MEXU, XAL). Oaxaca, cerro Corral de Piedra, *Delgadillo* 4844 (DUKE). Puebla, *Hermann* 26448 (DUKE); Pico de Orizaba, entre Tezmola y San Miguel, *De Luna* 1443 (MEXU, XAL). Tlaxcala, al norte de Villareal, *De Luna* 2647 (XAL), 2717 (XAL); volcán La Malinche, *Marin* 239 (XAL). Veracruz, Cofre de Perote, *De Luna* 2287 (XAL), 2711 (XAL), 2713 (XAL). Nuevo León, Peña Nevada, *Nelson and Wells* 6 (DUKE). [Crum \(1994\)](#). **EL SALVADOR.** [Allen \(2010\)](#). **GUATEMALA.** San Marcos, *Sharp* 5449 (DUKE). [Bartram \(1949\)](#). **COSTA RICA.** *Holz et al.* 99-0913 (DUKE); San José, *Crosby* 3888 (DUKE, MO). [Allen \(2010\)](#). **HONDURAS.** *Allen* 12255 (MO). **DOMINICAN REPUBLIC.** La Vega, *Norris et al.* 5680 (DUKE); La Vega, *Steere* 23037 (DUKE), 23104 (DUKE). [Sastre-De Jesús et al. \(2010\)](#).

SOUTH AMERICA

VENEZUELA. Mérida, *Griffin III* PV-510 (DUKE, MO). [Delgado and León-Vargas \(2017\)](#). **COLOMBIA.** Sumapaz, *Cleef* 149 (QCA); Belén, *Cleef* 2127 (QCA); Bogotá, Chapinero, *Lindig* 2005 (BM); Antioquia, *Churchill et al.* 13342 (DUKE); Cundinamarca, *Schultes* 12262 (DUKE). [Churchill and Linares \(1995\)](#). **ECUADOR.** Azuay, Cerro Urucaca, south of Cuenca, *Lewis* 78-2202 (F, NY), as *Braunia cirrhifolia*; Cañar, *Lewis* 78-2379 (QCA); Cajas, *Lewis* 78-2278 (F, QCA), 78-3236 (F, QCA); Cajas, *Steere* 27716 (NY, QCA); Cajas, *Sastre-De Jesús* 697 (QCA); entre Sigsig y Ludo, al sureste de Cuenca, *De Luna* 2010 (DUKE, XAL), Sierra de Cajas, camino de Cuenca a Molleturo, *De Luna* 1991 (DUKE, XAL); Chimborazo, alrededor de Achupallas, *De Luna* 2018 (DUKE, XAL); Coto-

paxi, Quevedo - Latacunga road, *Holm-Nielsen et al.* 3381 (AAU, S, US), as *B. cirrhifolia*; cerca de Mulalo, *De Luna* 1902 (DUKE, XAL); Volcán Cotopaxi, *De Luna* 1946 (DUKE, XAL), 1953 (DUKE, XAL), 1958 (DUKE, XAL); Cotopaxi, *Buck* 10298 (NY, QCA); Rio Cutuchi, *Gradstein et al.* 124 (QCA), *Bryophyta Neotropica Exiccatae* 113 (QCA); Pichincha, camino al volcán Pululahua, cerca de San Antonio, *De Luna* 1879 (DUKE). [Steere \(1948\)](#). **PERU.** Cuzco, *Herrera* 2386 (F), 2391 (F), as *B. secunda*; Lima, *Hampe s.n.* (slide 3817, BM), as *Braunia secunda*; *Mathews s.n.* (QCA); Lima, Lomas de Granados, *Vargas* 9554 (MICH). [Menzel \(1986\)](#). **BOLIVIA.** Sorata, *Balslev* 1097 (MO, NY, QCA); Cochabamba, *Hermann* 25155 (MO); *Herzog* 3254 (JE), as *Braunia macrocalyx*; Cochabamba, l.1908, *Herzog s.n.*, (JE); l.1908, *Herzog s.n.* (JE), as *B. subplicata*; Chuquisaca, al sur de Tarabuco, *Lewis* 1628 (MO); al noroeste de Santa Elena, *Lewis* 1948 (MO); Cochabamba, Ayopaya, *De Luna* 2122 (DUKE), 2124 (DUKE), Chaparé, *De Luna* 2111 (DUKE); Tunari, Monte Tunari, *De Luna* 2128 (DUKE), 2134 (DUKE); La Paz, Larecaja, *De Luna* 2047 (DUKE), 2060 (DUKE), 2063 (DUKE, MO); Larecaja, alrededores de Sorata, *De Luna* 2065b (DUKE). [Hermann \(1976\)](#). **CHILE.** Cordillera de la Costa, 4.XI.1897, *Dusén* 344 (JE, NY). [Mahú \(1979\)](#), [He \(1998\)](#), [Müller \(2009\)](#), as *H. integrifolium*. **ARGENTINA.** Argentina subtropica, Siambon regione Aliso, *Lorentz s.n.* (JE), as *Braunia rhabdocarpa* *Hampe*; Argentina Patagonica, Sierra Ventana, l.III.1881, *Lorentz s.n.* (JE), as *B. patagonica*; Buenos Aires, Cerro de la Ventana, *Roivainen* 460 (MICH), as *B. patagonica*; Cordoba, cerro Uritoco, *Hosseus* 360 (BM, BR, NY); Cordoba, *von Hübschmann* 5 (NY); Tandil, IX.1907, *Hicken* 18 (JE); *Churchill and Schiavone* 19993e (MO). [Blockeel et al. \(2003\)](#), as *H. integrifolium*. **BRAZIL.** Rio de Janeiro, *Glaziou* 9070 (NY); Sierra do Itatiaia, 17.VI.1902, *Dusén s.n.* (B, JE), as *Braunia macrocalyx*; Jaquirana, *Wasum et al.* 6041 (DUKE); *Vital* 7111 (MO); Serra Geral, *Ulé* 79 (JE, US), as *Hedwigidium serrae*. [Costa and Lima \(2005\)](#), [Yano \(2004, 2011\)](#), as *H. integrifolium*.

Verified specimens, worldwide distribution and habitat range

Since its establishment, *Hedwigidium* was first known from Europe, and later found throughout the mountains in Mexico, South America, Africa, New Zealand and Australia. For the first time, a list of specimens is provided, and the world-

wide geographical distribution of the genus is documented and mapped. The specimens listed above were used for mapping the distribution of genus *Hedwigidium*. The map also includes literature country records (Fig. 8).

Hedwigidium imberbe was originally described from a specimen growing on rocks in Glengarriff, southwestern Ireland. Afterwards, a second specimen was collected in a locality in Lofoten, northwestern Norway (Bruch and Schimper, 1946). Shortly after, Müller (1851) cited these two specimens (“Ad rupes prope Glengarriff Hiberniae: Miss Hutchins, Wilson; in insula Osteröe Finmarkiae: Blytt”) and added the following three specimens from southern France: “in Pyrenaeis ad Bagnères de Bigorre in rupib. porphyraceis: W.P. Sch., ad saxa granitica pr. Laruns: Spruce et in rupib. schistosis pr Pouzac et Gazos: Philippe”. Currently, *H. imberbe* is well-documented in Europe from northern, western and southwestern regions, where it is listed as rare and vulnerable (Hodgetts, 2015). European specimens have short perichaetial leaves, less than twice the length of vegetative leaves. *Hedwigidium imberbe* is present at low to moderate elevations in England. Wil-

son (1841) recorded “It is found rather plentifully near Llanberis, and near Beddgelert in N. Wales”. In modern times, Smith (1978: 493) documented this taxon from North Wales, West Scotland, north to Skye and West Ross. He used the name *Hedwigia integrifolia*, but the description certainly corresponds to *H. imberbe*. In Norway, Nyholm (1960) treated this taxon as *Hedwigia integrifolia*, but the description of elongate and non-ciliate perichaetial leaves undoubtedly corresponds to *Hedwigidium imberbe*. This species was reported erroneously in Germany, according to Düll (1992). In France this species is rare and it has recently been rediscovered (Hugonnot, 2015; Le Bail, 2015, as *Braunia imberbis*). It is listed for Italy with a report of *Braunia imberbis* based on collections published before 1962 (Ros et al., 2013). It was rediscovered in Italy in the area east of Lake Como, according to Frahm (1976, as *Hedwigidium integrifolium*). It has also been confirmed for Spain (Ros et al., 2013).

Hedwigidium is not known to occur in northern North America. However, in Mexico *Hedwigidium imberbe* is fairly common in high mountain areas, mostly above 3000 m.

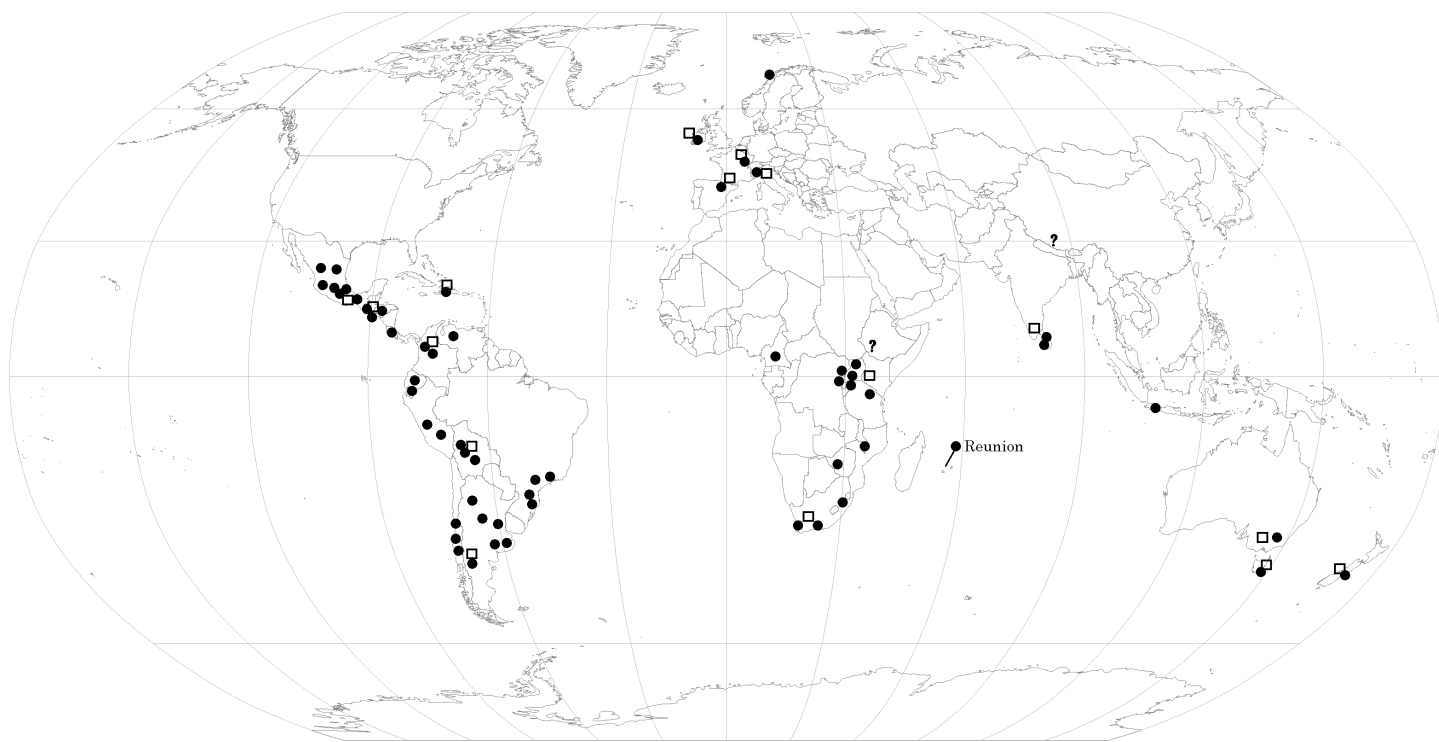


Figure 8: Map of the worldwide distribution of *Hedwigidium* Bruch & Schimp. A little square on the map indicates a literature citation. Each point on the distribution map indicates a particular specimen, of which I have corroborated the identity (see “Specimens examined” section). A question mark indicates a literature record not verified yet.

In Central America *H. imberbe* is also common on rocks at high elevations (“On rocks at high to very high altitudes” fide Bartram, 1949: 233; Allen, 2010). In the Dominican Republic the species has been collected in La Vega, a high elevation mountain (Sastre-De Jesús et al., 2010).

In northern, western and southern South America *Hedwigidium* has been documented in localities at high elevations along the Andes and also in southern Brazil. The illustrations of *H. imberbe* from Colombia correctly depict the morphology of this species (Churchill and Linares, 1995: fig. 101 a-f). In Ecuador, *Hedwigidium* grows mixed with *Hedwigia*, above 2400 m. I found infrequent populations on the Pulumahua volcano, only growing on rocks covered under small bushes. In contrast, every rock had abundant *Hedwigidium*, but not *Hedwigia* or *Braunia*, in a locality nearby Mulaló, above 3000 m. Also, *Hedwigidium* is abundant in localities on the skirts of Cotopaxi volcano, between 2800 and 3200 m (see e.g., De Luna 1946 (DUKE), 1953 (DUKE)). In the area close to Achupallas, at 3000 m, *Hedwigidium* grows abundantly on rocks in open agricultural fields (see e.g., De Luna 2027 (DUKE), 2030 DUKE). Britton (1896) discussed early collections of *Hedwigidium* in Bolivia and compared these with those in Colombia and Peru. Later, Herzog (1916: 104) reported two taxa of *Hedwigidium* from Bolivia. One was *H. imberbe* var. *macrocalyx* (Müll. Hal.) Herzog, based on his collection nr. 3254. I have seen this Herzog specimen at JE; indeed, it has extremely long perichaetial leaves reaching six times the size of vegetative leaves. Others of his collections (nrs. 3583 and 4914) were reported as *Hedwigidium imberbe*. In Bolivia, sterile populations of *Braunia* growing on rocks can be easily confused as *Hedwigidium*. But close examination reveals some actually are *Braunia subplicata*, a species that also has ovate-lanceolate leaves and strongly revolute margins, but exerted capsules (see e.g., De Luna 2082 (DUKE), 2129 (DUKE)). In Chile, Mahú (1979) recorded the presence of the genus, and it has been documented along the western side of the Andes, from Santiago to Valdivia (He, 1998; Müller, 2009, as *Hedwigidium integrifolium*).

The genus is also recorded in Argentina. Recently *Hedwigidium* was found in northern Patagonia, the most southerly locality of the genus in the Americas (Blockeel et al., 2003). Blockeel et al. (2003) believed that the Lorentz

specimen cited in the original report by Müller (1879), as *Braunia rhabdocarpa* was probably lost with Müller’s herbarium. However, I was able to locate a specimen in JE collected by P.G. Lorentz, labelled “*Braunia rhabdocarpa* Hampe, Argentina subtropica, Siambon regione Aliso”, an area that corresponds to northwestern Tucumán. This Lorentz specimen has the immersed capsules, entire perichaetial leaves, and other gametophytic features, which indicate it is clearly a genuine *Hedwigidium* from Argentina. In Brazil, Costa and Lima (2005) recorded *H. imberbe* (as *H. integrifolium*) in the montane and upper montane Atlantic rainforest of southeastern Brazil (1500-2700 m). Yano (2004, 2011) examined new specimens of this species (as *Hedwigidium integrifolium*) collected in six states in Brazil.

In Africa, *H. imberbe* is well-known from high altitude mountains in western, central, eastern and southern regions (O’Shea, 2006). Sim (1926) recorded localities at middle elevations (1500 m) with plants up to 5 cm long, but noted that at that time, sporophytes were not known in South Africa. More recently, Magill and van Rooy (1998) presented a detailed map of known localities of *Hedwigidium* in southern Africa. In Africa, the gametophytes of *H. imberbe* are very similar to those of *Braunia rupestris*. With some frequency, I have found specimens wrongly identified as *Braunia rupestris*, but on close examination, and having found sporophytes, undoubtedly these belong to *Hedwigidium*. The report of *Hedwigidium* from Ethiopia (Bizot et al., 1978: 274) is not correct, since the two specimens cited are from localities (21 and 33) not in this country. According to their map in p. 261, one locality is in Kenya, and the other site is on Tanzania. A few years later, Kis (1985: 88) listed several specimens of *Hedwigidium* for Tanzania, Uganda and Kenya, but none for Ethiopia. O’Shea (2006) listed *H. imberbe* (as *H. integrifolium*) from Cameroon, Cape Verde Island, Kenya, Lesotho, Réunion, Rwanda, South Africa, Swaziland, Tanzania, Uganda, Democratic Republic of Congo (former Zaire), and Zimbabwe. Recently, *Hedwigidium* was first reported from Malawi (Wigginton et al., 2020). I can confirm such record with four specimens found at BM: Hodgetts 7227, 7735, Porley M16a (cited in Wigginton et al., 2020), and Wigginton M1302a (cited in Wigginton et al., 2020). The latter specimen mostly consists of *Hedwigidium*, but it is mixed with some *Hedwigia*. Capsules have a very

wide-open mouth, and the perichaetial leaves are strongly undulate.

In Asia, *Hedwigidium imberbe* has been recorded from Palni Hills, southern India (Chopra, 1975). Vashistha (1998) and Daniels (2010) also listed this species, as *Hedwigidium integrifolium*, from southern India. Additionally, I was able to confirm collections from Sri Lanka (formerly Ceylon, Herzog 2320 (DUKE); II.1906, Herzog s.n. (JE)) and Indonesia (10.V.1901, Fleischer s.n. (BM, JE, NY)).

In Australia and New Zealand, *Hedwigidium imberbe* is well-documented, although Sainsbury (1955) and Scott and Stone (1976) incorrectly named this taxon as *Hedwigia integrifolia*. In southern Australia, plants are more than 6 cm long, with frequent flagelliform shoots. The illustrations in Gilmore (2012) and Fife (2014) are good representations of the morphological features of this taxon. Catcheside (1980: 295) also misapplied the name *Hedwigia integrifolia*, but the description fits very well the taxonomic concept of *Hedwigidium imberbe*. There are six drawings of *Braunia novae-seelandiae* in Plate xxvi in Beckett (1894). One leaf is shown as shortly ovate (Beckett, 1894: fig. 2), with perichaetial leaves twice the size of vegetative leaves (Beckett, 1894: figs. 5, 6). Previously, Dixon (1927: 240) considered that *B. novae-seelandiae* was a synonym of *Hedwigidium integrifolium*, a taxonomy with which Fife (2014) also agreed. I am also interpreting these features as an indication that *Braunia novae-seelandiae* Beckett belongs in *Hedwigidium*.

The records of *Hedwigidium* (as *Braunia obtusiuscuspe* Broth.) from China, by He and De Luna (2004) might be *Braunia alopecura* as re-interpreted by Wang (2011) and Dalton et al. (2013). However, my recent re-examination of the type specimen, Handel-Mazzetti 788 (S), is not so conclusive. The specimen has no sporophytes and the flat leaf apex indeed resembles that of *Hedwigidium*, not the tubulose leaf apex of *B. alopecura*. Thus, I prefer to leave this identification as doubtful.

Author contributions

EDL conceived and designed the study, carried out the statistical analyses, wrote the manuscript, reviewed, and approved the final version.

Funding

The author thanks the Instituto de Ecología, A.C. (INECOL, CONACYT) for the continued support for visits to MO (St. Louis, MO, USA) and BM (London, UK). 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 of reviewers in correcting the text for this published version. The careful revision of the editorial team and Marie-Stéphanie Samain is deeply appreciated.

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