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A synopsis of *Braunia* (Hedwigiaceae, Bryopsida) in Mexico, with the lectotypification of *Braunia andrieuxii*

Una sinopsis de *Braunia* (Hedwigiaceae, Bryopsida) en México, con la lectotipificación de *Braunia andrieuxii*

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Abstract:

Background and Aims: Four species of *Braunia* are known in Mexico: *Braunia andrieuxii*, *B. secunda*, *B. squarrulosa* and *B. plicata*. A taxonomic study of the species of *Braunia* in Mexico has not been undertaken before. Moreover, among several “*Andrieux*” specimens currently available, there is no certainty as to which particular collection is the type.

Methods: The four species of *Braunia* known in Mexico and neighboring areas in the southern United States of America, Central America and the Caribbean Islands were studied together for the first time. Based on over 450 collections from several herbaria, a taxonomic treatment and a key to the species of *Braunia* in this geographical region are presented.

Key results: The four species are described and illustrated. A specimen *Andrieux* 23 located at BM is selected as the lectotype for *B. andrieuxii*, with isoelectotypes in the herbaria BM and NY. A key is provided for the identification of the species of *Braunia* in Mexico, and neighboring USA, Central America, and the Caribbean.

Conclusions: Morphological features most likely to be informative for the distinction of the four species in Mexico are the leaf margins, leaf apices, upper leaf cells, and sporophytes. The leaf apex is hyaline and dentate only in *B. plicata*, while it is concolorous and entire or scabrous in the other three species of *Braunia* from Mexico. The upper leaf cells are quadrate to short-rectangular in *B. andrieuxii* and *B. plicata*; whereas the upper leaf cells are elongate in *B. secunda* and *B. squarrulosa*.

Key words: Hedwigiales, mosses, taxonomy.

Resumen:

Antecedentes y Objetivos: Se conocen cuatro especies de *Braunia* en México: *Braunia andrieuxii*, *B. secunda*, *B. squarrulosa* y *B. plicata*. Anteriormente no se había realizado ningún estudio taxonómico de las especies de *Braunia* en México. Además, entre varios especímenes colectados por “*Andrieux*” disponibles, no hay certidumbre sobre cual ejemplar en particular es el tipo.

Métodos: Las cuatro especies de *Braunia* conocidas en México y áreas vecinas en el Sur de Estados Unidos de América, Centroamérica y las islas del Caribe se estudiaron juntas por primera vez. Con base en más de 450 especímenes de varios herbarios, se presenta un tratamiento taxonómico y una clave para las especies de *Braunia* en esta región geográfica.

Resultados clave: Se describen e ilustran las cuatro especies. Se selecciona como lectotipo para *B. andrieuxii* el ejemplar *Andrieux* 23 localizado en el herbario BM, con isoelectotipos en los herbarios BM y NY. Se provee una clave para la identificación de las especies de *Braunia* en México, el sur de los EUA, Centroamérica y el Caribe.

Conclusiones: Los atributos morfológicos más probables que sean informativos para la distinción de las cuatro especies en México son los márgenes de la hoja, los ápices foliares, las células foliares superiores y los esporofitos. El ápice foliar es hialino y dentado solo en *B. plicata*, mientras que el ápice es verde y entero o escabroso en las otras tres especies de *Braunia* en México. Las células foliares superiores son cuadradas a corto-rectangulares en *B. andrieuxii* y *B. plicata*; mientras que las células superiores son alongadas en *B. secunda* y *B. squarrulosa*.

Palabras clave: Hedwigiales, musgos, taxonomía.

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Introduction

The Hedwigiaceae consist of four genera of acrocarpous and mostly epilithic mosses (De Luna, 1995) currently classified in the order Hedwigiales. The monotypic genus *Pseudobraunia* (Lesq. & James) Broth. is endemic to the western side of North America in the USA and Canada. The other three genera are present in Mexico and Central America (De Luna, 1995). In this geographical area, the genus *Braunia* Bruch & Schimp. can be set apart by the presence of exserted capsules on a long seta (3–20 mm), whereas the seta is very short (0.7–1.5 mm) in *Hedwigidium* Bruch & Schimp. and *Hedwigia* P. Beauv. An immersed sporophyte, surrounded by very long perichaetial leaves without cilia, helps to distinguish *Hedwigidium* reliably (Allen, 2010; De Luna, 2021a). The whitish leaves and hyaline leaf apices easily identify species of *Hedwigia*. However, when the sporophyte distinction cannot be used, *Hedwigidium imberbe* (Sm.) Bruch & Schimp. and the species of *Braunia* present in Mexico are very difficult to identify, since leaf shape and leaf cell papillae are so similar (Sharp et al., 1978). The genus *Braunia* is characterized by the ecostate leaves, thick-walled, sinuous leaf cells with multiple papillae over the longitudinal walls, long setae, eperistomate and usually cylindrical capsules, cucullate calyptrae, and an exosporic globular protonema (De Luna, 1990, 1995, 2016). In the area including the southern United States of America, Mexico, Central America and the Caribbean Islands, there are four species of *Braunia* known: *Braunia secunda* (Hook.) Bruch & Schimp., *B. andrieuxii* Lorentz, *B. squarrosa* (Hampe) Müll. Hal., and *B. plicata* (Mitt.) A. Jaeger.

Braunia was established as a genus in the Hedwigiaceae (Bruch and Schimper, 1846) to include the European species, *Braunia sciuroides* (Bals.-Criv. & De Not.) Bruch & Schimp. (= *B. alopecura* (Brid.) Limpr.), and two species from Mexico (*B. secunda* and *B. squarrosa*). Later, Müller (1851) described *Neckera sphaerocarpa* Müll. Hal. and *N. liebmanniana* Müll. Hal.; eventually both species were added to *Braunia*. Subsequently, Lorentz (1864) described yet another species from Mexico as *B. andrieuxii*. In the worldwide catalogue of mosses by Jaeger (1876), only three species were recognized for Mexico: *B. secunda*, *B. andrieuxii*, and *B. liebmanniana*. Early in the 20th cen-

tury, Brotherus (1909) listed the same three species for Mexico. Shortly after, two additional taxa from Mexico were added to the genus. First, Cardot (1911) described *Braunia plicata* var. *canescens* Cardot from two specimens collected by Pringle in central Mexico (Hidalgo and Estado de México). Lastly, Thériot (1926) described *B. secunda* var. *crassiretis* Thér. based on a collection by Arsène also in central Mexico (Michoacán).

In modern times, Crum (1951) recognized three species of *Braunia* in Mexico. He considered *B. andrieuxii* and *B. secunda* var. *crassiretis* as synonyms of *B. secunda*. Likewise, Crum (1951) treated *B. liebmanniana* and *B. sphaerocarpa* as synonyms of *B. squarrosa*. Remarkably, he accepted the records of *B. plicata* as genuine. However, the current understanding of the number of species of *Braunia* in Mexico has been based on Crum (1994); he re-interpreted the morphological diversity of *Braunia* in this area as consisting of just two species: *B. secunda* and *B. squarrosa*, suggesting that “Mexican records of *B. plicata* (Mitt) Jaeger, a South American species, can perhaps also be included in *B. secunda*.” A taxonomic study of the species of *Braunia* in Mexico had not been undertaken before. A taxonomic treatment and a key to the species of *Braunia* in Mexico is presented, including illustrations, maps and a summary of the known distribution. This treatment should be useful also for the species of *Braunia* in the southern United States of America, Central America and the Caribbean Islands.

Material and Methods

In this paper the four *Braunia* species known in Mexico and neighboring areas in the southern United States of America, Central America and the Caribbean Islands were studied together for the first time. Specimens of over 450 collections from the following herbaria were included: B, BM, DUKE, F, FH, FLA, G, H, JE, LPA, MEXU, MICH, MO, NY, S, US, and XAL (Thiers, 2016). Species distribution maps were prepared with the ZeeMaps software (Zee Source, 2021). Also, examination of original descriptions, protologues, and type specimens in several herbaria worldwide revealed the need of lectotypification for one name. The necessary lectotypification is documented for *B. andrieuxii*.

Results

Taxonomy

In order to facilitate identification of the four genera of Hedwigiaceae, here I offer the following key.

Key to the genera of Hedwigiaceae

- 1a. Medial and upper leaf cells with 1-4 papillae per cell, papillae tall, centered over cell lumen; gametophytes without stoloniferous branches 2
- 1b. Medial and upper leaf cells with 1-6 papillae per cell, papillae low, marginal and arching over cell lumen; gametophytes with stoloniferous branches 3
- 2a. Seta short, (0.5-)0.8-1(-1.2) mm, capsules immersed; operculum low, plano-convex, rostrum small mammillate; capsule stomata cryptoporic; perichaetial leaf margins ciliate *Hedwigia* P. Beauv.
- 2b. Seta long, (4-)6-7(-10) mm, capsules exserted; operculum high-conic, short-rostrate; capsule stomata phaneroporic; perichaetial leaf margins entire *Pseudobraunia* (Lesq. & James) Broth.
- 3a. Capsules immersed, urn turbinate-urceolate, subglobose, mouth wide; operculum high-conic, rostrum small mammillate; perichaetial leaf margins undulate; seta short, (0.8-)1-3(-4) mm *Hedwigidium* Bruch & Schimp.
- 3b. Capsules exserted, urn cylindric, ellipsoid, ovate, or turbinate, mouth wide or narrow; operculum low-conic, long-rostrate; perichaetial leaf margins not undulate; seta long, (4-)7-12(-17) mm *Braunia* Bruch & Schimp.

Braunia Bruch & Schimp., Bryol. Eur. 3: 159. 1846. (nom. cons., De Luna, 1999).

TYPE: *Braunia sciuroides* (Bals.-Criv. & De Not.) Bruch & Schimp. (= *Anoetangium sciuroides* Bals.-Criv. & De Not. 1836).

Hedwigia sect. *Braunia* (Bruch & Schimp.) Mitt., J. Linn. Soc., Bot. 12: 404. 1869.

Braunia sect. *Macromidium* Müll.Hal., Linnaea 42: 380. 1879.

Hedwigia subg. *Braunia* (Bruch & Schimp.) Kindb., Eur. N. Amer. Bryineae (Mosses) 1: 5. 1897.

Robust plants (3-5 cm tall) in loose or dense, dull, rigid tufts or mats, dark green or red-brown; stems sympodially branched, plagiotropic, tips ascending; most branches terete and blunt, some stoloniform; pseudoparaphyllia foliose, often deeply dentate, cells papillose; leaves imbricate, spreading or squarrose, concave, plicate, ovate to wide-oblong, cuspidate or acuminate; leaves ecostate; leaf apex concolorous or hyaline, crenulate or serrulate; margins reflexed below or revolute up to the base of acumen; upper leaf cells thick-walled, strongly sinuous, subquadrate or rectangular (28-40 µm long, 8-12 µm wide), with several low rounded, unbranched papillae, marginal, overarching to the lumen; apical cells broad oblong to narrowly elongate, smooth or papillose; leaf basal cells, linear, yellow, cell walls straight, porose, with 3-5 luminal, unbranched papillae or smooth, gradually broad elliptic to subquadrate, cell lumina subcruciform at basal margins; autoicous or rarely synoicous; perichaetia terminal on sympodial stems, becoming lateral because of innovations, perichaetial leaves erect, elongate, plicate, long-acuminate to cuspidate; paraphyses uniseriate, long, yellowish to deep orange, commonly exserted; setae yellow to reddish, short to elongate, straight or twisted near the neck, smooth; neck very short, ampullaceous or long, attenuate; capsule exserted, erect, symmetric, rarely inclined, urceolate, subglobose, broadly ellipsoid to cylindric, smooth or longitudinally ribbed, slightly constricted below the rim, commonly microstomous; operculum base conic, rostrum slender, long, oblique; exothecial cells broadly subquadrate, rectangular or polygonal, thick-walled, gradually subquadrate or oblate and darker in several suboral rows; annulus and peristome absent; stomata superficial, restricted to neck; spores yellow-brown, vermiculate papillose or rugulose, unicellular, weakly tetrahedral, or pluricellular; calyptrae large, cucullate, smooth or rarely hairy, beak narrow, long, base broad open or strongly concave, naked, 4-7 cell layers thick.

Morphological features most likely to be informative for the distinction of the four species in Mexico are the leaf margins, leaf apices, upper leaf cells, and sporophytes. For example, a detailed morphometric analysis of variation helped to reveal differences between *Braunia secunda* and *B. andrieuxii*, in the extent of the revolute leaf margins

and upper leaf cell lengths (De Luna and Gómez-Velasco, 2008). The seta is short, up to 5-6 mm long, and the capsule is widely urceolate only in *B. squarrulosa*. However, sporophytes are of no use for distinguishing *B. andrieuxii*, *B. secunda*, and *B. plicata*, because of overlapping variation in cylindrical to ellipsoid capsule shape and seta lengths (9-14 mm). Without sporophytes, the leaf apex, and the upper leaf cells help to discriminate species. The leaf apex is hyaline and dentate only in *B. plicata*, while it is concolorous and entire or scabrous in the other three species of *Braunia* from Mexico. Also, the apical cells are strongly papillose only in *B. plicata*. The upper leaf cells are quadrate to short-rectangular in *B. andrieuxii* and *B. plicata*; whereas the upper leaf cells are elongate in *B. secunda* and *B. squarrulosa*.

The morphological features listed above are emphasized in the following key. Since the four species of *Braunia* present in Mexico are distributed also in the Southern United States of America, Central America and the Caribbean, this key should be useful to identify species of *Braunia* in those areas.

Key to the species of *Braunia* in Mexico

- 1a. Leaf apex dentate, hyaline; capsule cylindrical *Braunia plicata* (Mitt.) A. Jaeger
- 1b. Leaf apex entire or scabrous, concolorous 2
- 2a. Leaf apex long-acuminate, narrow, flexuose; capsule turbinate, globose; setae (3-)5-6(-7) mm long *Braunia squarrulosa* (Hampe) Müll. Hal.
- 2b. Leaf apex short-acuminate; capsule cylindrical, narrow; setae (5-)9-14(-20) mm long 3
- 3a. Leaf margin revolute, extending from the base up 3/4 the leaf length; upper leaf cells rectangular, (8.2-)11-16.8(-21.9) μm long, (3.7-)4.9-6.5(-8.2) μm wide, 2-3:1, cell walls sinuose *Braunia secunda* (Hook.) Bruch & Schimp.
- 3b. Leaf margin plane, or revolute, extending from the base up 1/3 the leaf length; upper leaf cells sub-quadrate, (7.2-)9.2-13 (-17.2) μm long, (4.4-)5.3-6.7(-8) μm wide, 1.5-2:1, cell walls smooth *Braunia andrieuxii* Lorentz

Braunia andrieuxii Lorentz, Moosst. 164. 1864. Figs. 1,2.

$\equiv$ *Braunia secunda* (Hook.) Bruch & Schimp. var. *andrieuxii* (Lor.) Thér., Smith. Misc. Coll. 78(2): 24. 1926. Type citation: "Mexico, in monte St. Felipe prope Oaxacam leg. Andrieux". TYPE (Lectotype designated here): MEXICO. Oaxaca, in monte San Felipe, prope Oaxacam, IV. 1834, *Andrieux* 23 (Herb. Hooker-BM000960769!; isolectotypes, BM000960761!, BM000960765!, BM000960766!; H!, Herb. Mitten-NY00913938!, NY00913939!).

Plants medium-sized in dense mats; stems with sympodial branching, plagiotropic, (3-)4-5(-6) cm long, scarcely branched; branches short, erect; flagelliform branches rare; pseudoparaphyllia foliose, with papillose cells; leaves ovate, widest point at or above middle of leaf; acumen abruptly differentiated, to 1/6 length of leaf, short-acuminate, concolorous, 1.7-1.9 $\times$ 0.9-1.2 mm, leaf lamina flat or slightly concave, imbricate, erect-patent when dry, spreading when moist, weakly plicate; *margins reflexed or recurved from base up 1/2 the leaf length or less, margin plane above* (italics show the diagnostic characters), serrulate to erose at acumen; apical leaf cells 13-22 μm long, elliptic (3-4:1), sinuose, with few low marginal papillae; *upper and median leaf cells (7.2-)9.2-13(-17.2) μm long, quadrate to rectangular (2-3:1)*, walls weakly sinuose, papillae low, on side walls, overarched lumina; autoicous; archegonia distal on long vaginula (1.3-1.5 mm); perichaetial leaves oblong lanceolate, 2.3-2.7 mm long, slightly longer than vegetative leaves, acuminate, plicate; perichaetial paraphyses biseriate at base, 2-3 times longer than archegonia, immersed; setae (5-)7-11(-13) mm long; capsule exserted, necks 0.3-0.4 mm long, gradually differentiated, slender, urns 1.2-1.6 mm long, cylindrical, mouth narrow, nearly 1/2 the urn width, capsule walls smooth, or wrinkled when dry, exothecial cells polygonal; stomates superficial; opercula base conical, short obliquely rostrate; calyptrae cucullate, large, 2.8-3.7 mm, hairy; spores unicellular, 25-32 μm in diameter.

Nomenclatural note: There is a single collection, "*Andrieux*", cited in the protologue, although without

Figure 1: Lectotype of *Braunia andrieuxii* Lorentz. A. lectotype specimen at Hooker herbarium (BM), *Andrieux 23*, Herb. Hooker-BM000960769; B. detail of specimen showing elongate setae and elliptic capsules; C-D. vegetative leaves; E. leaf cells at the apex; F. upper leaf cells (A-F, from *Andrieux 23*, Herb. Hooker-BM).

Figure 2: Morphological features of *Braunia andrieuxii* Lorentz in Mexico. A. branching system with a sporophyte; B. detail of a branch showing leaf stance; C. vegetative leaf; D. perichaetial leaf; E. upper leaf cells (A-E, from *Cárdenas 348*, MEXU, Mexico, Zacatecas).

collection number and year. Among several “*Andrieux*” specimens currently available, there is no certainty as to which particular collection is the type. I examined several “*Andrieux*” specimens collected in Mexico without collection numbers, or without collection dates (BM000960759, BM000960760, BM000960767, BM000960768); the identity of these specimens is indeed *B. andrieuxii*. Some of these specimens are from Oaxaca, but there is no additional information to be sure if they are part of the original material. Therefore, here I am designating as lectotype a specimen located at the Hooker herbarium (“*Andrieux 23*”, BM000960769), clearly labeled as collected in the type locality (Fig. 1). The selection of this numbered specimen as lectotype facilitates the future recognition of additional duplicates in other herbaria. The duplicate of *Andrieux 23* in the Mitten herbarium (NY) consists of three small packets, two are good isotypes of *B. andrieuxii*, but the identity of the third plant (NY00913937) is actually *B. secunda*. Other specimens of *B. andrieuxii* collected by Andrieux are very likely not types, since these are not from Oaxaca (Mexico, Santa Fé, *Andrieux 18*, Herb. Hampe-BM) or there is no precise locality information (Mexique, 1834, *Andrieux s.n.*, Herb. Mus. Paris-BM; Mexico, *Andrieux s.n.*, Herb. Besch.-BM). I have seen an additional non-type specimen collected by Andrieux but the identity is *B. secunda* (Mexico, Pedregal, *Andrieux 20*, Herb. Hampe-BM).

Habitat: this species commonly grows on igneous rocks, in exposed habitats and within forests at middle elevations (1300–2500 m).

Distribution: United States of America (Arizona, New Mexico, fide Allred et al., 2016, Texas), Mexico, Guatemala (Allen, 2010), Colombia (as *B. secunda* in Churchill and Linares, 1995). Fig. 3.

Illustrations: Bartram (1949, Pl. 106 D–F, as *B. secunda*); Crum (1994, Fig. 497 a–f, as *B. secunda*); Churchill and Linares (1995, Fig. 100 h–k, as *B. secunda*); Figs. 1–2.

Selected specimens examined: MEXICO. Aguascalientes, Sierra Fría, *Cantrall 54* (MO). Baja California Sur, Sierra La Laguna, S of Pico La Aguja, *D. E. Breedlove and*

D. Axelrod 43286 (G); Sierra de La Laguna, 15 miles E of Todos Los Santos, *F. Bowers 5166* (DUKE, MO, XAL); *F. Bowers 5201-a* (MO); Sierra de la Laguna, *C. Delgadillo 3091* (MEXU). Chihuahua, 20 mi N of Las Nieves, *F. Bowers 6296-b* (DUKE, MO). Municipio Urique between Basigochic and Quirire, *R. Bye 6129* (MO); 38 mi S de Creel, Río Urique, Cañón del Cobre, *C. Delgadillo 3268* (MEXU); San Pedro Springs, *L. N. Godding 2123* (MO); 15 mi WSW of Madera, *G. L. Nesom 52* (DUKE, MO); 15 mi WSW of Madera, *G. L. Nesom 53* (DUKE, MO); 30 mi W of the La Junta, *K. J. Torke 1015* (MO). Ciudad de México (formerly Distrito Federal), Santa Fé, *Andrieux 18* (BM); Santa Ana, hacia el Mirador, *A. Cárdenas 1438* (DUKE, MEXU); Pedregal de San Angel, *C. Delgadillo 1642* (MEXU); *C. Delgadillo 2085* (MEXU); near Contreras, *A. J. Sharp 1189* (MO, US). Durango, 34.5 mi E of El Salto on Rt. 40, *T. Stuessy 409* (DUKE, NY); 45 km W of Durango, *F. Bowers 5284* (MO); Otinapa, *E. D. Palmer 438* (MO); eastern foothills of the Sierra Madre Occidental, *Weber 9856* (MO); Tejaman, *E. D. Palmer 475* (MO); Rocky ledge, a few km before Palos Colorados W of Durango, *A. J. Sharp 1747* (MO); 34 mi E of El Salto on Rt. 40, *Irving 409* (MO); 18 km S. de V. Matamoros, *C. Delgadillo 3250* (MEXU). Estado de Mexico, 10.5 km SW villa Nicolás Romero, *A. Cárdenas 1855* (DUKE); Sierra de Calpulalpan, *A. Cárdenas 2308* (MO). Municipio Tepotzotlan, 4 km de Magu, Sierra de Alcaparrosa, *A. Cárdenas 3798* (DUKE, MEXU); Sierra de Alcaparrosa, *A. Cárdenas 1820* (DUKE, XAL). Municipio Tepotzotlan, 2 km al W de Magu, *Cruz 1698* (XAL), *1700* (XAL). Municipio Texcoco, La Purificación, *A. Cárdenas 1886* (DUKE). Guanajuato, 5 km SW de Acámbaro, *A. Cárdenas 4461* (DUKE). Municipio Jerécuaro, Sierra de los Agustinos, *A. Cárdenas 5351* (MO). Guerrero, municipio Taxco de Alarcón, Caverna “La Joya”, *J. Castrejon 434* (MEXU, MO). Hidalgo, 2 km NW de San Francisco Sarabia, *A. Cárdenas 5636* (MEXU, MO); 5 km NE de Almoloya, *C. Delgadillo 5393* (MEXU); 60 km S of San Juan del Río gen Tula, *R. Düll 122* (JE); 10 km al W de Alfajayucan, *González 2696* (XAL); Cuyamaloya, *C. G. Pringle 10627* (B, F, FH, G, S). Jalisco, about 58 km W of Jiquilpan, Mich., on the road to Ciudad Guzman, *C. Delgadillo 2761* (DUKE, MEXU); Sierra de Bolaños, *García s.n.* (MO); mountains above (W of) Hacienda Chinampas, *R. McVaugh 17033* (DUKE, MO); Guadalupe, *C. G. Pringle 10619* (MO); 8 miles N of los Volcanes,

Figure 3: Distribution map of *Braunia andrieuxii* Lorentz. Each dot is one of the specimens listed in the text.

A. Whittemore 2127 (DUKE). Michoacán, Andames, Vicinity of Morelia, G. Arsène 4832 (MO); Dos Tetillas, G. Arsène 7658 (BM, MO); Cerro San Miguel, G. Arsène 4869 (BM, DUKE, MO), 5045 (BM, MO), 5050 (DUKE), 5077 (BM), 5104 (BM, MO); San Miguel prope Morelia in civit Michoacán, G. Arsène 3596 (BM, MO); Punguato, G. Arsène 5047 (DUKE, MO); Uripitio, 11 km NE de Maravatio, C. Delgadillo 4892 (MEXU); 13 km NE de Cotija de la Paz, C. Delgadillo 5053 (MEXU); 2 km N de Acuitzio del Canje, C. Delgadillo 5268 (MEXU); 19 km SSW de Jacona, C. Delgadillo 5339 (MEXU); 20 km N de Cherán, C. Delgadillo 5524 (MEXU); 2 km N de Cuamajo, C. Delgadillo 5475 (MEXU); Los Azufres, 3 km al S del campamento CFE, E. De Luna 1765 (XAL); camino al volcán Parícutín, cerca de San Lorenzo, E. De Luna 1779 (XAL), 1781 (XAL); above Carapan, W. Kiener 18328 (MO);

Pátzcuaro, C. G. Pringle 742 (JE, MO), 744 (JE, NY, MO). Morelos, seven Autoban zw. Mexico City u. Cuernavaca, ca 50 km ht. Mex, R. Düll 179 (B). Oaxaca, municipio San Juan, Miahuatlán, E. Hunn OAX-1206 (MEXU); El Punto on Highway 175, A. J. Sharp 2281 (MO); Cerro Jecote, 1.5 km W de Magdalena, Cruz 1890 (XAL); 43 km an der Str. F190 Oaxaca - Huajuapán, Eggers 792022 (MEXU); in Monte San Felipe, Andrieux 23 (lectotype BM, isolectotypes H, NY); 6 km al NW de Mitla, C. Delgadillo 73 (MEXU). Puebla, Cerro Tepoxuchitl, vicinity of Puebla, G. Arsène 4523 (BM, MO), 4851 (BM, MO); loc. cit., Nicolas 5126 (DUKE); along route 119, 8 miles S, F. J. Hermann 26462 (DUKE). Querétaro, El Batán, Argüelles 1459 (MEXU). Sonora, El rancho del Roble, White 4206 (DUKE); NE of El Tigre, White 4211 (MICH); Bavispe región, El Bilito, White 4811 (DUKE, MICH); Cerro

Saguarivo, E of San Bernardo, *Pennell s.n.* (MO). Veracruz, Jalapa, *Wagner s.n.*, 1896 (JE, S); Los Limones, *G. Juárez* 929 (MO, XAL). Zacatecas, Cerro de la Bufa, *A. Cárdenas* 348 (MEXU, MO), 349 (MEXU), 355 (MEXU, MO). Municipio Cerro Gordo, 3 km SE de la colonia Hidalgo, *A. Cárdenas* 741 (MEXU), 745 (MEXU). Municipio Tlaltenango, Cerro del Moro, 29 km W de Jalpa, *A. Cárdenas* 830 (MEXU, MO). Municipio Tlaltenango, 37 km W de Jalpa, *A. Cárdenas* 876 (MEXU). Municipio Valparaíso, 14 km N de Valparaíso, *A. Cárdenas* 796 (MEXU, MO); 7 km S de la Laguna Grande, *A. Cárdenas* 3034 (DUKE, MEXU). Municipio Fresnillo, 2 km S de San Juan de los Hornillos, *A. Cárdenas* 751 (MEXU). Municipio Chalchihuites, 2 km E de Gualterio, *A. Cárdenas* 1080 (MEXU); *A. Cárdenas* 1075 (MEXU). Municipio Jiménez de Teul, Rancho el Madroño, *A. Cárdenas* 1101 (MEXU); Road to Huejuquilla de Alto, Jal. 1 mi W of the road-junction, *R. McVaugh* 17766 (MO).

Additional specimens examined: COLOMBIA. Antioquia, Río Chico, près de Bogotá, 18.IX.1906, *F. Apollinaire s.n.* (G); près de Bogotá, 8.IX.1907, *F. Apollinaire s.n.* (G); Medellín, Andes, 17.VIII.1911, *F. Idinöel s.n.* (G); Cundinamarca, San Cristóbal, 19.VIII.1909, *F. Apollinaire s.n.* (G). **GUATEMALA.** Quetzaltenango, *P. C. Standley* 83237 (F, FH, NY#02120995). San Marcos, *T. B. Croat* 41046 (MO). **UNITED STATES OF AMERICA.** Arizona, ravine on Red Mt., Patagonia Mts., *E. B. Bartram* 617 (BM, MO); White House Canyon, Santa Rita Mountains, *E. B. Bartram* 60 (DUKE, MO), *E. B. Bartram* 4529 (MO), *E. B. Bartram* 1849 (MO); Patagonia Mountains, *E. B. Bartram* 13 (DUKE); Sycamore Canyon near Ruby, *I. M. Haring* 3277 (MO); Santa Cruz Co., near McBeth Campground near Josephine saddle above Madera, *D. Norris* 76567 (DUKE, MO); trail from Maple Camp to South Fork Campground SW of Portal, *D. Norris* 75380 (DUKE); Madera Canyon, *W. Schofield* 105057 (DUKE, MO); Chiricahua Mts., *W. Schofield* 105088 (DUKE); Chochise County, Chiricahua National Monument, trail from Sugarloaf to Echo Park, *C. Weber* B-42783 (MO). New Mexico, Fide *Allred et al.* (2016). Texas, South Rim Trail to Emory Peak, Chisos Mts, Big Bend Nat. Park, *L. E. Anderson* B-2879 (DUKE, MO); Travis Mountains, *Berkman* 121 (DUKE); Brewster County, Chisos Mountains, summit of Emory Peak, Big Bend National Park, *R. Magill* 2008 (MO); Chisos Moun-

tains, shortcut trail between Laguna Meadow and Boot, *R. Magill* 1855 (MO); Chisos Mountains, *R. Magill* 1883 (MO); Jeff Davis County, Madera Canyon, *R. Magill* 184 (MO); 215 (DUKE, MO); NE side of Mount Livermore, SW of SH 118, *R. Magill* 152 (MO); Rockpile State Park, SH 166, *R. Magill and Hatch* 531 (MO); Mount Livermore, Madera, *Hinckley* 1151 (MO); Madera Canyon near Mt. Livermore, *Hinckley* 1149 (MO); Chisos Mtns., 80 mi S of Marathon, *Pedano* 837 (MO); Boot Canyon Trail, *A. Stoneburner* 1791 (DUKE); 1805 (DUKE); Chisos Mtns, lower Boot Spring Canyon, *Warnock s.n.* (MO); between Boot Springs and South Rim, *Warnock s.n.* (MO); at Laguna, Chisos Mtns, *Warnock* 1561 (DUKE); Chisos Mountains, Emory Peak, *T. Wieboldt* 8050 (DUKE); Chisos Mountains, trail to Boot Springs, *E. Whitehouse* 24616 (DUKE, MO).

Discussion: in the original description of *B. andrieuxii*, *Lorentz* (1864) correctly compared this species with the European *B. alopecura*: “*B. sciuroidi simillima, differ autem folis perichaetialibus angustioribus, longioribus, ...*” Indeed, leaf shape in *B. andrieuxii* and *B. alopecura* is very similar. This morphological similarity and a misunderstanding of the species concept of *B. secunda* led *Frahm* (2013) to believe *B. alopecura* and *B. secunda* were the same species. The two figures *Frahm* (2013, Figs. 4-5) presented as *B. secunda* are in fact *B. andrieuxii*. Similarities in upper leaf cells and leaf shape are correct, but as *Lorentz* (1864) correctly pointed out, the perichaetial leaves in *B. andrieuxii* are elongate, whereas they are short in *B. alopecura*, almost the same size as vegetative leaves. In Mexico, *B. andrieuxii* is distinguished from other species in the genus by the leaf margins plane or reflexed to weakly recurved only at the leaf base and an elliptic capsule with polygonal exothecial cells. The distinctions made by *Thériot* (1926) between *B. andrieuxii* and *B. secunda* were correct. Nevertheless, this species was traditionally considered a synonym of *B. secunda*. Certainly, both species share a cylindrical to ellipsoidal capsule and a somewhat similar leaf shape. However, in *B. andrieuxii* the upper leaf margins are plane, the leaf cells are shorter and less sinuous, and the short acumen is sharply differentiated from a broader upper leaf lamina. These differences are most evident in mature leaves close to branch tips.

Braunia plicata (Mitt.) A. Jaeger, Ber. St. Gall. Naturw. Ges. 1874-1875: 171. (Adum. 2: 87). 1876.

≡ *Hedwigia plicata* Mitt., J. Linn. Soc., Bot. 12: 406-407. 1869. Type citation: "Andes Quitensis, Jameson. In Bolivia, *Bridges* in herb. Hooker". TYPE (Lectotype designated by De Luna, 2021b): BOLIVIA. 1846, *Bridges s.n.* (Herb. Hooker-BM000960770!; isolectotypes, Herb. Wilson-BM!, NY!).

= *Braunia plicata* var. *canescens* Cardot, Rev. Bryol. 38: 38. 1911. Type citation: "État de Hidalgo: Cuyamaloya, rochers (*Pringle*, 1908, no. 10627). État de Mexico: Toluca (*Pringle*, 1908, no. 15171)". TYPE (Lectotype designated by De Luna, 2021b): MEXICO. Toluca, 4.VIII.1908, *Pringle 15171* (Herb. Cardot-PC0701219!); isolectotypes (FH! (*pro parte*, the specimen at FH contains mostly plants of *B. andrieuxi*), NY#00792519!, S!,,).

Plants in dense mats; main stems sympodial, plagiotropic, (3-)4-5(-7) cm long, closely branched; *branches elongate, ending in obtuse, rosulate tips*; flagelliform branches common; pseudoparaphyllia foliose, with papillose cells; leaves ovate or broadly ovate, 1.9-2.2 mm long, 0.8-1.1 mm wide, concave, imbricate, spreading when moist, *strongly plicate*; margins recurved to acumen; *high base, widest point at or above middle of leaf*; apex cuspidate, *hyaline, margins sharply dentate*; apical leaf cells homogeneously elongate, narrow elliptic (5-7:1), 18-28 µm long, not sinuose, with many marginal papillae; upper and median leaf cells 14-18 µm long, sub-quadrate to short-elliptic (2:1), walls sinuose, papillae 2-3, low, on side walls, overarching lumen; autoicous; archegonia medial on short vaginula (1.4-1.6 mm); perichaetial leaves narrowly lanceolate, 2.4-2.9 mm long, *less than twice the length of vegetative leaves*, covering 1 mm of seta, acuminate, plicate, perichaetial paraphyses biseriolate at base, immersed; setae (7-)9-10(-12) mm long; capsule exserted, necks 0.3-0.4 mm, broad, gradually attenuated, urns 1.7-2.5 mm long, narrowly elliptic, mouth narrow, nearly 1/2 as wide as urn, capsule walls smooth, exothecial cells rectangular; stomates superficial; opercula base conical, short oblique rostrate; calyptrae cucullate, large; spores 29-31 µm in diameter.

Habitat: this species commonly grows on trees, but also colonizes andesitic rocks in exposed habitats within forests at middle to high elevations (1500-2700 m).

Distribution: Mexico (Aguascalientes, Estado de México, Hidalgo, Nuevo León, Oaxaca, Querétaro, Tlaxcala), Peru, Bolivia (De Luna, 2021b); Fig. 4.

Illustrations: De Luna (2021b, figs. 1-4); Fig. 5.

Selected specimens examined: MEXICO. Aguascalientes, San José de Gracia, La Congoja, *Villalobos 8* (MEXU, NY). Estado de México, San Martín de las Pirámides, Cerro Gordo, *B. Allen 12943* (MO); Cerro Gordo, *A. Cárdenas 2200* (DUKE). Toluca, *C. G. Pringle 15171* (FH *pro parte*, NY, S). Hidalgo, Cuyamaloya, *C. G. Pringle 10627* (BM, H, JE, MO, NY, S, US); ridge above Real del Monte, near Pachucá, *A. J. Sharp 797* (MICH, US); S of San Juan del Río, *Rauh and R. Düll 122* (H). Nuevo León, Cerro del Viejo, 15 mi W Dulces Nombres, *Meyer and Rogers 149* (G, NY); 3 mi NW of Picacho Onofre, *G. L. Nesom and Wells 34* (DUKE). Oaxaca, procedente de Trelan, *C. Conzatti 4739b* (F). Querétaro, cerro El Pinguical, cerca de Pinal de Amoles, *G. Ocampo 620* (XAL). Tlaxcala, cerca de Villareal, al NE de Huamantla, *E. De Luna 2646* (XAL); 2718 (XAL); 2720 (XAL); Mt. Tlacuapanga, *A. J. Sharp 433* (MICH).

Additional specimens examined: BOLIVIA. 1846, *Bridges s.n.* (BM, NY); alrededores de Sorata, *E. De Luna 2094* (DUKE, LPB); in market at Cochabamba, *F. J. Hermann 25280* (NY); Santa Cruz, Comarapa und Abra de Catalina, *T. Herzog 3703* (JE, S); in der Cordillere von Santa Cruz, *T. Herzog 3482* (JE, S); Carasani and Niño Karine, NNW of Chuma, *M. Lewis 79-947* (F). **PERU.** Cusco, Calca, Pisac, *Marin 622* (F); Laguna Uripancha, near Huacarpay, *H. Inoue 828* (JE).

Discussion: This is the same species concept from that of Mitten (1869). Morphological characters distinguishing *B. plicata* in Mexico are the leaves imbricate, strongly plicate, and concave (Fig. 5B). The leaf apex is cuspidate, hyaline, and dentate (Fig. 5J). Shoots are often dark green to brownish, especially darker green along the leaf plications, which contrasts sharply with the hyaline leaf

Figure 4: Distribution map of *Braunia plicata* (Mitt.) A. Jaeger. Each dot is one of the specimens listed in the text.

acumens (Fig. 5A-B). *Braunia plicata* is mostly montane Andean. In Mexico *B. plicata* is not as frequent as *B. secunda* or *B. andrieuxii*, but it is common in Peru and Bolivia.

Braunia secunda (Hook.) Bruch & Schimp., Bryol. Eur. 3 (fasc. 29-30): 161. 1846.

≡ *Hedwigia secunda* Hook., Musci Exot. 1: 46. 1818 (*Anoetangium secundum* Brid., Bryol. Univ. 2: 165. 18. 1827, *nom. inval.* *Harrisonia secunda* Spreng., Syst. Veg. IV, l: 145. 1827, *nom. inval.*); ≡ *Neckera secunda* (Hook.) Müll. Hal., Syn. Musc. Frond. 2: 103. 1851. Type citation: "In regni

Mexicani montosis apricis, juxta Toluccam ad radices montis perpetua nive obtecti, regione frigida, altitudine 1640 hexapodarum". TYPE (Lectotype designated in De Luna, 2016): MEXICO. In Nevado de Toluca, leg. Humboldt & Bonpland s.n. (Herb. Hooker no. H.1784-BM000960762!; isolectotypes, herb. Hampe-BM!, NY!, P!).

= *Braunia secunda* var. *crassiretis* Thér., Smiths. Misc. Coll. 78(2): 24. 1926. Type citation: "(Mexico), Morelia, Campanario (Arsène) (7448)". TYPE (Lectotype designated in De Luna, 2016): MEXICO. Vicinity of Morelia, Campanario, 2200 m., XI.1911, leg. Arsène 7448 (BM001226211!; isolectotypes, DUKE!, FI!, US!).

Figure 5: Morphological features of *Braunia plicata* (Mitt.) A. Jaeger in Mexico. A. branching system with a stoloniform branch and a sporophyte; B. detail of a branch showing leaf stance and leaf plications (A-B, from De Luna 2720, XAL, Mexico, Tlaxcala); C-F. vegetative leaves (C, from Pringle 10627, JE, Mexico, Hidalgo; D, from Pringle 10627, NY, Mexico, Hidalgo; E, from Sharp 433, MICH, Mexico, Tlaxcala; F, from Pringle 15171, NY, Mexico, Toluca); G-H. perichaetial leaves (G, from Pringle 15171, NY, Mexico, Toluca; H, from Pringle 10627, NY, Mexico, Hidalgo); I. upper leaf cells; J. leaf apex cells (I-J, from De Luna 2720, XAL, Mexico, Tlaxcala).

Not: *Anoetangium secundum* Mont., Musc. Neelgher. Ann. Sci. Nat. Bot. Ser. 2, t17: 251. 1842. 32. Patria. India Orientalis, in montibus Neelgheriensibus, ad rupes basalticas prope Kaitie lectum = *Braunia macropelma* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. Gen. Sp. Musc. 2: 87. 1876.

Plants in dense mats; main stems sympodial, plagiotropic, (3-)4-5(-6) cm long, scarcely branched; branches short; flagelliform branches rare; pseudoparaphyllia foliose, with papillose cells; leaves ovate or ovate-lanceolate, 1.9-2.2 mm long, 0.8-1.1 mm wide, flat or slightly concave, imbricate, erecto-patent, spreading erect when

moist, weakly plicate; *margins recurved extending from the base up 3/4 the leaf length*, sometimes reflexed; low base, widest point below middle of leaf; apex gradually differentiated, short acuminate to aristate, concolorous, margins erose-dentate; apical leaf cells mixed short (3-4:1) and narrow elliptic (5-7:1), 18-28 μm long, sinuose, with few low marginal papillae; *upper and median leaf cells 14-20 μm long, elliptic (3-5:1)*, walls nodulose, sinuose, papillae low, on side walls, overarching lumen; parocious; archegonia distal on long vaginula (1.4-1.6 mm); perichaetial leaves oblong lanceolate, 2.4-2.9 mm long, longer than vegetative leaves, covering 2 mm of seta, acuminate, plicate, perichaetial paraphyses biseriate at base, exserted; setae (8-)13-15(-20) mm long; capsules exserted, necks 0.3-0.4 mm long, gradually differentiated, broad, urns 1.7-2.5 mm long, narrowly elliptic to broadly ellipsoid, mouth narrow, nearly 1/2 as wide as urn, capsule walls smooth, or wrinkled when dry, exothecial cells polygonal; stomata superficial; opercula base conical, long oblique rostrate; calyptrae cucullate, large; spores unicellular, 29-31 μm in diameter.

Habitat: this species commonly grows on igneous rocks, in exposed habitats and within forests at middle elevations (1300-2500 m).

Distribution: United States of America (Arizona, Texas), Mexico (Chiapas, Chihuahua, Ciudad de México, Durango, Estado de México, Guanajuato, Hidalgo, Jalisco, Michoacán, Morelos, Nuevo León, Oaxaca, Puebla, Tlaxcala, Veracruz), Guatemala, Dominican Republic, Haiti, Venezuela, Bolivia; **Fig. 6.**

Illustrations: De Luna (2016, Figs. 1-2); **Fig. 7.**

Selected specimens examined: **MEXICO.** Chiapas, municipio of Motozintla, *D. E. Breedlove* 25803 (MO); Barrio de San Felipe de Ecatepec, *G. Gómez-Velasco* 277 (XAL); 2 km N of San Cristóbal de Las Casas, *den Held et al. HM34* (MO). Chihuahua, Ejido de Bocyna, W of Creel, *R. Bye* 7306 (MO); 30 mi N de San Juanito, *C. Delgadillo* 3302b (MEXU). Ciudad de México (formerly Distrito Federal), Santa Rosa, *Amable* 1510 (BM); Pedregal, *Andrieux* 20 (Herb.

Hampe-BM); Desierta Vieja, 1860, *Bourgeau s.n.* (BM, NY); Pedregal, Valle de México, *Bourgeau* 687 (BM); Ajusco, 1868, *Hahn s.n.* (BM); Cima, *C. G. Pringle* 10549 (BM, MO); Contreras, 4° Dinamo, *M. Vivas* 307 (DUKE). Durango, 9 miles W of La Ciudad, *F. Bowers* 5067 (MO, XAL); Hwy. 40 about 9 mi W of La Ciudad. *F. Bowers* 5075-b (MO); near Puerto Buenos Aires, *D. E. Breedlove* 69153 (DUKE); 69172 (DUKE); 13 km SE de La Ciudad, *C. Delgadillo* 3160 (MEXU); *C. Delgadillo* 3163 (MEXU); Metate, N of Cueva, *Pennell* 18400a (MO); near Salto, *A. J. Sharp* 1817 (DUKE, MO); 34.5 km E of El Salto on rt 40, *T. Stuessy* 407 (NY, MO). Estado de México, municipio San Martín de Las Pirámides, Cima del Cerro Gordo, valle de Teotihuacán, *B. Allen* 12938 (DUKE, MO); Valle de México, *Amable* 1291 (DUKE). Municipio Ixtapaluca, 1 km W de la Colonia Agrícola Manuel Ávila Camacho, *A. Cárdenas* 4360 (MO). Municipio Temascalapa, Cerro Gordo, *A. Cárdenas* 2199 (MO); Nevado de Toluca, *Humboldt and Bonpland s.n.* (type, BM, NY); Sierra de Las Cruces, *C. G. Pringle* 25a (BM, JE, MO, S). Guanajuato, 13 km NE de la ciudad de Guanajuato, *A. Cárdenas* 5312 (MEXU, MO); 9 km NE de Guanajuato, *C. Delgadillo* 5698 (MEXU); Mountains east of Comanja and 20 mi by road N of Leon, *R. McVaugh* 10426 (DUKE). Hidalgo, Casas Quemadas, Real del Monte, *Arreguín* 853 (CAS, MO). Municipio Epazoyucan, Peñas Largas, *A. Cárdenas* 3277b (MEXU, MO); El Cerezo al NW de la ciudad de Pachuca, *A. Cárdenas* 3331 (DUKE); 6 km N de Pachuca, Parque Nacional El Chico, *García* 101 (MO); Agua Blanca, Noroeste de Tulancingo, *Gimate s.n.* (XAL); Real del Monte, *I. Mexía* 2770 (BM, MO); Cuyamaloya, *C. G. Pringle* 10627 (MICH, NY); Tepeapulco, *M. Vivas* 81 (XAL); Parque Nacional "El Chico", *M. Vivas* 34 (XAL); 151 (XAL); 9 (XAL). Jalisco, slopes of La Ferrería, above Manantlán, *H. A. Crum* 776 (MICH); 1167 (S). Michoacán, Campanario, vicinity of Morelia, *G. Arsène* 7442 (BM, MO); 7448 (BM, MO, US); 7571 (MO); 9 km W de Mil Cumbres, hacia Puerto Garnica, *C. Delgadillo* 496 (MEXU); Paracho, about 6 km Northward along highway to Cheran, *T. C. Frye and E. W. Frye* 3073 (DUKE, MO). Morelos, municipio Tepoztlán, Sierra de Chichinautzin, *A. Cárdenas* 1059 (MEXU, MO); Tres cumbres, Cuernavaca, *R. Düll* 186 (B, MO); Mirador near kilometer marker 67, Cuernavaca, *R. Magill* 2508 (MO). Nuevo León, Picacho Onofre, Peña Nevada, *G. L. Nesom and Wells* 6 (DUKE). Oaxaca,

Figure 6: Distribution map of *Braunia secunda* (Hook.) Bruch & Schimp. Each dot is one of the specimens listed in the text.

distrito de Coixtlahuacán, Cerro de Tamazulapan, 3 km al E de San Francisco Teopa, *Cisneros* 2241 (XAL); 16 km al E. de Mitla, hacia San Lorenzo, *C. Delgadillo* 68 (MEXU, XAL); 37-38 km NE de Oaxaca, hacia Ixtlan, *C. Delgadillo* 129 (MEXU); 698 (MEXU, XAL); 2 km E de Ixtlan, *C. Delgadillo* 738b (MEXU); 20 km NNE de Tlacolula, *C. Delgadillo* 106 (MEXU); roadside at km 218 of Hwy. 175 at La

Cumbre, *Jim and Rosemary* 3107 (MO). Puebla, on cerro Pinar, 1945, *Alexander* #A (DUKE); Tepoxuchitl frie Puebla, *Nicolas s.n.* (JE); Las cuevas on Ixtaccihuatl above Huejotzingo, *A. J. Sharp* 4321 (MO); above Río Frío, *A. J. Sharp* 229 (MO). Tlaxcala, cerca de Villareal al N de Huamantla, *E. De Luna* 2643 (XAL), 2644 (XAL). Veracruz, Cofre de Perote, *C. Delgadillo* 3930 (MEXU, XAL); Rincón de Atotonilco,

Figure 7: Morphological features of *Braunia secunda* (Hook.) Bruch & Schimp. in Mexico. A. detail of a branch showing leaf stance; B. upper half of vegetative leaf; C. upper leaf cells; D. leaf cells at the apex. (A-D, from De Luna 2643, XAL, Mexico, Tlaxcala).

laderas del Pico de Orizaba, *E. De Luna* 1655 (XAL); Las Vigas, entre Perote y Jalapa, *E. De Luna* 1803 (XAL); Cima del Cofre de Perote, *E. De Luna and R. Keller* 2245 (XAL); 25 km W of Orizaba im pedregal, *R. Düll* 43 (JE, MO); Los Pescados, Cofre de Perote, *G. Gómez-Velasco* 3 (XAL); La Joya, *G. Gómez-Velasco* 1 (XAL); Camino al Cofre de Perote, *D. Hernández* 129 (MO, XAL); “El Volcancillo” entre la “Joya” y Rafael Ramírez, *G. Juárez* 554 (MO, XAL); Santa Marta del Monte, *G. Juárez* 830 (MO, XAL); Pedregal de las Vigas, above La Joya, *Rickett* 23 (MEXU); 33 (DUKE, MEXU); 17 km NE of Jalapa, *R. Pursell* 5005 (MO).

Additional specimens examined: **BOLIVIA.** Auf Felsblocken uri Chocayatal, *T. Herzog* 2585 (JE). **DOMINICAN REPUBLIC.** San Juan, Pico Duarte, *W. R. Buck* 8436 (FLAS), along trail up Pico Duarte, *W. R. Buck* 14174 (NY). **GUATEMALA.** Quetzaltenango, S of Ilano de Pinal, W slopes of Volcán Santa María, *T. S. Quedensley* 4566 (NY); mtns. above San Juan Ostuncalco, *P. C. Standley* 85253 (NY). **HAITI.** La Vega, Constanza, *von Türckheim* s.n. 1910 (H). **UNITED STATES OF AMERICA.** Arizona, Madera Canyon, Santa Rita Mts., Santa Cruz Co., *W. Schofield* 103112 (MO). Texas, Brewster Co., Upper Boot Canyon, Big Bend National Park area, *Muller C4a* (BM); 21270 (MO); Davis Co., Davis Mountains, *E. D. Palmer* 34297 (MO); Mt. LiverMore, Davis Mts.,

E. D. Palmer 34278 (DUKE, MO); Davis Mountains, Madera Canyon, *Worthington* 25422 (MO). **VENEZUELA.** Mérida, Quebrada Gavidia, S de Mucuchíes, *D. Griffin and J. Duarte* 1143 (F, FLAS, H, MICH, NY).

Discussion: paroicous stems are a character that clearly circumscribes this species. Other characters that distinguish *B. secunda* are the nearly flat, narrowly lanceolate leaves, with margins revolute up to acumen. The apex is acuminate, scabrous dentate; apical cells are a mix of oval and elliptic cells (Fig. 7). Also, the perichaetial paraphyses are frequently exserted and the capsules are ellipsoid, inflated at the base and slightly constricted below the mouth. The capsule wall is irregularly wrinkled when dry.

Braunia secunda, as recognized by De Luna (2016), is exclusively Neotropical and commonly grows on rocks in forests at middle elevations (1500-2000 m). This is a much narrower circumscription than previously accepted (Dixon, 1920; Brotherus, 1925). It does not include populations distributed in Africa and India. In Mexico it is indeed difficult to separate sterile material of *Braunia squarrolosa*, *Hedwigidium imberbe* and *B. secunda* as discussed by Sharp et al. (1978). Leaf margins are revolute up to the acumen in *B. secunda* and *H. imberbe*, but the margin is revolute only

at the base in *B. squarrulosa*. In Mexico, it is also difficult to distinguish gametophytes of *B. secunda* from those of *B. andrieuxii* and *B. plicata*. Leaves are broader, obovate and the upper leaf cells are shorter in the latter two species. Additionally, *B. andrieuxii* has the leaf margins erect or reflexed but only at the base. On the other hand, *B. plicata* has strongly plicate leaves with a broad, hyaline, strongly papillose, and dentate acumen.

Braunia squarrulosa (Hampe) Müll. Hal., Linnaea 42: 380. 1879.

≡ *Harrisonia squarrulosa* Hampe, Linnaea 12: 349-350. 1838 ≡ *Hedwigidium squarrulosum* (Hampe) Bruch & Schimp., Bryol. Eur. 3: 161. 1846 ≡ *Hedwigia squarrulosa* (Hampe) Mitt., J. Linn. Soc. Bot. 12: 407. 1869. Type citation: "Mexico, Inter muscos Mexicanos, terrestres?". TYPE (Lectotype designated in De Luna, 2009): MEXICO. *Schlechtendahl s.n.* (Herb. Hampe-BM!; isoelectotypes, BM!, NY!).

= *Neckera sphaerocarpa* Müll. Hal., Syn. Musc. Frond. 2: 105. 1851 ≡ *Braunia sphaerocarpa* (Müll. Hal.) Müll. Hal., Bull. Herb. Boiss. 5: 201. 1897. Type citation: "Mexico: C. Ehrenberg. E Guatemala copiose communicavit Kegel." TYPE (Lectotype designated in De Luna, 2009): MEXICO. Mineral del Monte, in arbor. C. Ehrenberg s.n. (BM!).

= *Neckera liebmanniana* Müll. Hal., Syn. Musc. Frond. 2: 668. 1851 ≡ *Hedwigidium liebmannianum* (Müll. Hal.) Schimp., Syn. Musc. Eur. Ed. 1, p. 239, 1860 ≡ *Hedwigia liebmanniana* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 407. 1869 ≡ *Braunia liebmanniana* (Müll. Hal.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 185. 1872 ≡ *Braunia liebmannii* Kindb., Enum. Bryin. Exot. 8, 1888, *nom. illeg.* Type citation: "Mexico. In monte Orizabensi: Liebmann". TYPE (Lectotype designated in De Luna, 2009): MEXICO. Orizaba, *Liebmann s.n.* (BM!; isoelectotypes, BM!, NY!).

Plants robust in dense mats; stems with sympodial branching, plagiotropic, (3-)5-7(-10) cm long, scarcely branched; branches arcuate, flexuose-flagelliform branches frequent; pseudoparaphyllia foliose, with papillose cells; leaves ovate or oblong-lanceolate, widest point below middle of leaf; large 2-2.5 × 0.8-1.3 mm, concave, erect-spreading to squarrose, strongly plicate; *leaf acumen*

gradually differentiated, to 1/4 length of leaf, acuminate to cuspidate, concolorous, sometimes ending in a flexuose hyaline point; margins reflexed, sometimes recurved in lower 1/2, entire or papillose-crenulate at acumen; apical leaf cells elliptic, 22-31 µm long, narrow (4-7:1), sinuous, with few low marginal papillae; upper and medial cells elliptic, 12-20 µm long, narrow (3-5:1), walls nodulose, sinuous, papillae low, on side walls, overarching lumina; autoicous; archegonia distal on short vaginula (1.4-1.6 mm); perichaetial leaves oblong lanceolate, 2.4-2.6 mm long, slightly longer than vegetative leaves, acuminate, plicate; paraphyses biseriate at base, 2-3× longer than archegonia, immersed; setae (3-)4 - 5(-8) mm long; capsule exserted; necks 0.3-0.4 mm long, sharply differentiated, broad; urns 1.2-1.6 mm long, *urceolate to globose, mouth broad, nearly as wide as urn*; capsule walls smooth, or wrinkled when dry; exothecial cells polygonal; stomata superficial; operculum base conical, short oblique-rostrate; calyptrae cucullate, large, hairy; *spores multicellular, 35-42 µm in diameter.*

Habitat: this species is mainly epiphytic on the base of trees, on oak trunks, on bark of *Juniperus* L, on trunk of *Cupressus* L, on fallen tree branches. Also forming carpets on very decayed logs, and on volcanic rocks, rarely on soil. It is common in coniferous and broadleaf forests at middle elevations (1500-2900 m).

Distribution: Mexico (Chiapas, Chihuahua, Ciudad de México, Durango, Estado de México, Guerrero, Hidalgo, Jalisco, Michoacán, Nayarit, Oaxaca, San Luis Potosí, Veracruz, Zacatecas), Guatemala, Honduras, Costa Rica, Panama (De Luna, 2009). Fig. 8.

Illustrations: Hampe (1844, Icon. Musc. 19, as *Harrisonia squarrulosa*); Bartram (1949, p. 235, Fig. 106, A-C); Crum (1994, p. 666, Fig. g-i); De Luna (2009, Figs. 1-17); Fig. 9.

Selected specimens examined: MEXICO. Chiapas, 1 km above Aguacatenango, D. E. Breedlove 68944 (DUKE); 68973 (DUKE); 9 km südlich San Cristobal, R. Düll 8 (B, MO); NE of Cerro Boquerón, on road from El Rosario to Niquivil,

Figure 8: Distribution map of *Braunia squarrulosa* (Hampe) Müll. Hal. Each dot is one of the specimens listed in the text.

Figure 9: Morphological features of *Braunia squarrulosa* (Hampe) Müll. Hal. in Mexico. A. branch with sporophytes (A, from Dieterle 3192, DUKE, Mexico, Guerrero); B-D. vegetative leaves; E. apical leaf cells (B-E, from Schlechtendahl s.n., Herb. Hampe-BM, 1846, lectotype).

D. E. Breedlove 68923 (DUKE); 10 km NW of Comitán on side road to Zaragoza, *D. E. Breedlove* 70423 (DUKE); Laguna Chamula, between Amatenango and Comitán, *D. E. Breedlove* 70073 (DUKE); between Teopisca and Comitán, *J. P. Frahm* 79-2277 (B); along route 190, *F. J. Hermann* 26429 (BR, DUKE, NY); Lake Jusnájay, NW of Comitán, *A. J. Sharp* 3538 (DUKE). Chihuahua, 29 mi along road from San Francisco del Oro to Guadalupe y Calvo, *Kimnach and Brandt* 1040 (MEXU). Ciudad de México (formerly Distrito Federal), mountain Tlaxpehualco, 26.VIII.1926, *M. S. Antipovich s.n.* (MO); Cima, *C. G. Pringle* 10550 (BM, F, NY). Durango, near Puerto Buenos Aires, *D. E. Breedlove* 69154 (DUKE). Estado de México, Temascaltepec, *Dzieskanowski et al.* 2005 (BM, MO); Valle de Bravo, *R. Düll* 55a (JE). Guerrero, about 40 km W of Chilpancingo, *Dieterle* 3192 (DUKE, MO); about 30 km W of Chilpancingo, *A. J. Sharp* 1106 (MO, TENN). Hidalgo, Mineral del Monte, *Ehrenberg s.n.* (lectotype, BM); Jacala, *T. C. Frye and E. W. Frye* 2713 (DUKE, G). Jalisco, El Cuartón, above Manantlán, *H. A. Crum* 1175 (DUKE); Sierra Madre W of Bolaños, *Rose #e* (NY). Michoacán, vicinity of Morelia, Cerro Azul, *G. Arsène* 4536 (BM, F, MO), *G. Arsène* 4539 (BM, F); 4776 (DUKE); W of Ciudad Hidalgo, *C. Delgadillo* 457 (MEXU, XAL); Mil Cumbres, cerca de Puerto Garnica, 20 km al E de Morelia, *E. De Luna* 1772 (DUKE, XAL); 1777 (DUKE, XAL); Uruapan, *C. G. Pringle* 15085 (F, NY); San Miguel del Monte Morelia, 1908, *Solorzano s.n.* (JE). Nayarit, La Cienega, on ridge about 10 miles NW of Mesa del Nayar, *D. Norris and D. J. Taranto* 14452 (FLAS). Oaxaca, El Punto, NE of Oaxaca, *J. Conrad and R. Conrad* 3160 (DUKE); 23 km NE of Oaxaca, *C. Delgadillo* 628 (MEXU, XAL); al Este de Ixtlán, *C. Delgadillo* 709 (MEXU, XAL); Sierra de Juárez, *R. Düll* 66 (JE); La Cumbre, between Oaxaca and Ixtlán de Juárez, *A. J. Sharp et al.* 2609 (F); towards cerro San Felipe from Oaxaca, *A. J. Sharp* 4015 (DUKE, F). San Luis Potosí, Alvarez, *C. Orcutt* 6530 (F). Sinaloa, about 6 mi W of Las Palmitas, *D. Norris et al.* 20444 (BR). Veracruz, Tlacotepec near Huayacocotla, *G. Juárez* 1014 (XAL); Orizaba, *Liebmman s.n.* (lectotype BM, isolectotypes BM, NY). Zacatecas, municipio Chalchihuites, Gualterio, *A. Cárdenas* 1068 (MEXU, MICH, XAL).

Additional specimens examined: **COSTA RICA.** San José, Copey De Dota, *Fournier and Fournier* 1030b (USJ);

Valle de Copey, ca. 30 km S de Cartago, *D. Griffin and I. Morales B* 97 (NY); Copey De Dota, *I. Morales* 704 (USJ). **GUATEMALA.** No locality, *Kegel s.n.* (BM); 3/48, *Kegel* #10004 (syntypes BM, JE, NY); Huehuetenango, near Paquix, above Huehuetenango, *A. J. Sharp* 4766 (DUKE); N of Chiantla, *P. C. Standley* 82548 (NY); Quetzaltenango, mountains N of Olinstepeque, *P. C. Standley* 85220 (NY); cerro Pixpíx, above San Ildefonso Ixtahuacán, *J. A. Steyermark* 50604 (NY). **HONDURAS.** Lempira, Montaña de Celaque, Filo Seco, 13 km SW of Gracias, *B. Allen* 12095 (DUKE, MO). **PANAMA.** Chiriquí, E slope of volcán Chiriquí (Barú), WNW of Boquete, *G. Davidse and D'Arcy* 10190A (G, MO).

Discussion: a short seta (5-6 mm), globose, smooth-walled capsules, leaves wide spreading to squarrose, and multicellular spores help in distinguishing this from all other species in the genus. Without the sporophyte, the variability in leaf shape and leaf cells makes it difficult to identify it. In general, the leaves are more strongly plicate, the leaf base is broader, the acumen is slender, long cuspidate, and the apical cells are narrower in *B. squarrolosa* than in *B. secunda* and *Hedwigidium imberbe*. These differences are more evident when comparing juvenile leaves in the three species.

Author contributions

EDL conceived and designed the study, wrote the manuscript, reviewed, and approved the final version.

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