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Goniothalamus flagellistylus Tagane & V. S. Dang (Annonaceae), a new species from Mt. Hon Ba, Vietnam

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Abstract

A new species, *Goniothalamus flagellistylus* Tagane & V. S. Dang, **sp. nov.** from Hon Ba Nature Reserve in Khanh Hoa Province, South Vietnam is described and illustrated. This species is most similar to *Goniothalamus tortilipetalus* M.R.Hend., but distinct in having 308–336 stamens (vs. ca. 170–260) and ca.120 carpels (vs. ca. 50–100) per flower, and Stigma and pseudostyles ca.8.5 mm (vs. 4–4.5 mm) long.

Keywords

Annonaceae, *Goniothalamus*, Hon Ba Nature Reserve, Vietnam

Introduction

The genus *Goniothalamus* (Blume) Hook. f. & Thomson, with more than 130 species (Nakkhuntod et al. 2009, Tang et al. 2013), is one of the largest genera in the Annonaceae family. The species is characterized by mostly solitary, axillary and pendent flowers, two whorls of petals with inner petals smaller than the outer ones, the inner petals connivent and forming a distinctive dome over the stamens and carpels acting as a pollination chamber and stamens having apical connectives. Most species

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of *Goniothalamus* are distributed in lowland evergreen rain forests in Southeast Asia, extending from India to Australia, also in New Caledonia (Jessup 1986, Mat-Salleh 2001, Saunders 2002, Saunders 2003, Kundu 2006, Saunders and Munzinger 2007, Saunders and Chalermglin 2008, Turner and Saunders 2008). In Vietnam, the following 19 species of *Goniothalamus* are recorded: *G. chartaceus* H.L.Li, *G. chinensis* Merr. & Chun, *G. donnaiensis* Finet & Gagnep., *G. elegans* Ast, *G. expansus* Craib, *G. gabriacianus* (Baill.) Ast (Synonym, *Goniothalamus saigonensis* Pierre ex Finet & Gagnep.), *G. gracilipes* Bân, *G. laoticus* (Finet & Gagnep.) Bân, *G. macrocalyx* Bân, *G. multiovulatus* Ast, *G. ninhianus* Bân, *G. takhtajanii* Bân, *G. tamirensis* Pierre ex Finet & Gagnep., *G. tenuifolius* King, *G. touranensis* Ast, *G. undulatus* Ridl., *G. vietnamensis* Bân, *G. wightii* Hook.f. & Thomson and *G. yunnanensis* W.T.Wang (Finet and Gagnepain 1907, Hô 1999, Bân 2000).

During the botanical survey of Hon Ba Nature Reserve in South Vietnam, we encountered an undescribed species of *Goniothalamus* in Mt. Hon Ba at 400 m elevation. We here describe and illustrate this new species, *Goniothalamus flagellistylus* Tagane & V. S. Dang, sp. nov.

Materials and methods

Morphological observations

In order to verify the validity of this new species we undertook a thorough literature review, consulted specimens from the following herbaria FU, BKF, KYO, MBK and VNM, as well as online digitized plant specimens (e.g. JSTOR Global Plants).

The thickness of leaves, sepals and petals was measured using a digital caliper (Absolute Digimatic 547-401, Mitutoyo, Japan, resolution 0.001 mm).

DNA barcoding

For DNA isolation, leaf material was collected and desiccated using silica gel in the field. DNA was extracted using a modified CTAB method in which silica-dried leaves were ground in a TissueLyser (QIAGEN), and the powder washed five times with 1 mL buffer (0.1 M HEPES, pH 8.0; 2% mercaptoetanol; 1% PVP; 0.05 M ascorbic acid) before DNA extraction. We sequenced the partial genes for the large subunit ribulose-1,5-bisphosphate carboxylase oxygenase (*rbcL*) and maturase K (*matK*), following published protocols (Kress et al. 2009; Dunning and Savolainen 2010).

Taxonomy

***Goniothalamus flagellistylus* Tagane & V. S. Dang, sp. nov.**
urn:lsid:ipni.org:names:77147106-1
Figs 1, 2

Diagnosis. Similar to *Goniothalamus tortilipetalus* M.R.Hend., but differing from that species in having 308–336 stamens (vs. ca. 170–260) and ca.120 carpels (vs. ca. 50–100) per flower, and stigmas and pseudostyles ca.8.5 mm (vs. 4–4.5 mm) long.

Type. Vietnam, Khanh Hoa Province, Hon Ba Nature Reserve, in evergreen forest near stream, 12°06.51'N, 108°59.23'E, alt. 400 m, *Tagane S., Kanemitsu H., Dang V.S., Tran H. with Hanh N., Loi X.N., Thach N.D., Dinh N., Hieu P.N.H. V1497*, 12 July 2014, Fl., holotype: KYO!; isotypes: BKF!, FU!, K!, VNM!, the herbarium of Hon Ba Nature Reserve!).

Description. Small trees, 11 m tall, DBH 8 cm. Young twigs sparsely covered with brown hairs, soon glabrous, blackish when dry. Petioles 1–1.2(–1.5) cm long, 2.5–3.5 mm in diam., glabrous, black when dry. Leaf blades narrowly oblong-elliptic, 31–45 × 8.2–11.5 cm, length/width ratio 2.7–4.0, 185–225 µm thick, base acute to obtuse, margin entire, revolute when dry, apex acuminate, acumen ca. 1.5 cm long, leathery, slightly shiny above, glabrous on both surfaces; midribs impressed above, prominent below, glabrous on both surfaces, secondary veins 16–20 pairs, arising at an angle of 60–70 degrees from a midrib, prominent on both surface when dry, glabrous on both surfaces, tertiary veins distinct above, slightly distinct below. Flowers solitary, arising from main trunks and older branches, pendent; pedicels 19–25 mm long, 1.5–2.5 mm in diam., glabrous; bracts 3–4, very broadly triangular to hemiorbicular, ca. 1.6 mm long, brownish pubescent outside, glabrous inside, margin sometimes ciliate. Sepals ovate-triangular, 2.2–2.8 × 2.2–2.8 cm in flower, accrescent, increasing to 3.3 × 3.8 cm in fruit, 200–210 µm thick, basally connate, greenish in vivo, glabrous outside, sparsely covered with brown hairs inside, veins reticulated, distinct outside, indistinct inside. Outer petals oblong-ovate to narrowly ovate, 6–9. 2 × 2.2–3.1 cm, length/width ratio 2.7–3.4, 380–450 µm thick, greenish, glabrescent outside, sparsely covered with short brown hairs inside, except at base velutinous, veins faintly visible outside, indistinct inside. Inner petals rhombic, 1.6 × 0.7 cm, length/width ratio ca. 1.9, 1100–2100 µm thick, greenish, pubescent outside, velutinous inside with 12–14 basal grooves. Stamens 308–336 per flower, flattened-oblong, 3.8–4.8 × 0.6 mm, glabrous; connectives long-apiculate, 1.2–1.5 mm long, apiculate length 0.5–0.9 mm long, densely covered with cream-white hairs. Carpels ca. 120 per flower; ovary 1.4–1.7 × ca. 0.3 mm, densely covered with golden-brown hairs; stigmas and pseudostyles flagellate, ca.8.5 mm long, L-shaped curved in the middle, yellowish in vivo, blackish when dry, glabrous, tip awl-shaped. Fruits with persistent calyx, fruiting pedicels 2.7 cm long, 3–4.5 mm in diam. Monocarps 22, ellipsoid, 1.6–1.7 cm long, ca. 1.0 cm in diam., base attenuate, apex apiculate, glabrous, reddish-brown, pericarp ca. 0.5 mm thick when dry; stipes 0.6–1.2 mm long, ca. 2 mm in diam., glabrous. Seeds one per

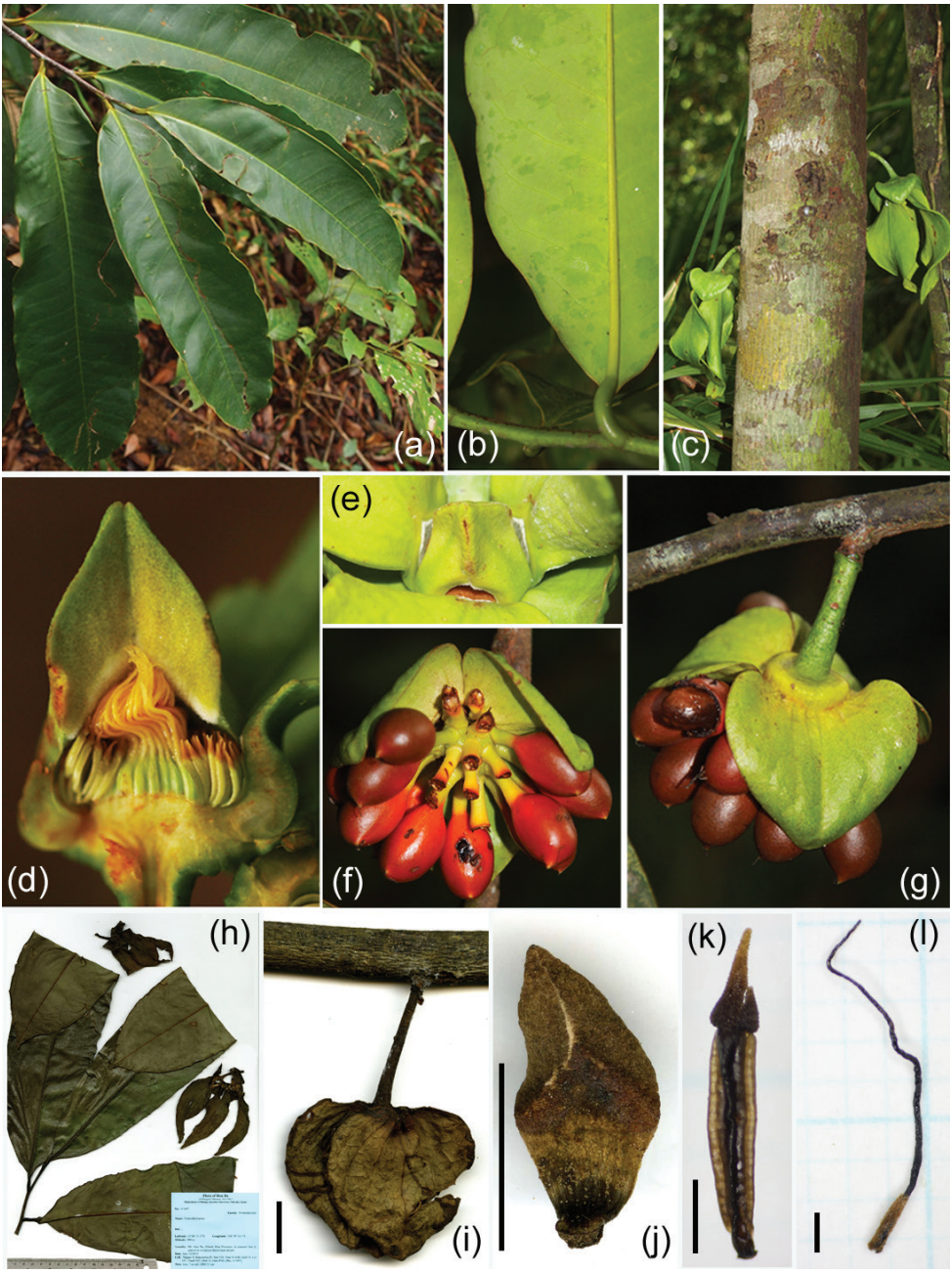

Figure 1. *Goniothalamus flagellistylus* sp. nov. (**a**) Leafy branch, (**b**) portion of abaxial leaf surface, (**c**) flowers on main trunk, (**d**) vertical section of flowers, (**e**) apertures between inner petals, (**f–g**) mature fruit on older blanch, (**h**) holotype, (**i**) pedicel and sepals on old branch, (**j**) adaxial side of inner petal, (**k**) stamen, (**l**) carpel. (**h–l**) From *Tagane et al. 1497*. Scale bars (**i**, **j**) = 1 cm, (**k, l**) = 1 mm.

monocarp, 1.5 cm long, 0.8–1.0 cm in diam., yellowish brown, glabrous, seeds with copious surrounding mucilage.

Phenology. Mature flowers and fruits were collected in July and November, respectively.

Distribution and habitat. This species is known only from Mt. Hon Ba, Khanh Hoa Province, South Vietnam. The small population was found on a slope in broad-leaved evergreen forest, ca. 100 m apart from a rapid river, where *Ixonanthes reticulata* Jack, *Palaquium* sp., *Gironniera subaequalis* Planch., *Archidendron chevalieri* (Kosterm.) I.C.Nielsen, *Barringtonia augusta* Kurz, *Barringtonia macrostachya* (Jack) Kurz, *Camellia krempfii* (Gagn.) Sealy, *Streblus indicus* (Bureau) Corner, *Xerospermum noronhianum* Blume and *Pandanus fibrosus* Gagnep. are dominated.

Other specimen examined. Vietnam, Khanh Hoa Province, Hon Ba Nature Reserve, in evergreen forest near stream, 12°06.51'N, 108°59.23'E, alt. 400 m, *Toyama H., Tagane S., Dang V.S., Nagamasu H., Naiki A., Tran H., Yang C.J. with Cuong N.Q., Hieu H.N.P. V1972*, 22 November 2014, Fr. (FU!, KYO!, NTU!, VNM!, the herbarium of Hon Ba Nature Reserve!).

Etymology. The specific epithet is in reference to its flexuous styles which is too long to insert straight in the pollination chamber that formed by the inner petals.

GeneBank accession No. *Tagane et al. V1497*: LC010815 (*rbcL*), LC010816 (*matK*).

Similar species. *Goniothalamus flagellistylus* is morphologically similar to *G. calvicarpus* Craib, *G. griffithii* Hook.f. & Thomson, and *G. tortilipetalus*, all of which form a monophyletic group (Nakkuntod et al. 2009) and are characterized by relatively large sepals with distinct veins and stamens with long apiculate connectives (Saunders and Chalermglin 2008). Among the three species, *G. flagellistylus* is most similar to *G. tortilipetalus*, which is distributed in the Malay Peninsula, in having more than 200 stamens and more than 50 carpels. In fact, The BLAST similarity search based on the *matK* sequence of *G. flagellistylus* resulted in homology as high as 734/736 bp with the sequence of *G. tortilipetalus* (GeneBank accession no. EU715081) in the DNA database. However, as described in the diagnosis above, the two species can be easily distinguished by the number of stamens and carpels per flower, and style length (Table 1). Also, *G. flagellistylus* is different from *G. tortilipetalus* in that flowers arise not only from the main trunk but also from the older branches as in *G. calvicarpus* and *G. griffithii* (Saunders and Chalermglin 2008).

Conservation status. Data deficient. *Goniothalamus flagellistylus* is known from a single population, including only six individuals: only one produces flowers/fruits while the others are just saplings. This situation satisfies the CR (critically endangered) status in criterion D of IUCN Red List Categories (IUCN 2014). However, more individuals could be found if neighboring areas are more thoroughly surveyed. Thus, we regard the conservation status as DD. In Mt. Hon Ba, large areas of primary evergreen forest below 300–400 m elevation had been cleared or selectively logged before the Hon Ba Nature Reserve established, and it is likely that some habitats of this species were lost. The forest habitat where we found *G. flagellistylus* remains less disturbed

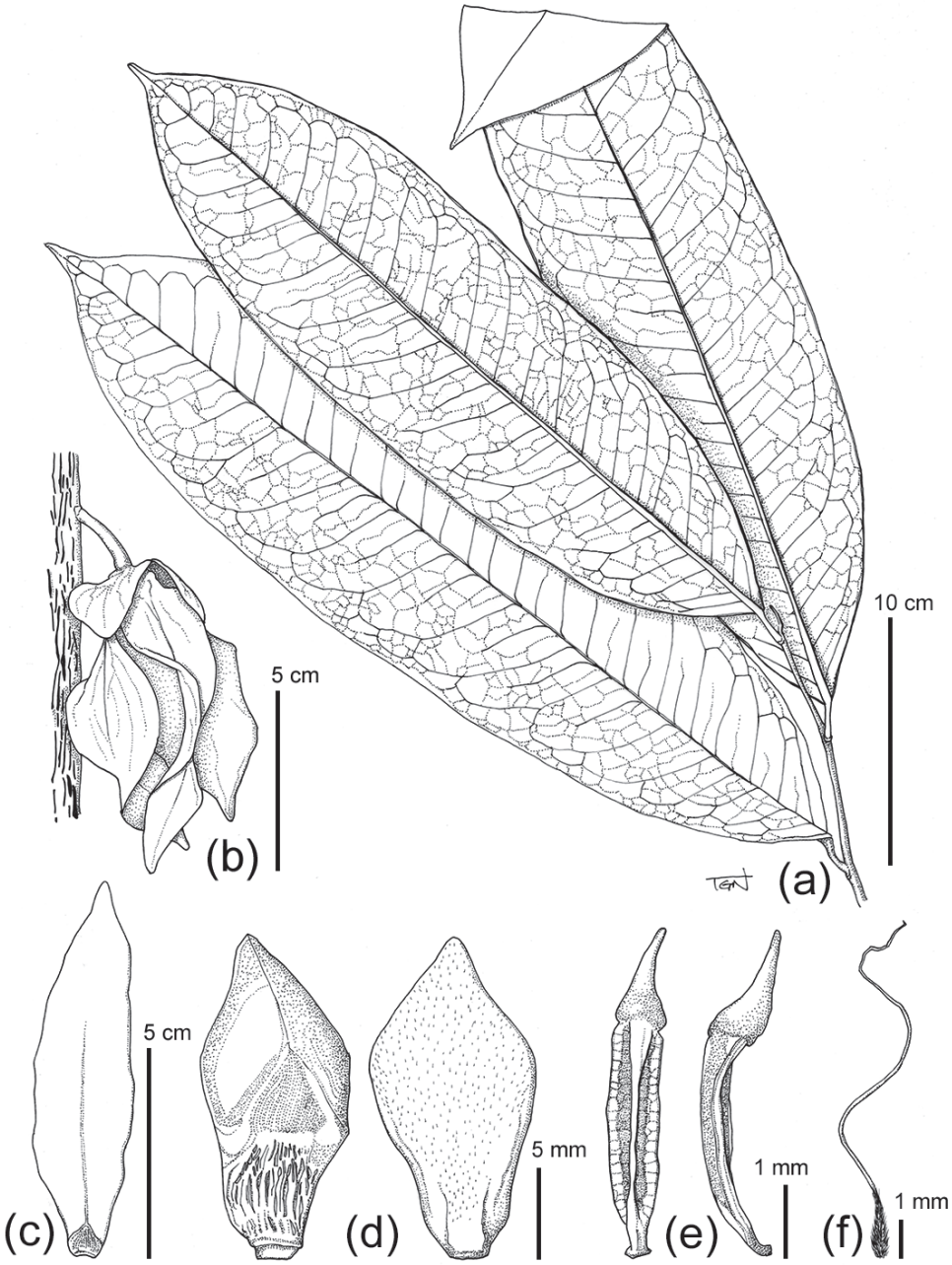

Figure 2. Line drawing of *Goniothalamus flagellistylus* sp. nov. (**a**) leafy twig, (**b**) flower on main trunk, (**c**) outer petal (adaxial), (**d**) inner petals (ad- and abaxial), (**e**) Stamens, (**f**) Carpel. Materials from *Tagane et al. V1497*.

Table 1. Morphological comparison between *Goniothalamus flagellistylus* sp. nov. and *G. tortilipetalus* (modified from Henderson 1933; Saunders 2003; Saunders and Chalermglin 2008).

Characters	*G. flagellistylus*	*G. tortilipetalus*
Flowers position	On main trunk and older branches	On main trunk only
Pedicel length	19–25 mm	20–37 mm
Sepals in flowering	22–28 by 22–28 mm	19–31 by 15–26 mm
Outer petals	60–92 by 22–31 mm	35–100 by 10–25 mm
Inner petal length/width ratio	1.9	2.2–3.1
Stamen number per flower	308–336	~170–260
Carpel number per flower	120	~50–100
Stigmas and pseudostyles	ca. 8.5 mm long	4–4.5 mm long
Ovary indument	densely hairy	(Very) densely hairy

under a lower level of logging activities probably because of its landform of the steep slope near the rapid river. The forest in this Nature Reserve is currently protected well from anthropogenic activities, and recovering better and better. The current data available are not enough for a risk evaluation, we therefore need special attention to the individuals/populations of *G. flagellistylus* and its distribution.

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References

Bân NT (2000) Thực vật chí Việt Nam, Vol. 1. Science and Technics Publishers, Hanoi.

Dunning LT, Savolainen V (2010) Broad-scale amplification of matK for DNA barcoding plants, a technical note. Botanical Journal of the Linnean Society 164: 1–9. doi: 10.1111/j.1095-8339.2010.01071.x

Finet AE, Gagnepain F (1907) *Goniothalamus*. In: Lecomte H, Gagnepain F (Eds) Flore générale de l'Indo-Chine. Masson, Paris, 1, 86–90.

Henderson MR (1927) Additions to the flora of the Malay Peninsula. Gardens' Bulletin, Straits Settlements, Series 3(7): 87–127.

Hô PH (1999) Cay Co Viet Nam: An Illustrated Flora of Vietnam Vol. 1. Published by the author Montreal.

IUCN (2014) The IUCN Red List of Threatened Species. Version 2014.3. http://www.iucnredlist.org [accessed 30.01.2015]

Jessup LW (1986) The genus *Goniothalamus* (Blume) JD Hook. & Thomson (Annonaceae) in Australia. Austrobaileya 2(3): 224–226.

Kress WJ, Erickson DL, Jones FA, Swenson NG, Perez R, Sanjur O, Bermingham E (2009) Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. Proceedings of the National Academy of Sciences of the United States of America 106(44): 18621–18626. doi: 10.1073/pnas.0909820106

Kundu SR (2006) A synopsis of Annonaceae in Indian subcontinent: Its distribution and endemism. Thaiszia Journal of Botany 16: 63–85.

Mat-Salleh K (2001) New and noteworthy species of Bornean *Goniothalamus* (Annonaceae). Folia Malaysiana 2: 75–116.

Nakkuntod M, Su YC, Seelanan T, Saunders RMK (2009) Molecular phylogenetic and morphological evidence for the congeneric status of *Goniothalamus* and *Richella* (Annonaceae). Taxon 58(1): 127–132.

Saunders RMK (2002) The genus *Goniothalamus* (Annonaceae) in Sumatra. Botanical Journal of the Linnean Society 139(3): 225–254. doi: 10.1046/j.1095-8339.2002.00061.x

Saunders RMK (2003) A synopsis of *Goniothalamus* species (Annonaceae) in Peninsular Malaysia, with a description of a new species. Botanical Journal of the Linnean Society 142(3): 321–339. doi: 10.1046/j.1095-8339.2003.00177.x

Saunders RMK, Chalermglin P (2008) A synopsis of *Goniothalamus* species (Annonaceae) in Thailand, with descriptions of three new species. Botanical Journal of the Linnean Society 156(3): 355–384. doi: 10.1111/j.1095-8339.2007.00762.x

Saunders RMK, Munzinger J (2007) A new species of *Goniothalamus* (Annonaceae) from New Caledonia, representing a significant range extension for the genus. Botanical Journal of the Linnean Society 155(4): 497–503. doi: 10.1111/j.1095-8339.2007.00718.x

Tang CC, Xue B, Saunders RMK (2013) A new species of *Goniothalamus* (Annonaceae) from Palawan, and a new nomenclatrual combination in the genus from Fiji. Phytokes 32: 27–35. doi: 10.3897/phytokeys.32.6663

Turner I, Saunders RMK (2008) Four new species of *Goniothalamus* (Annonaceae) from Borneo. Nordic Journal of Botany 26: 329–337. doi: 10.1111/j.1756-1051.2008.00359.x

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SHORT COMMUNICATION

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Lectotypification of names of Himalayan Brassicaceae taxa currently placed in the genus *Cardamine*

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Abstract

Lectotypes of twenty-eight names of taxa currently recognized or synonymized in *Cardamine* are designated as part of the work on the account of the genus for the Pan-Himalayan Flora. Among them, the previous first-step lectotypification of the name *C. calthifolia* is finalized. In cases when specimen images are available online, stable identifiers for specimens, other permanent links, or links via JSTOR Global Plants are provided.

Keywords

Cardamine, Himalaya, nomenclature, stable identifiers for specimens, taxonomy, typification

Introduction

During the work by the last author on the Brassicaceae (Cruciferae) account for the Pan-Himalayan Flora (PHF), it became evident that the majority of accepted names and their synonyms in that flora require lectotypification. The present paper focuses on the lectotypification of names of taxa currently placed in *Cardamine* L., a genus with 43 species in the PHF.

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Materials and methods

Herbarium specimens, especially types and authentic collections, deposited at B, BM, E, F, G, GH, K, LE, MO, NAS, NY, P, US, W, and WU were examined during the past two decades. In cases when specimen images are available online, stable identifiers for specimens (Hyam et al. 2012, Güntsch and Hagedorn 2013, Hagedorn et al. 2013; in the case of specimens from herbaria B, E, K), other permanent links (herbaria W, WU, see JACQ Consortium 2004 onwards; F, MO, P) or links via JSTOR Global Plants (https://plants.jstor.org/; herbaria BM, GH, NY, US) are provided. We suggest that the practice of providing stable indentifiers or other kind of permanent links to images of herbarium specimens should be adopted as standard one for lectotypification papers. It will make eventual registration or evidence of designated types much easier. The bibliographical citations in the original publications and databases such IPNI (The International Plant Names Index; http://ipni.org/), Tropicos (http://www.tropicos.org/), and The Plant List (http://www.theplantlist.org/) were also checked.

In lectotypifying names of taxa, we strictly followed the International Code of Nomenclature for algae, fungi, and plants (McNeill et al. 2012) and the recommendations recently presented by McNeill (2014). In cases where a single specimen is known that was used by the describing author and no duplicates were found or were not expected to exist, that particular specimens is considered a holotype, provided that it meets the criteria given in the publications above. In cases where one or more duplicates of the type collection exist (or possibly or likely existed) or more than one syntype was cited in the original publication, we first checked the material housed in the institution where the author(s) of the name worked. For example, for taxa described by Adrien René Franchet, Joseph Dalton Hooker, and Otto Eugen Schulz, we first checked the material deposited in the herbaria P, K, and B, respectively. The best of all duplicates that do not contradict the protologue or the guidelines in the *Code* is designated as the lectotype. If the home institution of the author of the name does not have any original material and no herbarium was cited, we put emphasis on the material annotated by that name author. If none of the above cases applies, the designation was based on the best representative material.

Entries are arranged alphabetically by their basionyms, and names in boldface are those of currently accepted names of taxa. Bibliographic citations are given for all names and only examined and designated lectotypes and their duplicates are listed. Barcode numbers of lectotypes and isolectotypes are given (if available) following the herbarium acronym.

Results

The type status of the following names of taxa is determined, and justifications for their typification is presented.

1. *Cardamine brachycarpa* Franch., Bull. Soc. Bot. France 26: 83. 1879, nom illeg. (http://ipni.org/urn:lsid:ipni.org:names:280196-1:1.4), non Opiz, Naturalientausch 11: 411. 1826 (http://ipni.org/urn:lsid:ipni.org:names:280195-1:1.3). Described from: [JAPAN] "Insul. Nippon, prov. Etchigo, circa Niigata, secus vias humidas (R. P. Faurie)". Lectotype (designated here): [JAPAN, Prefecture Niigata], "Nippon, Niigata, secus vias, [*U. J.*] *Faurie 23*" – P! (P00747512 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747512]); Isolectotype – P! (P00747513 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747513]). = ***Cardamine flexuosa*** subsp. ***debilis*** O.E.Schulz

Franchet (1879) cited only one unnumbered collection, but the only specimens at P that carry the name and exact locality information as given in the protologue are numbered [*U. J. or R. P.*] *Faurie 23*. The duplicate annotated with the species name in Franchet's handwriting is designated here as the lectotype.

2. ***Cardamine calthifolia*** H. Lév., Bull. Géogr. Bot. 24: 281. 1914 (http://ipni.org/urn:lsid:ipni.org:names:280217-1:1.1.2.1.1.3). Described from: [CHINA, Yunnan] "Vallée de Kiao-Mé-Ti, 3000 m., mai 1913". Lectotype [designated here (second step lectotypification after Lauener 1965: 336)]: [CHINA, Yunnan] "vallée de Kiao-mé-ti, 3000 m, *E. E. M*[*aire*] *s.n.*" – E! (E00154675 [http://data.rbge.org.uk/herb/E00154675]); Isolectotypes – E! (E00083337 [http://data.rbge.org.uk/herb/E00083337]), P! (P00747535 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747535]).

A single collection was cited in the protologue of the name, but none of the three duplicates mentioned above carry the species name nor were they annotated by Hector Léveillé. Lauener (1965) indicated that the type is at E, but he did not specify which of the two sheets there is the type, and therefore a second-step lectotypification is provided here.

3. ***Cardamine circaeoides*** Hook.f. & Thomson, J. Proc. Linn. Soc., Bot. 5: 144. 1861 (http://ipni.org/urn:lsid:ipni.org:names:280232-1:1.1.2.1.1.3). Described from: [INDIA] "In Himalaya orientali temperata, Sikkim interiore, sylvis, alt. 5000-7000 ped. ! J. D. H. (v.v.)". Lectotype (designated here, or perhaps holotype): [Label 1]: [INDIA] "Hab. Sikkim, Regio temp., *J. D. H*[*ooker*]"; [Label 2]: [INDIA] "295 Hab. wet wood, Gohsun, Sikkim, 5000 ft." – K! (K000077050 [http://specimens.kew.org/herbarium/K000077050]); Doubtful isolectotypes – B! (B 10 0386925 [http://herbarium.bgbm.org/object/B100386925]), P! (P00747534 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747534]).

The K specimen above was collected at an elevation of 5,000 ft, which is in agreement with the protologue, whereas labels of the B and P sheets indicate the elevation of

6,000−10,000 ft. It is questionable whether the three specimens above were collected from the same area, and that is why we feel that the B and P specimens are doubtful isolectotypes.

4. ***Cardamine delavayi*** Franch., Bull. Soc. Bot. France 33: 397. 1886 (http://ipni.org/urn:lsid:ipni.org:names:280264-1:1.4). Described from: [CHINA], "Yun-nan, ad fontes prope Mo-so-yun, haud procul a Lankong; fl. fr. immat., 2 april. 1885 (Delav. n. 1838)". Lectotype (designated here): [CHINA] [Label 1, printed] "Plantes de Chine, Province du (Yun-nan)" [Label 2, written] "… fontes prés de Mo-so-yun (Lan Kong), 2 avril 1885, *J. M. Delavay 1838*" – P! (P00279370 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00279370]); Isolectotypes – P! (P00747533 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747533]), US! (US00324476 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.us00324476]).

A single collection was cited in the original publication of this species, but the existence of two duplicates of the same collection at P and one in US annotated by Franchet calls for lectotypification, which is done here.

5. ***Cardamine elegantula*** Hook.f. & Thomson, J. Proc. Linn. Soc., Bot. 5: 146. 1861 (http://ipni.org/urn:lsid:ipni.org:names:280285-1:1.1.2.1.1.3). Described from: [BHUTAN] "In Himalaya temperata orientali, Bhotan ! alt. 6500 ped., Griffith". Lectotype (here designated): "[BHUTAN] "Bhotan", 1838, [*W.*] *Griffith 1360*" – K! (K000247218 [http://specimens.kew.org/herbarium/K000247218]); Isolectotypes – B! (B 10 0241392 [http://herbarium.bgbm.org/object/B100241392]), P! (P05036298 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p05036298]).

Two collection numbers by William Griffith from Bhutan, *Griffith 1360* and *Griffith 1756*, are mounted on the same sheet at K. The latter collection carries no determination and is attached by two pins to the sheet of the former collection, whereas the lectotype designated here carries Hooker's determination as "Card. elegantula Hf. & T.", has well-developed fruits and is represented by duplicates at B and P.

6. *Cardamine hirsuta* var. *flaccida* Franch., Bull. Soc. Bot. France 33: 398. 1886. Described from: [CHINA] "Yun-nan in umbrosis et humidis ad Mo-so-yn, prope Lankong; fl. fr., 14 mart. 1885 (Delav. n. 1839)". Lectotype (designated here): "CHINA, Yun-nan, Lieux humides et ombragés à Mo-so-yn, (Lan Kong), 14 Mart 1885, *J. M. Delavay 1839*" – P! (P00747528 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747528]); Isolectotypes – E! (E00154697 [http://data.rbge.org.uk/herb/E00154697]), K! (K000697728 [http://specimens.kew.org/herbarium/K000697728]), P! (P00250221 [http://coldb.mnhn.fr/catalognum-

ber/mnhn/p/p00250221], P00250222 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00250222], P00279384 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00279384], P000747522 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p000747522]), US! (US00100035 [https://plants.jstor.org/stable/10.5555/al.ap.specimen.us00100035]). = ***Cardamine flexuosa*** subsp. ***debilis*** O.E.Schulz

Five duplicates of the type collection of *Cardamine hirsuta* var. *flaccida* are housed at P, and the most complete specimen with Franchet's annotation is designated here as the lectotype.

7. *Cardamine insignis* O.E.Schulz, Bot. Jahrb. Syst. 32: 439. 1903 (http://ipni.org/urn:lsid:ipni.org:names:280398-1:1.4). Described from: "China australis: prov. Yunnan in silvis 2000 m leg. A. Henry n. 13090 (H. B. [B])". Lectotype (designated here, or perhaps holotype): [CHINA] "Yunnan, N. Szemao, 6,000 ft., *A. Henry 13090*". – B! (B 10 0386926 [http://herbarium.bgbm.org/object/B100386926]); Isolectotypes – E! (E00154731 [http://data.rbge.org.uk/herb/E00154731]), K! (K000697718 [http://specimens.kew.org/herbarium/K000697718]), MO! (357226 [http://www.tropicos.org/Specimen/2035994]). = ***Cardamine circaeoides*** Hook.f. & Thomson (http://ipni.org/urn:lsid:ipni.org:names:280232-1:1.1.2.1.1.3).

Schulz (1903) listed a single collection in the protologue and cited only the herbarium B. Currently there is only one specimen of this collection at B. Nevertheless, as considerable part of the Berlin herbarium was destroyed in 1943, we cannot exclude that there was originally more than one specimen of this collection at B in the past. To be on the safe side, extant specimen is treated here as "lectotype, or perhaps holotype."

8. *Cardamine macrophylla* var. *dentariifolia* Hook.f. & T.Anderson, Fl. Brit. India 1: 139. 1872. Described from: [CHINA] "From Kumaon to Kashmir". Lectotype (designated here): [INDIA, Uttarakhand], "Hab. Himal. Bor. Occ., Regio Temp., *T. T.* [*T. Thomson*] *s.n.*" – K! (K000397478 [http://specimens.kew.org/herbarium/K000397478]). = ***Cardamine macrophylla*** Willd. (http://ipni.org/urn:lsid:ipni.org:names:280460-1:1.1.5.1.1.1).

9. *Cardamine macrophylla* var. *foliosa* Hook.f. & T.Anderson, Fl. Brit. India 1: 139. 1872. Described from: [INDIA] "Wall. Cat. 4779.— Kumaon and Kashmir". Lectotype (designated here): [INDIA, Uttarakhand], "Kamoon [Kumaon], Wall. Cat. 4779, *R.B.* [Robert Blinkworth] *s.n.*" – K! (K000247365 [http://specimens.kew.org/herbarium/K000247365]); Isolectotypes – B! (B 10 0241370 [http://herbarium.bgbm.org/object/B100241370], B 10 0241369 [http://herbarium.bgbm.

org/object/B100241369]), P! (P00747537 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747537]). = ***Cardamine macrophylla*** Willd. (http://ipni.org/urn:lsid:ipni.org:names:280460-1:1.1.5.1.1.1).

10. *Cardamine macrophylla* var. *lobata* Hook.f. & T.Anderson, Fl. Brit. India 1: 139. 1872. Described from: [INDIA] "Kashmir, 6000 ft.; Western Tibet, 13,000 ft." Lectotype (designated here): [INDIA] [Label 1]: "marshy meadows, Nira Zanskar, 12,900 ft, 2 July 1849 [?]", [Label 2]: "Hab. Himal. Bor. Occ., W. Tibet, Regio Temp., Alt. 12,900 ft, *T. T.* [*T. Thomson*] *s.n.*" – K! (K000397477 [http://specimens.kew.org/herbarium/K000397477]). = ***Cardamine macrophylla*** Willd. (http://ipni.org/urn:lsid:ipni.org:names:280460-1:1.1.5.1.1.1).

11. *Cardamine macrophylla* var. *sikkimensis* Hook.f. & T.Anderson, Fl. Brit. India 1: 139. 1872. Described from: "Inner ranges of Sikkim, 7,000-13,000 ft.". Lectotype (designated here): [INDIA], [Label 1]: "Lachomy, 12,000 ft, 3 September 1849", [Label 2]: "Hab. Sikkim, Regio Alp. Temp. *J. D. H.* [*Hooker*] *s.n.*" – K! (K000397479 [http://specimens.kew.org/herbarium/K000397479]); Isolectotypes – K! (K000397480 [http://specimens.kew.org/herbarium/K000397480], K000397481 [http://specimens.kew.org/herbarium/K000397481]). = ***Cardamine macrophylla*** Willd. (http://ipni.org/urn:lsid:ipni.org:names:280460-1:1.1.5.1.1.1).

Hooker and Anderson (1872) divided *Cardamine macrophylla* into four numbered varieties: "1. *dentarifolia*", "2. *foliosa*", "3. *lobata*", and "4. *sikkimensis*". The sheets at K are annotated by Hooker as "*C. macrophylla*, Willd." followed by α, β, γ, and δ. These clearly correspond to the numbers 1 to 4 cited in the above reference, respectively. The sheets best matching the descriptions of the above four varieties are designated as lectotypes.

12. *Cardamine macrophylla* var. *moupinensis* Franch., Pl. David. 2: 18. 1888. Described from: "Moupine, in umbrosis monatis. Fl. April. 1869". Lectotype (designated here): [CHINA], [Label 1 (handwritten)]: "Moupin, Thibet oriental, lieux frais en montagne, Avril 1869", [Label 2 (printed)] "Chine (Thibet Oriental), Province de Moupin, 1870 [sic!], *David s.n.*" – P! (P00747519 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747519]); Isolectotype – P! (00747518 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747518]). = ***Cardamine macrophylla*** Willd. (http://ipni.org/urn:lsid:ipni.org:names:280460-1:1.1.5.1.1.1).

The more complete specimen of the two P duplicates of the type collection is designated here as the lectotype. There is a single plant on the sheet and it seems that the year on the printed label is either a typing error or the date of accession at P.

13. ***Cardamine microzyga*** O.E.Schulz, Bot. Jahrb. Syst. 32: 545. 1903 (http://ipni.org/urn:lsid:ipni.org:names:280483-1:1.4). Described from: [CHINA] "Asia centralis ad fines prov. Tibet et West-Szechuen pr. Tachienlu 3000-4500 in leg. A. E. Pratt n. 265 ante 1890 (H. B. [B])". Lectotype (designated here, or perhaps holotype): [CHINA] "West Sichuan and Tibetan Frontier, chiefly near Tachienlu, at 9000-13,500 ft, purchased December 1890, *A. E. Pratt 265*" – B! (B 10 0386913 [http://herbarium.bgbm.org/object/B100386913]); Isolectotype – K! (K000077046 [http://specimens.kew.org/herbarium/K0000046]).

Schulz (1903) listed a single collection in the protologue and cited only the herbarium B. Currently there is only one specimen of this collection at B. Nevertheless, as considerable part of the Berlin herbarium was destroyed in 1943, we cannot exclude that there was originally more than one specimen of this collection at B in the past. To be on the safe side, as in the case of the type of the name *C. insignis* dealt with above, extant specimen is treated here as "lectotype, or perhaps holotype". When publishing the name *C. prattii*, Hemsley and Wilson (1906: 153), included in the circumscription of the taxon to which it was applied the only element mentioned in the protologue of *C. microzyga* (namely collection *A. E. Pratt 265*), making the name *C. prattii* illegitimate (under Art. 52 of the *Code*, McNeill et al. 2012). Therefore, *C. prattii*, following the Art. 7.5 of the *Code*, should be automatically typified by the type of the name *C. microzyga*.

14. ***Cardamine multijuga*** Franch., Bull. Soc. Bot. France 33: 399. 1886 (http://ipni.org/urn:lsid:ipni.org:names:280497-1:1.4). Described from: [CHINA] "Yunnan, in aquosis ad Mo-so-yn, prope Langkong; fl. 28 jun. 1884 (Delav. n. 697)". Lectotype (designated here): [CHINA, Yunnan] "Les fossés à Mo-so-yun (Lan Kong), 28 Juin 1884, *J. M. Delavay 697*" – P! (P00279390 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00279390]); Isolectotypes – BM!, E! (E00154552 [http://data.rbge.org.uk/herb/E00154552]), GH! (GH00112040 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00112040]), K! (K000697737 [http://specimens.kew.org/herbarium/K000697737], K000697738 [http://specimens.kew.org/herbarium/K000697738]), NY! (NY00468267 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.ny00468267]), P! (P00747516 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747516], P00747517 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747517]), US! (US00100044 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.us00100044], US01100650 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.us01100650]). ≡ *C. griffithii* subsp. *multijuga* (Franch.) O.E.Schulz.

A single collection was cited by Franchet (1886), and the best duplicate at P that he annotated is designated here as the lectotype.

15. *Cardamine multijuga* var. *gracilis* O.E.Schulz, Repert. Spec. Nov. Regni Veg. 17: 289. 1921. Described from: "China: Prov. Yunnan, im Gebiete Lichiang beim Dorfe Ugu leh keh an einem Sumpfe, ca. 2900 m ü. M. (Camillo Schneider, It. chin. 1914, no. 1862 – Mitte Juli in Blüte, Blumen weib-lila, hb. Berlin [B]". Lectotype (designated here, or perhaps holotype): "CHINA, Yunnan: in reg. Lichiang prope pagum Ngu leh tseh, ad stagnum. 18 Jul. 1914, Alt. circiter 2900, *Camillo Schneider 1862*" – B! (B 10 0386915 [http://herbarium.bgbm.org/object/B100386915]); Isolectotypes – GH! (GH00142216 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00142216]), K!, US! (US00100045 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.us00100045]). ≡ ***Cardamine gracilis*** (O.E.Schulz) T.Y.Cheo & R.C.Fang (http://ipni.org/urn:lsid:ipni.org:names:280343-1:1.2.1.4).

Schulz (1903) listed a single collection in the protologue and cited only the herbarium B. Currently there is only one specimen of this collection at B. Nevertheless, as considerable part of the Berlin herbarium was destroyed in 1943, we cannot exclude that there was originally more than one specimen of this collection at B in the past. To be on the safe side, as in the case of the type of the names *C. insignis* and *C. microzyga* dealt with above, extant specimen is treated here as "lectotype, or perhaps holotype."

16. ***Cardamine paucifolia*** Hand.-Mazz., Symb. Sin. 7(2): 359. 1931 (http://ipni.org/urn:lsid:ipni.org:names:280343-1:1.2.1.4). Described from: [CHINA] "Y. [Yunnan] In wtp. Wäldern zwischen Dawan und Gwanyilang bei Yungbei ("Yungpeh"), Sandstein, 2400–2600 m, 3. VII. 1914 (3432)". Lectotype (designated here): [CHINA] "Prov. Yünnan, prope urbem Yungbei, in regionis calide temperatae, silvis inter vic. Dawan et Gwangyilang, 2400–2600 m, 3. VII. 1914, *H. Freiherr v. Handel-Mazzetti 3432*" – WU! (WU024360 [http://herbarium.univie.ac.at/database/detail.php?ID=6859]); Isolectotype – W! (W1931-0001417 [http://herbarium.univie.ac.at/database/detail.php?ID=265002]).

Although Handel-Mazzetti (1931) cited a single collection of his, no indication was given as to where the type is deposited. We have been unable to find more than two sheets of the type collection, and both carry identical labels in Handel-Mazzetti's handwriting. The WU sheet is designated as the lectotype.

17. ***Cardamine rockii*** O.E.Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 9: 473. 1926 (http://ipni.org/urn:lsid:ipni.org:names:280627-1:1.4). Described from: "China: Southwestern Szechuan, Muli or Mili Kingdom, 3300–4650 m s. m., J. F. Rock, Juni 1922, n. 5585". Lectotype (designated here): "CHINA, Muli or Muli Kingdom, southwestern Szechuan, 10,000–14,000 ft, June 1922, *J. F. Rock 5585*" – B! (B 10 0241338 [http://herbarium.bgbm.org/object/B100241338]);

Isolectotypes – E (E00154543 [http://data.rbge.org.uk/herb/E00154543]), GH! (GH00312595 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00312595]), P! (P00747504 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747504]), US! (US00100053 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.us00100053]).

Schulz (1926) listed a single collection in his description of the species, and the duplicate at B is designated as the lectotype because it was studied and annotated by him.

18. *Cardamine scoriarum* W.W.Sm., Notes Roy. Bot. Gard. Edinburgh 11: 203. 1919 (http://ipni.org/urn:lsid:ipni.org:names:280650-1:1.3). Described from: "China: - Yunnan; flank of volcanic mountain to north-west of Teng-yueh. Lat. 25°10'N, Alt. 7000 ft. Moist shady situations in thickets. June 1912, G. Forrest. No. 8201. Yunnan; divide between the Shweli and Teng-yueh valleys. Lat. 25°N. Alt. 6000–7000 ft. Moist shady situations on the margins of thickets. May 1912. G. Forrest. No. 7947". Lectotype (designated here): [CHINA] "Yunnan, West China, flank of volcanic mountain north-west of Tenguyeh, 25°70¢N, 7000 ft., June 1912, *G. Forrest 8201*" – E! (E00154541 [http://data.rbge.org.uk/herb/E00154541]); Isolectotype – K! (000697740 [http://specimens.kew.org/herbarium/K000697740]). ° *Cochlearia scoriarum* (W.W.Sm.) Hand.-Mazz. (http://ipni.org/urn:lsid:ipni.org:names:281500-1:1.5.2.1) = ***Cardamine fragariifolia*** O.E.Schulz (http://ipni.org/urn:lsid:ipni.org:names:280320-1:1.4).

Smith (1919) cited two collections by George Forrest, those of *Forrest 7947* [E! (E00117483 [http://data.rbge.org.uk/herb/E00117483]), K! (K000697741 [http://specimens.kew.org/herbarium/K000697741])] were examined by us as well. The above lectotype collection is better than the other, and the E sheet was annotated in Smith's handwriting as "type", and it carries the original printed label with Forrest's handwritten locality data. By contrast, label of the K duplicate was typed at some later time.

19. ***Cardamine simplex*** Hand.-Mazz., Symb. Sin. 7(2): 361. 1931 (http://ipni.org/urn:lsid:ipni.org:names:280661-1:1.3.2.1). Described from: "NW-Y. [Yunnan], Sumpfwiesen der tp. St. ober Ganhaidse bei Lidjiang, Sandstein, 3200 m, 22. VII. 1914 (4310). Offene Stellen an Bächen am Osthange des Beimaschan zwischen Djinscha-djiang und Mekong, 28°12', 3300 m, VI. 1917 (Forrest 13840)". Lectotype (designated here): [CHINA] "Prov. Yünnan bor.-occid.: Supra vicum Ganhaidse ad urbem Lidjiang ("Likiang"), in regionis temperatae pratis paludosis, alt. s. m. ca. 3200 m, 22. VII. 1914, *H. Freiherr von Handel-Mazzetti 4310*" – WU! (WU0024361 [http://herbarium.univie.ac.at/database/detail.php?ID=6858]); Isolectotypes – E! (E00154534 [http://data.rbge.org.uk/herb/E00154534]),

GH! (GH00112038 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00112038]), NAS!, W! (1931-0011416 [http://herbarium.univie.ac.at/database/detail.php?ID=264999]).

Two collections were cited by Handel-Mazzetti (1931) in the original description of the species, and all specimens/duplicates studied were annotated by the author/collector of the species/specimens in his handwriting as "*Cardamine simplex* Hand.-Mazt., sp. nova." Specimen of his own collection is designated here as the lectotype. Annotated specimen of the collection *Forrest 13840* was found at W! (W1929-0013606 [http://herbarium.univie.ac.at/database/detail.php?ID=216904]).

20. ***Cardamine tangutorum*** O.E.Schulz, Bot. Jahrb. Syst. 32: 360. 1903 (http://ipni.org/urn:lsid:ipni.org:names:280688-1:1.4). Described from: "China: Prov. Kansu in terra Tangutorum leg. N. M. Przewalski 1872 (H. B. Boiss. [G], H. P. Ac. [LE]), 1873 (H. B. [B]), 1880 (H. P. Ac. [LE]), prov. Kansu orient, leg. G. N. Potanin 1885 (H. B. [B]), occid. leg. idem (H. P. [LE]); prov. Schensi sept.: Miao Wang-san pr. Paoki-scen leg. J. Giraldi 1899 No. 3379, in alto monte Thaepei-san leg. idem No. 3378 (H.B. [B]); prov. Schansi leg. Potanin 1884 (H.P.Ac. [LE]); Flora Pekinensis, in m. Siao-Wu-Tai-shan 1660–2330 m leg. O. v. Möllendorff 1879 (H. B. [B]); prov. Szetschuan sept. leg. idem 1885 (H.P.Ac. [LE]), ad Tsakulao leg. V. Rosthorn 1891 No. 2583 (H. B. [B])". Lectotype (designated here): "CHINA occidentalis, Terra Tangutorum, (prov. Kansu [Gansu Province]), 1873, *N. M. Przewalski s.n.*" – B! (B 10 0241335 [http://herbarium.bgbm.org/object/B100241335]); Isolectotypes – K! (K000697742 [http://specimens.kew.org/herbarium/K000697742]), LE!.

Schulz (1903) cited 10 syntype collections under this species and gave the institutional abbreviations where the duplicates are housed. The lectotype was annotated by him, and we have examined its duplicates in other herbaria (K, LE).

21. ***Cardamine trifoliolata*** Hook.f. & Thomson, J. Proc. Linn. Soc., Bot. 5: 145. 1861 (http://ipni.org/urn:lsid:ipni.org:names:280717-1:1.1.2.1.1.3). Described from: "In Himalaya orientali, reg. temp., Bhotan ! Griffith." Lectotype (designated here): [BHUTAN] "Bootan, [1838], *W. Griffith 1757*" – K! (K000247214 [http://specimens.kew.org/herbarium/K000247214]).

Two of Griffith's collection numbers from Bhutan, *Griffith 1757* and *1359*, are mounted on the same sheet. The former collection was cut off and mounted on the sheet of the other, and it is the one with Hooker's annotation as "*C. trifoliolata*, Hf & T" that we designate herein as the lectotype.

22. *Cardamine violifolia* O.E.Schulz, Bot. Jahrb. Syst. 32: 440. 1903 (http://ipni.org/urn:lsid:ipni.org:names:280743-1:1.4). Described from: "China centralis: prov. Hupeh pr. Ichang leg. A. Henry 10. 1887 n. 3298 (H. B. [B], H. B. Boiss. [G], H. C. [GH])". Lectotype (designated here): [CHINA] "Central China, prov. Hupeh [Hubei], *Ichang and intermediate neighborhood* [more detailed information in italic is given on the other specimens of this collection than lectotype], 1885-1888, *A. Henry 3298*" – B! (B 10 0386924 [http://herbarium.bgbm.org/object/B100386924], except middle plant on the sheet); Isolectotypes – BM! (BM000587602 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.bm000587602]), E! (E00154597 [http://data.rbge.org.uk/herb/E00154597]), G (ex Herbarium Barbey-Boissier)!, GH! (GH00112032 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00112032], except the plant on the right; GH00112031 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00112031]), K!, P! (P05036305 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p05036305]), US! (US00100059 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.us00100059]). = ***Cardamine circaeoides*** Hook.f. & Thomson (http://ipni.org/urn:lsid:ipni.org:names:280232-1:1.1.2.1.1.3).

Schulz (1903) listed one collection and cited the duplicates at B, G, and GH. We have examined all four sheets that he cited, and any of them could have served as the lectotype, but Schulz's institutional affiliation was the reason to designate the B duplicate as the lectotype.

23. *Cardamine violifolia* var. *diversifolia* O.E.Schulz, Bot. Jahrb. Syst. 32: 440. 1903. Described from: "Saepe cum specie typica." Lectotype (designated here): [CHINA] "Central China, prov. Hupeh [Hubei], *Ichang and intermediate neighborhood* [more detailed information in italic is given on other specimens of this collection than lectotype], 1885-1888, *A. Henry 3298*" – B! (same as above) (B 10 0386924 [http://herbarium.bgbm.org/object/B100386924], middle plant on the sheet); isolectotype – GH! (GH00112032 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.gh00112032], plant on the right). = ***Cardamine circaeoides*** Hook.f. & Thomson (http://ipni.org/urn:lsid:ipni.org:names:280232-1:1.1.2.1.1.3).

According to his annotations on the herbarium sheets, both the B and GH sheets were considerd by Schulz (1903) as a mixed collection of the type variety and var. *diversifolia*. The latter variety was said to differ by having slightly lobed vs. unlobed leaves, though this variation is quite frequently encountered in almost every population of the species and, therefore, we considered it trivial and not worth of taxonomic classification.

24. ***Cardamine yunnanensis*** Franch., Bull. Soc. Bot. France 33: 398. 1886 (http://ipni.org/urn:lsid:ipni.org:names:280759-1:1.4). Described from: "[CHINA] Yun-nan,

in silvis ad Ta-long-tan, prope Tapin-tze, alt. 1800 m.; fl., fr. 26 jul. 1885 (Delav. n. 1843)". Lectotype (designated here): [Label 1, printed]: "Plantes de Chine (Province du Yun-nan)", [Label 2, handwritten] "Les bois de Ta-long-tan, près de Ta pint tze, à 1800m d'altitude, 26 juillet 1885, *J. M. Delavay 1843*" – P! (P00747493 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747493]); Isolectotypes – BM!, E! (E00154592 [http://data.rbge.org.uk/herb/E00154592]), F! (F0092968F [http://cornelia.fieldmuseum.org/285/783/V0092968F.jpg]), NY! (NY00468268 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.ny00468268]), P! (P00747494 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747494], P00747495 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p0074495]), US! (US00100060 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.us00100060], US00503998 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.us00503998]).

A single collection was cited in the original publication. Of the three duplicates of the type collection at P, two have Delavay's handwritten label and Franchet's annotation. The most complete one is designated here as the lectotype.

25. *Dentaria repens* Franch., Bull. Soc. Bot. France 32: 5. 1885 (http://ipni.org/urn:lsid:ipni.org:names:281996-1:1.5). Described from: [CHINA] "Plantes du Yunnan. In faucibus Han-tchang-kiou, secus viam e Tali ad Ho-kin ducentem; 27 maj. 1884; n°65". Lectotype (designated here): [CHINA, Yunnan] "Gorges de San tchang kiou. Ho Kin, 22 May 1884, *J. M. Delavay s.n.*" – P! (P00747505 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747505]); Isolectotype – P! (P00747506 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747506]). ≡ ***Cardamine repens*** (Franch.) Diels (http://ipni.org/urn:lsid:ipni.org:names:280619-1:1.3). ≡ *C. tenuifolia* var. *repens* (Franch.) Franch. ° *Loxostemon repens* (Franch.) Hand.-Mazz. (http://ipni.org/urn:lsid:ipni.org:names:286642-1:1.3.2.1.1.1).

Franchet (1885) dealt with Delavay's collections and listed only collection number 65 under the species. The only material at P with *Delavay 65* is a unicate of *Saxifraga diversifolia* var. *hematophylla* Franch. (P00136633). However, two sheets at P with the exact locality data (Han tchang-kiou, Ho-Kin) but without any collection number carry Franchet's annotation as "*Cardamine tenuifolia* Turcz. var. *repens* Franch.," and both were collected on May 22 (not 27, as in the protologue) of 1884. The sheet with the original hand-written label by Delavay, which carries the name "*Dentaria repens* Franch.", is designated herein as the lectotype. There are no other Delavay specimens of *Cardamine* or *Dentaria* at P that carry the above information and, therefore, it is safe to conclude that Franchet (1885) made mistakes in collection day and number.

26. *Erysimum violaceum* D.Don, Prodr. Fl. Nepal.: 202. 1825 (http://ipni.org/urn:lsid:ipni.org:names:284251-1:1.2.2.1.1.1). Described from: [NEPAL]

"Hab. in Gosaingsthan. *Wallich*." Lectotype (designated here): [NEPAL] "Gosain Than, *N. Wallich 4782*" – K! (K000247213 [http://specimens.kew.org/herbarium/K000247213]); Isolectotypes – BM! (BM000521637 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.bm000521637]), B! (B 10 0241325 [http://herbarium.bgbm.org/object/B100241325]), E! (E00154660 [http://data.rbge.org.uk/herb/E00154660]), GZU! (GZU000276995 [http://plants.jstor.org/stable/10.5555/al.ap.specimen.gzu000276995]). ≡ ***Cardamine violacea*** (D.Don) Wall. ex Hook.f. & Thomson (http://ipni.org/urn:lsid:ipni.org:names:280742-1:1.2.1.1.2.1.1.1).

According to Stafleu and Cowan (1988: 37–38), Nathaniel Wallich's complete set of Himalayan plants is currently deposited at K, and David Don's types in the "*Prodromus florae nepalensis*" (Don 1825) that were based on Wallich's collections were sent to him by Lambert and partially housed at BM. The duplicate at K is the most complete of all that we examined, and it is designated herein as the lectotype.

27. *Loxostemon delavayi* Franch., Bull. Soc. Bot. France 33: 400. 1886 (http://ipni.org/urn:lsid:ipni.org:names:286639-1:1.4), non *Cardamine delavayi* Franch., Bull. Soc. Bot. France 33: 397. 1886 (http://ipni.org/urn:lsid:ipni.org:names:280264-1:1.4). Described from: [CHINA] "Yun-nan ad juga nivalia Li-kiang post nives deliquescentens florens; fl. 9 jul. 1884 (Delavay)". Lectotype (designated here): [CHINA] [Label 1, printed] "Yunnan", [Labe1 2, written] "parmi les pierres après la fonte des neiges au Glacier Li Kiang, 9 iuillet 1884, *J. M. Delavay 35*" – P! (P00279378 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00279378]); Isolectotypes – P! (P00747524 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747524], P00747525 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747525]). ≡ ***Cardamine franchetiana*** Diels (http://ipni.org/urn:lsid:ipni.org:names:280322-1:1.3).

No collection number was given by Franchet (1886) in the original publication of *Loxostemon delavayi*, and the only collection carrying Franchet's annotation of the species and collected on the exact date cited in that publication is *Delavay 35*. That number was cited by Diels (1912) in renaming the species during transferring it to *Cardamine* to avoid the creation of a later homonym of *C. delavayi*, which is an entirely different species. The lectotype is the more complete of the three sheets at P and has five plants mounted on the sheet, together with author's drawing of details of flowers and fruit.

28. *Loxostemon pulchellus* Hook.f. & Thomson, J. Proc. Linn. Soc., Bot. 5: 147. 1861 (http://ipni.org/urn:lsid:ipni.org:names:286641-1:1.1.2.1.1.3). Described from: [CHINA] "In Himalaya orientali temperata; Sikkim graminosis humidis! alt. 10000-13000 ped., J. D. H. (fl. Jun.) (v.v.)". Lectotype: [INDIA] [La-

bel 1, printed] "Hab. Sikkim, Regio Alp" [Label 2, writeen] "Streams, Lachen, 12,000 ft, 9 June 1849, *J. D. Hooker s.n.*" – K! (K000397471 [http://specimens.kew.org/herbarium/K000397471]); Possible isolectotypes – B! (B 10 0241277 [http://herbarium.bgbm.org/object/B100241277]), P! (P00747596 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747596], P00747597 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747597], P00747598 [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00747598]). ≡ ***Cardamine pulchella*** (Hook.f. & Thomson) Al-Shehbaz & G.Yang (http://ipni.org/urn:lsid:ipni.org:names:1002420-1:1.1.2.1.1.2).

Six collections of Joseph Dalton Hooker from Sikkim are mounted on two herbarium sheets at K, and they vary in the elevations and dates of collection. The single collection in which the habitat was given is designate herein as the lectotype. The Sikkim duplicates at B and P do not carry the exact elevations and collection dates of the lectotype and, therefore, we are uncertain if they are part of the same collection.

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References

Diels L (1912) Plantae Chinenses Forrestianae. Notes from the Royal Botanic Garden Edinburgh 5: 161–304.

Don D (1825) Prodromus florae nepalensis, sive enumeratio vegetabilium, quae in itinere per Nepaliam proprie dictam et regiones conterminas, ann. 1802–1803. J. Gale, London, XII + 256 pp.

Franchet A (1879) Stirpes novae vel rariores florae Japonicae. Bulletin de la Société Botanique de France 26: 82–90. doi: 10.1080/00378941.1879.10825735

Franchet A (1885) Plantes du Yun-nan récoltées par M. l'Abbé Delavay. Bulletin de la Société Botanique de France 32: 3–11. doi: 10.1080/00378941.1885.10828278

Franchet A (1886) Plantas Yunnanensis A Cl. J. M. Delavay collectas. Bulletin de la Société Botanique de France 33: 358–467. doi: 10.1080/00378941.1886.10828470

Güntsch A, Hagedorn G (2013) Stable identifiers for specimens – A CETAF ISTC initiative supported by pro-iBiosphere. http://www.pro-ibiosphere.eu/news/4296_stable%20identifiers%20for%20specimens%20-%20a%20cetaf%20istc%20initiative%20supported%20by%20pro-ibiosphere/ [accessed 23 April 2015]

Hagedorn G, Catapano T, Güntsch A, Mietchen D, Endresen D, Sierra S, Groom Q, Biserkov J, Glöckler F, Morris R (2013) Best practices for stable URIs. http://wiki.pro-ibiosphere.eu/wiki/Best_practices_for_stable_URIs [accessed 23 April 2015]

Handel-Mazzetti H (1931) Sympolae Sinicae. Botanische Ergebnisse der Expedition der Akademie der Wissenschaft in Wien nach Südwest-China 1914/1918. Part 7 (Lief. 2). Verlag von Julius Springer, Wien, 211−448.

Hemsley WB, Wilson EH (1906) Some new Chinese plants. Bulletin of the miscellaneous information. Royal Botanic Gardens, Kew, 147−163. doi: 10.2307/4111296

Hooker JD, Anderson T (1872) Cruciferae. In: Hooker JD (Ed.) Flora of British India. Vol. 1. L. Reeve & Co., London, 128–167

Hyam RD, Drinkwater RE, Harris DJ (2012) Stable citations for herbarium specimens on the internet: an illustration from a taxonomic revision of *Duboscia* (Malvaceae). Phytotaxa 73: 17–30.

JACQ Consortium (2004 onwards) Virtual Platform for Botanical Specimens. http://herbarium.univie.ac.at/database/search.php

Lauener LA (1965) Catalogue of the names published by Hector Léveillé: III. Notes from the Royal Botanic Garden Edinburgh 26: 333−346.

McNeill J (2014) Holotype specimens and type citations: General issues. Taxon 63: 1112−1113. doi: 10.12705/635.7

McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, Prud'homme van Reine WF, Smith GF, Wiersema JH, Turland NJ (2012) International code of nomenclature for algae, fungi, and plants (Melbourne Code). Adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Koeltz Scientific Books, Königstein, XXX + 208 pp. [Regnum Vegetabile 154]

Schulz OE (1903) Monographie der Gattung *Cardamine*. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 32: 280−623.

Schulz OE (1926) Diagnosen neuer, hauptsächlich in China gesammelter Cruciferen. Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9: 473−477. doi: 10.2307/3994368

Smith WW (1919) Diagnoses specierum novarum Chinensium in herbario Horti Regii Botanici Edinburgensis cognitarum CCCCI−CCCCL. Notes from the Royal Botanic Garden Edinburgh 11: 191−232.

Stafleu FA, Cowan RS (1988) Taxonomic Literature: a selective guide to botanical publications and collections with dates,commentaries and types. Volume VII: W-Z. Ed. 2. Bohn, Scheltema & Holkema, Utrecht, [LVI] + 653 pp. [Regnum Vegetabile 116]

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SHORT COMMUNICATION

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The correct name in *Oenothera* for *Gaura drummondii* (Onagraceae)

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Abstract

In 2007, Wagner and Hoch proposed the new name *Oenothera xenogaura* W.L.Wagner & Hoch for the species then known as *Gaura drummondii* (Spach) Torrey & A. Gray (non *O. drummondii* Hooker, 1834). However, the authors overlooked the availability of *Gaura hispida* Bentham (1840) for this species. Accordingly, we herewith make the appropriate new combination for this species, *O. hispida* (Bentham) W.L.Wagner, Hoch & Zarucchi, and place *O. xenogaura* in synonymy.

Keywords

Gaura drummondii, *Gaura hispida*, *Oenothera hispida*, *Oenothera xenogaura*, nomenclature

Introduction

The only member of *Oenothera* sect. *Gaura* subsect. *Xenogaura* is a distinctive allopolyploid species that occurs from eastern Texas south through Mexico as far south as Oaxaca. When the genus *Gaura* L. is recognized, the correct name for this species is *G. drummondii* (Spach) Torrey & A. Gray, which was used in the revision of the group by Raven and Gregory (1972). Since that time, molecular studies (Hoggard et al. 2004; Levin et al. 2004; Ford and Gottlieb 2007) have shown that *Oenothera* is strongly supported as monophyletic only with the inclusion of *Calylophus* Spach, *Gaura*, and *Stenosiphon* Spach. These four groups also have in common a stigma that either is

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peltate to discoid, or is deeply to shallowly 4-lobed and then subtended by a more or less conspicuous peltate indusium. These data led Wagner et al. (2007) to broaden the concept of *Oenothera* by including within it *Calylophus*, *Gaura*, and *Stenosiphon*. The new name *Oenothera xenogaura* W.L.Wagner & Hoch was proposed in 2007 for this species when *G. drummondii* was transferred to *Oenothera* because use of *G. drummondii* is blocked by *O. drummondii* Hooker of sect. *Oenothera*. Within the protologue of their new combination, Wagner and Hoch did not cite any other taxonomic synonym. However, at that time, they failed to take into account *G. hispida* Bentham (1840), one of the synonyms included for *G. drummondii* by Raven and Gregory (1972). Thus, they missed the opportunity of transferring *G. hispida* to *Oenothera* and making the new combination. We herewith correct the mistake and make the appropriate new combination namely *O. hispida* W.L.Wagner, Hoch & Zarucchi. Additionally, along with other synonyms cited by Raven and Gregory, *O. xenogaura*, a legitimate replacement name, is here placed into synonymy. Since Wagner and Hoch did not cite any taxonomic synonym, their Ô. *xenogaura* was not superfluous when published [Art. 52.1; McNeill et al. 2012].

Taxonomic part

***Oenothera hispida* (Bentham) W.L.Wagner, Hoch & Zarucchi, comb. nov.**
urn:lsid:ipni.org:names:77147316-1
Fig. 1

Basionym. *Gaura hispida* Bentham, Pl. Hartw. 288. 1840.

Type. Mexico: In fields near Leon, Guanajuato, June 1837, *Thomas Hartweg 1603* (Holotype: K! [Kew image]; Isotypes: BM, CAMB, G, LD!).

Schizocarya drummondii Spach, Nouv. Ann. Mus.Hist. Nat. 4: 382. 1836 ["1835"]. *Gaura drummondii* (Spach) Torrey & A. Gray, Fl. N. Amer. 1: 519. 1838. *Oenothera xenogaura* W.L.Wagner & Hoch, Syst. Bot. Monogr. 83: 213. 2007.

Type. U.S.A. Texas: Travis Co., Austin, 1833–1834, *T. Drummond III.36* (Holotype: G; isotypes: BM!, GH!, NY!, P). Note: the BM isotype is mounted on a sheet with two non-type collections of the same species: Purpus 3387 and Purpus 5383.

Gaura roemeriana Scheele, Linnaea 21: 579. 1848.

Type. U.S.A. Texas: Comal Co., New Braunfels, 1846, *Ferdinand Roemer s.n.* (Lectotype: MO-1833107!, here designated; Isolectotypes: CAS, HAL). The holotype at B was destroyed in World War II.

Schizocarya crispa Spach, Nouv. Ann. Mus. Paris 4: 384. 1835. *Gaura crispa* (Spach) D.Dietr., Syn. Pl. 2: 1298. 1840.

Type. Mexico: Tamaulipas, Matamoros, April 1831, *J. L. Berlandier 2313* (Holotype: G; Isotypes: BM, K, P).

Plant rhizomatous, perennial, forming extensive colonies, strigillose and often also villous. Stems 20–60(-120) cm tall, sometimes strict with a single unbranched main

Figure 1. *Oenothera hispida* (Bentham) W.L.Wagner, Hoch & Zarucchi **A** Habit, Mexico, Nuevo León, *Roybal 34* (US) **B** Flower, lateral view, *Roybal 34* (US) **C** Flower, face view, digital image (Ray Pistrum as "Gaura drummondii fresh flower" [http://redsgoodvsevilcowbarn.blogspot.com/2012/06/chigger-chow-and-gaura-drummondii.html]) **D** Base of staminal filaments showing basal scales, *Roybal 34* (US) **E** Capsule, Texas, Hall 213 (US) **F** *Oenothera suffrutescens* (Ser.) W.L.Wagner & Hoch capsule, New Mexico, *Standley 6481* (US).

stem but usually somewhat decumbent with several branches from the base and usually irregular branching above. Leaves in a basal rosette and cauline, 0.5–7.5 (-9.5) × 0.1–2.2 cm; subsessile; blade narrowly lanceolate to elliptic, margin subentire to shallowly sinuate-dentate. Inflorescence a spike. Flowers 4-merous, zygomorphic, opening near sunset; floral tube 4–14 mm; sepals 7–11(-14) mm; petals white, fading red, 6-10 mm; staminal filaments 4–8.5 mm, anthers 3-6 mm; style 12–26 mm. Capsule 7–13 × 3–5 mm, erect, the body ellipsoid or ovoid, 4-angled, distal half pyramidal, the base of the pyramidal portion distinctly bulging, then immediately and sharply constricted to the terete proximal part. Seeds (2-)3-4(-8), 2–2.5 × 1–1.25 mm, ovoid, usually flattened on one or several sides by crowding in the fruit, reddish brown. 2n = 28.

Phenology and distribution. Flowering from May through July, but sporadically as late as November. *Oenothera hispida* grows in sandy loam soils from the eastern half of Texas south through Mexico as far south Oaxaca. It is naturalized in Arkansas (Sevier Co.), coastal southern California, Georgia (Glynn Co.); its current status in both Arkansas and Georgia should be verified. It is considered an invasive species in California.

Oenothera hispida is the sole member of *Oenothera* sect. *Gaura* subsection *Xenogaura*. Raven and Gregory (1972) suggested that *O. hispida* arose following interspecific hybridization between *O. suffrutescens* (Ser.) W.L.Wagner & Hoch (subsect. *Campogaura* (P. H. Raven & D. P. Gregory) W.L.Wagner & Hoch) and a species in subsect. *Stipogaura* (P. H. Raven & D. P. Gregory) W.L.Wagner & Hoch, possibly near *O. mckelveyae* (Munz) W.L.Wagner & Hoch. Hoggard et al. (2004) found that the pistillate parent of *O. hispida* was indeed *O. mckelveyae* or a close relative, but that the staminate parent probably came from a lineage related to *O. dodgeniana* Krakos & W.L.Wagner or *O. lindheimeri* (Engelm. & A.Gray) W.L.Wagner & Hoch in subsect. *Gaura* (L.) W.L.Wagner & Hoch. *Oenothera hispida* is not easily distinguished morphologically from *O. suffrutescens* (subsect. *Campogaura*), with which it shares the character of a thick stipe, and occasionally hydridizes in Texas. *Oenothera hispida* is an aggressively rhizomatous perennial with fruits conspicuously bulging on the distal half (Raven and Gregory 1972). Since *O. hispida* and *O. suffrutescens* can be difficult to distinguish we have included a capsule of the latter in the figure (Fig. 1-F) for comparison of key features for correct separation of the two species. The rhizomatous habit makes this species potentially invasive, despite its self-incompatibility, but so far it has established itself most aggressively only in coastal southern California (Wagner et al. 2007). There are no other Hartweg collections of this species that anyone has seen other than the one cited above as the type collection. We have seen the holotype as an image on the Kew web site that was mistakenly filed under *G. coccinea* Pursh. The label information corresponds to the published locality given and is marked as in the Bentham herbarium.

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References

Dietrich W (1978 ["1977"]) The South American species of *Oenothera* sect. *Oenothera* (*Raimannia*, *Renneria*; Onagraceae). Ann. Missouri Bot. Gard. 64: 425–626. doi: 10.2307/2395257

Ford VS, Gottlieb LD (2007) Tribal relationships within Onagraceae inferred from PgiC sequences. Syst. Bot. 32: 348–356. doi: 10.1600/036364407781179725

Hoggard GD, Kores PJ, Molvray M, Hoggard RK0 (2004) The phylogeny of *Gaura* (Onagraceae) based on ITS, ETS and *TrnL-F* sequence data. Amer. J. Bot. 91: 139–148. doi: 10.3732/ajb.91.1.139

Levin RA, Wagner WL, Hoch PC, Hahn WJ, Rodriguez A, Baum DA, Katinas L, Zimmer EA, Sytsma KJ (2004) Paraphyly in Tribe Onagreae: Insights into phylogenetic relationships of Onagraceae based on nuclear and chloroplast sequence data. Syst. Bot. 29: 147–164. doi: 10.1600/036364404772974293

McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, Prud'homme van Reine WF, Smith GF, Wiersema JH, Turland NJ (Eds) (2012) International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Koeltz Scientific Books, Königstein, Germany. [Regnum Veg. 154]

Raven PH, Gregory DP (1972) A revision of the genus *Gaura* (Onagraceae). Mem. Torrey Bot. Club 23: 1–96.

Wagner WL, Hoch PC, Raven PH (2007) Revised classification of the Onagraceae. Syst. Bot. Monogr. 83: 1–240.

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The correct name for a section of *Ludwigia* L. (Onagraceae)

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Abstract

In 1953, Hara provided new combinations for many sectional and species names when he combined *Jussiaea* L. with *Ludwigia* L., and at the time, *Ludwigia* sect. *Oligospermum* (Micheli) H.Hara was the correct name for one well-defined section. However, subsequent changes to/clarifications of the botanical code have necessitated a change for that name in that now an autonym is treated as having priority over the name or names of the same date and rank that established it. Since Hara's combination was based on *Jussiaea* sect. *Oligospermum* Micheli, the correct name for this section is *Ludwigia* sect. *Jussiaea* (L.) Hoch, W.L.Wagner, & P.H.Raven.

Keywords

Ludwigia, *Jussiaea*, sect. *Oligospermum*, nomenclature

Introduction

The cosmopolitan group of species known since 1953 as *Ludwigia* sect. *Oligospermum* is one of the most distinctive in the genus (Raven 1963, Wagner et al. 2007). Among the diplostemonous sections of *Ludwigia* – which formerly were segregated as the genus *Jussiaea* L. – this section differs by having woody, subcylindrical capsules with uniseriate seeds firmly embedded in woody pieces of endosperm and pollen released singly

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rather than as tetrads or polyads. Most species of the section, which grow in warm-temperate to subtropical moist or wet habitats worldwide, are vigorously aquatic and some (*L. peploides* (Kunth) P.H.Raven, *L. hexapetala* (Hook. & Arn.) Zardini, H.Y.Gu & P.H.Raven) can be invasive weeds in wetlands and other wet areas, most recently so in California (Wood 2006, Hoch and Grewell 2012). This polyploid section comprises a group of nine highly variable species that includes three diploid species (n = 8), four tetraploid species (n = 16), one hexaploid species (n = 24, *L. grandiflora* (Michx.) Greuter & Burdet), and one decaploid species (n = 40, *L. hexapetala*; see also Nesom and Kartesz 2000). Most species in this section have native distributions restricted to the New World, but two species are restricted to the Old World, *L. stolonifera* (Guill. & Perr.) P.H.Raven throughout Africa and Madagascar, extending to Turkey and Iraq, and *L. adscendens* (L.) H.Hara across tropical Asia from India to New Guinea, and from southern Japan to northern Australia, and probably naturalized in Madagascar (Raven 1963, Wagner et al. 2007).

While editing the treatment of *Ludwigia* for the Flora of North America, Jim Zarucchi noticed a problem with the name used for this section, and after consultation with Kanchi Gandhi informed us that a change was necessary. We are grateful to Zarucchi and Gandhi for pointing out this problem for us. We are making this change now so that the correct combination can be available for FNA.

In his treatment for the Flora Brasiliensis (Martius 1875), Micheli divided the genus *Jussiaea* into three sections: sect. *Eujussiaea*, sect. *Oligospermum*, and sect. *Macrocarpon*. This division of the genus has been widely followed in subsequent treatments. Munz (1942) provided a treatment for New World species of *Jussiaea* in which he recognized the same three sections, but provided different names for two of them (no change for sect. *Macrocarpon* Micheli). For sect. *Eujussiaea* Micheli, he used the new name sect. *Myrtocarpus* Munz, and for sect. *Oligospermum* Micheli, he used sect. *Eujussiaea* Munz. His rationale was that the section that included the type species of the genus had to retain the generic name, and since Hitchcock and Greene (1929) effectively lectotypified *Jussiaea* with *J. repens* L. [= *Ludwigia adscendens* (L.) Hara], he proposed the name sect. *Eujussiaea* for the section that included *J. repens* (this lectotypification has been attributed incorrectly in the past to Britton and Brown (1913)).

Hara (1953), following the conclusion by Brenan (1953) and others that *Ludwigia*, *Jussiaea*, and *Isnardia* (a group sometimes segregated) formed a single genus (as *Ludwigia*, as established by Baillon 1877), recognized the sections in question as *Ludwigia* sect. *Oligospermum* (Micheli) H.Hara, sect. *Myrtocarpus* (Munz) H.Hara, and sect. *Macrocarpon* (Micheli) H.Hara. He noted that he was "strictly following the Code" (Hara 1953: 290). This treatment was widely accepted, including by Raven (1963) as well as Munz (1965). Most recently Wagner et al. (2007), in a synopsis of Onagraceae, included all three sections as proposed by Hara.

However, changes made to the ICBN in 1981 and retained in subsequent editions (McNeill et al. 2012), specifically as Article 11.6, invalidated part of this treatment. Article 11.6 states that "an autonym is treated as having priority over the name or

names of the same date and rank that established it." So when the transfer of names from *Jussiaea* to *Ludwigia* was made, the correct sectional name combination for *Jussiaea* sect. *Oligospermum* should have been *Ludwigia* sect. *Jussiaea*, since this is the section that includes the type of the genus. Therefore, we make the following change in compliance with the ICBN.

Nomenclature

***Ludwigia* L. sect. *Jussiaea* (L.) Hoch, W.L.Wagner, & P.H.Raven, comb. nov.**
urn:lsid:ipni.org:names:77147317-1

Jussiaea L., Sp. pl. 1: 388. 1753. [*Jussia* Adans., Fam. 2: 85, 565. 1763, orth. var.]; *Jussiaea* L. sect. *Eujussiaea* Munz, Darwiniana 4: 184. 1944.
Type. *Jussiaea repens* L. [=*Ludwigia adscendens* (L.) H.Hara] (Lectotype, designated by Hitchcock & Greene, Prop, Brit. Bot. 153. 1929).

Jussiaea L. sect. *Oligospermum* Micheli in Martius, Fl. bras. 13(2): 149, 162. 1875. *Ludwigia* L. sect. *Oligospermum* (Micheli) H.Hara, J. Jap. Bot. 28: 290. 1953.
Type. *Jussiaea hookeri* Micheli [=*Ludwigia hookeri* (Micheli) H.Hara] (Lectotype, designated by Raven, Reinwardtia 6: 335. 1963).

Cubospermum Lour., Fl. Cochinch. 258, 275. 1790.
Type. *Cubospermum palustre* (L.) Lour. [= *Ludwigia adscendens* (L.) H.Hara].

Adenola Raf., Aut. Bot. 36. 1840.
Type. *Adenola grandiflora* (Michx.) Raf. [= *Ludwigia grandiflora* (Michx.) Greuter & Burdet]. (Lectotype, designated by Pennell, Bull. Torrey Bot. Club 48: 93. 1921).

Oocarpon Micheli, Flora 57: 303. 1874. *Ludwigia* sect. *Oocarpon* (Micheli) P.H.Raven, Reinwardtia 6: 336. 1963.
Type: *Oocarpon jussiaeoides* Micheli [= *Ludwigia torulosa* (Arn.) H.Hara].

Description. Perennial herbs, stems creeping, floating, or emergent and ascending to erect, rooting at nodes, when floating often forming spongy white pneumatophores at nodes, when erect with spongy base, terete. Leaves alternate; blades with one submarginal vein. Flowers 5(6)-merous; petals present, yellow or white; stamens twice as many (rarely as many) as sepals, pollen shed in monads. Capsules cylindrical, terete, often curved up, woody with thick walls, irregularly and tardily dehiscent. Seeds in one row per locule, pendulous, and firmly embedded in a woody coherent segment of endocarp, with inconspicuous raphe. 2n = 16, 32, 48, 80, 96.

Taxa included. *Ludwigia adscendens* (L.) H.Hara, *L. grandiflora* (Michx.) Greuter & Burdet, *L. helminthorrhiza* (Mart.) H.Hara, *L. hexapetala* (Hook. & Arn.) Zardini, H.Y.Gu & P.H.Raven, *L. hookeri* (Micheli) H.Hara, *L. peduncularis* (C.Wright ex Griseb.) M.Gómez, *L. peploides* (Kunth) P.H.Raven subsp. *glabrescens* (O. Kuntze) P.H.Raven, *L. peploides* subsp. *montevidensis* (Sprengel) P.H.Raven, *L. peploides* sub-

sp. *peploides*, *L. peploides* subsp. *stipulacea* (Ohwi) P.H.Raven, *L. stolonifera* (Guill. & Perr.) P.H.Raven, *L. torulosa* (Arn.) H.Hara.

Acknowledgments

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References

Baillon HE (1877) Onagraceae. Histoire des plantes 6: 305–516.

Brenan JPM (1953) Notes on African Onagraceae and Trapaceae. Kew Bulletin 8: 163–172. doi: 10.2307/4117169

Britton NL, Brown A (1913) An illustrated flora of the northern United States, Canada and the British possessions, Ed 2, 2: 1–735.

Hara H (1953) *Ludwigia* versus *Jussiaea*. Journal of Japanese Botany 28: 289–294.

Hitchcock AS, Greene ML (1929) Standard species of Linnean genera of Phanerogamae (1753–54). International Botanical Congress. Cambridge (England), 1930: Nomenclature. Proposals by British Botanists, H.M.S.O., London, 110–199.

Hoch PH, Grewell BJ (2012) *Ludwigia*. In: Baldwin BG, Goldman DH, Keil DJ, Patterson R, Rosatti TJ, Wilkin DH (Eds) The Jepson Manual: Vascular Plants of California, Second Edition. Univ. California Press, Berkeley, 948–949.

Martius CFP de (1875) Onagraceae. Flora Brasiliensis 13(2): 146–182.

McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, PrudPhomme van Reine WF, Smith GF, Wiersema JH, Turland NJ (2012) International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Koeltz Scientific Books, Königstein, Germany. [Regnum Veg. 154]

Munz PA (1942) Studies in Onagraceae XII. A revision of the new world species of *Jussiaea*. Darwiniana 4: 179–284.

Munz PA (1965) Onagraceae. North American Flora, ser. 2, 5: 1–278.

Nesom GL, Kartesz JT (2000) Observations on the *Ludwigia uruguayensis* complex (Onagraceae) in the United States. Castanea 65: 123–125.

Raven PH (1963) The Old World species of *Ludwigia* (including *Jussiaea*), with a synopsis of the genus (Onagraceae). Reinwardtia 6: 327–427.

Wagner WL, Hoch PC, Raven PH (2007) Revised classification of the Onagraceae. Systematic Botany Monographs 83: 1–240.

Wood M (2006) Squelching water primrose. Agricultural Research Magazine 54(5): 13.

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Eremogone (Caryophyllaceae): new combinations for Old World species

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Abstract

Twenty-one new combinations in *Eremogone* (Eremogoneae, Caryophyllaceae) are proposed to accommodate placement of all Old World taxa of *Arenaria* subg. *Eremogone* and *Eremogoneastrum* within *Eremogone*.

Keywords

Eremogone, *Arenaria*, Caryophyllaceae

Introduction

In their study of relationships in *Arenaria* L. and major lineages within the Alsinoideae, Harbaugh et al. (2010) found that members of *Arenaria* subg. *Eremogoneastrum* F.N. Williams and *Eremogone* (Fenzl) Fenzl, as well as *Minuartia* L. subg. *Spergella* (Fenzl) McNeill and *Thylacospermum* Fenzl, clustered in a clade that was both distantly related to the rest of *Arenaria* and sister to the Caryophylloideae. The tribe Eremogoneae was described in that paper to place this clade within the context of their tribal classification of the family.

Three subsequent molecular studies have confirmed the placement of the *Arenaria* and *Minuartia* species in Eremogoneae (Greenberg and Donoghue 2011; Dillenberger and Kadereit 2014; Sadeghian et al. in press). The first two studies included a similar

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complement of taxa in the tribe with the exception of *Thylacospermum*, which clustered with *Spergula arvensis* L. in those studies. While Harbaugh et al. (2010) proposed that the genus *Phlebanthia* Rchb. be resurrected for the species of *Minuartia* subg. *Spergella*, Dillenberger and Kadereit (2014) instead proposed new combinations in *Eremogone* for these taxa, noting there was not a clear segregation among the sampled taxa. We follow the results of Greenberg and Donoghue (2011) and Dillenberger and Kadereit (2014) by excluding *Thylacospermum* from *Eremogone* at this time.

Eremogone, as now defined, consists of the former *Arenaria* subg. *Eremogone* (~ 70 sp.), subg. *Eremogoneastrum* (22 sp.), and *Minuartia* subg. *Spergella* (3 sp.). Sadeghian et al. (in press) included a larger sample of taxa now placed in *Eremogone* than earlier studies; they concluded that infrageneric relationships were still unclear. While many combinations in *Eremogone* have been published (esp., Ikonnikov (1973, 1990) and Hartman and Rabeler (2004)), most members of *Arenaria* subg. *Eremogoneastrum* lack combinations in *Eremogone*. With active flora projects in India (Flora of India Checklist, in prep.) and China (Flora of China, e.g. Wu et al. 2001) bringing more information to light about these regions we feel that it is time to supply the 21 additional combinations to make all currently recognized taxa available in *Eremogone*.

The information about type specimens of the basionyms of the new combinations that we have included is based on examining protologues and searching major indices (Tropicos – http://www.tropicos.org/; JSTOR Global Plants – https://plants.jstor.org/) for extant specimens. Herbarium abbreviations follow Index Herbariorum (Thiers 2015). In cases where specimen deposition is not clearly stated in a protologue, we have added "?" after the abbreviation where, based on information about the location of the herbarium where the author worked and/or deposited their herbaria (see Index of Botanists – http://kiki.huh.harvard.edu/databases/botanist_index.html), we expect, but cannot confirm, a type specimen should be deposited.

In the cases where syntypes are cited, we have refrained from designating lectotypes. It is not a requirement for the names to be validly and effectively published and we consider those decisions should be made during the course of a taxon-level revision where a serious study of all specimens would lead to the best selections.

Taxonomic part

Eremogone Fenzl, Vers. Darstell. Alsin. 13. 1833

Lectotype. (see McNeill in Notes Roy. Bot. Gard. Edinburgh 24: 120. 20 Sep 1962): *E. graminifolia* Fenzl, Vers. Darstell. Alsin. 37. 1833.

Description. Plants perennial, sometimes densely cespitose or pulvinate or with a stout woody caudex, very rarely annual. Leaves filiform to subulate, often long-linear and grass-like, sometimes short and setaceous or needle-like, congested in vegetative rosettes and at or near base of flowering stems, margin sometimes scarious, apex of-

ten apiculate. Inflorescence of one or more terminal cymes, sometimes compressed to head-like, sometimes flowers solitary or paired. Flowers weakly perigynous. Sepals often hardened at base, veins 1–3, margins often white-scarious. Petals white, rarely pink. Floral glands (nectaries) at base of the antisepalous filaments often lobed, conspicuous.

New combinations

***Eremogone aksayqingensis* (L.H.Zhou) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147449-1

Arenaria aksayqingensis L.H.Zhou, Acta Biol. Plateau Sin. 6: 25. 1987.

Type. CHINA. Xinjiang: Aksayqing, ca. 4900 m. Northwest Plat. Inst. Biol. Acad. Sin. Exped. 3723 (holotype, NWBI).

***Eremogone commagenae* (Çeleb. & Favarger) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147450-1

Arenaria commagenae Çeleb. & Favarger, Candollea 44: 329. 1989.

Type. TURKEY: Adiyaman, Mt. Nemrut Dagi, 1950 m, 5 July 1983, T. Çelebioğlu 83-8/1 (holotype, ISTF).

***Eremogone depauperata* (Edgew.) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147452-1

Arenaria depauperata (Edgew.) H.Hara, J. Jap. Bot. 51: 129. 1976, non Gay (1846). *Stellaria depauperata* Edgew., Fl. Brit. India [J.D. Hooker] 1(2): 234. 1874.

Type. INDIA: Alpine Sikkim Himalaya, Yeumtong in gravelly places, alt. 15000 ft.; J.D. Hooker s.n. (holotype, K?; possible isotype, GH, GH00353889 [JSTOR image!]).

***Eremogone ferruginea* (Duthie ex Williams) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147453-1

Arenaria ferruginea Duthie ex Williams, J. Linn. Soc., Bot. 33: 410. 1898.

Type. INDIA: Kumaon, Kali Valley, on rocks near Byans, 2800–3000 m, J.F. Duthie 2762 (BM?).

Eremogone festucoides **(Benth.) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147454-1

Arenaria festucoides Benth., Ill. Bot. Himal. Mts. 1: 81, pl. 21, f. 3. 1834.

Type. Kunawar (K?).

Eremogone festucoides **(Benth.) Rabeler & W.L.Wagner var.** ***imbricata*** **(Bieb.) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147455-1

Arenaria festucoides Benth. var. *imbricata* (Bieb.) Edgew. & J.D. Hooker, Fl. Brit. India [J.D. Hooker] 1(2): 234. 1874. *Arenaria imbricata* M.Bieb., Fl. Taur.-Caucas. 1: 344. 1808.

Type. Caucasus. circa Kobi (LE?).

Eremogone gerzensis **(L.H.Zhou) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147456-1

Arenaria gerzensis L.H.Zhou, Rep. Invest. Fl. Fauna Ah Li Reg. Tibet. 126. 1979.

Type. CHINA. Xizang: Ngari Diqu, Geze, 4500–4700 m, collector unknown 4346 (holotype, NWBI).

Eremogone grueningiana **(Pax & K. Hoffmann) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147457-1

Arenaria grueningiana Pax & K. Hoffmann in Pax, Repert. Spec. Nov. Regni Veg. Beih. 12: 366. 1922.

Syntypes. CHINA: Tschili (Hebei). Hsiau Wu tai schan, Felsen des Gipfels, 3050 m, 3 Aug 1912, H.W. Limpricht 600 (WRSL?, WU, WU0029891 [JSTOR image!]); Gipfelfelsen des Pe tai, 4050 m, Kalk, 26 Jun 1915, H.W. Limpricht 2563 (WRSL?, WU, WU0029892 [JSTOR image!]); Felsen des His tai, 3000 m, H.W. Limpricht 2982 (WRSL?). West-Tibet: Hor Tschango, Schtiala, Geröll des Schao kirr bu, 4700 m, H.W. Limpricht 2095 (WRSL?); Kanse, Tsokoma-Stock, Geröllhalden, 5000 m, H.W. Limpricht 2127 (WRSL?). Batang-Litang Pungtschamu, Felsen des Passes Dshagala, 5260 m, H.W. Limpricht 2262 (WRSL?).

This combination is proposed based on the placement of this taxon in subg. *Eremogone* in Wu et al. (2001). Pax and Hoffmann (Pax 1922) originally thought it was close to *A. przewalskii* Maxim., placed in subg. *Dolophragma* (Fenzl) McNeill in Wu et al. (2001). Neither taxon has been included in a molecular analysis as of this writing.

***Eremogone haitzeshanensis* (Tsui ex L.H.Zhou) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147458-1

Arenaria haitzeshanensis Tsui ex L.H.Zhou, Acta Biol. Plateau Sin. 13: 1. 1997.

Type. CHINA. Sichuan: Dege, Haizi Shan, 3800 m., Sichuan Exped. D-7475 (holotype, WUG).

***Eremogone ischnophylla* (F.N.Williams) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147459-1

Arenaria ischnophylla F.N.Williams, J. Linn. Soc., Bot. 38: 400. 1909.

Type. CHINA. Xizang: Khamba Fort, 17 July 1903, F.E. Younghusband 107 (holotype, K, K000723883 [JSTOR image!]; E, E00317561 = photo of specimen at K!).

***Eremogone juncea* (M.Bieb.) Fenzl var. *glabra* (Regel) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147461-1

Arenaria juncea var. *glabra* Regel, Bull. Soc. Imp. Naturalistes Moscou 35: 246. 1862.

Type. CHINA: northern China, A.A. Tatarinoff (LE?).

***Eremogone kumaonensis* (Maxim.) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147462-1

Arenaria kumaonensis Maxim., Fl. Tangut. 86. 1889.

Syntypes. INDIA: Kumaon, Ralam valley, 12500 ft., R. Strachey & J.E. Winterbottom 3 (BM, BM000946338 [JSTOR image!]; K, K000742179 [JSTOR image!]; LE?); Ralam valley, 14000-16000 ft., 1884, J.F. Duthie 2757 (LE?); Tihri-Garhwal, J.F. Duthie s.n. (LE?).

***Eremogone lancangensis* (L.H.Zhou) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147463-1

Arenaria lancangensis L.H.Zhou, Acta Phytotax. Sin. 18: 357. 1980.

Type. CHINA. Yunnan: Weixi, 4000 m, T.T. Yü 8966 (holotype, PE).

Eremogone mukerjeeana **(Majumdar) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147464-1

Arenaria mukerjeeana (Majumdar) H.Hara, J. Jap. Bot. 51: 7. 1976, *Stellaria mukerjeeana* Majumdar, Blumea 16: 267. 1968.

Type. NEPAL: Muktinath, 4250 m, T.B. Shrestha & Bista 2462A (holotype, CAL).

Eremogone potaninii **(Schischk.) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147465-1

Arenaria potaninii Schischk. in Komarov, Fl. URSS 6: 536. 1936, nom nov. for *Arenaria pentandra* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 26: 429. 1880, non (J. Gay) Ardoino (1867), Turcz. (1834), Wallr. (1822), Dufour (1820).

Type. Songaria, non procul a finibis Mongoliae, in montibus Kitschni-ne-tau, prope fortalitium Saissan, in rupibus, Potanin (LE?).

Eremogone pulvinata **(Edgew.) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147466-1

Arenaria pulvinata Edgew., Fl. Brit. India [J.D. Hooker] 1(2): 238. 1874.

Type. INDIA. Sikkim: 14000-17000 ft. [Lana Kayna, 15000 ft., 24 July 1849 (on additional label on K sheet)], J.D. Hooker, Hooker & Thomson, Herb. Ind. Orient. 3 (Holotype, K, K000723992 [JSTOR image!]; isotypes, BM, BM000946339 [JSTOR image!], BM000946343 [JSTOR image!]).

Eremogone qinghaiensis **(Tsui & L.H.Zhou) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147467-1

Arenaria qinghaiensis Tsui & L.H.Zhou, Acta Phytotax. Sin. 18: 358. 1980.

Type. CHINA. Qinghai: Dulan Xian, 4200 m, Qinghai-Gansu Exped. 1194 (holotype, WUG).

***Eremogone roborowskii* (Maxim.) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147468-1

Arenaria roborowskii Maxim., Fl. Tangut. 87. 1889.

Type. CHINA. Tibet: ad fl. Yang-tze, 20 July 1884, Przewalski? (LE?).

***Eremogone shannanensis* (L.H.Zhou) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147469-1

Arenaria shannanensis L.H.Zhou in C.Y. Wu, Fl. Xizang. 1: 677. 1983.

Type. CHINA. Xizang: Lunzhe, ca. 4300 m, B.Z. Guo et al. 22435 (holotype, NWBI).

***Eremogone taibaishanensis* (L.H.Zhou) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147470-1

Arenaria taibaishanensis L.H.Zhou, Acta Phytotax. Sin. 18: 361. 1980.

Type. CHINA. Shaanxi: Meixian, side of Dayehai, ca. 4000 m, Shaanxi Chin. Herb. Medic. Exped. 390 (holotype, WUG).

***Eremogone zadoiensis* (L.H.Zhou) Rabeler & W.L.Wagner, comb. nov.**
urn:lsid:ipni.org:names:77147471-1

Arenaria zadoiensis L.H.Zhou, Acta Biol. Plateau Sin. 6: 26. 1987.

Type. CHINA. Qinghai: Zado, ca. 4400 m, S.W. Liu 110 (holotype, WUG).

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References

Dillenberger MS, Kadereit JW (2014) Maximum polyphyly: Multiple origins and delimitation with plesiomorphic characters require a new circumscription of *Minuartia* (Caryophyllaceae). Taxon 63: 64–88. doi: 10.12705/631.5

Greenberg AK, Donoghue MJ (2011) Molecular systematics and character evolution in Caryophyllaceae. Taxon 60: 1637–1652.

Harbaugh DT, Nepokroeff M, Rabeler RK, McNeill J, Zimmer EA, Wagner WL (2010) A new lineage-based tribal classification of the family Caryophyllaceae. International Journal of Plant Science 171: 185–198. doi: 10.1086/648993

Hartman RL, Rabeler RK (2004) New combinations in North America *Eremogone* (Caryophyllaceae). Sida 21: 237–241.

Ikonnikov SS (1973) Notae de Caryophyllaceis, 1. Novosti Sistematiki Vysshchikh Rastenii 10: 136–142.

Ikonnikov SS (1990) Notae de Caryophyllaceis, 9. Novosti Sistematiki Vysshchikh Rastenii 27: 63–65.

Pax F (1922) Aufzählung der von Dr. Limpricht in Ostasien gesammelten Pflanzen. Repertorium Specierum Novarum Regni Vegetabilis, Beihefte 12: 298–515.

Sadeghian S, Zarre S, Rabeler RK, Heubl G (in press) Molecular phylogeny of *Arenaria* (Caryophyllaceae: tribe Arenarieae) and its allies inferred from nuclear DNA ITS and plastid DNA rps16 sequences. Botanical Journal of the Linnaean Society.

Thiers B (2015) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih [continuously updated]

Wu Z, Zhou L, Wagner WL (2001) *Arenaria*. In: Zhengyi W, Raven PH, Deyuan H (Eds) Flora of China, volume 6. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 40–66.

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A new species of *Brevianthus* (Brevianthaceae, Marchantiophyta) from New Caledonia with unusual underleaf production

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Abstract

Brevianthus is a distinctive genus of leafy liverwort in its succubously inserted, entire leaves, lack of underleaves, restriction of sexual organs to lateral-intercalary branches, scattered rhizoids and dense leaf-surface ornamentation. The sole species, *Brevianthus flavus*, is divided into two subspecies, one in Tasmania the other in New Zealand. A second species, *Brevianthus hypocanthidium*, is described as new and is the first record of the genus for New Caledonia. Among its distinguishing characters are its shallowly bilobed leaves, and triangular underleaves present on small to medium-sized shoot sectors, the lack of a hyaline leaf margin, and the crenulate leaf margin formed by heavily thickened external cell walls. The most unusual features of the new species are the presence of underleaves between lateral leaf insertion lines that reach the ventral stem mid-line, and the absence of underleaves from larger shoots. To explain these features we propose a competitive model of shoot formation wherein the ventral merophyte progressively loses vigor as its relative stature decreases, and its derivative cells become discontinuous and isolated along the ventral stem surface, with intervening areas occupied by derivatives of the more vigorous lateral merophytes.

Keywords

Bryophyte, liverwort, *Brevianthus flavus*, New Zealand, Tasmania, Australasia

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Introduction

Brevianthus J.J.Engel & R.M.Schust. possesses a highly distinctive suite of morphological characters incongruent with its phylogenetic relationships. The restriction of sexual organs to abbreviated lateral-intercalary branches, the lack of underleaves, and the scattered rhizoids were thought to immediately remove the plant from the Lophocoleaceae De Not. (Engel and Schuster 1982), whereas the combination of succubously inserted, undivided leaves, with coarse trigones, lack of underleaves, undifferentiated stems, and short androecial branches suggest the isolated genus *Jackiella* Schiffn., within which the type species was originally described by Grolle (1970) on the basis of sterile and androecial individuals. The discovery of fertile, perianth- and sporophyte-bearing material prompted the species' removal from Jackiellaceae R.M.Schust. due to the well-developed perianth and the comparatively large and undifferentiated seta. The female structures in combination with the minute androecia with strongly ventricose and monandrous bracts, the uniseriate antheridial stalks suggested relationships with the Adelanthaceae Grolle. However, the exclusively lateral intercalary branching (both vegetative and sexual), lack of stolons, lack of secondary pigmentation, and the 3-4 stratose capsule were all inconsistent with placement within the Adelanthaceae (Engel and Schuster 1982).

The wide-mouthed obscurely trilobed perianths, the isophyllous gynoecium, the 1-phase development of the outer capsule layer, and the seta anatomy all suggested affinity with the old Geocalycineae R.M.Schust. (including the Lophocoleaceae and Plagiochilaceae Müll. Frib. & Herzog). However the spherical capsules, scattered rhizoids and apparent absence of a ventral merophyte were anomalous with that suborder so *Brevianthus* was placed, with the Chonecoleaceae R.M.Schust. ex Grolle, into an independent new suborder, Brevianthineae J.J.Engel & R.M.Schust. by Engel and Schuster (1982). These authors also proposed a monogeneric family Brevianthaceae J.J.Engel & R.M.Schust.

Molecular phylogenetic studies led to considerable changes in the classification of liverworts (Crandall-Stotler et al. 2009) and supported the reinstatement of Lophocoleaceae (Hentschel et al. 2007) for the perianth-bearing elements of Geocalycaceae Endl. sensu Crandall-Stotler and Stotler (2000) and others.

The first molecular phylogenetic study including *Brevianthus*, on the basis of a New Zealand specimen, resolved the genus sister to the Lophocoleaceae element *Tetracymbaliella* Grolle, then *Plagiochila* (Dumort.) Dumort. in a monophylum also containing *Chiloscyphus* Corda (He-Nygren et al. 2006), placing it firmly within the Lophocoleaceae-Plagiochilaceae familial complex in contradiction to much of the morphological evidence. Subsequent molecular phylogenetic studies seem to corroborate the sister relationship of *Brevianthus* and *Tetracymbaliella*, and resolved this clade as sister to the rest of the Lophocoleaceae (Feldberg et al. 2014).

Once believed endemic to Tasmania, *Brevianthus* was discovered on South Island (Blackball), New Zealand in 1998 (Glenny 2000), and has since been collected from a small number of sites on the West Coast of the South Island and in the upper North Island. The first New Zealand collection was made in the North Island in 1990 but

went unrecognized. New Zealand plants differ morphologically from Tasmanian, and were given subspecific status by Engel (2011).

In 2006 the late Elizabeth Brown made a relatively copious collection of *Brevianthus* at Mont Kouakoué in New Caledonia, sufficient to facilitate the identification of several distinctive morphological characters warranting its assignment as a separate species. We outline this proposition below, and provide additional observations on the ecology and distribution of the two subspecies of *B. flavus* (Grolle) J.J.Engel & R.M.Schust.

Taxonomic treatment

***Brevianthus* J.J.Engel & R.M.Schust., Phytologia 47: 317. 1981.**

Type. *Brevianthus flavus* (Grolle) J.J.Engel & R.M.Schust., Phytologia 47: 318. 1981.

Key to species

1 Leaf margins crenulate; leaves bifid at least on small stature shoots; leaf cell surface ornamentation lacking urceolate papillae over the cell junctions **2**

– Leaf margins entire, not crenulate; leaves undivided; leaf cell surface ornamentation with urceolate papillae over the cell junctions on the medial-basal cells of some or all leaves..... ***Brevianthus flavus* subsp. *flavus*.**

2 Small triangular underleaves present on small to medium-sized shoot sectors, absent from large shoots; leaf margin not hyaline; leaf apex always distinctly bifid; leaf margin crenulate by thickened cell walls, marginal cells similar in size to internal cells.... ***Brevianthus hypocanthidium* M.A.M.Renner & J.J.Engel**

– Underleaves entirely absent; leaf margin hyaline; leaf apex bifid on small leaves but undivided on large leaves, leaf margin crenulate by bulging cells, marginal cells smaller than internal cells..... ***Brevianthus flavus* subsp. *crenulatus* J.J.Engel**

Table 1. Characters differentiating *Brevianthus* taxa.

	B. flavus* subsp. *flavus	***B. flavus* subsp. *crenulatus***	***B. hypocanthidium***
Leaf margin	Entire	Crenulate by bulging cell lumen	Crenulate by thickened cell walls
Leaf marginal cells	Hyaline	Hyaline	Chlorophyllous
Underleaves	Absent	Absent	Present on small and medium sized shoot sectors
Leaf apex	Unlobed	Unlobed on large leaves, bifid on small leaves	Uniformly bifid
Leaf shape	Ovate-oblate	Ovate-oblate	Ovate-rotund
Leaf cell trigones	Triangular to bulging	Triangular to bulging	Block-like
Leaf cell surface ornamentation	Urceolate papillae over cell junctions of at least medial and basal cells of some leaves on each shoot	Without urceolate papillae over cell junctions	Without urceolate papillae over cell junctions

Brevianthus hypocanthidium **M.A.M.Renner & J.J.Engel, sp. nov.**
Figures 1, 2

Diagnosis. Distinguished from both subspecies of *Brevianthus flavus* by the triangular underleaves produced on small- to medium-sized shoot sectors, the consistently but shallowly bilobed leaves, the crenulate leaf margins formed by heavily thickened exterior cell walls, and the chlorophyllous marginal leaf cells similar in size to the medial cells.

Type. New Caledonia, Province Sud, Mont Kouakoué, slightly west of base camp at helicopter landing site, without date, *E.A. Brown 2006/17*, holotype: NOU; isotypes: NSW, F.

Description. Plants closely prostrate, creeping, shoots sinuous, dull whitish green, opaque, water repellent, axes cylindrical, vermiform, to 2 mm wide and 30 mm long, the axes slightly laterally flattened. Branches sporadic, lateral-intercalary. Stolons and flagellae absent. Stems wiry, narrow for plant size, densely papillose, cortical cells oblong, all walls heavily thickened, in cross section 7–8 cells high, cortex undifferentiated, cells same size as medulla, with massive, nodular thickenings either confluent or separated by short stretches of unthickened primary wall. Rhizoids scattered on ventral side of stem, colourless, non-septate, tips often branched. Leaf insertion strongly succubous, nearly horizontal at postical end, not recurved at antical end, extending to stem mid-line on ventral side of large, but not small shoots, not extending to dorsal stem midline, leaving 1–2 cell rows leaf-free. Leaves strongly dorsally assurgent, not connivent over the dorsal stem surface, the axis appearing channeled in dorsal view with the stem partly or completely visible, the leaves unistratose throughout, densely imbricate, concave, ovate-rotund, lacking a hyaline border; apex shallowly but distinctly bifid; margins crenulate by thickened cell walls; dorsal margin rounded, not or slightly decurrent, ventral margin rounded, the base weakly auriculate on small leaves and not auriculate on large leaves, not overlapping the ventral stem surface, not totally obscuring the stem in ventral view. Leaf cells not tiered, polygonal but typically hexagonal, isodiametric, with massive coarse, nodular trigones, confluent or separated by narrow stretches of unthickened primary wall, primary walls visible within trigones, 39–50 µm diameter; marginal cells thick walled, external wall heavily thickened, especially medially, trigones coarse, not confluent, consistently separated by unthickened primary wall, lumena not reduced, cells only slightly smaller than median cells, quadrate, 40–50 µm long and 27–36 µm wide, long axis parallel with margin. Intramarginal cells on abaxial surface covered with dense circular and confluent to bacilliform anastomosing ornamentation continuous over cell junctions; urceolate to clavate 'papillae' over cell junctions absent. Cells, both marginal and intramarginal, on adaxial surface with similar ornamentation, comprised circular and confluent to weakly anastomosing ornamentation. Underleaves present on small- to medium-sized shoot sectors, triangular, 4–6 cells wide at base and 8–9 cell tiers high, apex acute, formed by a single cell; 230–300 µm long by 9–140 µm wide at base, margins crenulate; ventral merophyte 0–2 cells wide. Asexual reproduction by leaf-borne regenerants arising from the adaxial leaf surface.

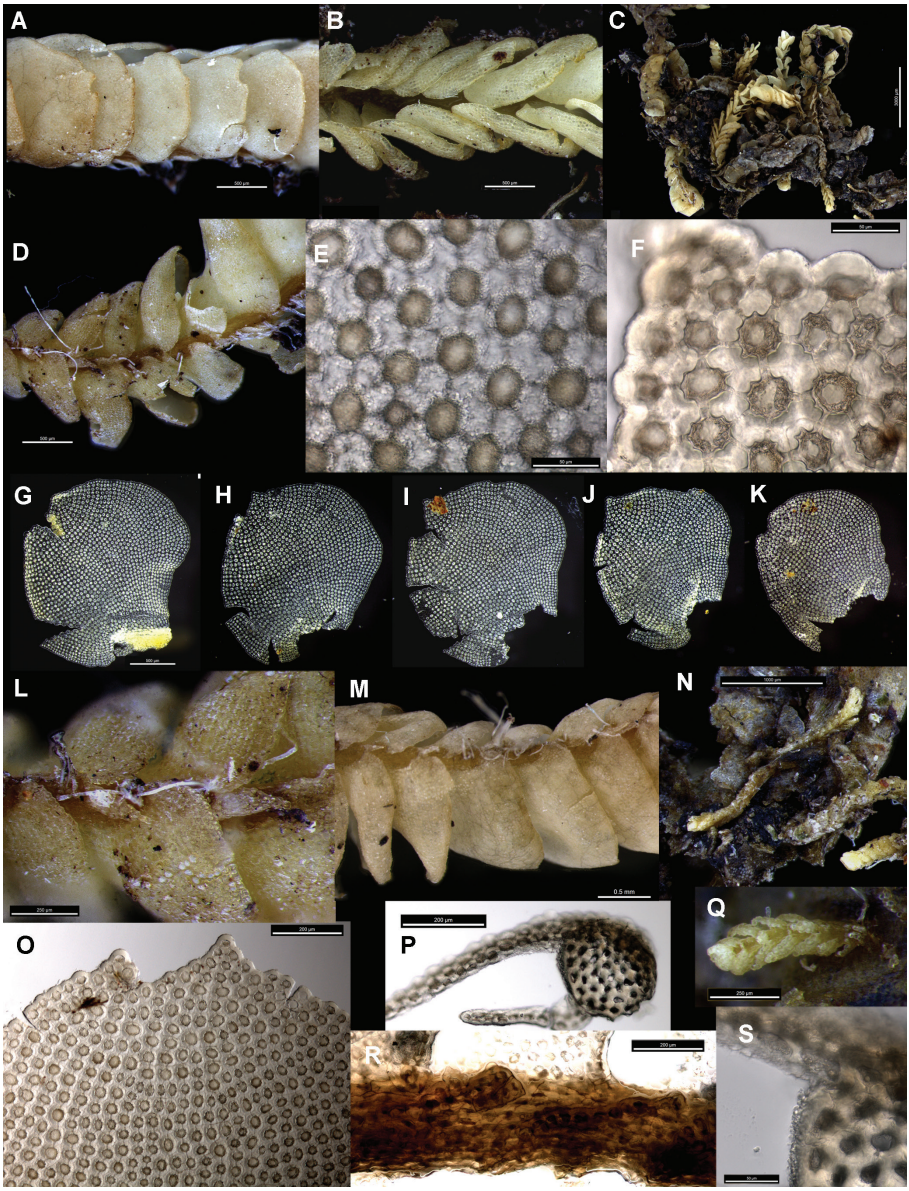

Figure 1. *Brevianthus hypocanthidium*: **A** lateral view of shoot **B** dorsal view of shoot **C** habitus **D** ventral view of shoot **E** abaxial leaf cell surface **F** cell margin at leaf apex, one leaf-lobe featured **G–K** leaves dissected and flattened **L** underleaves **M** ventral view of shoot showing underleaf absence from largest shoot sector (middle of image) **N** regenerants on old shoot sector **O** leaf apex **P** stem transverse section **Q** ventral view of regenerant attached to adaxial side of single cell at shoot base, showing variable expression of triangular underleaves on distinct ventral merophyte **R** lateral view of stem, with apex to left, leaves removed showing linear succubous insertion, J-shaped at ventral end, note cells of stem insertion projecting ventrally **S** transverse section of stem showing dense ornamentation on dorsal stem surface. All from NSW791547. Scale: 500 µm (**A, B, D, G–K, M**); 3000 µm (**C**); 50 µm (**E, F, S**); 200 µm (**L, O, P, R**); 1000 µm (**N**); 250 µm (**Q**).

Sexual structures not seen.

Etymology. hypocanthidium: υπο- hypo-, below; αχανθα- acantha (f.) spine, thorn, prickle; -ιδιον -idion, a diminutive suffix.

Distribution and ecology. So far as known, endemic to New Caledonia. The type collection occurred on a ridge bearing forest 3 m tall with open canopy and high light at ground level, where it grew with *Schistochila vitreocincta* (Herzog) X.-L.He & Glenny at the base of the trunk on a 'mostly dead' *Leucopogon* R.Br. The Schuster specimen occurred in an open, disturbed (old burn) *Dacrydium araucarioides* Brong. & Gris-*Callitropsis* Oerst. scrub.

Recognition. The genus *Brevianthus* is highly distinctive among leafy-liverworts in the white or nearly white, water-repellent, cylindrical shoots with dorsally assurgent and succubously inserted leaves and no or inconspicuous underleaves, and scattered rhizoids. The shoots are typically sinuous in growth, either down or across the substrate, and lay closely appressed to it. They do not often overlap one another. This combination of macro-morphological characters facilitates field identification.

The three *Brevianthus* taxa recognized here all share these features, and are similar in their gross morphology. They differ primarily in micromorphological, microstructural, and anatomical details. However, characters vary in their manifestation with the stage of shoot stature and maturity, such that diagnostic differences must be sought within shoots of the appropriate age or size.

The triangular underleaves found only in *B. hypocanthidium* (Fig. 1L) are a case in point. Not only are these partly obscured by adjacent leaves, they are produced only on small and medium sized shoot sectors. They are absent from the largest stature shoot sectors. As such, they are inconsistently present along a shoot, and may be entirely absent if the shoot examined is uniformly large. The other two *Brevianthus* taxa never produce underleaves, regardless of shoot stature.

Characters of the leaf apex and margins are useful in distinguishing the taxa of *Brevianthus*. The leaf apex of *B. hypocanthidium* (Fig. 1O) is shallowly but distinctly bifid, and this is a consistent feature of leaves of all sizes, though on the smallest leaves of leaf-borne propagules this is obscure. In *B. flavus* subsp. *crenulatus* small leaves are bifid (Fig. 5O, P), while medium and large leaves have an undivided apex (Fig. 5G–L). In *B. flavus* subsp. *flavus* the leaf apex is always undivided and entire (Fig. 3E–J).

The leaf margin provides several diagnostic differences between the three taxa that are of more consistent manifestation. In *B. hypocanthidium* the leaf margin (Fig. 1F) is crenulate by virtue of its heavily thickened exterior cell wall, and the marginal leaf cells are chlorophyllous and similar in size to the medial cells. In *B. flavus* subsp. *crenulatus* the leaf margin (Fig. 5F) is crenulate by virtue of bulging marginal cell lumena, and the marginal cells are colourless and smaller than medial cells. In *B. flavus* subsp. *flavus* the leaf margin (Fig. 3L) is entire, the marginal cells are again colourless and smaller than medial cells.

Trigones in leaf-cells differ between species. In *B. hypocanthidium* (Fig. 1E) they are block-like and angular with truncate ends and straight sides. In both subspecies of *B. flavus* (Figs 3L, 5F) they are coarse to bulging but with curved sides, and never as large or angular as observed in *B. hypocanthidium*.

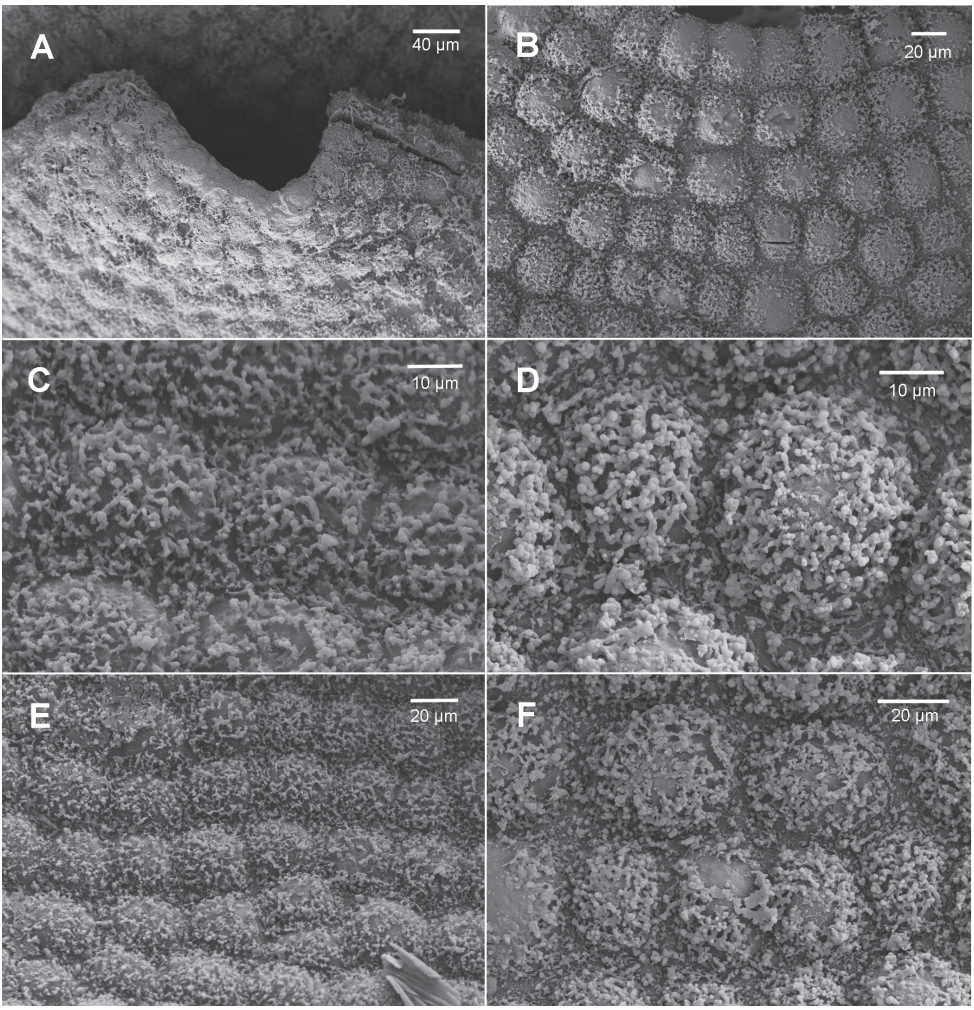

Figure 2. *Brevianthus hypocanthidium*: **A** leaf apex **B** cells at base of sinus on abaxial leaf surface **C** abaxial leaf surface at mid-leaf **D** abaxial leaf surface scale **E** adaxial leaf surface scale **F** adaxial leaf surface detail scale. All from NSW791547. Scale: 40 µm (**A**); 20 µm (**B, E, F**); 10 µm (**C, D**).

Leaf surface ornamentation may exhibit species-specific differences though there is intra-individual variation; our interpretation, however, may suffer from the relatively small number of observations we have made via SEM. Individuals of *Brevianthus flavus* subsp. *flavus* (Figs 3K; 4C, D) possess urceolate to clavate 'papillae' over the cell junctions on the abaxial leaf surface, at least between cells in the median-basal to basal portions of leaves, and at least sporadically on leaves along a single shoot. These 'papillae' have not been observed in individuals of *B. flavus* subsp. *crenulatus* (Figs 5E; 6C, D) or the type of *B. hypocanthidium* (Figs 1E; 2C, D). Parts of these structures are removable with chloroform, providing evidence that they partly consist of surface waxes (Heinrichs and Reiner-Drehwald (2012)).

Other leaf characters differentiate the taxa. The interstices between cells also appears to exhibit species-specific differences. In *B. flavus* subsp. *crenulatus* (Fig. 6) leaf cell junctions appear recessed within the leaf such that the upper and lower parts of the cell appear surrounded by a narrow trench, which is less pronounced or absent in both *B. hypocanthidium* (Fig. 2) and *B. flavus* subsp. *flavus* (Fig. 4).

Leaf shape, orientation and imbrication also differ. In both *B. flavus* subsp. *crenulatus* (Fig. 5D, M) and *B. flavus* subsp. *flavus* (Fig. 3D) the leaves are imbricate over the ventral stem surface, obscuring stem tissue in ventral view, while in *B. hypocanthidium* (Fig. 1D, L, M) the ventral stem surface is often partially visible between the leaves. The leaves of *B. hypocanthidium* (Fig. 1A, G–K) are ovate-rotund, and when viewed *in situ* laterally, have their antical margin orientated more or less perpendicular to the stem. *Brevianthus flavus* subsp. *flavus* (Fig. 1A, E–I) has ovate to oblate leaves whose antical margin is inclined in lateral view, with the lowest part of the margin closest to the shoot apex. The same is true of *B. flavus* subsp. *crenulatus* (Fig. 5A, H–L) though the angle of inclination is not so steep.

Conservation status. That *B. hypocanthidium* is known from two gatherings precludes inference of its likely distribution and abundance, we therefore recommend the species be considered Data Deficient.

Additional specimen examined. New Caledonia, Montagne des Sources, above St. Louis: Pic Buse and vicinity, 650–750 m, *R.M. Schuster 57820* (F).

Brevianthus flavus (Grolle) J.J.Engel & R.M.Schust. subsp. *flavus* Phytologia 47: 318. 1981

Figures 3, 4

Basionym: *Jackiella flava* Grolle, Journal of the Hattori Botanical Laboratory 33: 222. 1970.

Type. Tasmania, Recherche Bay, Catamaran, 14 Jan 1911, *W.A. Weymouth 1232* as *Jamesoniella occlusa*, holotype: NY.

For a full description of *B. flavus* see Engel and Schuster (1982).

Distribution and ecology. *Brevianthus flavus* subsp. *flavus* is widespread on the wetter western, south-western and southern sectors of Tasmania, between 300 and 900 m altitude where it occurs in a wide variety of habitat types encompassed by this altitudinal range. *Brevianthus flavus* occurs within or on the margins of a wide variety of forest types, for example riparian scrub dominated by *Leptospermum* J.R.Forst. & G.Forst., *Acacia* Mill. and *Banksia* J.R.Forst. & G.Forst., with dense thicket of *Bauera* Banks ex Andrews on alluvial terrace in a gully with south-easterly aspect at Condominium Creek, or montane forest of *Nothofagus cunninghamii* (Hook.) Oerst., *Eucryphia* Cav., *Arthrotaxis* Endl., *Atherosperma* Labill. and *Richea dracophylla* R.Br. with broken canopy to 8 m tall on a ridge with southerly aspect on Mt Dundas. The species also occurs in subalpine and alpine scrub such as that dominated by *Eucalyptus* L'Hér., *Sprengelia* Sm., *Leucopogon*, *Banksia*, *Orites* R.Br. and *Gymnoschoenus* Nees as at Mount Eliza, and dominated by *Astelia* Banks & Sol. ex R.Br., *Richea* and *Nothofagus* Blume at Mount Hesperus. *Brevianthus flavus* is

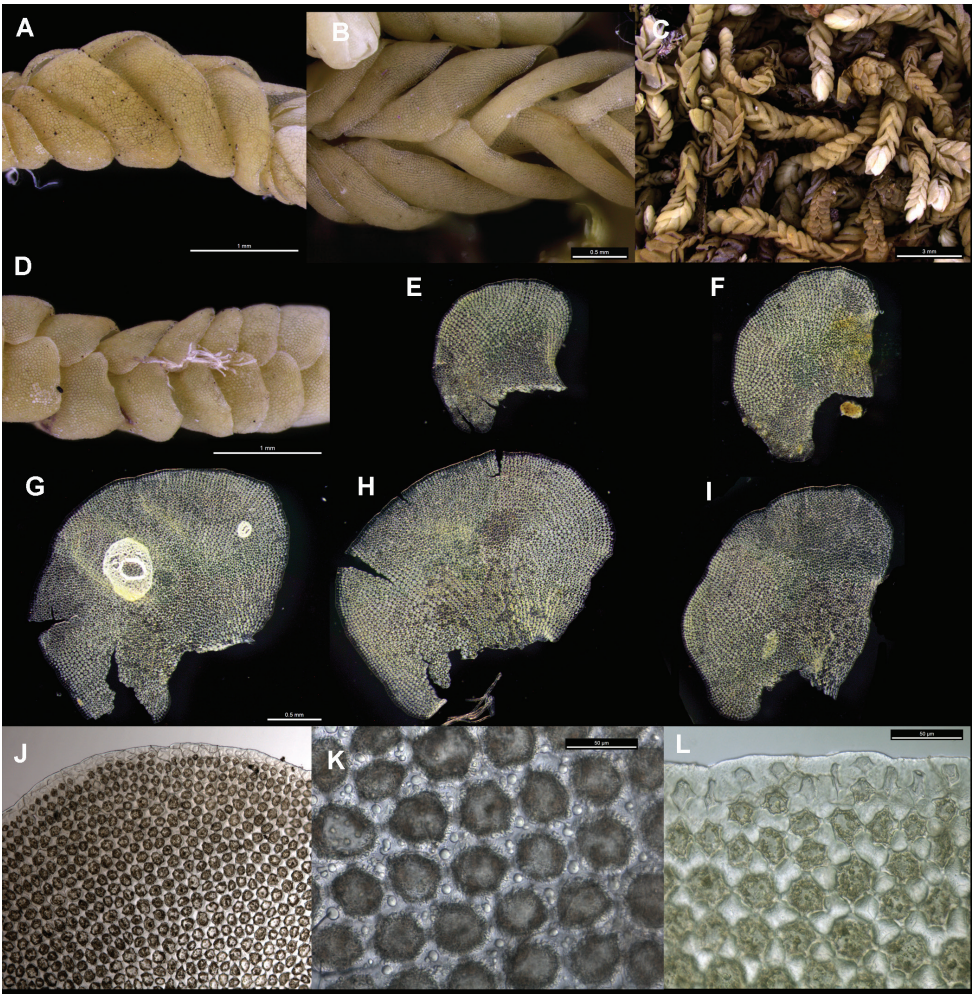

Figure 3. *Brevianthus flavus* subsp. *flavus*: **A** lateral view of shoot **B** dorsal view of shoot **C** habitus **D** ventral view of shoot **E–I** leaves dissected and flattened **J** leaf apex **K** abaxial leaf cell surface **L** leaf margin at apex. All from NSW892112. Scale: 500 µm (**A, B, E–I**); 3000 µm (**C**); 1000 µm (**D**); 200 µm (**J**); 50 µm (**K, L**).

for most part an epiphyte on tree trunks, including *Banksia*, *Lagarostrobos* Quinn, and *Nothofagus*. It sporadically occurs as a lithophyte on rock outcrops where it may inhabit crevices or sides sheltered by surrounding vegetation. It co-occurs with a wide variety of species, including *Acromastigum cavifolium* R.M.Schust., *Frullania* Raddi spp., *Heteroscyphus* Schiffn. spp., *Radula multiamentula* E.A.Hodgs. on rocks; *Bazzania* Gray, *Schistochila* Dumot. spp., *Lepidolaena brachyclada* (Lehm. ex Lehm.) Trevis., *Lepidozia ulothrix* (Schwägr.) Lindenb., *Schistochila pinnatifolia* (Hook.) Trevis., *Radula* spp., *Acromastigum cavifolium*, *Acrobolbus cinerascens* (Lehm. & Lindenb.) Schiffn., *A. ochrophyllus* (Hook.f. & Taylor) R.M.Schust., *Frullania* etc on trunks of *Nothofagus cunninghamii*.

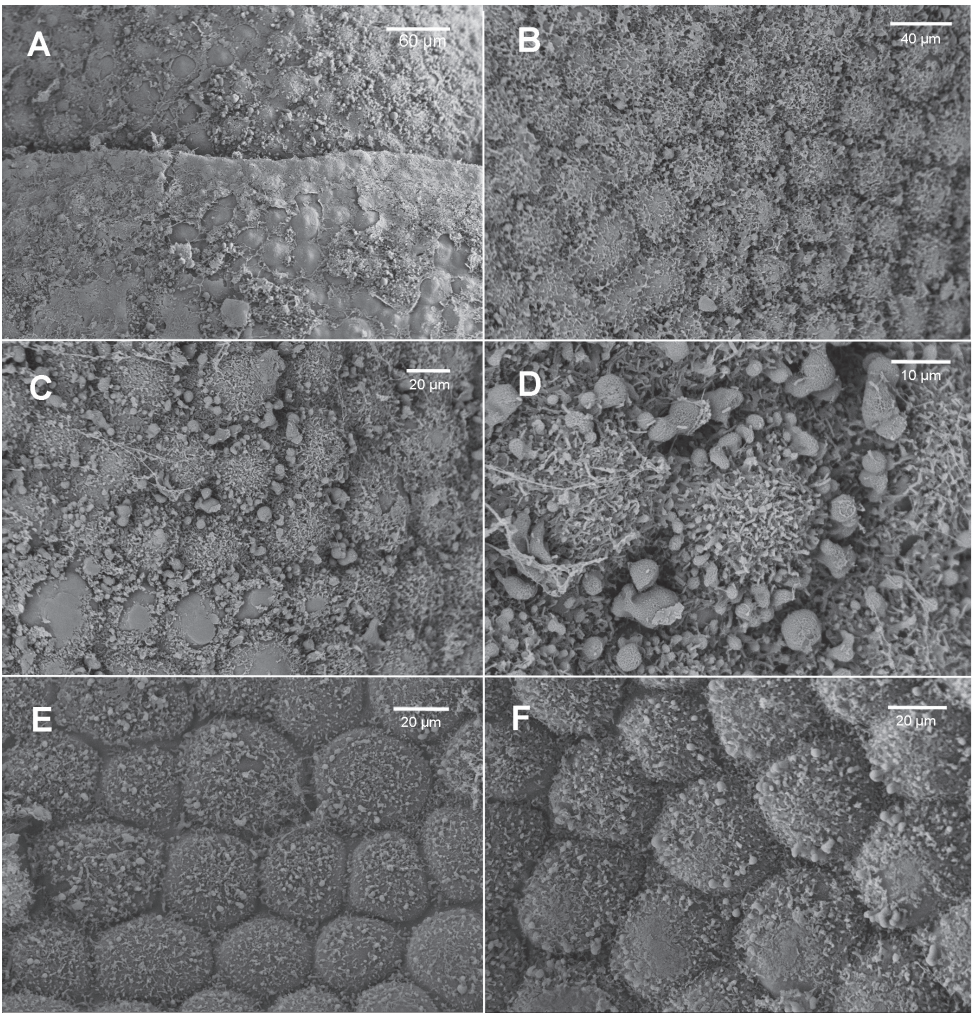

Figure 4. *Brevianthus flavus* subsp. *flavus*: **A** leaf apex scale **B** cells below apex on abaxial leaf surface scale **C** abaxial leaf surface at mid-leaf scale **D** abaxial leaf surface scale **E** adaxial leaf surface **F** adaxial leaf surface detail. All from NSW89112. Scale: 60 µm (**A**); 40 µm (**B**); 20 µm (**C, F**); 10 µm (**D**).

Conservation status. *Brevianthus flavus* subsp. *flavus* appears widely distributed in western and southern Tasmania, however collecting and survey effort to date provides insufficient basis for an accurate appraisal of the species' threat status. We therefore recommend *B. flavus* subsp. *flavus* be regarded as Data Deficient pending a more informed assessment.

Specimens examined. Australia, Tasmania, West: Highway B28, east of Mt Murchison, Quinn Creek, 41°50'S, 145°37'E, 600 m, 20 Feb 1998, *J.E. Braggins 98064B*, AK255753; West Coast: Mount Dundas Regional Reserve, Mount Dundas, track to summit from south, 41°54'32"S, 145°28'3 2"E, 845 m, *M.A.M. Renner 6008 & E.A.*

Brown, NSW855958; South West: Serpentine River valley, south of the Gordon River, just below the dam, 42°47'S, 145°57'E, 300m, 18 Feb 1998, *J.E. Braggins 98052A*, AK255728; South West Conservation Area: Mount Eliza, Condominium Creek, 42°57'22"S, 146°21'56"E, 350 m, 23 Jan 2012, *M.A.M. Renner 5927 & E.A.Brown*, NSW895251; Mount Eliza, unnamed catchment S of Mount Anne track, 42°57'45"S, 146°23'32"E, 860 m, 22 Jan 2012, *M.A.M. Renner 5898 & E.A.Brown*, NSW892112; Arthur Range, Mount Hesperus, S of track to summit at top of hill, 43°06'41"S, 146°13'9"E, 820 m, 24 Jan 2012, *M.A.M. Renner 5958*, NSW880771.

***Brevianthus flavus* subsp. *crenulatus* J.J.Engel, Nova Hedwigia 93: 406. 2011**

Type. New Zealand, South Is., Westland Prov., Lake Kaniere Scenic Reserve, Lake Kaniere Rd, 125 m, *J.J. Engel 24815, M.J. von Konrat & J.E. Braggins*. holotype: F; isotype: CHR.

Distribution and ecology. *Brevianthus flavus* subsp. *crenulatus* exhibits a discontinuous distribution within New Zealand's, cool hyper-humid forest environments from Waipoua Forest in western Northland southward at least as far as Blackball on the West Coast of the South Island. *Brevianthus flavus* subsp. *crenulatus* is often, though not exclusively, associated with forests including *Lepidothamnus intermedius* (Kirk) Quinn or *Manoao colensoi* (Hook.) Molloy, where these occur in podocarp-broadleaf forests, as at the summits of Hirakimata (Mount Hobson) on Aotea (Great Barrier Island, M.A.M. Renner *pers. obs.*) and Mount Rowe; or in podocarp-beech forest as at Craigieburn. *Brevianthus flavus* subsp. *crenulatus* is typically a trunk epiphyte, but may occur as a lithophyte, as at the head of the Croesus Track, near Blackball.

In Northland *Brevianthus flavus* subsp. *crenulatus* may be a common and even dominant component of epiphytic communities on the southern side of *Metrosideros robusta* A.Cunn. and *Agathis australis* (D.Don) Loudon trunks in open *A. australis* ricker forest on clearing edges, where it occurs with *Dendromastigophora flagellifera* (Hook.) R.M.Schust., *Lepicolea attenuata* (Mitt.) Steph., *Lopholejeunea colensoi* Steph., *Radula pseudoscripta* M.A.M.Renner, *Heteroscyphus menziesii* (Mitt.) J.J.Engel, and *Hymenophyllum armstrongii* (Baker) Kirk. Despite its often luxuriant growth in these situations, no fertile material has yet been observed.

From the Auckland Region southward *B. flavus* subsp. *crenulatus* tends to be an epiphyte on trunks of *Lepidothamnus intermedius*, *Manoao colensoi* and sometimes *Nothofagus solandri* (Hook.f.) Oerst. var. *cliffortioides* (Dippel) Poole, where these grow in mixed podocarp-beech and podocarp-broadleaf forests, such as the *Lepidothamnus intermedius*, *Dacrydium cuppressinum* Sol ex G.Forst., *Phyllocladus* aff. *alpinus* Hook.f., *Weinmannia silvicola* L.f., *Quintinia serrata* A.Cunn., *Pseudopanax discolor* (Kirk) Harms forest on boggy ground on the summit ridge of Mt Rowe, here *B. flavus* subsp. *crenulatus* grew in association with *Lepicolea scolopendra* (Hook.) Dumort. ex Trevis.,

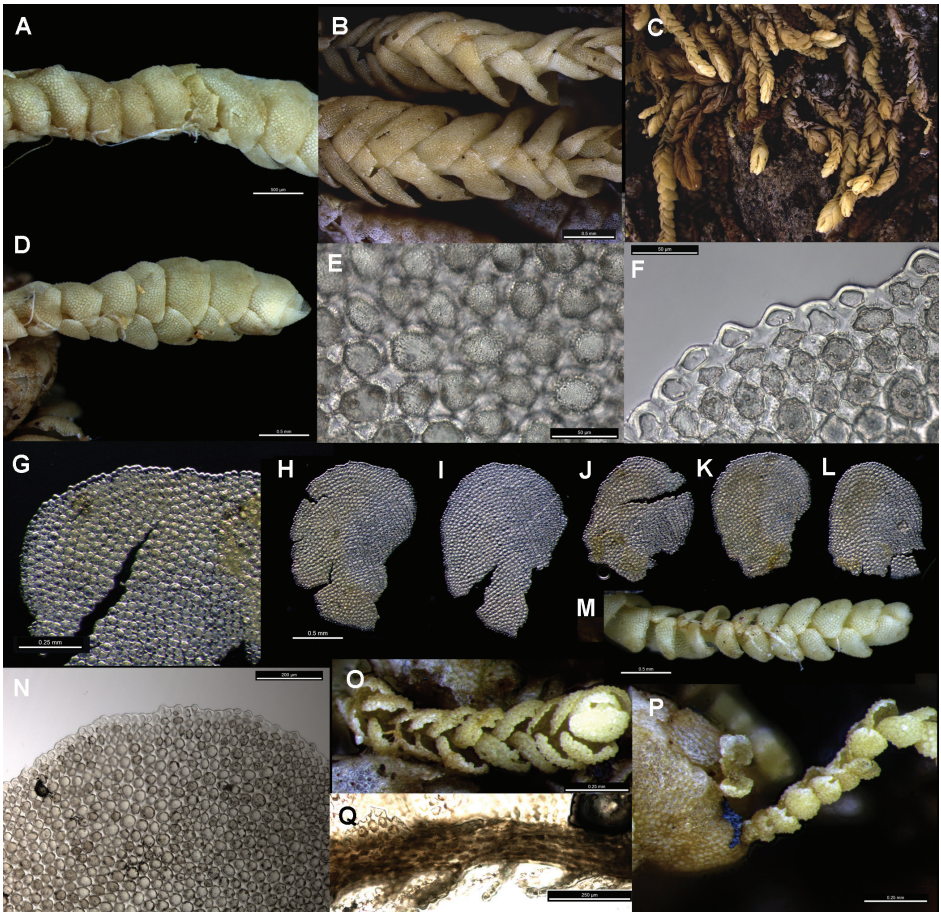

Figure 5. *Brevianthus flavus* subsp. *crenulatus*: **A** lateral view of shoot **B** dorsal view of shoot **C** habitus **D** ventral view of shoot **E** abaxial leaf cell surface **F** cell margin at leaf apex, one leaf-lobe featured **G** leaf showing crenulate hyaline cells prominent on dorsal margin **H–L** leaves dissected and flattened **M** ventral view of shoot **N** leaf apex **O** dorsal view of regenerant showing bulging cells and bifid leaf apices **P** lateral view of regenerant attached to adaxial side of single cell near the leaf margin at shoot base **Q** lateral view of stem, apex to left. All from NSW745726. Scale: 500 µm (**A, B, D, H–M**); 3000 µm (**C**); 50 µm (**E, F**); 250 µm (**G, O, P, Q**); 200 µm (**N**).

Lepidozia microphylla (Hook.) Lindenb., *Heteroscyphus* sp., *Acrochila biserialis* (Lehm. & Lindenb.) Grolle, *Acromastigum cavifolium*, *Schistochila tuloides* (Hook.f. & Taylor) Steph., *Radula multiamentula*, and *Thysananthus anguiformis* (Hook.f. & Taylor) Taylor ex Gottsche, Lindenb. & Nees.

At the head of the Croesus track *B. flavus* subsp. *crenulatus* grew on vertical granite of bluffs overhanging the start of the Croesus track, with *Heteroscyphus menziesii*, *Radula multiamentula*, *Acrobolbus epiphyticus* (Colenso) Briscoe, *Herbertus* Gray, *Acromastigum anisostomum* (Lehm. & Lindenb.) A.Evans, *Frullania* sp., *Lepidozia* (Dumort.) Dumort. spp. and *Hymenophyllum armstrongii*.

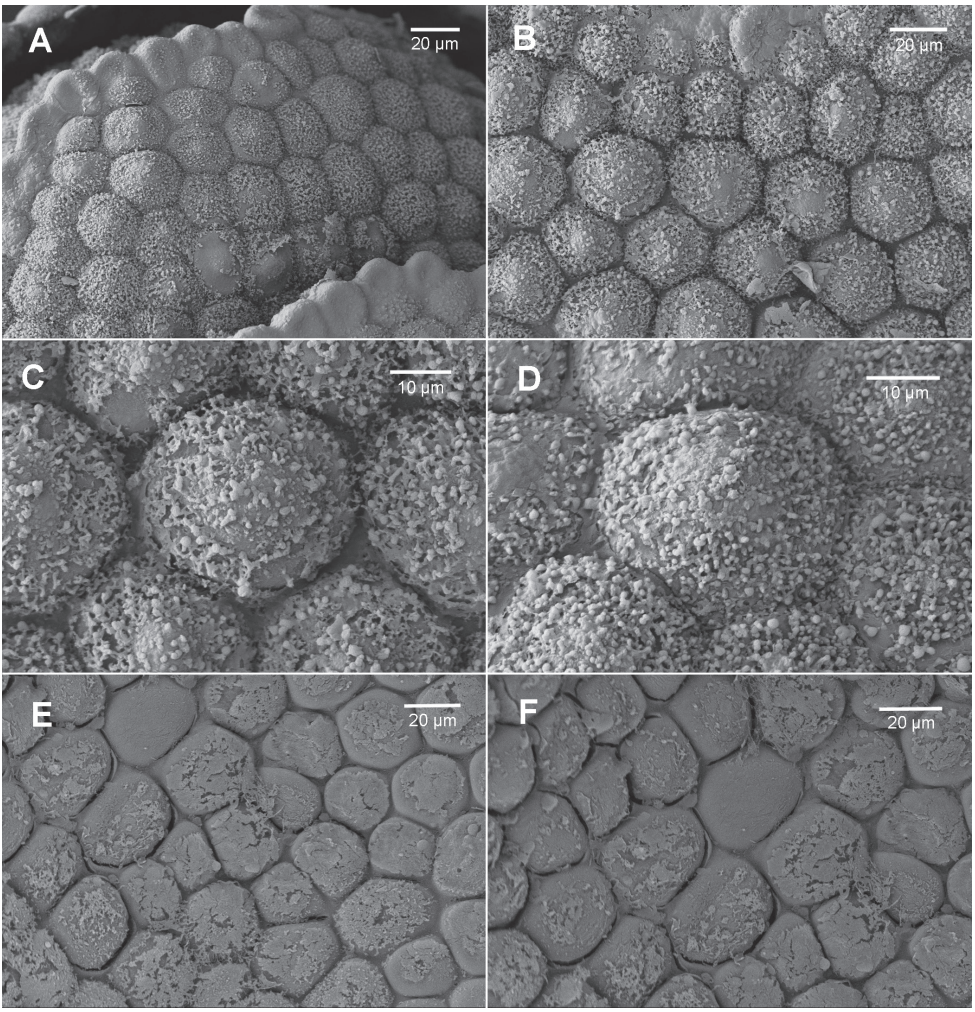

Figure 6. *Brevianthus flavus* subsp. *crenulatus*: **A** leaf apex **B** cells below apex on abaxial leaf surface **C, D** abaxial leaf surface at mid-leaf **E, F** adaxial leaf surface. All from NSW745726. Scale: 20 µm (**A, B, E, F**); 10 µm (**C, D**).

At Craigieburn Road on the West Coast of the South Island, *B. flavus* subsp. *crenulatus* is an occasional corticol on *Manoao colensoi* trunks in low forest with uneven, broken canopy comprised of *Leptospermum scoparium* J.R.Forst. & G.Forst. with *Nothofagus solandri* var. *cliffortioides*, *N. menziesii* (Hook.f.) Oerst., and emergent *Manoao colensoi*, on saturated soil of an old alluvial terrace. Here the species was common on *Manoao* trunks, occasional on *Nothofagus solandri* var. *cliffortioides*, but apparently absent from trunks of *N. menziesii*, and grew in association with *Acrochila biserialis*, *Acromastigum cavifolium*, *Heteroscyphus menziesii*, *Heteroscyphus* sp., *Schistochila tuloides*, *Radula multiamentula*, *Radula tasmanica* Steph., *Frullania ptychantha* Mont., *Frullania* sp., *Macromitrium longipes* (Hook.) Schwägr., *Dicnemon calycinum* (Hook.) Schwägr., and *Hymenophyllum armstrongii*.

Conservation status. *Brevianthus flavus* subsp. *crenulatus* was listed as Naturally Uncommon, with qualifier 'Sparse' by the New Zealand Department of Conservation's, Threat listing Bryophyte specialist panel (Glenny et al. 2014).

Specimens examined. New Zealand, North Island: Western Northland Ecological Region, Tutamoe Ecological District, Waipoua Forest, Tarahoka clearing, 35°37'S, 173°33'E, 380 m, 16 Oct 2000, *M.A.M. Renner 00/125*, AK280186; Tutamoe Ecological District, Waipoua Forest, lookout loop, Toatoa Grove, c. 280m, 35°40'30"S, 173°33'46"E, 21 Feb 1990, *J.E. Braggins 90/42*, AK325216; Waipoua Forest, track to Te Matua Ngahere, 35°36'S, 173°31'E, ca. 340 m, 1997, *J.J. Engel 22543* (F); Thames Ecological District, ridge NW of Mount Rowe on track to summit, 37°02'16"S, 175°40'19"E, 720 m, 14 Feb 2007, *M.A.M. Renner 2548*, NSW745726; Coromandel Ecological Region, Thames Ecological District, Ridge NW of Mt Rowe, track to Mt Rowe, 37°02'16"S, 175°40'19"E, 720m, 14 Feb 2007, *M.A.M. Renner 2535*, AK298528; Coromandel Ecological Region, Thames Ecological District, Ridge NW of Mt Rowe, track to Mt Rowe, 720 m, 37°02'16"S, 175°40'19"E, 14 Feb 2007, *M.A.M. Renner 2618*, AK299749; Coromandel State Forest Park, summit of Table Mt., 37°03'S, 175°40'E, 835 m, 1997, *J.J. Engel 22381* (F); South Island: North Westland Ecological Region, Blackball Ecological District, Craigieburn, Craigieburn Road east, 220 m, 42°13'43"S, 171°37'30"E, 06 Dec 2000, *J.E. Braggins*, AK287110; North Westland Ecological Region, Blackball Ecological District, Craigieburn, Craigieburn Road east, 190 m, 42°14'S, 171°38'E, 28 Mar 2001, *M.A.M. Renner 01/200*, AK280202; North Westland Ecological Region, Maimai Ecological District, Cragieburn Road, near Doolan Creek headwaters, west of Atarau Road, some 400m south of *Pinus* plantation in dense low mixed podocarp/*Nothofagus* forest, 205 m, 42°14'S, 171°38'E, 30 Apr 2003, *Y. Qiu NZ03115 & J.E. Braggins*, AK283714; North Westland Ecological Region, Blackball Ecological District, Paparoa Range, Croesus track, Blackball Road end, 42°20'S, 171°24'E, 330m, 26 Mar 2001, *M.A.M. Renner s.n.*, AK280201.

Discussion

The presence of underleaves in *Brevianthus hypocanthidium* reduces the morphological distance between this isolated genus and more typical Lophocoleaceae species including those belonging to *Tetracymbaliella*, which was shown to be sister to *Brevianthus* in the analysis of He-Nygren et al. (2006). The retention of at least partial underleaf production in *B. hypocanthidium* is probably plesiomorpic and the complete absence of underleaf production in *B. flavus* probably derived. The variable production of underleaves and a ventral merophyte by mature gametophyte shoots in *B. hypocanthidium* is unusual within species of the Lophocoleaceae-Plagiochilaceae complex, and perhaps all Jungermanniopsida Stotler & Crand.-Stotl. Only in broad phylogenetic terms is a parallel seen, in that across the Jungermanniales Hedw. as a whole, as stature of the lateral merophytes increases so does anisophylly, which is at the expense of the ventral merophyte (Schuster 1966).

In Lophocoleaceae the narrow triangular underleaf is unusual in showing no evidence of lobing. While well-developed and unlobed underleaves are known within the Lophocoleaceae, as in *Chiloscyphus austrigenus* (Hook.f. et Taylor) R.M.Schust. et J.J.Engel (Engel 2010), and many species of *Heteroscyphus* (J.J.Engel unpublished data); all of these taxa have a wide ventral merophyte. Underleaves in most species of the family, however, are bilobed in all stages of expression. In the related Plagiochilaceae, whose species for the most part have reduced ventral merophytes, unlobed and ciliform underleaves are known, for example, in *Dinckleria fruticella* (Hook.f. & Taylor) J.J.Engel & Heinrichs. In both *D. fruticella* and *B. hypocanthidium* the underleaves are probably derivatives of a reduced ventral merophyte, whose abbreviated morphology reflects underlying developmental degeneracy.

What then of the variable underleaf production exhibited by *B. hypocanthidium*? That merophytes form continuous rows, two lateral and one ventral, all contributing stem and leaf tissue implies the leaf and underleaf insertions ought not exhibit overlap across shared cell rows along the stem. This generally holds across the Jungermanniopsida as a result of the orderly proliferation of cortical cells within each merophyte row.

Dorsal and ventral 'leaf-free' strips are readily reconciled via greater division of stem-producing derivatives of the merophyte initial. The converse, overlap of leaf and underleaf insertion lines across rows of cortical stem cells, is not so readily reconciled with a model of growth wherein each merophyte derivative contributes to discrete stem sectors.

In small stature shoots of *B. hypocanthidium* the leaf insertion lines do not reach the ventral stem mid-line, leaving a row or two of ventral cortical cell rows leaf-free, onto which the underleaves are inserted. In small stature shoots the merophyte rows appear both continuous and non-overlapping, and their growth is compatible with conventional liverwort development (Fig. 7).

However, in medium-sized shoot sectors where underleaves are produced, the insertion lines of the two lateral merophytes reach the ventral stem midline. The underleaf insertion line is completely overlapped by the insertion line of the non-adjacent leaf (Figs 1L, M; 7B). This is incompatible with a conventional growth model involving three continuous and discrete merophyte rows. How might the underleaves come to be completely nested within the overlapping leaf insertion lines? One explanation could be that the ventral merophyte row is not straight but perhaps zig-zags between the leaf insertion lines. Observation of ventral cortical cell rows is hampered by their surface ornamentation, rhizoids, and their overlap by both underleaves and lateral leaves. We have not undertaken destructive sampling of underleaf-bearing shoots to confirm this due to the relative paucity of the type material. So while we cannot categorically exclude this possibility by direct observation of cortical cell rows, it fails to explain why underleaves are not produced on large shoots.

The stature-correlated pattern of underleaf production in *B. hypocanthidium* provides clues to development, and there are a number of observations a developmental model must explain:

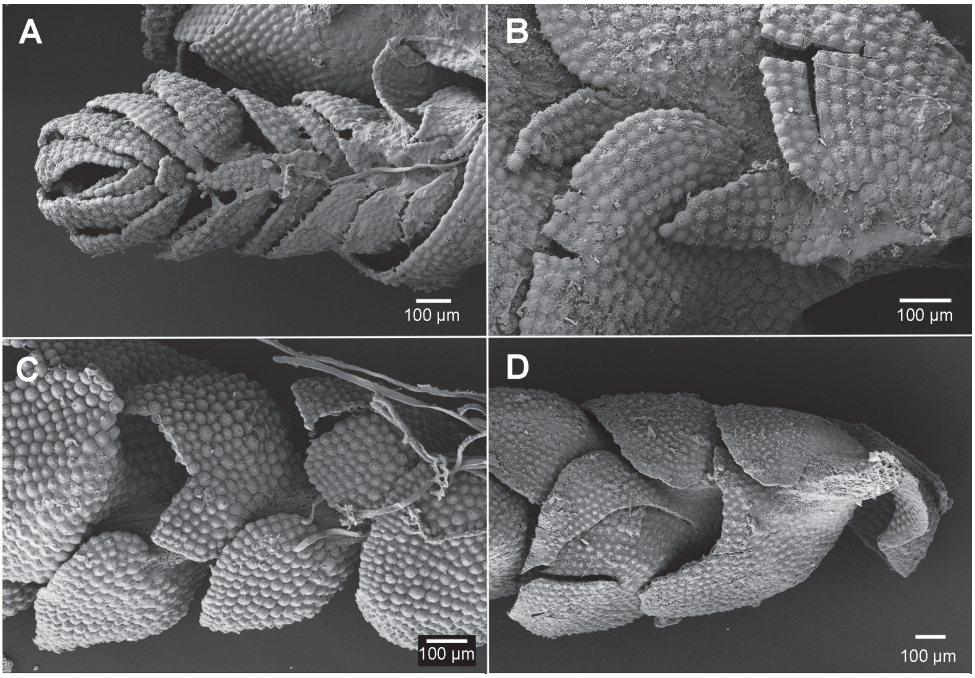

Figure 7. Ventral stem views. **A, B** *Brevianthus hypocanthidium* (NSW791547) **C** *Brevianthus flavus* subsp. *crenulatus* (NSW745726) **D** *Brevianthus flavus* subsp. *flavus* (NSW892112).

1) Shoot stature increases and underleaf size remains constant on small and medium sized shoots.
2) Underleaves are absent from large shoot sectors.
3) Lateral leaf insertion does not reach the ventral stem midline on small shoots, therefore a discrete and continuous merophyte row is present.
4) Lateral leaf insertion reaches the ventral stem midline on medium sized and large shoots, therefore a discrete and continuous merophyte row is lacking.
5) Underleaf insertion is completely overlapped by the leaf insertion lines on medium-sized shoots.
6) Underleaf position relative to the adjacent leaf on medium-sized shoots varies. Sometimes the underleaf is next to the adjacent leaf on a continuation of the same insertion line. At other times the underleaf is behind and a little more apical in position to the leaf on a separate line of insertion that overlaps the insertions of the adjacent leaf as well as the opposing leaf.

Assumption of a helical segmentation sequence seems reasonable given the apparent invariance across the Jungermanniales and its manifestation on at least small and medium-sized shoots, as evidenced by the sequence of merophytes. The most unusual and counter-intuitive features are the presence of underleaves when lateral leaf insertion lines reach the ventral stem mid-line, and the absence of underleaves from the larger shoots.

Here we posit a competitive model of shoot growth to explain the five observations above, wherein merophytes vie for occupancy of the mature shoot. An increase in shoot stature can be achieved by an increase in stature of the lateral merophytes only, or shoot stature can be increased by increasing the size of the lateral merophytes at the expense of ventral merophyte stature (Schuster 1966).

In *Brevianthus hypocanthidium* both may contribute, and our competitive model combining changes in both lateral and ventral merophytes is postulated as follows. The stature of lateral merophytes increases with shoot stature, while the stature of ventral merophytes does not, resulting in a decrease in relative stature of the ventral merophyte. With reduced stature comes a reduction in relative vigour of ventral merophyte derivatives, resulting in proportionally fewer cell divisions particularly those that contribute to the stem cells. The derivative cells fail to occupy the complete length of the potential ventral stem surface, they become localized to the region of initial deposition only. In such cases the 'vacant' ventral stem surface is occupied by tissue derived from lateral merophytes. These lateral merophyte derivates carry their leaf insertion lines to the ventral stem midline. The ventral merophytes become "marooned" or isolated at the sites of deposition. Growth of opposite and adjacent lateral merophytes causes the ventral merophyte to appear both laterally displaced and enveloped by the lateral merophytes. Perhaps eventually the ventral merophyte initials lose vigour to the extent that no divisions resulting in leafy tissue are completed. Developmental studies, perhaps including selective sequential sectioning, might test this model when more material becomes available.

Perianths and bracts. In *Plagiochila* shoot stature increases prior to gynoecium production. A female bracteole is often produced, as may be underleaves associated with one or two of the subtending gyres. In some members of this genus increase in shoot stature results in the re-expression of leafy appendages on the ventral merophyte. The same ought be true in *B. hypocanthidium*, given that in *B. flavus* bracteoles are expressed in the two cycles of female bracts on gynoecium-bearing branches. These bracteoles are either broadly connate or free from the adjacent bracts (Engel and Schuster 1982). The brevity of the lateral intercalary branches upon which gynoecia are borne in this species precludes assessment of transformation from normal leafy shoots. Location of fertile material of *B. hypocanthidium* would confirm the consistency of gynoecium position and associated characters within the *Brevianthus* lineage.

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References

Crandall-Stotler BJ, Stotler RE (2000) Morphology and classification of the Marchantiophyta. In: Shaw AJ, Goffinet B (Eds) Bryophyte Biology. Cambridge University Press, Cambridge, 21–70. doi: 10.1017/cbo9781139171304.003

Crandall-Stotler B, Stotler RE, Long DG (2009) Phylogeny and classification of the Marchantiophyta. Edinburgh Journal of Botany 66: 155–198. doi: 10.1017/S0960428609005393

Engel JJ (2010) Austral Hepaticae 45. A monograph of the genus *Chiloscyphus* Corda (Lophocoleaceae) for Australasia. Fieldiana Botany 48: 1–209. doi: 10.3158/0015-0746-48.1.1

Engel JJ (2011) Studies of New Zealand Hepaticae. 56–68. A miscellanea of new taxa and combinations. Nova Hedwigia 93: 401–410. doi: 10.1127/0029-5035/2011/0093-0401

Engel JJ, Schuster RM (1982) Austral Hepaticae 15. Brevianthaceae, a monotypic family endemic to Tasmania. The Bryologist 85: 375–388. doi: 10.2307/3242903

Feldberg K, Schneider H, Stadler T, Schäfer-Verwimp A, Schmidt A, Heinrichs J (2014) Epiphytic leafy liverworts diversified in angiosperm-dominated forests. Scientific Reports 4: 5974. doi: 10.1038/srep05974

Glenny D (2000) *Brevianthus flavus* new to New Zealand. Australasian Bryological Newsletter 42: 3.

Glenny D, Braggins JE, Renner MAM, von Konrat MJ, Engel JJ, Reeb C, Rolfe J, de Lange PJ (2014) Conservation status of New Zealand hornworts and liverworts, 2014. Department of Conservation, Wellington.

Grolle R (1970) Eine neue *Jackiella* aus Tasmanien. Journal of the Hattori Botanical Laboratory 33: 222–224.

Heinrichs J, Reiner-Drehwald ME (2012) Surface wax in *Dinckleria*, *Lejeunea* and *Mytilopsis* (Jungermanniidae). Cryptogamie, Bryologie 33: 81–86. doi: 10.7872/cryb.v33.iss1.2012.081

Hentschel J, Wilson R, Burghardt M, Zündorf HJ, Schneider H, Heinrichs J (2006) Reinstatement of Lophocoleaceae (Jungermanniopsida) based on chloroplast gene rbcL data: exploring the importance of female involucres for the systematics of Jungermanniales. Plant Systematics and Evolution 258: 227–250. doi: 10.1007/s00606-006-0408-y

He-Nygren Z, Juslén A, Ahonen I, Glenny D, Piippo S (2006) Illuminating the evolutionary history of liverworts (Marchantiophyta) – towards a natural classification. Cladistics 22: 1–31. doi: 10.1111/j.1096-0031.2006.00089.x

Schuster RM (1966) Hepaticae and Anthocerotae of North America. Volume 1. Columbia University Press.

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Seven new species of *Selaginella* subg. *Stachygynandrum* (Selaginellaceae) from Brazil and new synonyms for the genus

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Abstract

We describe seven new species of *Selaginella* subg. *Stachygynandrum* (*S. alstonii*, *S. blepharodella*, *S. crinita*, *S. mucronata*, *S. mucugensis*, *S. saltuicola*, and *S. sematophylla*) from Brazil and discuss their possible affinities and conservation status. Scanning electron micrographs of stem sections, leaves, and spores are provided to illustrate the new taxa. In *Selaginella alstonii* and *S. saltuicola* vegetative growth from strobilus tips is reported and discussed. Four of the new species are from the Espinhaço Mountain Range associated with Campos Rupestres (montane savannah/rocky fields) vegetation. Three of these (i.e., *Selaginella blepharodella*, *S. crinita*, and *S. mucugensis*) were collected in the northern part of the range in Chapada Diamantina, state of Bahia, while *S. alstonii* is from the southern part of the range in the state of Minas Gerais. *Selaginella mucronata* is found in Atlantic Rainforest vegetation in the state of Espírito Santo, whereas *S. saltuicola* inhabits Cerrado (tropical savannah) vegetation in the state of Mato Grosso. *Selaginella sematophylla* is the most widely distributed of the new species and was collected in Espírito Santo, Minas Gerais, and Rio de Janeiro states in Campos Rupestres and Atlantic Rainforest vegetation. *Selaginella alstonii* occurs in rocky caves, *S. blepharodella*, *S. crinita*, *S. mucugensis*, and *S. sematophylla* seem adapted to seasonally dry places, living on sandy or humid soils, *S. mucronata* occupies humid, forest understory, and *S. saltuicola* is adapted to wet places associated with rocks or logs in waterfalls. Of the seven new species, six are considered local endemics (except for *S. sematophylla*) because of their restricted

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currently known distributions to one or two localities within a single state in Brazil. Additionally, we propose new synonymy for *S. palmiformis* (syn. = *S. bahiensis* subsp. *manausensis*, ≡ *S. manausensis*) and *S. vestiens* (syn. = *S. fragillima*); the last species is endemic to Brazil, recorded in the states of Goiás and Minas Gerais. Finally, based on literature discussed and this study, we conclude that the number of well-documented Brazilian *Selaginella* species is 61, of which 58 are native and three introduced and naturalized. These statistics are likely to change with further work on *Selaginella* from Brazil.

Resumen

Describimos siete nuevas especies de *Selaginella* subg. *Stachygynandrum* (*Selaginella alstonii, S. blepharodella*, *S. crinita*, *S. mucronata*, *S. mucugensis*, *S. saltuicola* y *S. sematophylla*) de Brasil y discutimos sus posibles afinidades y estado de conservación. Micrografias electrónicas de barrido de secciones de los tallos, hojas y esporas se proveen para ilustrar los nuevos taxa. Igualmente, se describe y discute el crecimiento vegetativo a partir del ápice de los estróbilos en *Selaginella alstonii* y *S. saltuicola*. Cuatro de las especies nuevas proceden de la Cadena del Espinhaço asociadas a vegetación de Campos Rupestres (sabana montana). Tres de éstas (i.e., *Selaginella blepharodella*, *S. crinita* y *S. mucugensis*) fueron recolectadas en la parte norteña de la Cadena del Espinhaço en la Chapada Diamantina, estado de Bahia, mientras que *S. alstonii* se registra para la parte sureña en el estado de Minas Gerais. *Selaginella mucronata* se encuentra en vegetación de Bosques Lluviosos del Atlántico en el estado de Espírito Santo, mientras que *S. saltuicola* habita vegetación de Cerrado (sabana tropical) en el estado de Mato Grosso. De las nuevas especies, *Selaginella sematophylla* es la más ampliamente distribuida y se ha recolectada en los estados de Espírito Santo, Minas Gerais y Río de Janeiro en vegetación de Campos Rupestres y Bosques Lluviosos del Atlántico. *Selaginella alstonii* crece sobre rocas en cuevas, mientras que *S. blepharodella*, *S. crinita*, *S. mucugensis* y *S. sematophylla* parecen estar adaptadas a lugares estacionalmente secos, creciendo sobre suelos arenosos o húmedos; a su vez, *S. mucronata* crece en el sotobosque de bosques húmedos y *S. saltuicola* está adaptada a vivir en lugares húmedos asociada a rocas o troncos en cascadas. De las siete nuevas especies, seis son consideradas tentativamente endémicas locales (con la excepción de *S. sematophylla*) debido a su distribución restringida a una o dos localidades dentro de un sólo estado de Brasil. Adicionalmente, proponemos nuevos sinónimos para *S. palmiformis* (syn. = *S. bahiensis* subsp. *manausensis*, ≡ *S. manausensis*) y *S. vestiens* (syn. = *S. fragillima*), la cual se confirma como endémica de Brasil donde se registra para los estados de Goiás y Minas Gerais. Finalmente, de acuerdo con este estudio y la literatura discutida, estimamos que el número de especies brasileñas de *Selaginella* debidamente documentadas es de 61, de las cuales 58 son nativas y tres introducidas y naturalizadas. Esta estadística muy probablemente cambiará conforme se realicen estudios adicionales sobre *Selaginella* en Brasil.

Keywords

Atlantic Rainforest, Chapada Diamantina, Chapada dos Guimarães, Espinhaço Mountain Range, Mucugê, Serra do Sincorá

Palabras clave

Bosques Lluviosos del Atlántico, Chapada Diamantina, Chapada dos Guimarães, Cadena del Espinhaço, Mucugê, Serra do Sincorá

Introduction

The genus *Selaginella* P. Beauv. (Selaginellaceae) is cosmopolitan and comprises 600–750 species mostly distributed in tropical and subtropical regions of the world,

although some are adapted to live in dry, desert-like areas and some are circumboreal (Jermy 1990, Valdespino 1993a, Mickel et al. 2004).

Alston et al. (1981) recorded 45 species and two subspecies of *Selaginella* from Brazil, while Hirai (2015) listed 56 taxa, including two subspecies and three introduced species. As part of ongoing work on *Selaginella* by the senior author and a study of this genus in the state of Minas Gerais conducted by Heringer (2011) under the supervision of Salino, we now describe seven new taxa from Brazil: *S. alstonii* G. Heringer, Salino & Valdespino, *S. blepharodella* Valdespino, *S. crinita* Valdespino, *S. mucronata* G. Heringer, Salino & Valdespino, *S. mucugensis* Valdespino, *S. saltuicola* Valdespino, and *S. sematophylla* Valdespino, G. Heringer & Salino, and place them in subg. *Stachygynandrum* (P. Beauv.) Baker following Jermy's (1986, 1990) infrageneric classification.

Three of the new species *Selaginella blepharodella*, *S. crinita*, and *S. mucugensis* are reported from three localities (i.e., Pico das Almas in Serra do Rio de Contas and Ibicoara and Mucugê in Serra do Sincorá) of Chapada Diamantina in the state of Bahia, whereas *S. alstonii* was collected in Santo Antônio do Itambé in the state of Minas Gerais. These localities are within the Espinhaço Mountain Range, which is dominated by "Campos Rupestres" (montane savannah/rocky fields) vegetation (Melo 2000, São-Pedro and Feio 2011) and recognized as an important biodiversity and endemism center (Harley and Simmons 1986, Melo 2000, Rapini et al. 2008, Bünger et al. 2014). *Selaginella mucronata* was collected in Castelo, Parque Estadual do Forno Grande, a locality that has highland remnants of the rich, biodiverse Atlantic Rainforest vegetation in the state of Espírito Santo, southeastern Brazil (Meirelles and Goldenberg 2012, Silva-Soares and Scherrer 2013). *Selaginella saltuicola* is recorded from Chapada dos Guimarães, a high plateau in the state of Mato Grosso (Oliveira-Filho and Martins 1991) in the Central-West region of Brazil, where the species-rich (Ratter et al. 1997) "Cerrado" (tropical savannah) vegetation is dominant (Oliveira-Filho and Martins 1991) and waterfalls, caves, and ponds are common. Finally, *S. sematophylla* seems to be the most widely distributed species of all the spike mosses newly described herein, as it is recorded from Campos Rupestres vegetation in the localities of São Sebastião do Paraíso and Parque Estadual de Serra Nova, part of the Espinhaço Mountain Range, in the state of Minas Gerais and in mountane areas with some remnants of Atlantic Rainforest vegetation such as Pedra do Garrafão in Santa Maria do Jetibá, state of Espírito Santo and Santo Antônio do Imbé in the state of Rio de Janeiro. Because of their restricted currently documented distributions to one or two localities within a single Brazilian state, six of these new species, except for *S. sematophylla*, are tentatively considered local endemics.

Additionally, we propose the following updates to Hirai's (2015) list: *Selaginella arenaria* Baker = *S. brevifolia* Baker (Valdespino 2015), *S. bahiensis* subsp. *manausensis* (Bautista) Jermy & Rankin (≡ *S. manausensis* Bautista) is conspecific with and a synonym of *S. palmiformis* Alston ex Crabbe & Jermy (which see for details), *S. cladorrhizans* A. Braun = *S. tenella* (P. Beauv.) Spring (Valdespino 1995, Mickel et al. 2004), *S. fragillima* Silveira is conspecific with and a synonym of *S. vestiens* Baker (see discussion under *S. sematophylla* and *S. vestiens*), and *S. pedata* Klotzch = *S. parkeri* (Hook.

& Grev.) Spring (Alston et al. 1981). Furthermore, *S. gynostachya* Valdespino and *S. sandwithii* Alston, reported from Brazil by Góes-Neto et al. (2015) should be added to Hirai's account as well. Accordingly, there are 58 well-documented native Brazilian *Selaginella* species and if we were to take into account the introduced taxa listed by Hirai (2015), i.e., *S. kraussiana* (Kunze) A. Braun [native of Africa and Macaronesia (Alston et al. 1981)], *S. plana* (Desv. ex Poir.) Hieron. [native of Southeast Asia and Indonesia (Valdespino 1993b), and *S. vogelii* Spring [native of Africa (Stefanović et al. 1997)], then a total of 61 species of *Selaginella* would be recorded for Brazil. These statistics are likely to change as work on Brazilian *Selaginella* continues.

Material and methods

Herbarium specimens were examined from B, BHCB, BM, CAS, CESJ, COL, G, GH, INPA, K, MG, MO, NY, P, PMA, QCA, R, RB, UC, US, and W (Thiers 2015) and samples for Scanning Electron Microscopy (SEM) were taken from selected collections to document upper and lower surfaces of stems and leaves, as well as spore morphology. Although for each of the new species an effort was made to secure megaspore and microspore samples to determine sculpturing pattern, color, and diameter, these were not always available or, in some cases, were too immature to be utilized for those purposes. The SEM samples were prepared, viewed, and photographed at different magnifications using a Zeiss Model Evo 40 at 20–30 KV following standard techniques as described by Valdespino (1995) and Valdespino et al. (2014). Digitized SEM images were post-processed with Adobe Photoshop and assembled according to species in multipart figures.

In heterophyllous species of *Selaginella* (i.e., subg. *Stachygynandrum*, where the new taxa are classified, and subg. *Heterostachys* Baker) there are three kinds of vegetative leaves (i.e., lateral/ventral, median/dorsal, and axillary). The axillary leaves are located ventrally at branch forks on dorsiventral shoots and are usually morphologically similar to lateral leaves (Schoute 1938, Valdespino 1995) and, thus, in previous descriptions vegetative leaves are often referred to as "dimorphic". Nevertheless, on occasion, axillary leaves may be quite different morphologically from lateral leaves (Valdespino 1995) and to take this into account we decided to use the term "heteromorphic" when describing vegetative leaves in our species descriptions. Likewise, sporophylls are described as "monomorphic" because no significant differences in their size and form were found; however, their epidermal cell composition may be different according to their plane of insertion on the strobilus axis with respect to the main stem, which allows two types to be recognized: "dorsal sporophylls" (inserted in the same plane as the median/dorsal leaves) and "ventral sporophylls" (inserted in the same plane as the lateral/ventral leaves). Otherwise, descriptions of the new species were made according to terminology utilized by Valdespino (1995), while leaf and spore measurement methods and the terminology used to describe leaf surfaces are those explained in Valdespino et al. (2014). The description of spore morphology follows Valdespino (1995), Punt et al. (2007), and Hesse et al. (2009).

Taxonomy

***Selaginella alstonii* G. Heringer, Salino & Valdespino, sp. nov.**
urn:lsid:ipni.org:names:77147598-1
Figures 1, 2

Diagnosis. *Selaginella alstonii* resembles *S. acanthostachys* Baker, from which it differs by having the upper surfaces of the lateral leaves glabrous (vs. hairy near basiscopic margins), median leaves acuminate to short-aristate (vs. long-aristate) with each acumen (arista) ¼ or less the lamina length (vs. arista ⅓–½), with the outer and inner hyaline margins about the same width (vs. outer margin almost twice as wide as the inner one), and non stoloniferous stems (vs. stoloniferous).

Type. BRAZIL. Minas Gerais: Santo Antônio do Itambé, Parque Estadual do Pico do Itambé, 18°23'50,4"S, 43°19'55,5"W, 1676 m, 5 Oct 2006, *T.E. Almeida et al. 533* (holotype: BHCB!; isotype: PMA!).

Description. *Plants* epipetric. *Stems* prostrate to ascending, greenish to stramineous, to 10 cm long, 0.3–0.6 mm diam., exarticulate, not flagelliform or stoloniferous, 2- or 3-branched. *Rhizophores* ventral, borne on the proximal ⅔ of stems, filiform, 0.1–0.2 mm diam. *Leaves* heteromorphic throughout, chartaceous, both surfaces glabrous, upper surfaces green, lower surfaces silvery green. *Lateral leaves* distant, spreading to slightly ascending, oblong to oblong-lanceolate, 1.1–2.0 × 0.4–1.0 mm; bases rounded, acroscopic bases overlapping stems, basiscopic bases free from stems; acroscopic margins on upper surfaces hyaline along proximal ½–¾ in a band 1 or 2 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 row over each cell lumen, otherwise greenish distally with rounded to quadrangular, sinuate-walled cells, on lower surfaces hyaline in a band 2–5 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 row over each cell lumen, short-ciliate along proximal ⅓–½, otherwise serrate distally, basiscopic margins greenish on upper surfaces with rounded to quadrangular, sinuate-walled cells and on lower surfaces with elongate, sinuate-walled cells, entire along proximal ¾ and serrulate on distal ¼; apices acute to slightly cuspidate, each cusp 0.02–0.03 mm, tipped by 1–3 teeth; upper surfaces comprising rounded to quadrangular, sinuate-walled cells, without idioblasts or stomata, lower surfaces comprising elongate, sinuate-walled cells, with some obscure, papillate idioblasts and stomata along central portion of midribs and along basiscopic margins. *Median leaves* distant to slightly imbricate near the branch tips, ascending, elliptic to elliptic-lanceolate or ovate-elliptic, 0.7–1.4 × 0.4–0.7 mm; bases oblique; margins hyaline in a band 2–5 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 row over each cell lumen, inner margins serrate to short-ciliate, outer margins entire along proximal ½, otherwise serrate to short-ciliate distally; apices acuminate to short-aristate, each acumen (arista) 0.15–0.2 mm, entire or obscurely tipped by 1–3 teeth; both surfaces without conspicuous idioblasts, upper surfaces comprising quadrangular to rounded, sinuate-walled cells, some of these covered by 10–20 papillae, with stomata along midribs on distal half and submarginal and marginal along

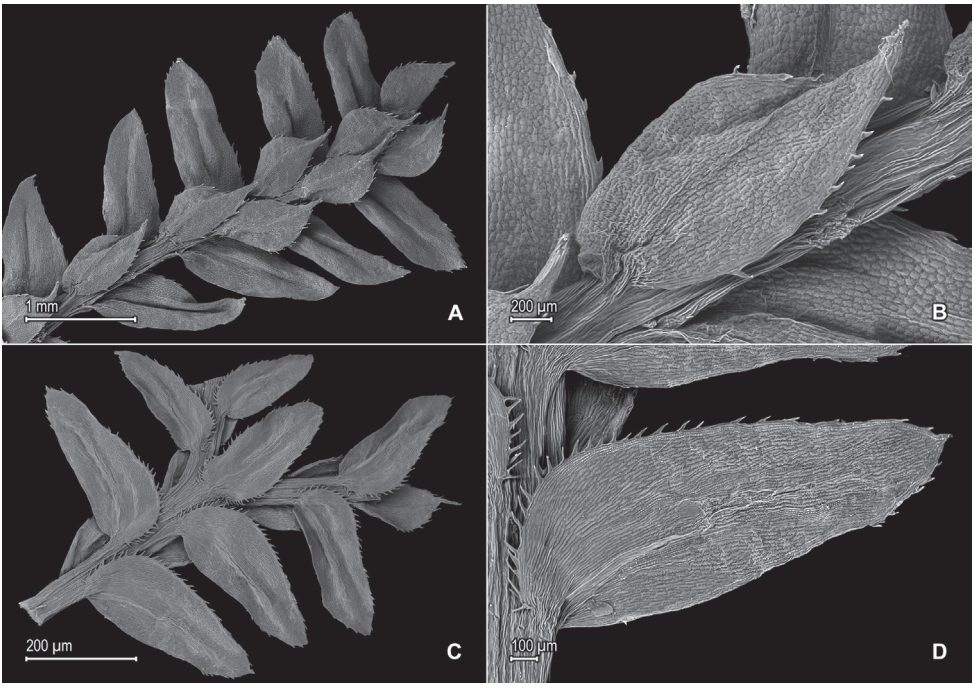

Figure 1. *Selaginella alstonii* G. Heringer, Salino & Valdespino. **A** Section of upper surface of stem **B** Upper surface of median leaf **C** Section of lower surface of stem **D** Lower surface of lateral leaf. **A–D** taken from isotype, *Almeida et al. 533* (PMA).

proximal half of outer margins, lower surfaces comprising elongate, sinuate-walled cells, without stomata. *Axillary leaves* similar to lateral leaves but with both margins ciliate along proximal ¼, otherwise short-ciliate to serrate distally. *Strobili* terminal on branch tips, compact, quadrangular, 1.5–4.0 mm. *Sporophylls* monomorphic, without a laminar flap, ovate to ovate-lanceolate, 0.7–1.1 × 0.4–0.6 mm, each with a dentate (teeth often caducous) keel along distal ½ of the midribs; bases rounded; margins narrowly hyaline, serrate; apices acute, entire or obscurely tipped by 1–3 teeth; *dorsal sporophylls* with upper surfaces green and cells as in median leaves, except for the half that overlaps the ventral sporophylls, there hyaline with elongate, sinuate-walled cells, lower surfaces silvery green and comprising elongate, sinuate-walled cells; *ventral sporophylls* with both surfaces hyaline to faintly greenish hyaline, comprising elongate, sinuate-walled cells. *Megasporangia* in proximal portion in 2 ventral rows; *megaspores* cream, with a cristate equatorial flange, rugulate on proximal faces, reticulate with low, cristate ridges on distal faces, with areolate-perforate microstructure on both faces, 250–300 µm diam. *Microsporangia* in 2 dorsal rows and, in distal portion, also in 2 ventral rows; *microspores* orange, psilate marginally and verrucate-rugulate towards the center with psilate microstructure on proximal faces, clavate (Fig. 2G, H) or echinulate to baculate (if apices of projected elements broken off, Fig. 2F, H) with striate to striate-reticulate microstructure on distal faces, 27–33 µm diam.

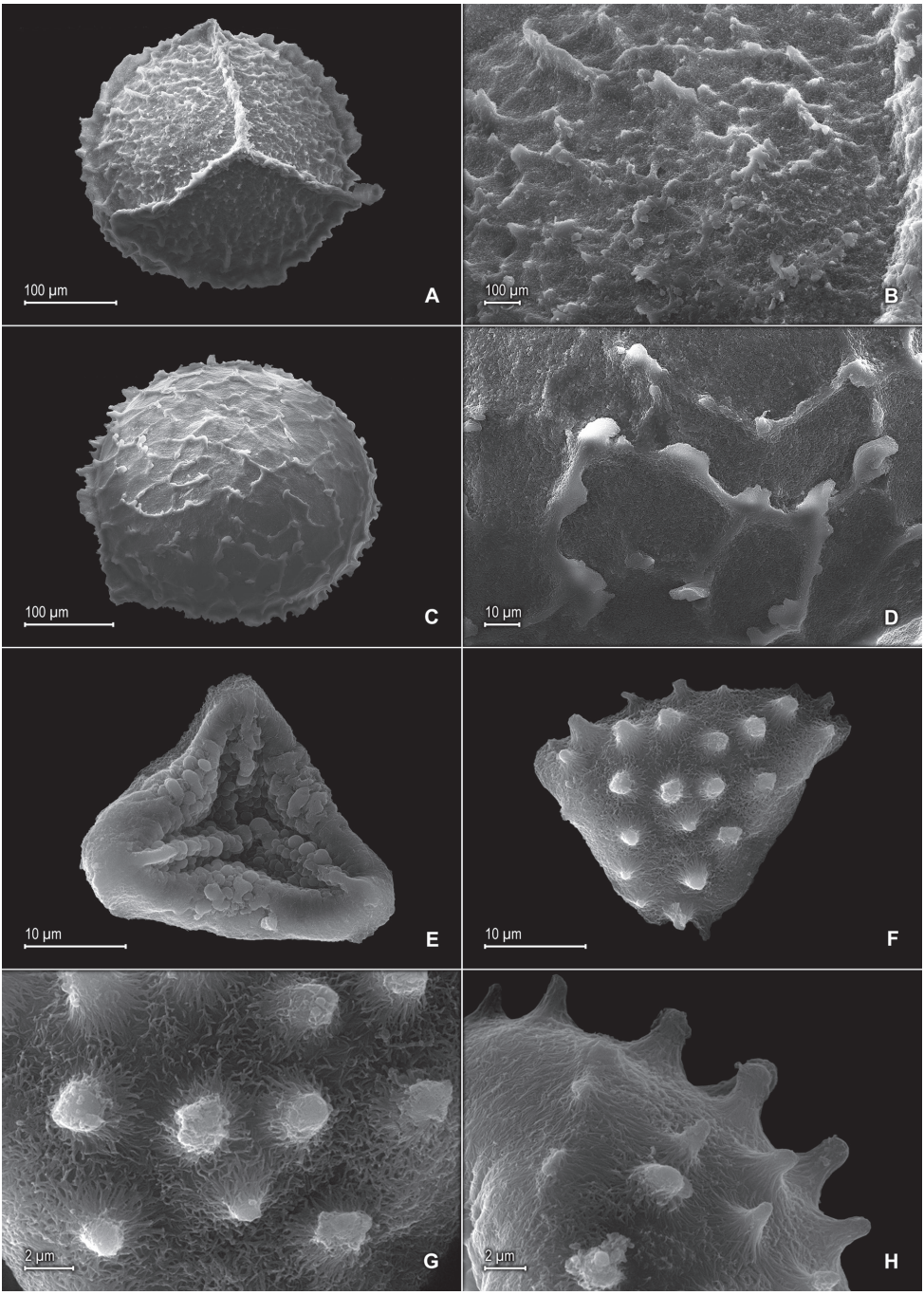

Figure 2. *Selaginella alstonii* G. Heringer, Salino & Valdespino. **A** Megaspore proximal face **B** Close-up of megaspore proximal face surface **C** Megaspore distal face **D** Close-up of megaspore distal face surface **E** Microspore proximal face **F** Microspore distal face **G** Close-up of microspore distal face surface **H** Close-up of microspore equatorial view surface **A–H** taken from isotype, *Almeida et al. 533* (PMA).

Habitat and distribution. *Selaginella alstonii* is epipetric on rocky caves in Campos Rupestres vegetation; the type and paratype were collected at an elevation range of 1676–1810 m. The species is known only from Parque Estadual do Pico do Itambé in Serra do Espinhaço, Minas Gerais, Brazil, where it may be a local endemic.

Etymology. *Selaginella alstonii* is named for Arthur Hugh Garfit Alston (1902–1958), a British pteridologist and one of the world's authorities on the genus *Selaginella*.

Conservation status. There is limited information on the conservation status and range distribution of *Selaginella alstonii*. Nevertheless, given that the localities where this species is presently known are located within the Espinhaço Mountain Range, a habitat threatened by human activities (Rapini et al 2008), we tentatively consider it vulnerable (VU) according to IUCN (2012) categories and criteria.

Additional specimen examined (paratype). BRAZIL. **Minas Gerais**: Santo Antônio do Itambé, Parque Estadual do Pico do Itambé, 18°23'50,4"S, 43°19'55,5"W, 1810 m, 5 Oct 2006, *Almeida et al. 535* (BHCB).

Discussion. *Selaginella alstonii* belongs to subg. *Stachygynandrum* and is characterized by its oblong to oblong-lanceolate lateral leaves with acroscopic margins short-ciliate along proximal ⅓–½ and elliptic to elliptic-lanceolate or ovate-elliptic median leaves with oblique bases (Fig. 1). Dried specimens of *S. alstonii* tend to develop a groove along midribs of lateral leaves (Fig. 1A), but it remains to be confirmed if this is a character observed in living plants or an artifact when plants are dried. The surfaces of the median and lateral leaves of *S. alstonii* do not show conspicuous idioblasts when observed with a stereoscope, but on SEM micrographs, idioblast-like, papillate elongate cells are observed on the lower surfaces of lateral leaves, with papillae in 1 row over each cell lumen, parallel to the midribs (Fig. 1D). Additionally, in some median leaves, the outer bases have 2–4 short cilia. In some plants of *S. alstonii*, as well as in *S. saltuicola* (which see for discussion), we observed vegetative growth from the tips of some strobili.

Selaginella alstonii resembles *S. acanthostachys* from Colombia, Ecuador, and Peru; however the characters given in the diagnosis separate them. Among other species of *Selaginella* from Minas Gerais, *S. alstonii* may be confused with *S. decomposita* Spring because of their similar texture and shape of the lateral leaves. *Selaginella decomposita*, however, has an ascending to erect habit and is a more robust plant.

Selaginella blepharodella **Valdespino, sp. nov.**

urn:lsid:ipni.org:names:77147599-1
Figures 3, 4, 5

Diagnosis. *Selaginella blepharodella* differs from similar *S. thysanophylla* A.R. Sm. in its short- (vs. non-) stoloniferous stems, median leaves broadly-ovate to ovate-elliptic (vs. ovate or orbicular), 0.6–1.0 × 0.4–0.6 (vs. 1.4 × 1.0) mm, with stomata on upper surfaces restricted to the midribs (vs. also on submarginal and marginal regions on proximal ¼ near outer bases), lateral leaves broadly ovate to ovate-oblong (vs. ovate or

orbicular), 0.8–2.0 × 0.5–0.8 (vs. 2.0 × 1.5) mm, and upper surfaces of sporophylls with long or short cilia along distal ½ of the midribs (vs. upper surfaces glabrous).

Type. BRAZIL. Bahia: Ibicoara, [13°24'00"S, 41°18'00"W], 26 Aug 2009, *P. Moraes & van der Werff 2933* (holotype: PMA!; isotypes: HUEFS-n.v., MO!, UC!).

Description. *Plants* terrestrial or epipetric. *Stems* decumbent to suberect, stramineous, 1.5–9.5 cm long, 0.3–0.4 mm diam., exarticulate, not flagelliform, short-stoloniferous, 1- or 2-branched. *Rhizophores* axillary or axillary-ventral, restricted to bases of stems, filiform, 0.1–0.2 mm diam. *Leaves* heteromorphic throughout, chartaceous, those on and above first branch of stems with both surfaces usually glabrous and those below the first branch of stems often with few, caducous cilia-like or dentate projections on the upper surfaces of the median leaves and sporophylls and on the lower surfaces of lateral leaves, upper surfaces green or brownish (when old), lower surfaces silvery green or shiny brown (when old). *Lateral leaves* imbricate, spreading or ascending, broadly ovate to ovate-oblong, 0.8–2.0 × 0.5–0.8 mm; bases rounded to subcordate, acroscopic bases overlapping stems (more so on leaves below first branch), basiscopic bases free from stems; acroscopic margins broadly hyaline, especially along proximal ⅓ in a band 3–15 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 or 2 rows over each cell lumen, long-ciliate along proximal ⅔ and short-ciliate to serrate along distal ⅓, basiscopic margins hyaline to greenish hyaline in a band 4–6 cells wide, the cells as on acroscopic margins, ciliate throughout or sometimes cilia absent from proximal ¼–⅓; apices acute, tipped by 1–4 teeth or 2 or 3 cilia, especially on leaves below first branch; upper surfaces comprising quadrangular to rounded, sinuate-walled cells covered by 5–15 papillae, without idioblasts or stomata, lower surfaces comprising elongate, sinuate-walled cells, most of these papillate and idioblast-like, papillae in 1 or 2(–3) rows over each cell lumen, with stomata in 2 or 3(–4) rows along midribs and some along proximal ¼ of basiscopic margins. *Median leaves* imbricate, ascending, broadly-ovate to ovate-elliptic, 0.6–1.0 × 0.4–0.6 mm; bases oblique, inner bases truncate, outer bases rounded and glabrous or these may also be ventricose (i.e., swollen) and each with a tuft of long cilia on leaves below first branch; margins broadly hyaline, especially the inner ones, in a band 5–15 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 or 2 rows over each cell lumen, long-ciliate throughout or infrequently along only distal ⅘; apices gradually tapering into a long acumen, each acumen 0.1–0.3 mm, tipped by 2 or 3 cilia; both surfaces without idioblasts, upper surfaces comprising quadrangular to rounded, sinuate-walled cells covered by 5–15 papillae, with stomata along midribs, lower surfaces comprising elongate, sinuate-walled cells, without stomata. *Axillary leaves* similar to lateral leaves. *Strobili* terminal on branch tips, compact, quadrangular, 1.2–9.0 mm long. *Sporophylls* monomorphic, without a laminar flap, ovate, 0.6–0.9 × 0.4–0.7 mm, each with a ciliate keel along distal ½ of the midribs; bases rounded; margins hyaline, long-ciliate; apices acute, tipped by 1 or 2 cilia; *dorsal sporophylls* with upper surfaces green and cells as in median leaves, except for the half that overlaps the ventral sporophylls, there hyaline with elongate, papillate, and slightly sinuate-walled cells, lower surfaces silvery green and comprising elongate, sinuate-walled cells (Fig. 4F); *ventral sporophylls* with both

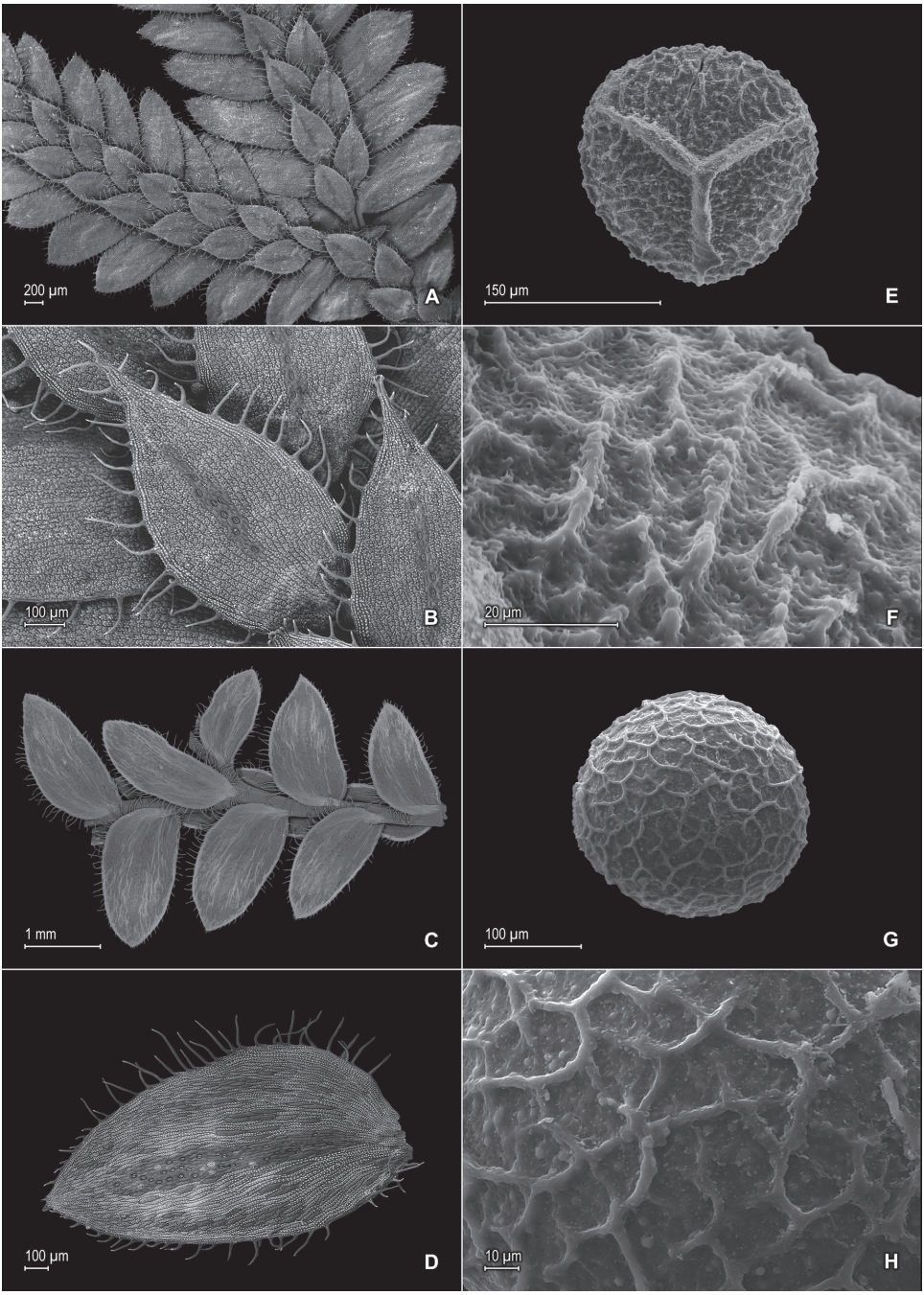

Figure 3. *Selaginella blepharodella* Valdespino. **A** Section of upper surface of stem **B** Upper surface of median leaf **C** Section of lower surface of stem **D** Lower surface of lateral leaf **E** Megaspore proximal face **F** Close-up of megaspore proximal face surface **G** Megaspore distal face **H** Close-up of megaspore distal face surface **A–D** taken from holotype, *Moraes & van der Werff 2933* (PMA) **E–H** taken from paratype, *Ule 7298* (B).

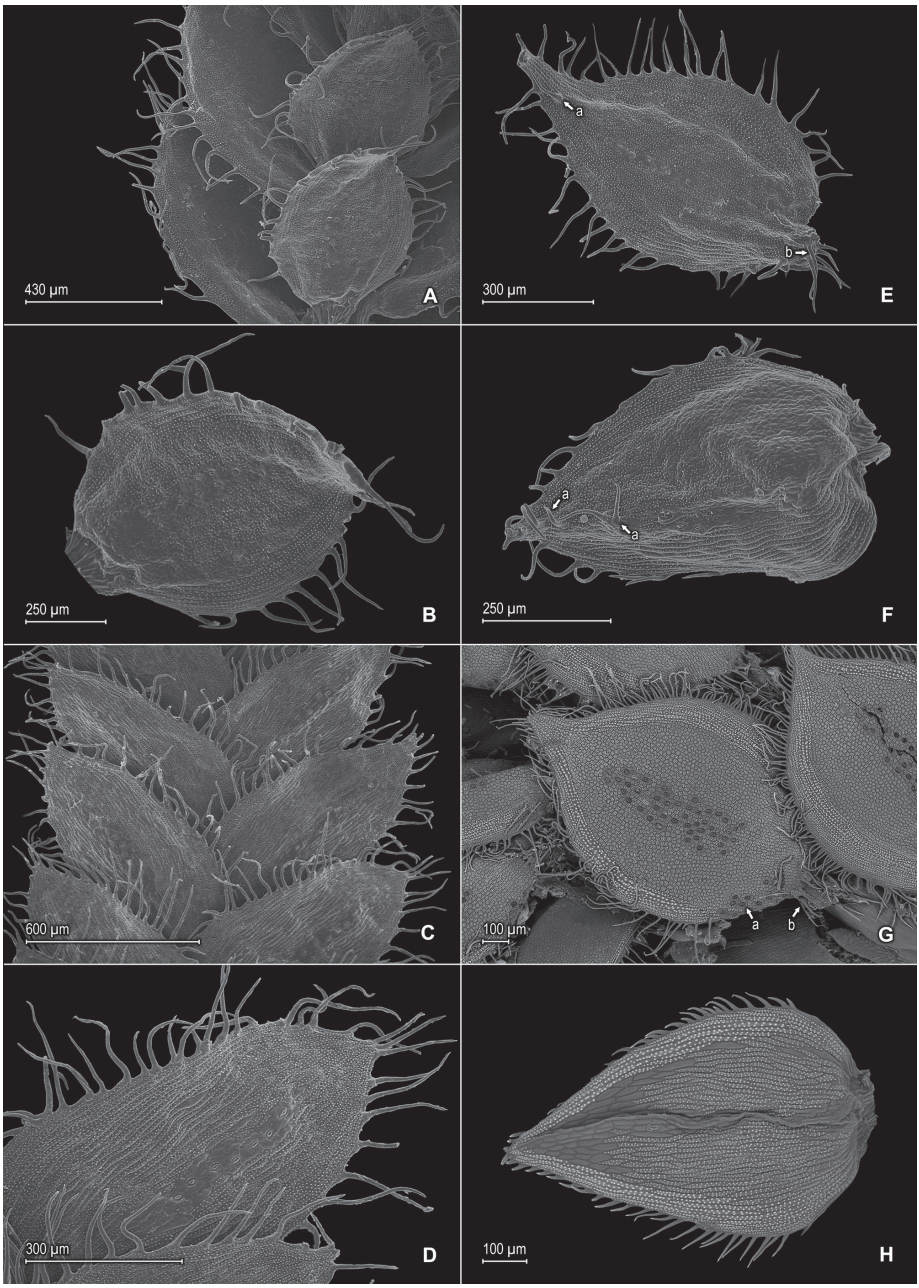

Figure 4. *Selaginella blepharodella* Valdespino. **A** Section of upper surface of stem **B** Upper surface of median leaf **C** Section of lower surface of stem **D** Lower surface of lateral leaf **E** Upper surface of median leaf, note: cilium-like or tooth projection (a) and long cilia on outer base (b) **F** Upper surface of dorsal sporophyll, note: cilia-like or teeth projections on distal portion of midrib (a) **A–F** taken from paratype *Ule 7298* (B). *Selaginella thysanophylla* A.R. Sm. **G** Upper surface of median leaf, note: stomata on submarginal and marginal regions on proximal ¼ near outer base (a) and outer base tufted with long cilia (b) **H** Upper surface of ventral sporophyll **G, H** taken from *Steyermark et al. 113322* (NY).

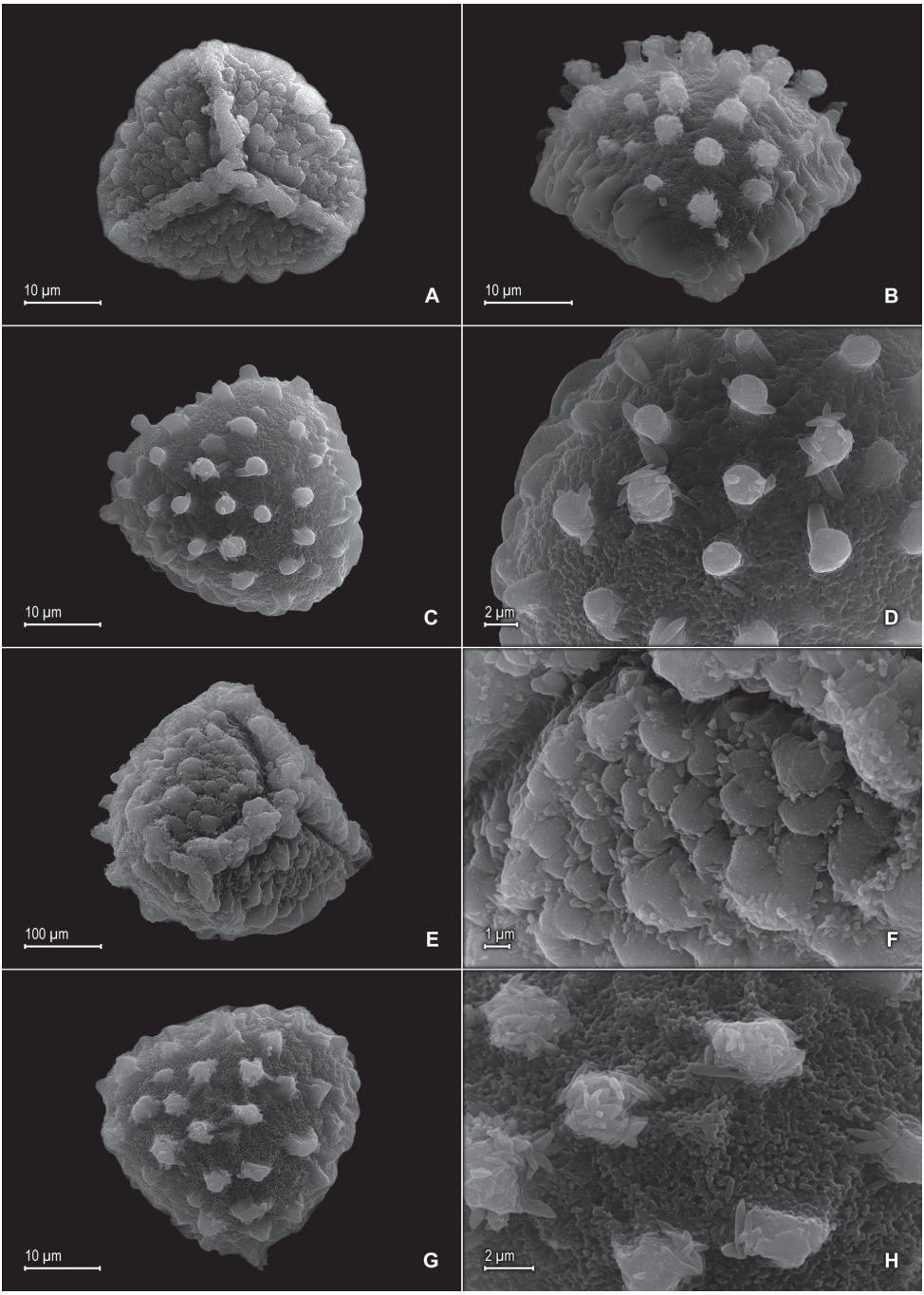

Figure 5. *Selaginella blepharodella* Valdespino. **A** Microspore proximal face **B** Microspore equatorial view **C** Microspore distal face **D** Close-up of microspore distal face surface **E** Microspore proximal-equatorial view **F** Close-up of microspore proximal face surface **G** Microspore distal face **H** Close-up of microspore distal face surface **A–H** taken from holotype, *Moraes & van der Werff 2933* (PMA).

surfaces hyaline to greenish, comprising elongate, sinuate-walled cells. *Megasporangia* in proximal portion in 2 ventral rows; *megaspores* light-yellow, rugulate-reticulate on proximal faces, reticulate on distal faces, with psilate-perforate microstructure on both faces, 200–230 μm diam. *Microsporangia* in 2 dorsal rows and, in distal portion, also in 2 ventral rows; *microspores* orange, verrucate-rugulate with granulate microstructure on proximal faces, broadly capitate to clavate (5B–D) or broadly baculate (if apices of projected elements broken off, Fig. 5G, H) with reticulate-perforate and echinulate microstructure on distal faces, ca. 30–38 μm diam.

Habitat and distribution. *Selaginella blepharodella* is presumed to be a local endemic of the Serra do Sincorá, Espinhaço Range, state of Bahia, Brazil, where it is known from only two localities, growing on sandy soil or overhanging from rocks at 1400 m.

Etymology. The epithet of the new species derives from the Greek *blepharis*, meaning eyelash, *ode* meaning similar to and *ella*, Latin diminutive suffix; this refers to the long-ciliate leaf margins that resemble miniature eyelashes.

Conservation status. *Selaginella blepharodella* is known from only two collections in Serra do Sincorá and may be expected to occur in places with similar vegetation types in the Chapada Diamantina region of the Espinhaço Mountain Range. The Chapada Diamantina region and the Espinhaço Mountain Range, in general, are still subject to anthropomorphic pressure, including low-scale mining (Pedreira 2002), subsistence agriculture accompanied by the slash-and-burn methods, and plant extraction for commerce (Rapini et al. 2008). Based on these threats and according to IUCN (2012) categories and criteria, this species is tentatively considered vulnerable (VU).

Additional specimen examined (paratype). BRAZIL. **Bahia**: Serra do Sincorá, 1400 m, Nov 1906, *Ule 7298* (B, BM, PMA-fragment).

Discussion. *Selaginella blepharodella* is a member of subg. *Stachygynandrum* and is defined here in a broad sense to encompass the morphological variability found within the two collections examined. In general, this species is characterized by long-ciliate leaves with broadly hyaline margins, lateral leaves imbricate, spreading to ascending with lower surfaces almost completely comprising elongate, papillate, sinuate-walled cells with papillae in 1–3 rows over cell lumina and stomata in 2 or 3(–4) rows along midribs amidst shortly elongate, sinuate-walled cells, and median leaves with apices ending in 2 or 3 cilia (Figs 3, 4). The type collection (*Moraes & van der Werff 2933*) has stems more than 3 cm tall, is 2- or 3-brached, and has lateral leaves mostly spreading to ascending and imbricate at branch tips (Fig. 3), whereas the paratype (*Ule 7298*) is a much smaller plant to 3 cm tall, is 1- or 2-branched, and has lateral leaves imbricate throughout (Fig. 4). In both specimens, the leaves below the first branch tend to be more imbricate, have wider hyaline margins and longer marginal cilia, and the outer bases of the median leaves may be ventricose and with a tuft of long cilia (Fig. 4E). Additionally, below the first branch, they may have scarce and caducous cilia-like projections on the upper surfaces of the median leaves and sporophylls (Fig. 4E, F) and on the lower surfaces of lateral leaves. In these characters, *Selaginella blepharodella*, especially the paratype, is similar and perhaps related to *S. thysanophylla* from Venezuela

(Fig. 4G). These two species also share similar megaspore color; however *Selaginella blepharodella* can be separated from *S. thysanophylla* by the characters discussed in the diagnosis. *Selaginella blepharodella* differs further from *S. thysanophylla* by having megaspores 200–230 (vs. 150–200) µm, lateral leaves with acute (vs. rounded to subacute) apices, median leaves with the inner margins hyaline in a band 5–15 (vs. 20–25) cells wide at least along proximal ⅓ with long-acuminate (vs. apiculate) apices, each acumen 0.1–0.3 (vs. acumen 0.05–0.1) mm, and sporophyll apices each tipped by 2 cilia (Fig. 4F) [vs. 2 teeth; (Fig. 4H)].

In Brazil, *Selaginella blepharodella* does not seem to have close relatives, but it shares some characters, e.g., hyaline and ciliate leaf margins, with the newly described *S. mucugensis* and *S. crinita* (which see for comparison).

Selaginella crinita **Valdespino, sp. nov.**
urn:lsid:ipni.org:names:77147600-1
Figures 6, 7

Diagnosis. *Selaginella crinita* is morphologically similar to and may be confused with the Brazilian endemic, *S. jungermannioides* (Gaudich.) Spring, but differs in its lateral leaves long-ciliate throughout the basiscopic margins (vs. along proximal ¼ and then serrulate distally), median leaves with margins long-ciliate throughout (vs. along proximal ¼, particularly on outer margins, otherwise short-ciliate to serrulate distally), and apices long-acuminate (vs. cuspidate to acuminate) with each acumen hyaline (vs. cusp or acumen green) tipped by 2–4 long cilia (vs. entire).

Type. BRAZIL. Bahia: Mun. Água Quente, Pico das Almas, Vertente Oeste, trilho do povoado da Sta. Rosa, 35 km W of the city, 13°31'S, 42°00'W, 1100–1300 m, 1 Dec 1988, *R. Harley & N. Taylor 27048* (holotype: NY!; isotypes: BM-n.v., CEPEC-n.v., K-n.v., PMA!, SPF-n.v.).

Description. *Plants* terrestrial. *Stems* prostrate, stramineous, to 10 cm long, 0.3–0.5 mm diam., exarticulate, not flagelliform or stoloniferous, 1- or 2-branched. *Rhizophores* axillary, borne throughout stems, filiform, 0.1–0.2 mm diam. *Leaves* heteromorphic throughout, chartaceous, both surfaces glabrous, upper surfaces green or brownish (when old), lower surfaces silvery green or shiny brown (when old). *Lateral leaves* imbricate or distant, spreading to ascending, ovate-oblong, 1.5–2.0 × 0.5–1.0 mm; bases rounded, acroscopic bases strongly overlapping stems, basiscopic bases free from stems; acroscopic margins hyaline in a band 2–7 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 or 2 rows over each cell lumen, long-ciliate along proximal ⅔ and short-ciliate along distal ⅓; basiscopic margins greenish to slightly hyaline in a band 1 or 2 cells wide, the cells as along acroscopic margins, long-ciliate throughout, apices obtuse to rounded, variously tipped by 1–5 cilia; upper surfaces comprising quadrangular to rounded, sinuate-walled cells, most of these covered by 15–30 papillae, without idioblasts or stomata, lower surfaces comprising elongate, sinuate-walled cells, most of these papillate and idioblast-like, papillae in 1 or

2 rows over each cell lumen, with stomata in 1 or 2 rows along midribs where cells are shortly elongate and sinuate. *Median leaves* imbricate, ascending, ovate-lanceolate to ovate-elliptic, 1.0–1.5 × 0.4–0.7 mm; bases rounded to truncate; margins hyaline in a band 2–5 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 or 2 rows over each cell lumen, long-ciliate throughout; apices gradually tapering into a long-acumen, each acumen 0.12–0.15 mm, tipped by 2–5 cilia; both surfaces without idioblasts, upper surfaces comprising quadrangular to rounded, sinuate-walled cells covered by 15–30 papillae, with stomata along midribs, lower surfaces comprising elongate, sinuate-walled cells, without stomata. *Axillary leaves* ovate-oblong to oblong, otherwise similar to lateral leaves. *Strobili* terminal on branch tips, compact, quadrangular, 1.5–2.0 mm. *Sporophylls* monomorphic, without a laminar flap, ovate, 0.7–1.1 × 0.4–0.6 mm, each usually with a slightly developed and ciliate (cilia often caducous) keel along distal ½ of midribs; bases rounded; margins narrowly hyaline, long-ciliate; apices acute, tipped by 1 or 2 cilia; *dorsal sporophylls* with upper surfaces green and cells as in median leaves, except for the half that overlaps the ventral sporophylls, there hyaline with elongate, papillate, and slightly sinuate-walled cells, lower surfaces silvery green and comprising elongate, sinuate-walled cells; *ventral sporophylls* with both surfaces hyaline to greenish, comprising elongate, sinuate-walled cells. *Megasporangia* in proximal portion in 2 ventral rows; *megaspores* white to creamy, rugulate-reticulate on proximal faces, reticulate-granular on distal faces, with granulate-echinulate and perforate microstructure on both faces, 250–258 μm diam. *Microsporangia* in 2 dorsal rows and, in distal portion, also in 2 ventral rows; *microspores* orange, rugulate-verrucate on proximal faces, broadly clavate or broadly baculate (if apices of projected, echinulate elements broken off) [Fig. 7F] on distal faces, with echinulate microstructure on both faces, 25–33 μm.

Habitat and distribution. *Selaginella crinita* is known only from the type collection from Pico das Almas, Serra do Rio de Contas, Bahia, Brazil, where it is probably a local endemic. It grows on shady rocky and sandy soil at 1100–1300 m.

Etymology. The specific epithet is derived from the Latin *crinitus*, meaning long haired; this refers to the many, long cilia along leaf margins.

Conservation status. There is insufficient data to definitively ascertain distributional range, abundance, and possible threats to this species. Nevertheless, since its type locality is in the Chapada Diamantina region of the Espinhaço Mountain Range, which is threatened by anthropomorphic activities (Rapini et al. 2008), *Selaginella crinita* is tentatively considered vulnerable (VU), according to IUCN (2012) categories and criteria.

Discussion. *Selaginella crinita* is a prostrate species that belongs to subg. *Stachygynandrum* and is characterized by its median leaves ovate-lanceolate to ovate-elliptic, with the inner and the outer margins symmetric, and apices tapering into a long-acumen with each acumen tipped by 2–5 cilia, lateral leaves ovate-elliptic to ovate-oblong, as well as long-ciliate leaf margins, and quadrangular to rounded sinuate-walled cells on upper surfaces of median and lateral leaves covered by many (15–30) papillae. Because of its imbricate and long-ciliate lateral leaves and leaves tipped by cilia, *Selaginella crinita* may be confused

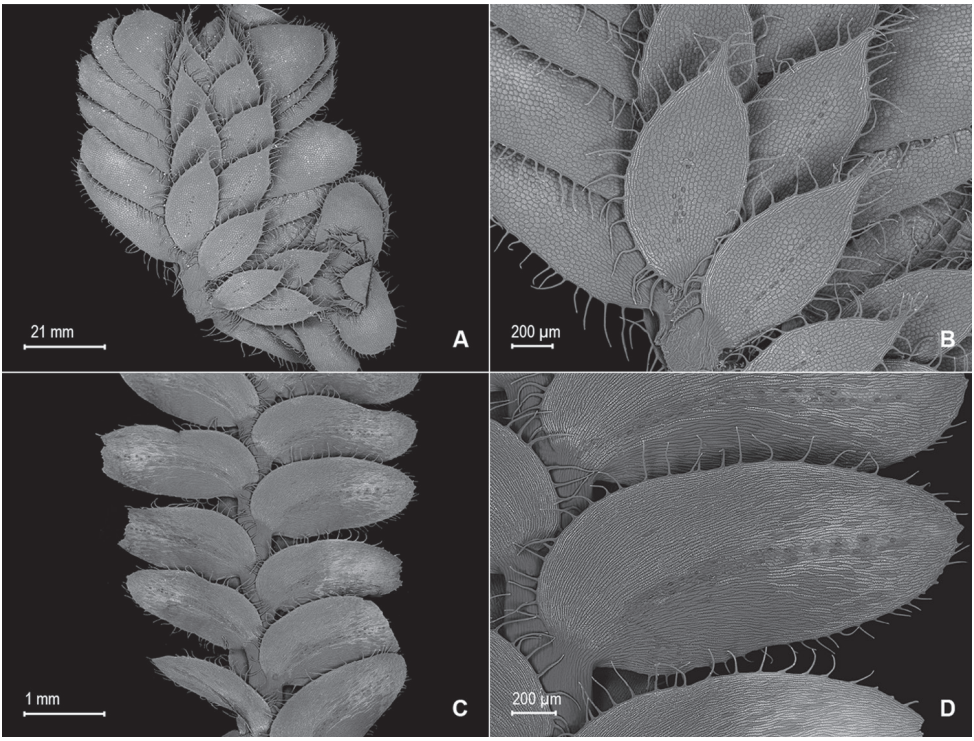

Figure 6. *Selaginella crinita* Valdespino. **A** Section of upper surface of stem **B** Upper surface of median leaves **C** Section of lower surface of stem **D** Lower surface of lateral leaf **A–D** taken from holotype, *Harley & Taylor 27048* (NY).

with *S. blepharodella*. *Selaginella crinita* is easily separated from *S. blepharodella* by its prostrate (vs. decumbent to suberect) habit, median leaves margins hyaline in a band 2–5 (vs. 5–15) cells wide, lateral leaves with obtuse to rounded (vs. acute) apices, and the cells of upper surfaces of median and lateral leaves covered by 15–30 (vs. 5–15) papillae.

Selaginella crinita belongs to a Neotropical group of *Selaginella* species, here informally termed the "*Selaginella jungermannioides* group", characterized mostly by creeping or prostrate habit, rhizophores usually distributed throughout the stems, median leaf apices acute, cuspidate, acuminate, or aristate, and lateral leaves often ovate-oblong or oblong with truncate, obtuse to broadly acute apices. The "*Selaginella jungermannioides* group" tentatively includes the South American taxa *S. applanata* A. Braun (Colombia, Venezuela, and Peru), *S. homaliae* A. Braun (Colombia and Brazil), *S. jungermannioides* (Brazil), *S. schultesii* Alston ex Crabbe & Jermy (Colombia), and *S. truncata* H. Karst. ex A. Braun (Colombia, Peru, and Bolivia), as well as *S. lindenii* Spring from southern Mexico. Among species in the "*Selaginella jungermannioides* group", *S. crinita* is morphologically close to *S. applanata*, *S. jungermannioides*, and *S. lindenii*. *Selaginella crinita* can be separated from *S. applanata* by its median leaves with inner and outer margins symmetric (vs. inner margins straight and outer

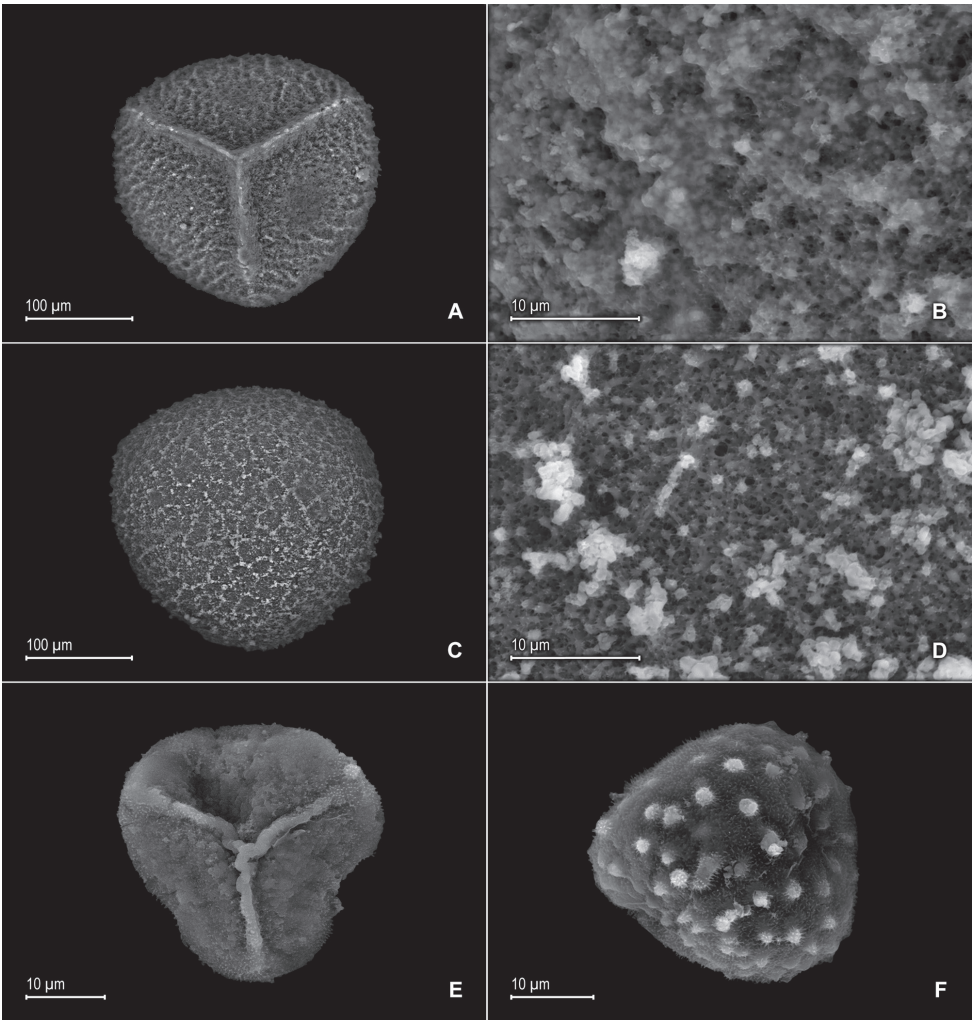

Figure 7. *Selaginella crinita* Valdespino. **A** Megaspore proximal face **B** Close-up of megaspore proximal face surface **C** Megaspore distal face **D** Close-up of megaspore distal face surface **E** Microspore proximal face **F** Microspore distal face **A–F** taken from holotype, *Harley & Taylor 27048* (NY).

margins convex), long-acuminate (vs. long-aristate) apices tipped by cilia (vs. entire), and acroscopic margins of lateral leaves ciliate throughout (vs. along proximal ½). It can be easily distinguished from *S. lindenii* by the upper surfaces of lateral and axillary leaves glabrous (vs. hispid), whereas from *S. jungermannioides* it differs by the characters of marginal projections of leaves and form of the median leaf apices, as discussed in the diagnosis. Additionally, *Selaginella crinita* may be confused with *S. homaliae* and *S. truncata*, but it is set apart from them by its median leaf apices long-acuminate (vs. acute to short-cuspidate) and margins long-ciliate throughout (vs. dentate to serrate in *S. homaliae* and in *S. truncata* inner margins denticulate and outer margins

sparingly long-ciliate along proximal ⅓, otherwise denticulate). *Selaginella crinita* also differs from the newly described *S. mucronata*, which may be part of the "*Selaginella jungermannioides* group", by its median leaves ovate-lanceolate to ovate-elliptic (vs. orbiculate to broadly elliptic), with stomata on upper surfaces along midribs (vs. distributed throughout the leaf laminae), and apices long-acuminate (vs. mucronate or infrequently acute), as well as by having the cells on the upper surfaces of the lateral and median leaves covered by 15–30 (vs. 5–10) papillae.

Selaginella mucronata G. Heringer, Salino & Valdespino, sp. nov.

urn:lsid:ipni.org:names:77147601-1
Figures 8, 9

Diagnosis. *Selaginella mucronata* seems morphologically related to *S. jungermannioides* but differs from it in having the upper surfaces of the leaves slightly rugose (vs. smooth), lateral leaves with the basiscopic margins entire to serrulate distally (vs. basiscopic margins long-ciliate along proximal ⅛, otherwise entire), median leaf bases rounded (vs. oblique with a slightly developed outer lobe), and margins hyaline (vs. greenish) and long-ciliate throughout (vs. inner margins denticulate and outer margins sparingly long-ciliate along proximal ⅓, otherwise denticulate).

Type. BRAZIL. Espírito Santo: Castelo, Parque Estadual do Forno Grande, [20°32'29"S, 41°07'17"W], [1200 m], 28 Jun 2008, *A. Salino, G. Heringer & V.A.O. Dittrich 13686* (holotype: BHCB!; isotype: PMA-fragment!).

Description. *Plants* epipetric. *Stems* creeping, stramineous, 5.5–8.0 cm long, 0.4–0.8 mm diam., exarticulate, not flagelliform or stoloniferous, 1- or 2-branched. *Rhizophores* ventral, axillary or dorsal, borne throughout stems, filiform, 0.1–0.2 mm diam. *Leaves* heteromorphic throughout, membranaceous to chartaceous, both surfaces glabrous, upper surfaces green, lower surfaces silvery green. *Lateral leaves* imbricate or distant, spreading, broadly ovate to ovate-oblong, 2.5–4.0 × 1.3–2.3 mm; bases rounded or hemicordate, acroscopic bases strongly overlapping stems, basiscopic bases free from stems; acroscopic margins greenish or hyaline in band 2–4 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 row over each cell lumen, long-ciliate along proximal ½–⅔ and serrulate to entire distally, basiscopic margins greenish or narrowly hyaline in a band 1 or 2 cells wide, the cells as along acroscopic margins, entire or entire along proximal ¾ and serrulate along distal ¼, apices mucronate or obtuse, tipped by 2 or 3 teeth; upper surfaces comprising rounded to quadrangular, sinuate-walled cells, most of these covered by 5–10 papillae, without idioblasts or stomata, lower surfaces comprising elongate, sinuate-walled cells, few of these papillate and idioblast-like, papillae in 1 row over each cell lumen, with stomata in 2 or 3 rows along midribs. *Median leaves* imbricate (especially at stem and branch apices), ascending, orbiculate to broadly elliptic, 1.4–2.6 × 1.1–2.1 mm; bases rounded; margins hyaline in a band 1–3 cells wide, the cells elongate and papillate parallel to margins, long-ciliate throughout; apices mucronate or infre-

quently acute, each mucro 0.14–0.16 mm, ending in 1–3 teeth; both surfaces without idioblasts, upper surfaces comprising rounded to quadrangular, sinuate-walled cells, many of these covered by 5–10 papillae, with stomata throughout the laminae and some near submarginal region of the outer bases, lower surfaces comprising elongate, sinuate-walled cells, without stomata. *Axillary leaves* ovate or slightly cordiform, bases rounded or cordate, margins and apices similar to lateral leaves. *Strobili* terminal on branch tips, compact, quadrangular, 4.0–7.0 mm. *Sporophylls* monomorphic to slightly dimorphic, without a laminar flap, ovate to lanceolate, 1.3–1.9 × 0.7–0.9 mm, each with or without a slightly developed denticulate keel along distal ½ of the midribs; bases rounded; margins narrowly hyaline, serrulate to short-ciliate; apices acute, tipped by 1–3 teeth; *dorsal sporophylls* with upper surfaces green and cells as in median leaves, except for the half that overlaps the ventral sporophylls, there hyaline and with elongate, papillate, and slightly sinuate-walled cells, lower surfaces silvery green and comprising elongate, sinuate-walled cells; *ventral sporophylls* with both surfaces silvery green and comprising elongate, sinuate-walled cells. *Megasporangia* in 2 ventral rows; *megaspores* creamy or light yellow, most observed immature, reticulate to reticulate-rugulate on proximal faces, reticulate on distal faces, with perforate microstructure on both faces, 200–230 µm. *Microsporangia* in 2 dorsal rows; *microspores* orange, psilate-rugulate on proximal faces, capitate or baculate (if apices of projected elements broken off) [Fig. 9E, G, H] on distal faces, with granulate microstructure on both faces, 20–27 µm diam.

Habitat and distribution. *Selaginella mucronata* is known only from the type collection from Parque Estadual do Forno Grande, state of Espírito Santo, growing on rocks in understory of Atlantic Rainforest vegetation at 1200 m. It could be considered a local endemic given its limited distribution and the vegetational type.

Etymology. The epithet mucronata refers to the apices of the median leaves.

Conservation status. The paucity of data available does not allow an assessment of abundance and possible threats to this species and, thus, we assign to it a Data Deficient (DD) conservation assessment according to IUCN (2012) categories and criteria.

Discussion. *Selaginella mucronata* belongs to subg. *Stachygynandrum* and is characterized by its creeping habit, orbicular to broadly elliptic, long-ciliate, mucronate or infrequently acute median leaves with stomata distributed throughout the upper surfaces (Fig. 8A–C). *Selaginella mucronata* seems to be morphologically most similar to *S. jungermannioides*; however, the characters of leaf texture, margin type, and shape of median leaf bases discussed in the diagnosis distinguish these two species. *Selaginella mucronata* could be confused with *S. crinita*, another member of the "*Selaginella jungermannioides* group," which see for discussion.

The upper surfaces of *Selaginella mucronata* may be slightly corrugate (Fig. 8A–C), perhaps as a drying artifact, and because of this and its creeping habit it could be confused, among other Brazilian species, with *S. flexuosa* Spring and *S. macrostachya* (Spring) Spring. *Selaginella mucronata* differs chiefly from those two species in having the apices of median leaves mucronate or acute (vs. long-aristate) with each acumen $^{1}/_{10}$–$^{1}/_{16}$ (vs. arista ¼–¾) the length of the leaf lamina. Additionally, *S. mucronata* dif-

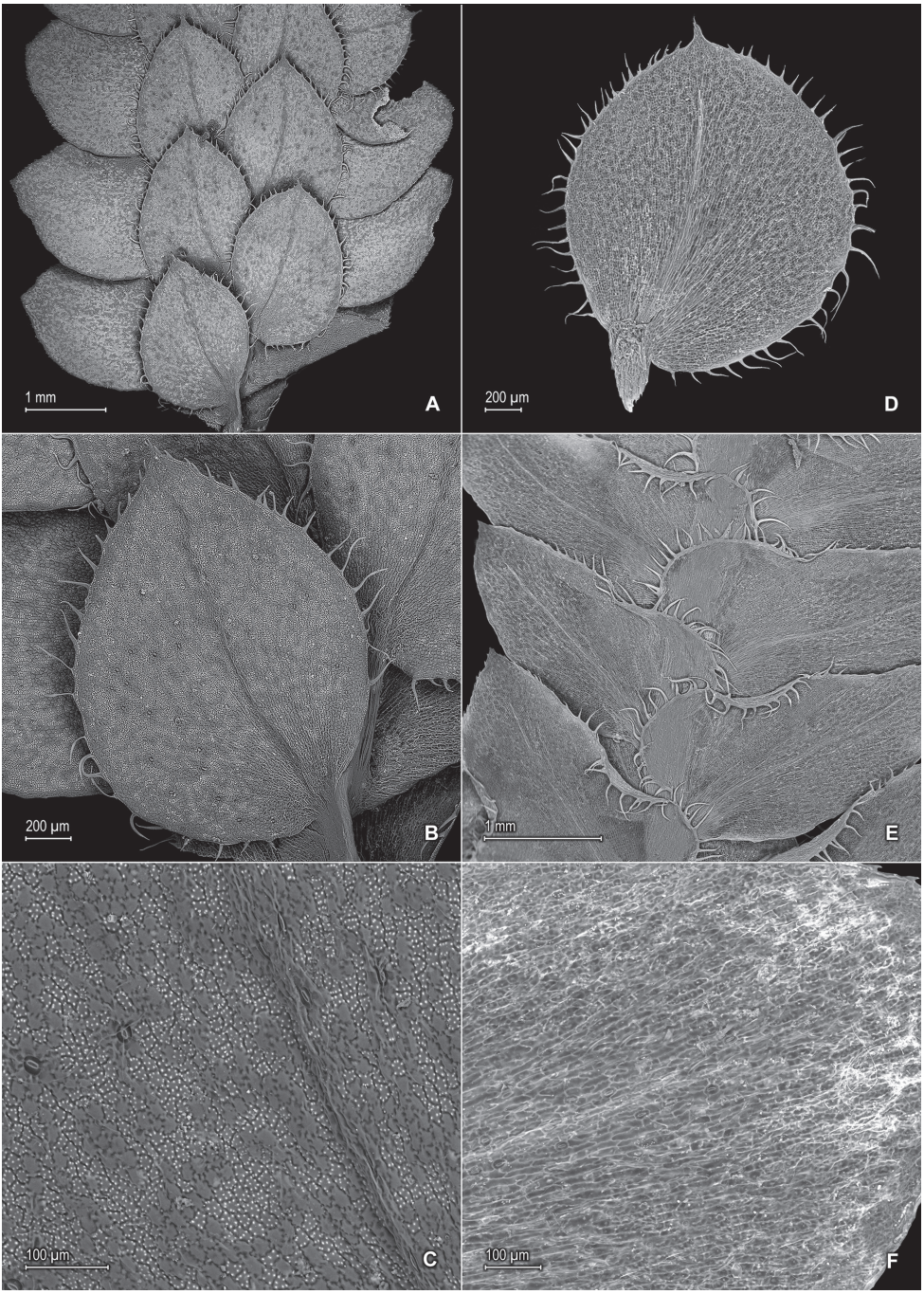

Figure 8. *Selaginella mucronata* G. Heringer, Salino & Valdespino. **A** Section of upper surface of stem **B** Upper surface of median leaf **C** Close-up of upper surface of median leaf **D** Lower surface of median leaf **E** Section of lower surface of stem **F** Close-up of lower surface of lateral leaf **A–F** taken from isotype, *Salino et al. 13686* (PMA).

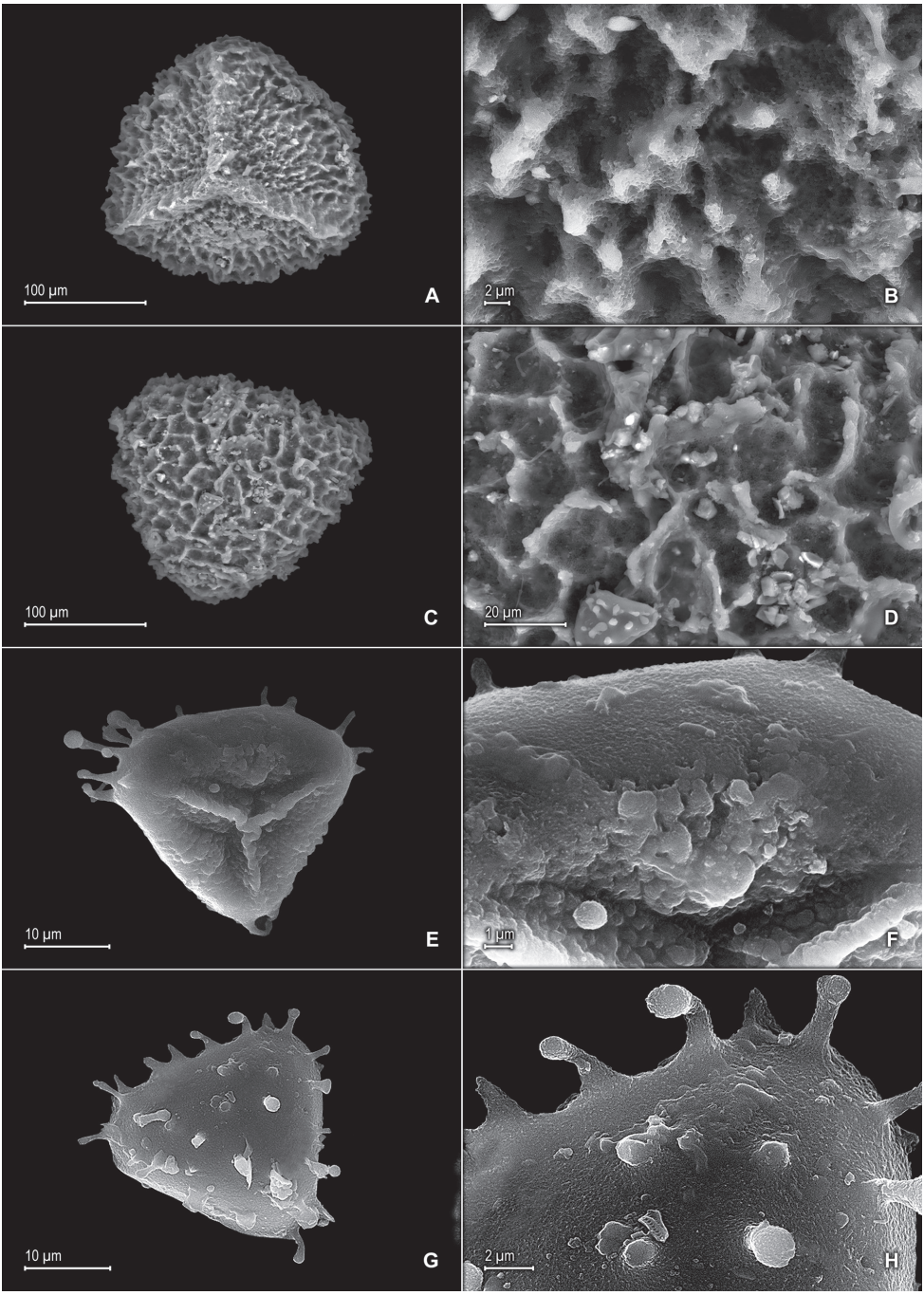

Figure 9. *Selaginella mucronata* G. Heringer, Salino & Valdespino. **A** Megaspore proximal face **B** Close-up of megaspore proximal face surface **C** Megaspore distal face **D** Close-up of megaspore distal face surface **E** Microspore proximal face **F** Close-up of microspore proximal face surface **G** Microspore distal face **H** Close-up of microspore distal face surface **A–H** taken from isotype, *Salino et al. 13686* (PMA).

fers from *S. flexuosa* by acroscopic margins of lateral leaves long-ciliate along proximal ½–$^{2}/_{3}$ and serrulate to entire distally (vs. denticulate along proximal ¼–½, otherwise entire distally) and the margins of the median and axillary leaves ciliate (vs. serrulate). It is further distinguished from *S. macrostachya* by its orbiculate to broadly elliptic (vs. cordate) median leaves with the outer bases glabrous (vs. tufted with short hairs) and lateral leaves with upper surfaces near basiscopic margins glabrous (vs. often with short, tooth-like hairs).

Selaginella mucugensis **Valdespino, sp. nov.**
urn:lsid:ipni.org:names:77147602-1
Figures 10, 11

Diagnosis. *Selaginella mucugensis* differs from *S. blepharodella* in having median leaves distant (vs. imbricate), ovate (vs. broadly-ovate to ovate-elliptic), with margins hyaline in a band 2–5 (vs. 5–15) cells wide with cilia 30–50 (vs. 130–180) µm long, stomata on upper surfaces on submarginal and marginal regions of the outer bases (vs. restricted to midribs), apices acute to short-acuminate (vs. long-acuminate), the acumen, if present, 0.02–0.08 (vs. acumen 0.1–0.3) mm, and lateral leaves with basiscopic margins entire along proximal ¼–½ and serrate to short-ciliate distally (vs. usually ciliate throughout).

Type. BRAZIL. Bahia: Mucugê, campo defronte ao cemitério, [ca. 13°00'S, 41°22'19"W], [ca. 984 m], 20 Jul 1981, *A.M. Giulietti et al. [CFCR 1430]* (holotype: NY!; isotypes: PMA- fragment!, SPF-n.v.).

Description. *Plants* terrestrial. *Stems* ascending to suberect, stramineous, 3–7 cm long, 0.2–0.4 mm diam., exarticulate, not flagelliform, probably shortly stoloniferous, 2- or 3-branched. *Rhizophores* axillary and axillary-dorsal, restricted to the bases of stems, filiform, 0.1–0.2 mm diam. *Leaves* heteromorphic throughout, chartaceous, both surfaces glabrous, upper surfaces green, lower surfaces silvery green or brownish (when old). *Lateral leaves* distant, slightly ascending, ovate to slightly ovate-oblong, 1.2–1.5 × 0.9–1.1 mm; bases rounded, acroscopic bases slightly to strongly overlapping stems, basiscopic bases free from stems; acroscopic margins hyaline in a band 2–8 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 row over each cell lumen, long- to short-ciliate along proximal ¾ and serrate to entire along distal ¼; basiscopic margins narrowly hyaline or greenish in a band 1 or 2 cells wide, the cells as along acroscopic margins, entire along proximal ¼–½ and serrate to short-ciliate distally, apices acute, tipped by 1–3 teeth; upper surfaces comprising rounded to quadrangular, sinuate-walled cells, some of these covered by 4–8 papillae, without idioblasts or stomata, lower surfaces comprising elongate, sinuate-walled cells, some of these papillate and idioblast-like, papillae in 2 rows over each cell lumen, with stomata in 2 or 3 rows along midribs and along proximal ½ of basiscopic margins. *Median leaves* distant, ascending, ovate, 0.8–1.3 × 0.5–0.7 mm; bases oblique, inner bases plane in profile, outer bases ventricose (i.e., swollen); margins hyaline in a

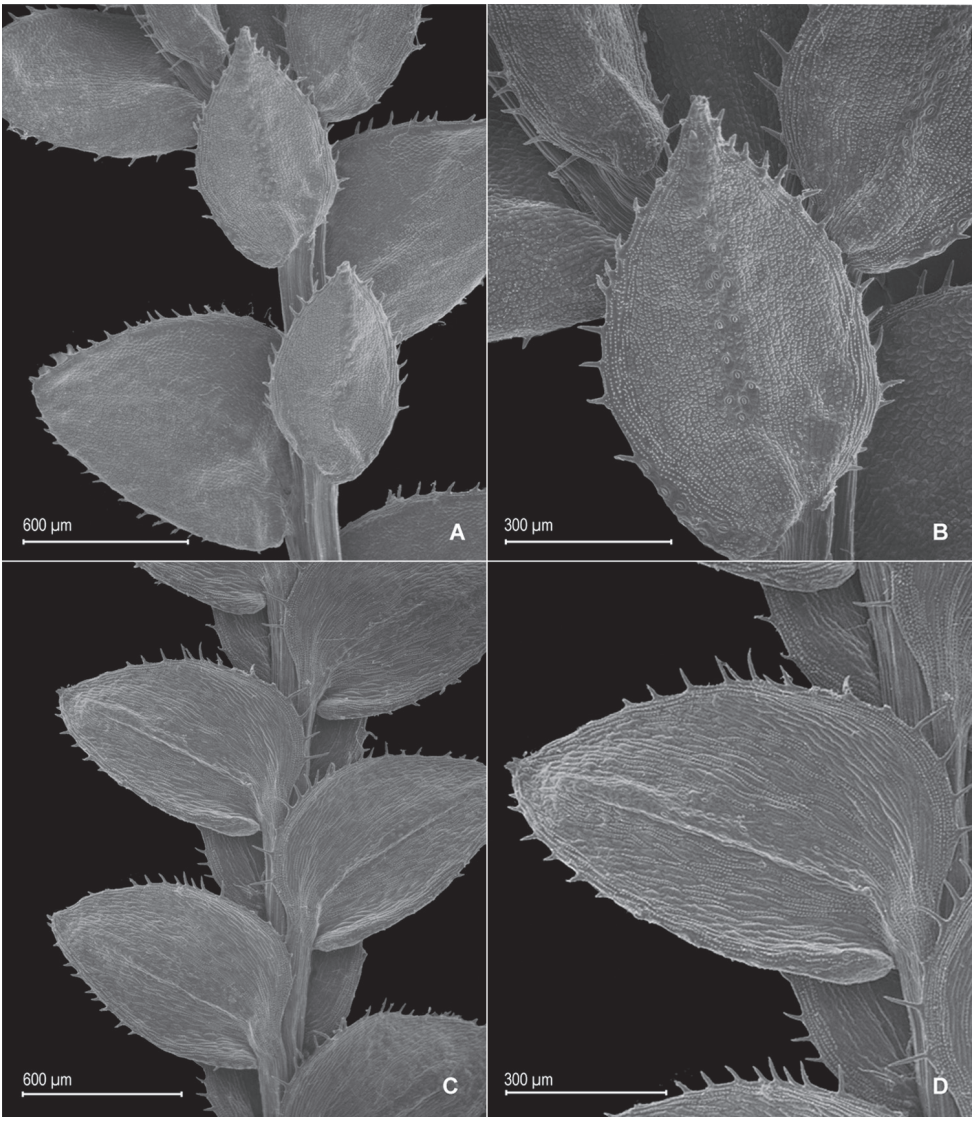

Figure 10. *Selaginella mucugensis* Valdespino. **A** Section of upper surface of stem **B** Upper surface of median leaf **C** Section of lower surface of stem **D** Lower surface of lateral leaf **A–D** taken from holotype, *Giulietti et al. [CFCR 1430]* (NY).

band 2–5 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 row over each cell lumen, shortly ciliate throughout; apices acute to short-acuminate, each acumen 0.02–0.08 mm, occasionally with 1 or 2 hairs on upper surfaces, tipped by 1–3 teeth; both surfaces without idioblasts, upper surfaces comprising rounded to quadrangular, sinuate-walled cells covered by 4–8 papillae, with stomata along midribs and some on submarginal and marginal regions of the outer bases, lower surfaces comprising elongate, sinuate-walled cells, without stomata. *Axillary leaves* similar to lateral

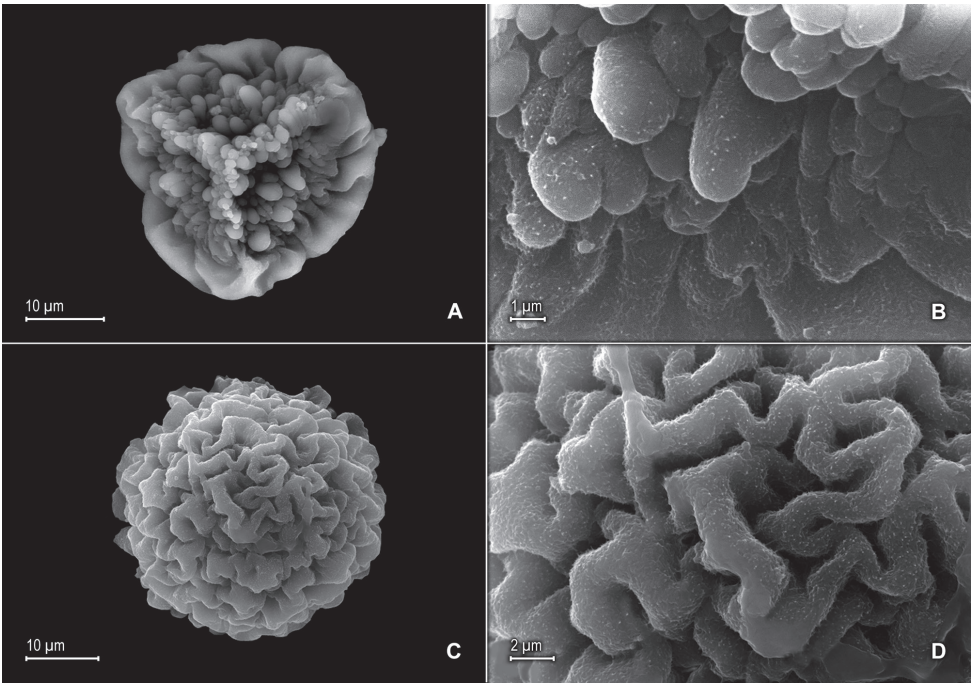

Figure 11. *Selaginella mucugensis* Valdespino. **A** Microspore proximal face **B** Close-up of microspore proximal face surface **C** Microspore distal face **D** Close-up of microspore distal face surface **A–D** taken from holotype, *Giulietti et al. [CFCR 1430]* (NY).

leaves. *Strobili* terminal on branch tips, compact, quadrangular, 2.0–7.0 mm. *Sporophylls* monomorphic, without a laminar flap, ovate, 0.8–1 × 0.4–0.5 mm, each with a well-developed, frequently puberulous keel along the midribs; bases rounded; margins hyaline, short-ciliate to serrate; apices acute, tipped by 1 or 2 teeth; *dorsal sporophylls* with upper surfaces green and cells as in median leaves, except for the half that overlaps the ventral sporophylls, there hyaline with elongate, papillate, and slightly sinuate-walled cells, lower surfaces silvery green and comprising elongate, sinuate-walled cells; *ventral sporophylls* with both surfaces hyaline, comprising elongate, sinuate-walled cells. *Megasporangia* frequently proximal in 2 ventral rows or the proximal megasporangia abortive and a few intermixed with microsporangia; *megaspores* lemon-yellow, mostly immature or absent, proximal faces not observed, reticulate on distal faces, 275–285 µm. *Microsporangia* in 2 dorsal rows and, in distal portion, also in 2 ventral rows; *microspores* orange, gemmate-rugulate or broadly baculate-rugulate with psilate to echinulate microstructure on proximal faces, vermiculate with echinulate microstructure on distal faces, 30–40 µm.

Habitat and distribution. *Selaginella mucugensis* is known only from the type collection from Mucugê, Serra do Sincorá, in the Chapada Diamantina region of the Espinhaço Mountain Range, where it is probably a local endemic. It grows terrestrially on damp soil in Campos Rupestres vegetation at ca. 984 m.

Etymology. This species is named for the type locality.

Conservation status. At present, there is limited information available to allow a conclusive determination of the conservation status of *Selaginella mucugensis*. Nevertheless, according to IUCN (2012) categories and criteria, we tentatively considered this species to be vulnerable (VU) on account that it is so far known from a single locality in the Espinhaço Mountain Range, which is threatened by human activities (Rapini et al. 2008).

Discussion. *Selaginella mucugensis* is a member of subg. *Stachygynandrum* and may be confused with *S. blepharodella* because they have similar leaf margins and indument on the upper surfaces in the distal region of median leaves and sporophylls (Fig. 7B). In fact, these two species may prove to be sympatric in the Serra do Sincorá, where both were collected. According to Harley and Simmons (1986), this area is an important center of diversity of the Brazilian montane flora. *Selaginella mucugensis* is distinguished from *S. blepharodella* by the characters discussed under the diagnosis.

Selaginella saltuicola **Valdespino, sp. nov.**
urn:lsid:ipni.org:names:77147603-1
Figures 12, 13

Diagnosis. *Selaginella saltuicola* is morphologically close to *S. prasina* Baker but differs from it by having median leaves on main stems ovate or ovate-elliptic (vs. oblong to oblong-elliptic), with acute (vs. obtuse) apices, distally entire (vs. toothed), inner margins entire (vs. dentate distally), narrowly hyaline (vs. green) with (vs. without) a band of 1–3 elongate and papillate cells, leaf bases rounded to oblique (vs. decurrent), strobili borne throughout the stems and weakly defined (vs. terminal and compact), with (vs. without) continuous, vegetative growth from the apices, sporophylls similar to (vs. well-differentiated from) vegetative leaves, and light-orange (vs. deep orange) megaspores.

Type. BRAZIL. Mato Grosso: Chapada dos Guimarães, Gorge of Véu de Noiva [ca. 15°24'21"S, 55°50'12"W], [ca. 720 m] 17 Oct 1973, *G.T. Prance et al. 19126* (holotype: NY!; isotypes: INPA!, PMA-fragment!).

Description. *Plants* epipetric or epiphytic. *Stems* creeping, stramineous to green, 1.5–3 cm long, 0.05–0.2 mm diam., exarticulate, not flagelliform or stoloniferous, 1-branched. *Rhizophores* axillary, borne throughout stems, filiform, 0.05–0.1 mm diam. *Leaves* heteromorphic throughout, thin-membranaceous, both surfaces glabrous, upper surfaces green, lower surfaces silvery green. *Lateral leaves* distant or imbricate apically, patent to slightly ascending, ovate, ovate-elliptic or ovate-oblong, 0.9–1.5 × 0.5–0.8 mm; bases rounded, acroscopic bases slightly to strongly overlapping the stems, basiscopic bases free from the stems; acroscopic margins on upper surfaces greenish or narrowly hyaline, if the latter, in a band 1 or 2 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 row over each cell lumen, on lower surfaces hyaline in a band 2–4 cells wide, the cells as on upper surfaces, entire or minutely serrulate

along distal ¼, basiscopic margins on upper surfaces greenish on lower surfaces, narrowly hyaline marginally in a band 2–4 cells wide, the cells as along acroscopic hyaline margins, entire or inconspicuously denticulate throughout; apices rounded to broadly acute, entire or tipped by 1–3 teeth; upper surfaces comprising rounded to quadrangular, sinuate-walled cells, some of these on or near basiscopic and apical regions of the laminae covered by 2–4 papillae, without idioblasts and with stomata along margins, lower surfaces comprising elongate, sinuate-walled cells, some of these papillate and idioblast-like, papillae in 1 row over each cell lumen, with stomata irregularly distributed along midribs, as well as on acroscopic half of the laminae and on both margins (visible in both surfaces of the laminae). *Median leaves* distant or imbricate apically, ascending to spreading, ovate or ovate-elliptic, 0.6–0.9 × 0.4–0.5 mm; bases rounded or oblique, ventricose (i.e., swollen); margins narrowly hyaline in a band 1–3 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 row over each cell lumen, entire; apices acute, entire (not distinctly tipped by teeth or cilia); both surfaces without idioblasts, upper surfaces comprising rounded to quadrangular, sinuate-walled cells, many of these covered by 2–4 papillae, with stomata throughout the laminae and some near submarginal region of the outer bases, lower surfaces comprising elongate, sinuate-walled cells, without stomata. *Axillary leaves* similar to lateral leaves. *Strobili* borne throughout the stems, weakly defined, lax, flattened, 1.0–2.0 mm. *Sporophylls* similar to or slightly differentiated from vegetative leaves, monomorphic to subdimorphic, without a laminar flap, ovate, 0.7–1.4 × 0.5–0.8 mm, each without a keel; bases rounded; margins narrowly hyaline, entire; apices acute, entire (not distinctly tipped by teeth or cilia); *dorsal sporophylls* with upper surfaces green and cells as in median leaves, except for the half that overlaps the ventral sporophylls, there hyaline to greenish hyaline with elongate, papillate, and slightly sinuate-walled cells, lower surfaces silvery green and comprising elongate, sinuate-walled cells; *ventral sporophylls* with both surfaces hyaline to greenish hyaline, comprising elongate, sinuate-walled cells. *Megasporangia* few in 1 ventral row; *megaspores* light-orange, mostly absent, proximal and distal faces not observed, not measured. *Microsporangia* in 2 dorsal rows and in 1 ventral row or few and in axils of median leaves; *microspores* deep orange, areolate-fossulate with granulate microstructure on proximal and distal faces, 25–31 μm.

Habitat and distribution. *Selaginella saltuicola* is unique among other species here described by its apparent adaptation to very wet areas near waterfalls and perhaps even partially submerged in water along creek banks in Cerrado vegetation. At present, this species is known only from the high plateau of the Chapada dos Guimarães, Mato Grosso, Brazil, where it may be a local endemic, growing on wet rocks or wet logs at 600–720 m.

Etymology. The epithet of the new species is derived from the Latin *saltus*, meaning jump, drop or fall and *cola*, meaning dweller, inhabitant, and alludes to it habitat near "cachoeiras" (waterfalls).

Conservation status. *Selaginella saltuicola* seems to be restricted to the Chapada dos Guimarães area, where the Cerrado vegetation is dominant and severely threatened by human activities (Oliveira-Filho and Martins 1991, Ratter et al. 1997, Strüssmann

and Mott 2009). *Selaginella saltuicola* may therefore be tentatively considered vulnerable (VU), according to IUCN (2012) categories and criteria, at least until additional distributional and conservation status studies can be carried out.

Additional specimens examined (paratypes). BRAZIL. **Mato Grosso**: Waterfall at first Igarapé after descending Chapada on road to Cuiabá, 600 m, 23 Oct 1973, *Prance et al. 19336* (INPA, NY), *19337* (INPA, K, NY); Chapada dos Guimarães, Gorge of Véu de Noiva, 17 Oct 1973, *Prance et al. 19123* (INPA, NY), *19127* (NY), *19128* (INPA, NY), *19136* (INPA, NY), *19138* (NY).

Discussion. *Selaginella saltuicola* belongs to subg. *Stachygynandrum* and is morphologically similar to *S. prasina* from Cuba, *S. salazariae* Valdespino from Panama, and *S. undata* Shelton & Caluff, from Cuba, because they share similar habit and overall vegetative leaf morphology, stomata throughout upper surfaces of median leaves, and midribs of lateral leaves restricted to ca. ¼ below apices. However, *S. undata* (isotype: *Shelton & Caluff 4514*, B!) falls within the morphological range of *S. prasina* and may be best considered conspecific with the latter. *Selaginella saltuicola* differs from *S. prasina* by the characters of median leaf shape, apex type, inner margin color and projections, leaf base shape, strobilus morphology, and megaspore color, as discussed in the diagnosis, as well as by having ovate, ovate-elliptic, or ovate-oblong (vs. obovate) axillary leaves and many cells on the upper surfaces of median leaves covered by 2–4 (Fig. 12B) [vs. without (Fig. 12E)] papillae. It differs from *Selaginella salazariae* in its median leaves ovate or ovate-elliptic (vs. obovate, obovate-elliptic, or broadly elliptic) with acute (vs. abruptly cuspidate to short-aristate) apices.

We note that Neotropical *Selaginella* species studied (i.e., *S. prasina*, *S. salazariae*, and *S. saltuicola*) that grow either partially underwater or constantly wetted by waterfalls, rivers, or creeks have numerous stomata distributed over the upper surfaces of median leaves (Fig. 12A, B, E) and broadly acute to obtuse, rounded (Fig. 12A, C, D) or truncate lateral leaves (Fig. 12F). At present, it is not clear if the shared characters among those species might be the result of adaptation to a similar habitat (i.e., wet rocks or logs on waterfalls or stream banks) by convergent evolution or synapomorphies that may phylogenetically relate them.

In some plants of *Selaginella saltuicola*, as well as in some of *S. alstonii*, we found strobili with continuous, vegetative growth from their apices. This condition was reported to occur in the genus by Hieronymus (1901), Williams (1931), Jermy (1990), and Valdespino (1993a, 1993b, 1995). In *Selaginella*, normally, fertile shoots (strobili) originate from the tips of vegetative shoots (i.e., stems and branches) in a "vegetative (V)/determinate fertile (F) growth pattern" or "V/F pattern," although in plants of some species, e.g., *S. decomposita* and *S. saltuicola*, microsporangial development was observed in axils of median leaves, similarly to what is seen in *S. denticulata* (L.) Spring where mega- and microsporangia are found in axils of lateral leaves below the weekly differentiated strobilus (see images in Quiles 2015). In the phenomenon described for *S. saltuicola* and *S. alstonii*, however, the fertile growth becomes indeterminate and the apices of strobili revert to a vegetative condition in what could be termed a "V/indeterminate F/V growth pattern" or "V/F/V pattern" that is also found in other

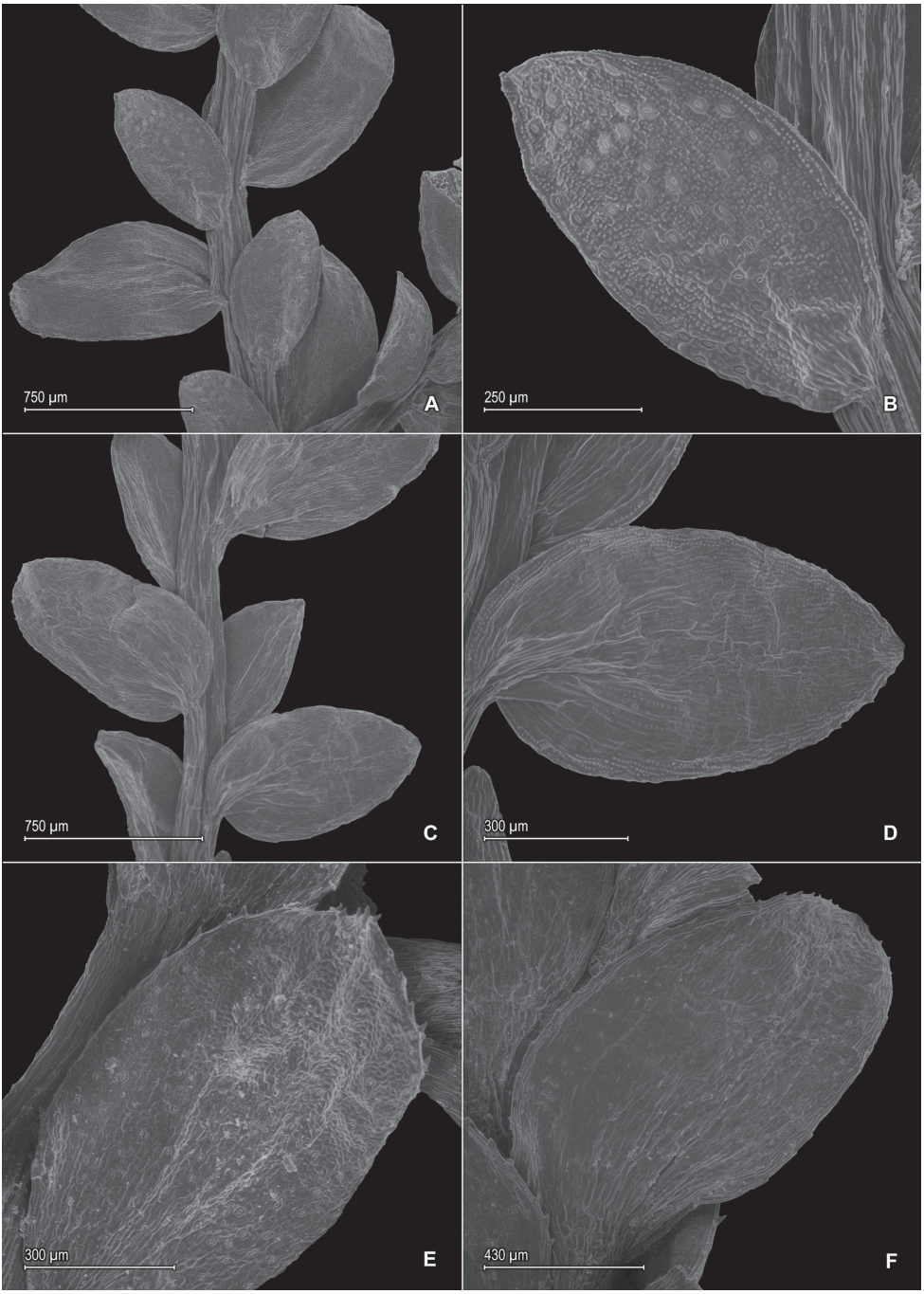

Figure 12. *Selaginella saltuicola* Valdespino. **A** Section of upper surface of stem **B** Upper surface of median leaf **C** Section of lower surface of stem **D** Lower surface of lateral leaf. **A–D** taken from paratype, *Prance et al. 19337* (NY). *Selaginella prasina* Baker **E** Upper surface of median leaf **F** Lower surface of lateral leaf **E**, **F** taken from *Smith et al. 115583* (GH).

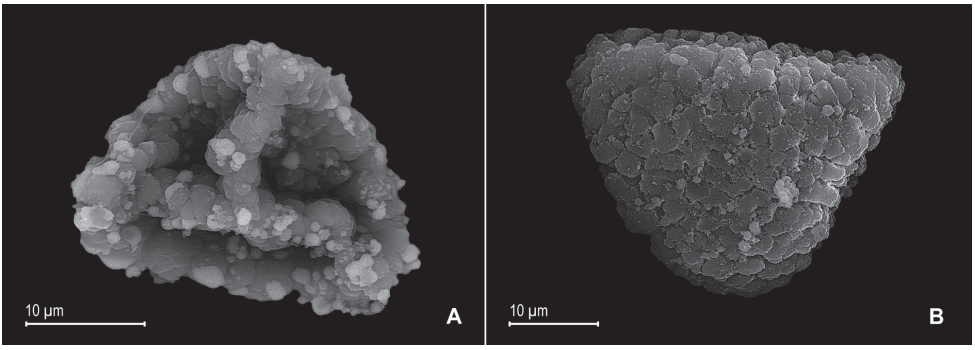

Figure 13. *Selaginella saltuicola* Valdespino. **A** Microspore proximal face **B** Microspore distal face **A, B** taken from holotype, *Prance et al. 19126* (NY).

species such as *S. finitima* Mickel & Beitel, *S. porphyrospora* A. Braun, and *S. tenella* (P. Beauv.) Spring in mainland in the Neotropics (Valdespino 1995), *S. orbiculifolia* Shelton & Caluff from Cuba (Caluff and Shelton 2003), and *S. wangpeishanii* Li Bing Zhang, H. He & Q. W. Sun from China, which Zhang et al. (2014) termed TST (where T is for trophophyll = vegetative leaf, and S is for sporophyll) arrangement of microphylls. In a third condition, the second vegetative growth of the V/F/V pattern of the shoot becomes fertile and indeterminate in a "V/F/ V/indeterminate F growth pattern" or "V/F/V/F" pattern, found for example in *Selaginella correae* Valdespino from Panama (Valdespino 1993b), *S. oregana* D.C. Eaton from temperate zones in western North America (Valdespino 1993a), and *S. tuberculata* Spruce ex Baker (e.g., *Steyermark 75483*, NY!) from South America. This V/F/V/F pattern consists of a shoot with alternating vegetative leaves, sporophylls, and vegetative leaves along the stems and is reminiscent of the pattern found in some species of *Huperzia* (Lycopodiaceae). Valdespino (1995) suggested these alternating patterns of vegetative stems and fertile shoot formation could be an adaptive strategy of *Selaginella*, or it could be a response to damage to the growing apices. In any case, hormones may probably mediate this phenomenon, which seems to be more common and found across geographically and phylogenetically different *Selaginella* taxa than previously acknowledged. The ecological advantages of such variation, phylogenetic significance, and possible genetic and/or hormonal origin remain to be determined.

Selaginella sematophylla **Valdespino, G. Heringer & Salino, sp. nov.**
urn:lsid:ipni.org:names:77147604-1
Figures 14, 15

Diagnosis. *Selaginella sematophylla* differs chiefly from *S. vestiens* in having (vs. lacking) idioblasts on upper surfaces of median leaves and dorsal sporophylls and on lower surfaces of lateral leaves, and by its acute (vs. acuminate to aristate, 0.4–0.7 mm) median leaves, and creeping (vs. ascending to suberect) habit.

Type. BRAZIL. Minas Gerais: São Sebastião do Paraíso, Baú, [ca. 20°53'52"S, 46°57'33"W], 26 Apr 1945, *A.C. Brade & A. Barbosa 17953* (holotype: MO!; isotypes: BM!, CESJ!, NY!, PMA-fragment!, RB-image!).

Description. *Plants* terrestrial. *Stems* creeping, stramineous, 2–3.5 cm long, 0.1–0.3 mm diam., exarticulate, not flagelliform or stoloniferous, 1-branched. *Rhizophores* axillary, borne throughout stems, filiform, 0.05–0.1 mm diam. *Leaves* heteromorphic throughout, thin-membranaceous to chartaceous, both surfaces glabrous, upper surfaces green, lower surfaces silvery green. *Lateral leaves* distant or imbricate distally, patent, ovate, 1.0–1.4 × 0.6–0.9 mm; bases rounded, acroscopic bases strongly overlapping the stems, basiscopic bases free from the stems; acroscopic margins hyaline to green-hyaline in a band 2–6 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 row over each cell lumen, short- to long-ciliate along proximal ¼–½ and serrulate distally; basiscopic margins hyaline in a band 2 or 3 cells wide, the cells as on acroscopic margins, short-ciliate along proximal ⅕, otherwise serrate to serrulate along distal ⅘; apices acute, tipped by 1–3 teeth; upper surfaces comprising quadrangular to rounded, sinuate-walled cells, some of these on or near basiscopic and apical regions of the laminae, which are covered by 1–5 papillae, without idioblasts or stomata, lower surfaces comprising elongate, sinuate-walled cells, some of these papillate and idioblast-like, papillae in 1 row over each cell lumen, with stomata along midribs and few irregularly distributed over laminae. *Median leaves* imbricate, ascending, lanceolate, 0.8–1.4 × 0.3–0.7 mm; bases oblique to rounded, margins hyaline in a band 3–7 cells wide, the cells elongate and papillate parallel to margins, papillae in 1 row over each cell lumen, serrate to denticulate throughout; apices acute, tipped by 1 or 2 teeth; upper surfaces comprising rounded to quadrangular, sinuate-walled cells, most of these covered by 1–7 papillae, and some idioblast-like, papillate, elongate cells with papillae in 1 row over each cell lumen along both sides of the midribs, with stomata in 1 or 2 rows along midribs and a few irregularly distributed on proximal region of inner half of the laminae, lower surfaces comprising elongate, sinuate-walled cells, without stomata. *Axillary leaves* similar to lateral leaves. *Strobili* terminal on branch tips, lax, slightly quadrangular, 2.0–8.0 mm. *Sporophylls* monomorphic to slightly dimorphic, without a laminar flap, lanceolate, 1–1.4 × 0.5–0.8 mm, each without a keel; bases rounded; margins hyaline, serrulate; apices gradually acute, tipped by 1–3 teeth; *dorsal sporophylls* with both surfaces having idioblasts, upper surfaces green with cells as in median leaves, except for the half that overlaps the ventral sporophylls, there hyaline to greenish hyaline and with elongate, papillate, and slightly sinuate-walled cells, lower surface silvery green comprising elongate, sinuate-walled cells; *ventral sporophylls* with both surfaces hyaline and comprising elongate, sinuate-walled cells. *Megasporangia* in 2 ventral rows; *megaspores* cream or light-yellow, rugulate-reticulate with granulate-perforate microstructure on proximal faces, reticulate or reticulate-granular with granulate-echinulate and perforate microstructure on distal faces, 275–290 µm. *Microsporangia* in 2 dorsal rows; *microspores* orange, psilate marginally to rugulate

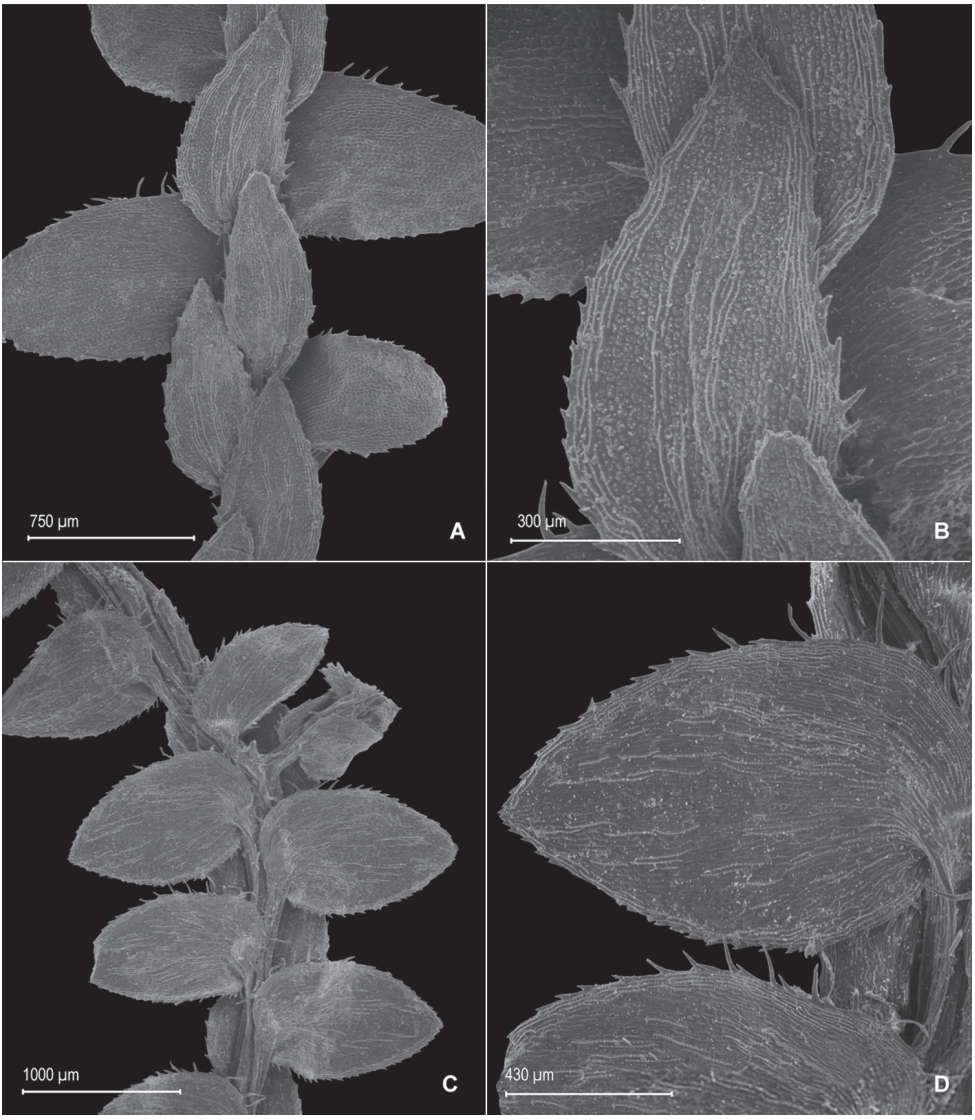

Figure 14. *Selaginella sematophylla* Valdespino, G. Heringer & Salino. **A** Section of upper surface of stem **B** Upper surface of median leaf **C** Section of lower surface of stem **D** Lower surface of lateral leaf **A–D** taken from paratype, *Brade et al. [Beta 109]* (R).

towards the center with granulate microstructure on proximal faces, rugulate-cristate or cristate with broad baculate-like projections and granulate microstructure on distal faces, 28–40 µm.

Habitat and distribution. *Selaginella sematophylla* is known from Minas Gerais, Espírito Santo, and Rio de Janeiro states in Brazil. It grows in Campos Rupestres and Atlantic Rainforest vegetation on sandy soil in shaded, wet places at 1000–1230 m.

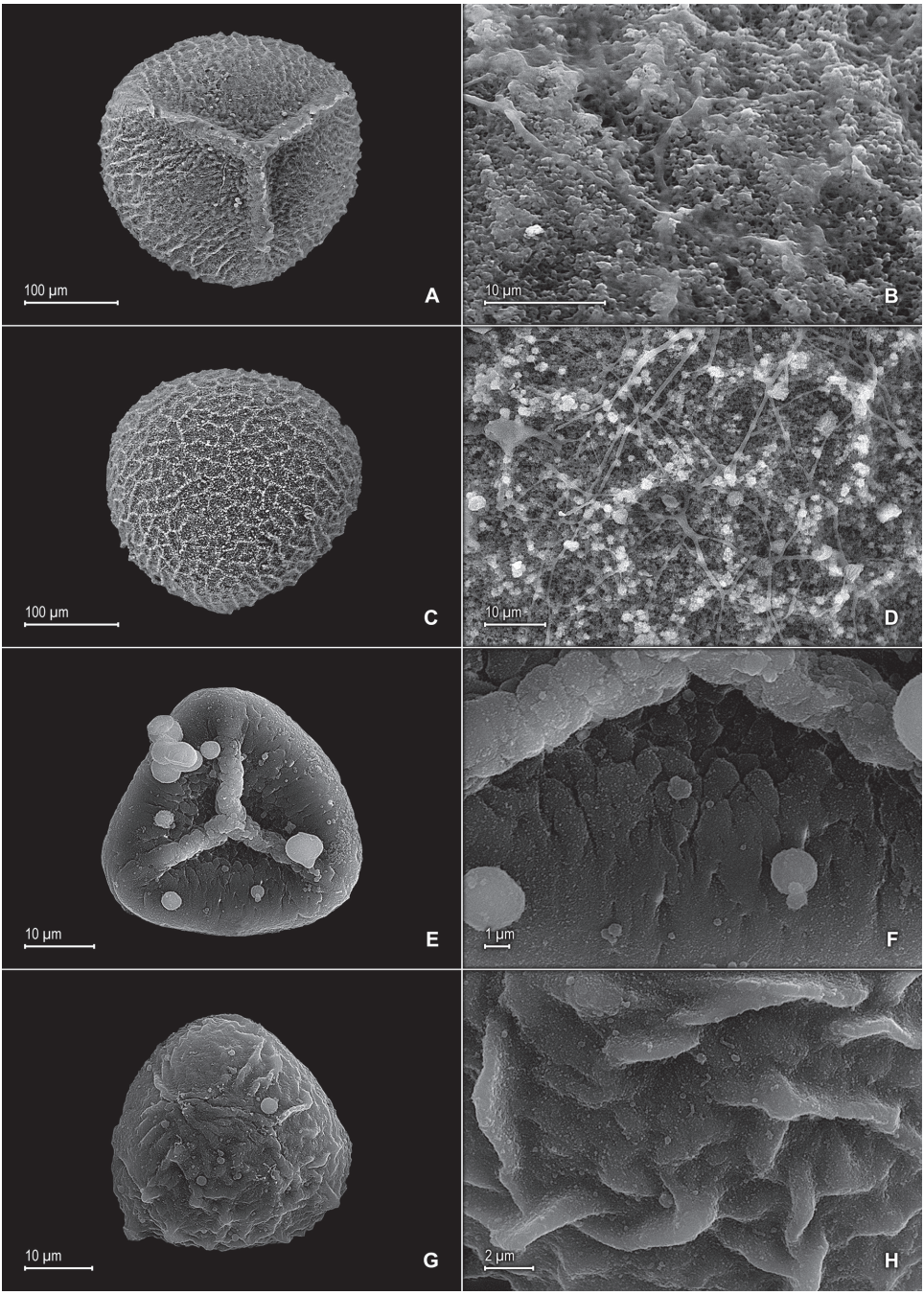

Figure 15. *Selaginella sematophylla* Valdespino, G. Heringer & Salino. **A** Megaspore proximal face **B** Close-up of megaspore proximal face surface **C** Megaspore distal face **D** Close-up of megaspore distal face surface **E** Microspore proximal face **F** Close-up of microspore proximal face surface **G** Microspore distal face **H** Close-up of microspore distal face surface **A–H** taken from holotype, *Brade & Barbosa 17953* (MO).

Etymology. The epithet of the new species derives from the Greek, *sema -tos*, meaning sign, flag, mark and *phyllon*, meaning leaf; this refers to the presence of conspicuous, hyaline idioblasts on upper leaf surfaces.

Conservation status. The distributional range of *Selaginella sematophylla* encompasses three southeastern states of Brazil, but the vegetation types it inhabits are in peril; thus, we believe advisable to consider it vulnerable (VU), according to IUCN (2012) categories and criteria.

Additional specimens examined (paratypes). BRAZIL. Minas Gerais: Arredores de São Sebastião do Paraíso, Apr 1945, *Brade et al. [Beta 109]* (R); Baú, 26 Apr 1949, *Brade 3461* (CESJ); Serra Nova, Rio Pardo de Minas, Parque Estadual de Serra Nova, 15°39'37,5"S, 42°45'53,7"W, 1000–1230 m, 13 Mar 2007, *Salino et al. 11734* (BHCB). **Espírito Santo**: Santa Maria do Jetibá, Garrafão, Pedra do Garrafão, 20°10'24,5"S, 40°55'6,8"W, 1081 m, 28 Aug 2009, *Salino et al. 14543* (BHCB, PMA). **Rio de Janeiro**: Santo Antônio do Imbé, Mandigueira, Apr 1932, *Brade & Santos-Lima 11670* (R).

Discussion. *Selaginella sematophylla* is a member of subg. *Stachygynandrum* and is characterized by having stems 1-branched, lateral and median leaves with hyaline margins, and idioblasts on upper surfaces of median leaves (Fig. 14A, B), lower surface of lateral leaves (Fig. 14C, D), and on both surfaces of sporophylls.

In the past, specimens of *S. sematophylla* were identified as *S. fragillima* (= *S. vestiens*, which see for discussion). *Selaginella sematophylla* differs from *S. vestiens* by cell types on leaf surfaces, median leaf apex shape, and habit, as discussed in the diagnosis.

Selaginella palmiformis Alston ex Crabbe & Jermy, 1973

Selaginella palmiformis Alston ex Crabbe & Jermy, Amer. Fern J. 63: 141. 1973. — Type. Venezuela. Amazonas: Near Salto de Huá, in western foothills of Sierra Imeri, 800 m, *E. Holt & E. Blake 490* (holotype: US!; isotypes: BM! [photo: NY!, QCA!], NY!).

Selaginella manausensis Bautista, Bol. Mus. Paraense Emílio Goeldi, n.s., Bot. 45: 2. 1974. —*Selaginella bahiensis* Spring subsp. *manausensis* (Bautista) Jermy & Rankin, Bull. Brit. Mus. (Nat. Hist.) Bot. 9: 260. 1981. —Type: Brazil. Amazonas: Estrada Manaus-Itacoatiara, Km 64, picada I, 10 Oct 1968, *Rodrigues, Coêlho & Monteiro 8588* (holotype: INPA-image!; isotype: MG!). **Syn. nov.**

Additional specimens examined. COLOMBIA. **Amazonas**: Corregimiento Araracuara, Caño Aduche, 30 Aug 1977, *Aguirre 907* (COL); Corr. Araracuara, Río Caquetá, 7 Aug 1977, *Idrobo 8939* (COL); La Pedrera, 2-3 km along E main road, 01°18'N, 69°32'W, 300 m, 10–11 Mar 1990, *Churchill 16094* (MO, NY); Río Caquetá, Cueva de los Guácharos, 250–500 m, 13 Aug 1979, *Echeverry 3364* (COL); Río Caquetá, cerca a Santa Isabel, 250 m, 26 Sep 1988, *Galeano & Miraña 1948* (COL). **Amazonas-Vaupés**: Río Apaporis, Raudal del Jirijirimo, 7 Aug 1951, *Schultes & Cabrera 13459* (BM, GH, MO, S, UC, US); Caño Oo-gö'-dja, Jenogojé, 26 Aug 1952, *Schul-*

tes & Cabrera 17058 (US). **Guainía**: Maimachi, Serranía del Naquén, Caño Culebra, 02°06'N, 68°11'W, 150 m, *Madriñan & Barbosa 822* (MO, NY); Río Guainía, Caño Guarinuma, 150 m, 10 Oct 1977, *Espina et al. 153* (COL). **Vaupés**: Río Guainía, near Sejal, June 1948, *Schultes & López 10162* (GH, MO); Río Kananarí, Cerro Isibukurí, 250-700 m, 28 Oct 1951, *Schultes & Cabrera 14465* (US); Río Piraparaná, 28 Aug 1952, *Schultes & Cabrera 17076* (UC, US); Río Piraparaná (tributary of Río Apaporis), Caño Teemeeña, 00°15'S-25'N, 70°30'W, 5 Sep 1952, *Schultes & Cabrera 17185* (GH p.p.), *Schultes & Cabrera 17190* (US), 10 Sep 1952, *Schultes & Cabrera 17369* (NY, US-2 sheets). **VENEZUELA**. **Amazonas**: Dpto. Atabapo, Alto Cunucunuma, 04°08'N, 65°35'W, 380 m, Feb 1992, *Chaviel 385* (NY), between Culebra and slope of Duida, 03°44'N, 65°44'W, 210 m, 16 Feb 1985, *Liesner 17568* (MO, NY, UC), camino entre Culebra y la falda del extremo N del Cerro Duida, SW of Comunidad de Culebra, 03°40'N, 65°45'W, 180–300 m, 28, 30 Jan and 1 Feb 1982, *Steyermark et al. 125726* (NY, UC); Río Cunucunuma, alrededores de Akanaña, 03°27'N, 65°44'W, 170 m, Apr 1990, *Fernández 7946* (MO-2 sheets, NY); Cerro Duida, base on N side opposite Culebra, 03°44'W, 65°44'N, 210–350 m, 10 Oct 1988, *Liesner 24640* (MO, NY, UC), slopes of Mount Duida, 750 ft [229 m], 15 Nov [1928?], *Tate 376* (NY), in saddle between Duida and Marahuaca near base of Duida, 03°34'N, 65°32'W, 1000 m, 25 Oct 1988, *Liesner 25363* (MO, NY, UC), slope of Huachamacari, 03°39'N, 65°42'W, 750 m, 6 Mar 1985, *Liesner 18382* (MO, UC), Cerro Huachamacarí, E slope, 03°49'N, 65°42'W, 600–700 m, 2 Nov 1988, *Liesner 25604* (MO, UC), Caño Negro, Río arriba desde la confluencia con Río Cunucunuma, 03°40'N, 65°45'W, 8 Feb 1982, *Steyermark 126269* (NY, UC); Río Cunucunuma, Río Orinoco, Playa Alta near river mouth, 100 m, 6 Nov 1950, *Maguire et al. 29452* (NY, US); Dpto. Río Negro, slopes of Cerro Aracamuni, 01°24'N, 65°38'W, 600 m, 21 Oct 1987, *Liesner & Delascio 22264A* (MO, NY, UC); Dpto. Río Negro, Neblina Base Camp on Río Bario (= Río Mawarinuma), SE of camp, 00°49'50"N, 66°09'40"W, 140 m, 27 Jan 1985, *Beitel & Buck 85065*, *Beitel & Buck 85066* (NY, UC), *Beitel & Buck 85067* (NY, UC). **PERU**. **Amazonas**: Dist. Bagua, Imaza, Aguaruna de Putuim, W of Putuim Village, 04°55'S, 78°19'W, 680 m, 12 Jun 1996, *Rodríguez et al. 968* (MO, NY), along road Imaza-Chiriaco, 05°03'24"S, 78°20'17"W, 400 m, 18 Mar 2001, *van der Werff et al. 16181* (MO). **Loreto**: Prov. Maynas, Dist. Iquitos, carretera del Caserio del Varillal, km 10, trail from Varillal, ca. 160 m, 4 Oct 1983, *Rimachi 7101* (NY). **BRAZIL**. **Acre**: Santa Lucia, km 40 on Transamazonica Highway E of Cruzeiro do Sul, 07°08'S, 72°33'W, 14 Oct 1987, *Pruski et al. 3466* (NY). **Amazonas**: Manaus, Rio Turumã, 23 Aug 1949, *Fróes 25063* (RB); Manaos [Manaus], Sep 1929, *Huebner 67* (B-2 sheets); Rio Cuieiras, 50 km upstream, 3 Apr 1974, *Campbell et al. P21811* (GH, K, MO, NY-2 sheets, R, S); Rio Urubú, between Serra da Lua and Iracema, 8 Aug 1979, *Calderón et al. 2978* (NY-2 sheets), between Cahoeira Iracema and Manaus-Caracarai Road, 6 Jun 1968, *Prance et al. 5017* (NY). **WITHOUT COUNTRY** [**BRAZIL**?]. *Bartlett s.n.* (W).

Discussion. *Selaginella palmiformis* is a member of subg. *Stachygynandrum* and is characterized by its usually 1-pinnate branches that look like miniature palm leaves.

According to Alston et al. (1981) this species was restricted to the Sierras of the Amazonian part of Venezuela and Colombia; however, Smith et al. (2005) recorded it in the Department of Loreto, Peru at 100–200 m and here we registered it in Amazonas Department of that country, where it was collected at 680 m. Both Departments are located in the Peruvian Amazon region. We also confirm the distribution range of *Selaginella palmiformis* to include the states of Acre and Amazonas in Brazil. It can be surmised that this species is widespread in the Amazon River basin in South America and that it grows in lowland tropical rainforests and in premontane wet forests from 100 to 1000 m.

Alston et al. (1981) considered *Selaginella manausensis* a subspecies of *S. bahiensis* Spring (= *S. bahiensis* subsp. *manausensis*). As part of his ongoing monographic work on the "*Selaginella flabellata* (L.) Spring group" the senior author studied the types of *S. bahiensis* [BRAZIL. Bahia: In vicinia urbis Soteropoleos, *Blanchet 2528* (holotype: G!; isotypes: photo BM!, G!, P-2 sheets!], *S. manausensis*, and *S. palmiformis*. Based on this we conclude that *S. manausensis* is not closely related to *S. bahiensis* but rather it is conspecific with *S. palmiformis* and, accordingly, it is synonymized here.

Selaginella vestiens **Baker, 1883**

Selaginella vestiens Baker, J. Bot. 21: 97. 1883. — *Selaginella cladostachya* Baker, J. Bot. 21: 97. 1883. — Type. Brazil. Goiás: Morro de Canto Gallo, *Burchell [7006]* (holotype: K!; isotype: B p.p.!).

Selaginella erythrospora A. Silveira, Bol. Commiss. Geogr. Geol. Est. Minas Geraes 5: 126. 1898. — Type: Brasil, Minas Geraes [Gerais], in rupibus, locis arenosis in Serra do Linheiro prope urbem S. João d' El Rei, Apr 1897, *A. Silveira s.n.*, *No. 2383 in herb. Com. Geog. et Geolog. Civitatis Minas Geraes* (holotype: R! [*as Hebarium Silveira No. 156*]; isotypes: B!, BM! [*as Hebarium Silveira No. 156*]).

Selaginella fragillima A. Silveira, Bol. Commiss. Geogr. Geol. Est. Minas Geraes 5: 127. 1898. — Type: Brasil, Minas Geraes [Gerais], in umbrosis sub rupibus in Serra de S. José d' El Rei prope Aguas Santas, Mar 1898, *A. Silveira s.n., No. 2622 in herb. Com. Geog. et Geolog. Civitatis Minas Geraes* (holotype: R! [as *Hebarium Silveira No. 149*]; isotypes: B!, P-image!). **Syn. nov.**

Selected specimens examined. BRAZIL. **Goiás**: same as type coll. **Minas Gerais**, Belo Horizonte, 9 Jul 1932, *Brade 11881* (R); Biribyri, Mar 1892, *Schwacke 8028* (RB); Campos de S. Sebastião, Ouro Preto, Jun 1907, *Damazio 1882* (B-2 sheets, P-image, RB); Catas Altas, RPPN do Caraçá, 20°05'28"S, 43°29'00"W, 1500 m, 1 Jun 2008, *Hirai et al. 563* (NY, PMA, UC); Christias, near Corriga dois Puntes, Diamantiha [Diamantina], *Mexia 5832* (BM, CAS, GH, MICH, MO, S, U); Matta, Jun 1934, *Brade 13962* (RB); km 138, Estrada Pilar, Serra do Cipó, 15 Apr 1935, *Barreto 581 & Brade 144404* (RB); Santa do Riacho, Serra do Cipó, km 125 da Rodovia Belo Horizonte-Conceicão do Mato Dentro, 1320–1370 m, 29 Jun 1991, *Pirani et al.*

CFSC12385 (NY); Serra do Cipó, Jun 1908, *Damaizo s.n.* (RB); Serra de Ouro Preto, *Ule s.n.* (B); Serra do Rio Grande, 1260 m, Diamantiha [Diamantina], *Mexia 5799a* (CAS, GH, MO, NY, UC); Serra do Espinhaço, ca. 18 km E. of Diamantina, Diamantina, 1050 m, 20 Mar 1970, *Irwin et al. 27953* (NY), slopes of Serra da Piedade, ca. 35 km E of Belo Horizonte, near BR-31, 1800 m, 18 Jan 1971, *Irwin et al. 28699* (NY); Without specific locality, *Schwacke s.n.* (B).

Discussion. *Selaginella vestiens* belongs to subg. *Stachygynandrum* and is characterized by its erect habit, stoloniferous stems, leaves seemingly monomorphic below first branch, and median leaves acuminate to aristate, ciliate, and broadly hyaline. *Selaginella fragillima* was a poorly known taxon that Alston et al. (1981) maintained as a distinct species. Our examination of type material of *S. fragillima* causes us to conclude that it is conspecific with *S. vestiens*, under which it is synonymized here. See comparison of *Selaginella vestiens* with *S. sematophylla* under the latter.

Alston et al. (1981) cited *Ule 7298* (B!, BM!) from Bahia and *Glaziou 11723* (BM!, P-image!, US!) from Rio de Janeiro as *Selaginella vestiens*. *Ule 7298* is here assigned to *Selaginella blepharodella*, while *Glaziou 11723* morphologically does not fit *S. vestiens*; therefore, we exclude Bahia and Rio de Janeiro from the range of the latter species. Specimens of *Selaginella vestiens* here cited and those cited by Heringer (2011) are either from Goiás (i.e., type collection) or from Minas Gerais in Brazil.

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References

Alston AHG, Jermy AC, Rankin JM (1981) The genus *Selaginella* in tropical South America. Bulletin of the British Museum (Natural History) Botany 9(4): 233–330.

Bünger M, Stehmann JR, Oliveira-Filho AT (2014) Myrtaceae throughout the Espinhaço Mountain Range of central-eastern Brazil: Floristic relationships and geoclimatic controls. Acta Botanica Brasilica 28(1): 109–119. doi: 10.1590/S0102-33062014000100011

Caluff MG, Shelton G (2003) The musciform *Selaginella* species (Selaginellaceae) with broad lateral leaves in the West Indies. Willdenowia 33: 425–437. doi: 10.3372/wi.33.33217

Góes-Neto LAA, Maciel S, Pietrobom MR, Valdespino IA (2015) Licófitas (Lycopodiophyta) do Corredor de Biodiversidade do Norte do Pará, Brasil. Rodriguésia 66(1): 229–244. doi: 10.1590/2175-7860201566114

Harley RM, Simmons NA (1986) Florula of Mucugê, Chapada Diamantina, Bahia, Brazil: A descriptive check-list of a campo rupestre area. Royal Botanic Gardens, Kew, 1–228.

Heringer G (2011) Selaginellaceae Willk. no estado de Minas Gerais, Brasil. Masters Thesis. Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, Belo Horizonte, 1–98.

Hesse M, Halbritter H, Zetter R, Weber M, Buchner R, Frosch-Radivo A, Ulrich S (2009) Pollen terminology. An illustrated handbook. Springer, Wein and New York, 1–264.

Hieronymus G (1901) Selaginellaceae. In: Engler A, Prantl K (Eds) Die Natürlichen Pflanzenfamilien 1(4). Leipzig, 621–715.

Hirai RY (2015) Selaginellaceae. Lista de Espécies da Flora do Brasil, Jardim Botânico do Rio de Janeiro, Brazil. http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB92047 [accessed 12.01.2015]

IUCN (2012) IUCN Red List Categories and Criteria, Version 3.1. Second edition. Prepared by the IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Jermy AC (1986) Subgeneric names in *Selaginella*. Fern Gazette 13: 117–118.

Jermy AC (1990) Selaginellaceae. In: Kramer KU, Green PS (Eds) Pteridophytes and Gymnosperms Vol. I. In: Kubitzki K (Ed.) The Families and Genera of Vascular Plants. Springer-Verlag, Berlin, 39–45. doi: 10.1007/978-3-662-02604-5_11

Meirelles J, Goldenberg R (2012) Melastomataceae do Parque Estadual do Forno Grande, Espírito Santo, Brasil. Rodriguésia 63(4): 831–855. http://www.scielo.br/pdf/rod/v63n4/a08v63n4.pdf

Melo E (2000) Polygonaceae da Cadeia do Espinhaço, Brasil. Acta Botanica Brasilica 14(3): 273–300. doi: 10.1590/S0102-33062000000300006

Mickel JT, Smith AR, Valdespino IA (2004) *Selaginella*. In: Mickel JT, Smith AR. The Pteridophytes of Mexico. Memoirs of the New York Botanical Garden 88: 550–602.

Oliveira-Filho AT, Martins FR (1991) A comparative study of five cerrado areas in southern Mato Grosso, Brazil. Edinburgh Journal of Botany 48(3): 307–332. doi: 10.1017/S0960428600003036

Pedreira AJ (2002) Serra do Sincorá, Chapada Diamantina, BA: Beleza paisagística e paleopláceres de diamante, SIGEP 85. In: Schobbenhaus C, Campos DA, Queiroz ET, Winge M, Berbert-Born MLC (Eds) Sítios Geológicos e Paleontológicos do Brasil. DNPM/CPRM - Comissão Brasileira de Sítios Geológicos e Paleobiológicos (SIGEP), Brasília, 187–194.

Punt W, Hoen PP, Blackmore S, Nilsson S, Le Thomas A (2007) Glossary of pollen and spore terminology. Review of Palaeobotany and Palynology 143: 1–81. doi: 10.1016/j.revpalbo.2006.06.008

Quiles J (2015) *Selaginella denticulata* (L.) Spring (images). In: Quiles J (webmaster) Flora Silvestre del Mediterráneo: Fotografías de flora silvestre del mediterráneo occidental. Valencia, España. http://www.florasilvestre.es/mediterranea/index.htm [accessed 03.04.2015]

Rapini A, Ribeiro PL, Lambert S, Pirani JR (2008) A flora dos campos rupestres da Cadeia do Espinhaço. Megadiversidade 4(1-2): 16–23. http://www.conservation.org.br/publicacoes/files_mega4/02_a_flora_dos_campos_rupestres_da_cadeia_do_espinhaco.pdf

Ratter JA, Ribeiro JF, Bridgewater S (1997) The Brazilian cerrado vegetation and threats to its biodiversity. Annals of Botany 80: 223–230. doi: 10.1006/anbo.1997.0469

São-Pedro VA, Feio RN (2011) Anuran species composition from Serra do Ouro Branco, southernmost Espinhaço Mountain Range, state of Minas Gerais, Brazil. Check List 7(5): 671–680. http://www.checklist.org.br/getpdf?SL020-11

Schoute JC (1938) Morphology. In: Verdoorn F (Ed.) Manual of Pteridology. Nijhoff, The Hague, 1–64. doi: 10.1007/978-94-017-6111-6_1

Silva-Soares T, Scherrer PV (2013) Amphibians of Parque Estadual do Forno Grande, state of Espírito Santo, southeastern Brazil: Species composition and conservation. North-Western Journal of Zoology 9(1): 113–120. http://biozoojournals.ro/nwjz/content/v9n1/nwjz.131502.Silva-Soares.pdf

Smith AR, León B, Tuomisto H, van der Werff H, Moran RC, Lehnert M, Kessler M (2005) New records of pteridophytes for the flora of Peru. Sida 21: 2321–2342.

Stefanović S, Rakotondrainibe F, Badré F (1997) Famille 14, Sélaginellacées. Flore de Madagascar et des Comores. Muséum National d'Histoire Naturelle, Paris, 1–68.

Strüssmann C, Mott T (2009) Sympatric amphisbaenids from Manso Dam region, Mato Grosso state, western Brazil, with the description of a new two-pored species of *Amphisbaena* (Squamata, Amphisbaenidae). Studies on Neotropical Fauna and Environment 44(1): 37–46. doi: 10.1080/01650520802628295

Thiers B (2015, continuously updated) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/ [accessed 06.02.2015]

Valdespino IA (1993a) Selaginellaceae. In: Flora of North America Editorial Committee (Eds) Flora of North America North of Mexico. Vol. 2. Pteridophytes and Gymnosperms. Oxford University Press, New York, 38–63.

Valdespino IA (1993b) Notes on neotropical *Selaginella* (Selaginellaceae), including new species from Panama. Brittonia 45(4): 315–327. doi: 10.2307/2807605

Valdespino IA (1995) A monographic revision of *Selaginella* P. Beauv. subgenus *Heterostachys* Baker in Central and South America. Doctoral Thesis. The City University of New York, New York, 1–405.

Valdespino IA (2015) Two new species and a new record of *Selaginella* (Selaginellaceae) from Bolivia. Novon 24: 96–105.

Valdespino IA, López C, Góes-Neto LAA (2014) Additions to Cuban *Selaginella* (Selaginellaceae). Phytotaxa 184: 235–244. doi: 10.11646/phytotaxa.184.4.4

Williams S (1931) An analysis of the vegetative organs of *Selaginella grandis* Moore, together with some observations on abnormalities and experimental results. Transactions of the Royal Society of Edinburgh 57(1): 1–24. doi: 10.1017/S0080456800016616

Zhang LB, Sun QW, He H (2014) *Selaginella wangpeishanii* (Selaginellaceae), a new lycophyte from a limestone cave in Guizhou, China. Phytotaxa 164: 195–199. doi: 10.11646/phytotaxa.164.3.5

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RESEARCH ARTICLE

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The resurrection of *Neohattoria* Kamim. (Jubulaceae, Marchantiophyta): a six decade systematic conflict resolved through a molecular perspective

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Abstract

The systematic placement of *Frullania herzogii* has been contentious since its description six decades ago. Over the years it has been interpreted as either a member of the genus *Frullania* or segregated into its own genus, *Neohattoria,* due to morphological similarities with both *Frullania* and *Jubula*. Here we provide molecular evidence that supports the recognition of the genus *Neohattoria* and its inclusion within the Jubulaceae, together with *Jubula* and *Nipponolejeunea*. Jubulaceae are placed sister to Lejeuneaceae rather than to the monogeneric Frullaniaceae.

Keywords

DNA sequence data, *Frullania*, Frullaniaceae, Japan, *Jubula*, Jubulaceae, Lejeuneaceae, liverwort, *Nipponolejeunea*

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Introduction

The liverwort *Frullania herzogii* S.Hatt. was originally described by Hattori (1955) from a poor, sterile specimen collected on Mt. Hayachine in Iwate Prefecture, northern Honshu, Japan. Since that time the generic and even familial placement of the species has remained controversial. The species also has remained poorly known partially because of its seemingly limited distribution in the subalpine coniferous forest zones of Honshu and Hokkaido, Japan, and the Kuril Islands (Inoue et al. 1981, Stotler and Crandall-Stotler 1987). Hattori (1955) remarked that the leaf morphology, with acute teeth along the margin, differed from all the other Japanese *Frullania* Raddi species known by him. A few years later, in his monograph of Japanese Frullaniaceae, Kamimura (1961) erected the new genus *Hattoria* Kamim. to separate this taxon from other *Frullania* species. He stated that although his new genus superficially resembled species of *Cololejeunea* (Spruce) Schiffn. or *Frullania*, there was an important similarity between the branching patterns of *Hattoria herzogii* (S.Hatt) Kamim. and species in the genus *Jubula* Dumort. In both *Jubula* and *Hattoria*, the branches replace the lobule of the leaf at the point of insertion, and the leaf lobes are attached to both the main stem and to the branch. Although Kamimura (1961) noted the similarity of cell shape between *Hattoria* and *Frullania*, he considered the combination of branching architecture and leaf denticulation sufficient to recognize *Hattoria* as a distinct genus. A year later he had to give a new name, *Neohattoria* Kamim., to his recently described genus (Kamimura 1962), because of the almost simultaneous although earlier description of *Hattoria* by Schuster for a liverwort in the Lophoziaceae (Schuster 1961).

Later Schuster (1963), in a key for the Southern Hemisphere genera of liverworts, expanded the circumscription of *Neohattoria* to include two more species, *Frullania microscopica* Pearson from New Caledonia, and *F. parhamii* (R.M.Schust.) R.M.Schust. ex von Konrat, L.Söderstr. & A.Hagborg from Fiji. He based his taxonomic decision on the morphology of the reduced leaves on branch bases, the subfloral innovations, and the sharply delimited bracts and bracteoles of *F. microscopica*, and on the toothed leaf lobes of this species. Schuster (1963) did not provide any argument for placement of the Fijian *F. parhamii* in *Neohattoria*, other than the hyaline margins of the leaves that can be seen in this species and in *F. microscopica* (as inferred from the key). However, his key is restricted to the Southern Hemisphere and did not include the type of the genus, which completely lacks a hyaline border in leaf lobes. Schuster (1970) later expanded this generic concept even further, including the Australasian *F. rostrata* (Hook.f. & Taylor) Hook.f. & Taylor ex Gottsche, Lindenb. & Nees (as *Neohattoria australis* R.M.Schust.) and *F. hodgsoniae* von Konrat, Braggins, Hentschel & Heinrichs (as *Neohattoria rostrata* R.M.Schust.), the SE Asian *F. junghuhniana* Gottsche var. *tenella* (Sande Lac.) Grolle & S.Hatt. [as *Neohattoria perversa* (Steph.) R.M.Schust.], the New Caledonian *F. chevalieri* (R.M.Schust.) R.M.Schust. and *F. neocaledonica* J.J.Engel

(as *Neohattoria caledonica* R.M.Schust.). Of these, *F. hodgsoniae* is now considered a member of *F.* subg. *Diastaloba* Spruce sect. *Inconditum* von Konrat, Hentschel & Heinrichs (von Konrat et al. 2010), while the rest of the taxa are currently included in *Frullania* subg. *Microfrullania* (R.M.Schust.) R.M.Schust. The current taxonomic placement of these taxa is based on both morphological (Hattori and Mizutani 1982, Schuster 1992) and molecular evidence (Hentschel et al. 2009, von Konrat et al. 2012).

Asakawa et al. (1979) demonstrated, based on chemical compound differences, that Jubulaceae *sensu lato* should be divided into three families, i.e. Jubulaceae, Frullaniaceae and Lejeuneaceae. This view has been confirmed by most molecular phylogenies published to date (e.g., Forrest et al. 2006, Heinrichs et al. 2005, 2007). Asakawa et al. (1979) listed 11 morphological characters that support the separation of Frullaniaceae and Jubulaceae, and placed *Neohattoria* together with *Jubula* in the Jubulaceae. Hattori (1982, 1984, 1986) and Hattori and Mizutani (1982) also accepted the separation between Jubulaceae and Frullaniaceae and argued that *Amphijubula* R.M.Schust., a genus formerly considered by Schuster (1970, 1980) as intermediate between *Jubula* and *Frullania*, should be placed within *Frullania.* This view was first held by Engel (1978), who had earlier reduced *Amphijubula* to a synonym of *Frullania*.

In 1987, Stotler and Crandall-Stotler published a thorough treatise of the taxonomic history of *Neohattoria herzogii* (S.Hatt.) Kamim. in the context of a detailed re-evaluation of its morphology, including the discovery of immature female inflorescences. In that contribution they came to the conclusion that this taxon should be considered within the circumscription of *Frullania*, although in its own subgenus, *F.* subg. *Dentatilobi* Stotler & Crand.-Stot. Their conclusion was based on both vegetative and reproductive characters, including the morphology of the bracts surrounding the female gametangia, lobule anatomy, leaf cell pattern, and the morphology of regenerants. Although they recognized that leaf-lobe insertion, branch morphology, and morphology of stylus are more similar to *Jubula* than to *Frullania*, they concluded that on the basis of the *Frullania*-like inflorescences and regenerants, *Neohattoria* should be synonomized with *Frullania*. This synonomy was adopted by Grolle and Meister (2004) who described a morphologically similar plant from Oligocene amber from Bitterfeld (Germany) as *Frullania* (subg. *Dentatilobi*) *hamatosetacea* Grolle. However, this fossil species appears morphologically closer to *F.* subg. *Microfrullania* than to *Neohattoria*, and this issue will be explored in detail in a forthcoming monograph of the latter subgenus.

Lack of useable specimens has previously precluded inclusion of *Neohattoria* in molecular phylogenetic studies. As a result of recent collecting activities, fresh material became available that allowed for successful DNA extraction and amplification. In the present study, we use molecular sequence data to investigate the phylogenetic position of *Neohattoria*. We investigate whether the genus should be placed in the Frullaniaceae or the Jubulaceae and evaluate whether molecular evidence supports the recognition of *Neohattoria* as a distinct genus.

Methods

Microscopy

For the production of microscopic images an Olympus BX51 microscope was used, equipped with both a QICAM Fast1394 camera from QIMAGING (Surrey, Canada), and a slide scanner (moving platform stage attached between the objectives and the condenser) from Objective Imaging Ltd. (Cambridge, UK). The software "Surveyor" from the latter company was used for the digitally rendered images.

DNA extraction, PCR amplification and sequencing

We worked with two independent datasets to address two different questions, (1) what is the position of *Neohattoria* relative to the Frullaniaceae, Jubulaceae and Lejeuneaceae, and once we obtained results from these analyses, we asked (2) what is the position of *Neohattoria* within the Jubulaceae. For dataset 1 sequences were generated for two mitochondrial (*nad*1, *rps*3), and two chloroplast loci (*psb*A, *rbc*L), following DNA extraction, amplification and sequencing methods described by Shaw et al. (2003), and using primer sequences provided in Cooper et al. (2011). For dataset 2 we used the aforementioned plastid regions (*psb*A and *rbc*L) together with the nuclear ITS region following the methods described by Shaw et al. (2003), and the chloroplast *trn*L-*trn*F region, amplified and sequenced as described in von Konrat et al. (2012). All sequences were edited and manually aligned in PhyDE v0.9971 (www.phyde.de) following the alignment rules and hotspot definitions presented in Kelchner (2000), Olsson et al. (2009), and Borsch and Quandt (2009).

Taxon sampling and outgroup selection

For dataset 1 seven species of *Radula* were selected as outgroup taxa following the results already published in recent liverwort phylogenies (Davis 2004, Forrest et al. 2006, Feldberg et al. 2014, Heinrichs et al. 2005, 2007). The same criteria were undertaken for dataset 2, including all taxa with sequences available in GenBank for *Jubula* and *Nipponolejeunea* S.Hatt. (Ahonen 2006, Ahonen et al. 2003, Konstantinova and Vilnet 2011, Pätsch et al. 2010, Wilson et al. 2004, 2007), using selected taxa of the Lejeuneaceae and species of *Frullania* as outgroup based on results from dataset 1. GenBank accession numbers for both newly generated sequences and for already published sequences are provided in Appendices 1 and 2 for datasets 1 and 2 respectively.

Phylogenetic inferences

Both datasets were analysed with PartitionFinder v1.1.0 (Lanfear et al. 2012, 2014) to develop best-fit partitioning schemes and models of molecular evolution. Dataset 1

was partitioned setting one separate data block for each of the four genes used, each of them divided in three according to each codon position; introns and/or spacers were coded as extra partitions. Dataset 2 was partitioned in four parts, corresponding to the regions included only, without inner codon partition for the coding regions analysed. For dataset 1, phylogenetic reconstructions under maximum likelihood (ML) were performed in GARLI v2.01 (Zwickl 2006), setting up seven different models for the eleven partitions determined by PartitionFinder. Two independent searches each with 100 bootstrap replicates were made, and the 50% majority-rule consensus tree from all obtained trees was obtained with SumTrees v3.3.1 included in the package DendroPy v3.12.2 (Sukumaran and Holder 2010). Bayesian Posterior Probabilities analyses (PP) were executed in MrBayes v3.2.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) also with the partitioned data set as given by PartitionFinder, and setting a different model for the individual partitions from the available options in MrBayes, with all characters given equal weight and gaps treated as missing data. The default settings of the program for a priori probabilities were used. Four runs, each with four MCMC chains (one million generations each) were run simultaneously, with the temperature of the heated chain set to 0.2 (default setting). Chains were sampled every 100 generations. Calculation of the consensus tree and posterior probabilities of clades was based on the set of trees sampled after the chains had converged, as observed graphically using Tracer v1.5 (Rambaut and Drummond 2007). For dataset 2, phylogenetic reconstructions under ML were performed in GARLI v2.01 and Bayesian analyses were executed with MrBayes v3.2.2 following the protocols as described above. For this dataset only three different partitions were suggested by PartitionFinder, and the models given by this software for each partition were incorporated into the settings of both the ML and the Bayesian analysis. Trees were edited and support values added using TreeGraph v2.0.54-364 beta (Stöver and Müller 2010).

Results

The complete alignment for dataset 1 including all four regions mentioned above, with flanking areas pruned to avoid ambiguous readings, comprised 4818 characters for 54 accessions, of which 694 were parsimony informative. A total of 101 new sequences were generated for this study (Appendix 1). In the analysis of the *Neohattoria* sequences with accessions of the Frullaniaceae, Jubulaceae and Lejeuneaceae (dataset 1), *Neohattoria* is strongly supported (as defined by Pedersen et al. 2007) as one of three clades belonging to the Jubulaceae in both ML and Bayesian analyses, with accessions of *Nipponolejeunea*, resolved in a second clade and those of *Jubula*, in a third clade (Fig. 1), although the latter with low support (ML = 52, PP = 0.6). The Jubulaceae is resolved as sister to the Lejeuneaceae with strong support in both types of analysis. The position of the Frullaniaceae as sister to this latter clade (Jubulaceae + Lejeuneaceae) was strongly supported by the Bayesian analyses (PP = 1.0), but it was not recovered by the ML analyses. The Bayesian analyses also resolved *Neohattoria* as sister to the rest of the Jubulaceae (*Nipponolejeunea* + *Jubula*) with strong support (PP = 1.0).

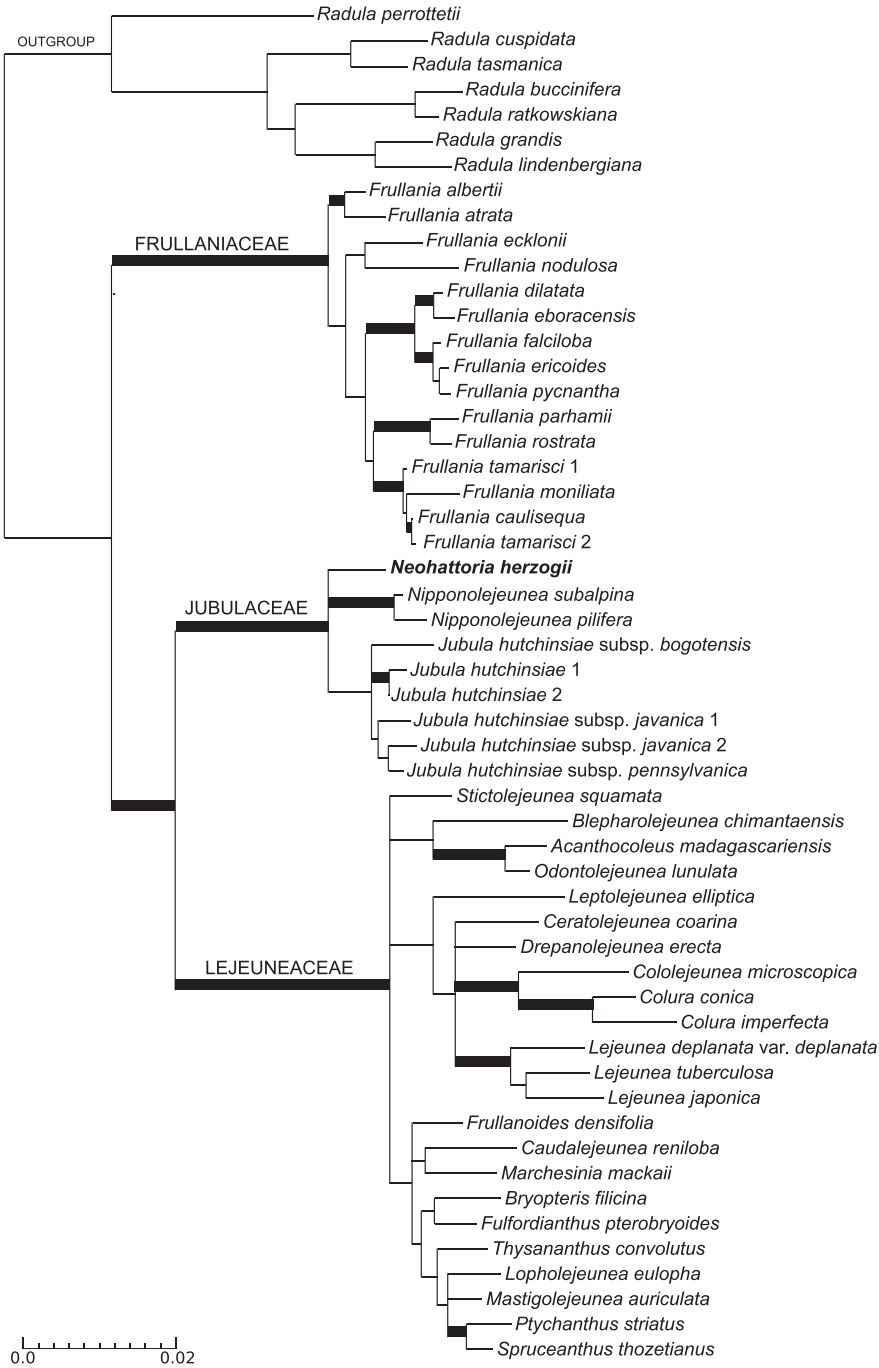

Figure 1. Maximum likelihood (ML) tree showing the systematic position of *Neohattoria* relative to the Jubulaceae, Frullaniaceae and Lejeuneaceae. Wide black branches indicate ML bootstrap support > 90 % and PP > 0.95.

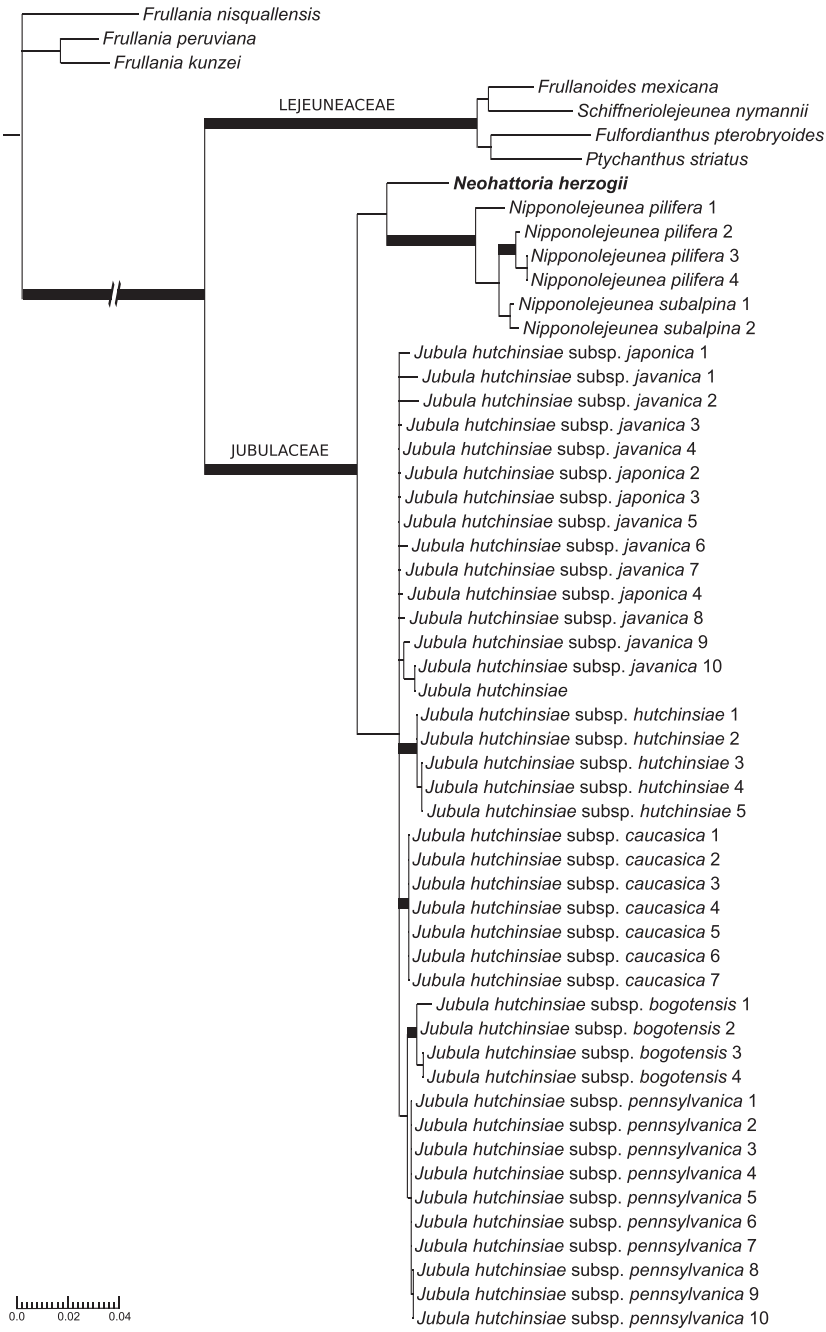

Figure 2. Maximum likelihood (ML) tree showing the systematic position of *Neohattoria herzogii* within the Jubulaceae. Only 1/2 of the length of the branch between the Frullaniaceae and the Lejeuneaceae/Jubulaceae clade is depicted. Wide black branches indicate ML bootstrap support > 90 % and PP > 0.95.

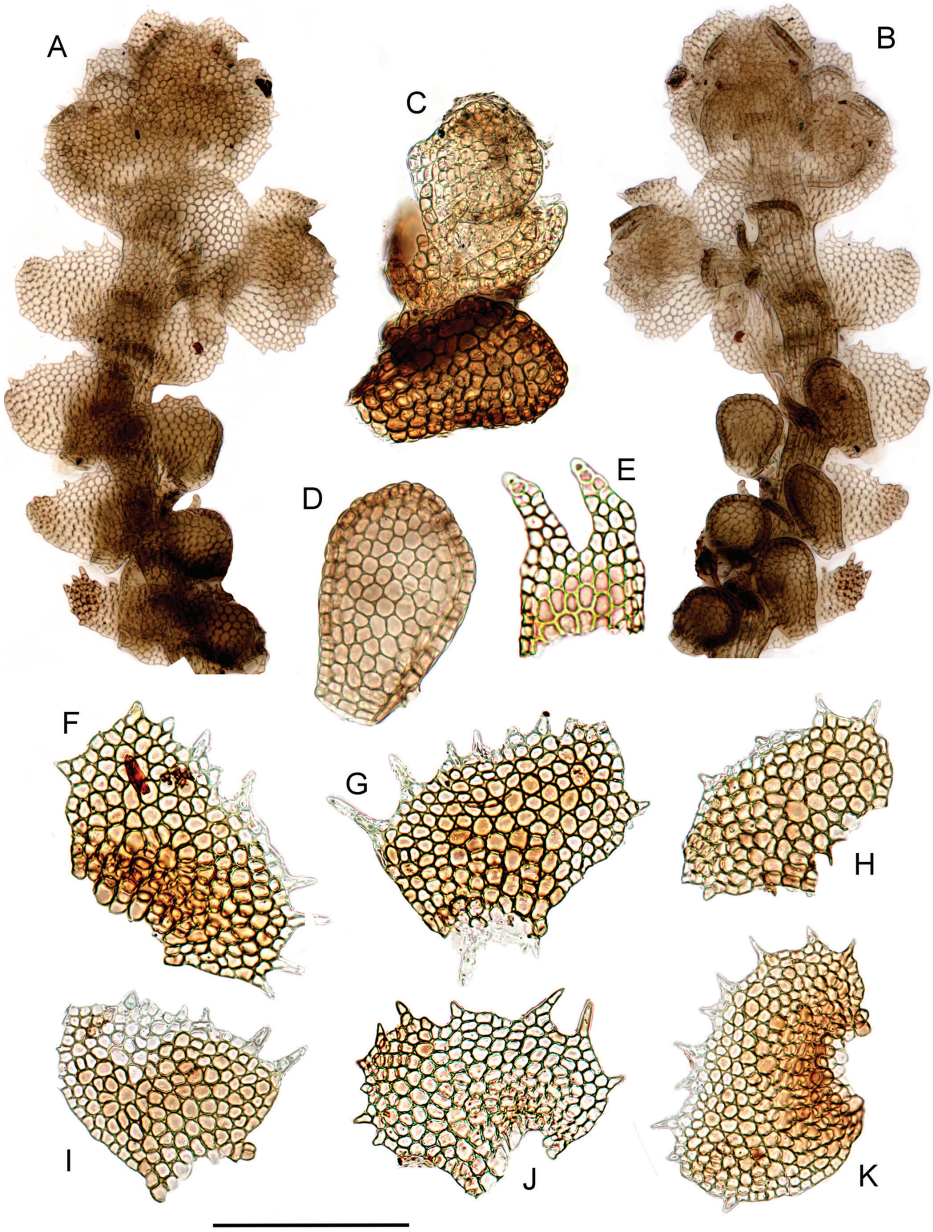

Figure 3. *Neohattoria herzogii*. **A** Habit, dorsal view **B** Habit, ventral view with distal lobules detached **C** Regenerant shoot originating from a detached lobule **D** Lobule **E** Underleaf **F–K** Leaves. All from Furuki 22673 (F). Scale bar: 350 µm (**A, B**), 200 µm (**C**), 180 µm (**D**), 300 µm (**E**), 150 µm (**F–K**).

The complete alignment for dataset 2 including all four regions included, and after pruning the flanking areas to avoid ambiguous readings and deleting unalignable areas of the ITS region, comprised 3737 characters for 55 accessions, of which 548 were

parsimony informative. The four different regions were not equally represented in the matrix, as shown in Appendix 2. The results of the analyses (Fig. 2) confirm with strong support the placement of *Neohattoria* within the Jubulaceae (ML = 100, PP = 1.0), and forming a sister clade to *Nipponolejeunea*, although recovered with strong support only by the Bayesian analysis (ML = 64, PP = 0.97). *Jubula* was resolved as the sister clade to the *Neohattoria-Nipponolejeunea* clade, although with low support (ML = 65, PP = 0.5).

The voucher of *Neohattoria herzogii* used for DNA extraction is illustrated in Figure 3.

Discussion

Our molecular analyses support recognition of the genus *Neohattoria* as distinct from the genus *Frullania,* as first proposed by Kamimura (1961) almost 55 years ago. Moreover, our molecular analysis strongly supports its inclusion within the Jubulaceae, together with *Jubula* and *Nipponolejeunea*. A close relationship with *Jubula*, based on similarities in branch morphologies, was first suggested by Kamimura (1961, p. 94), and also accepted by Hattori et al. (1972). Inoue et al. (1981) provided new karyological, chemical and ecological data on *N. herzogii* and concluded that the biosystematic evidence collected suggested distance between *Jubula* and *Neohattoria*, but, nonetheless, retained *Neohattoria* in the Jubulaceae. While morphologically closer to *Jubula* than *Nipponolejeunea* to which it is sister, it is clearly not nested in the *Jubula* clade. This combination of molecular and morphological evidence, in fact, supports its recognition as a distinct genus in the Jubulaceae.

Circumscription and relationships of the Jubulaceae

Our results strongly support the position of the Jubulaceae (containing *Jubula*, *Nipponolejeunea* and *Neohattoria*) sister to the Lejeuneaceae, and the Frullaniaceae as sister of the latter clade, although without significant support (Fig. 1). These results agree with several molecular phylogenies (e.g. Ahonen 2004, Forrest et al. 2006, Heinrichs et al. 2005, 2007). Thus the traditional view of a widely circumscribed Jubulaceae including *Frullania* is further rejected in this study.

These three families (Frullaniaceae, Jubulaceae and Lejeuneaceae) share several morphological characters, including the leaves divided into two (or three) parts [lobe, lobule (and stylus)], the beaked perianths, the sporophyte enclosed in a stalked true calyptra, the bistratose capsule wall, and the vertically aligned elaters that are attached to the valve apices (Crandall-Stotler et al. 2009, Gradstein et al. 2001, Schuster 1992). However, these characters need to be carefully evaluated to understand their evolution and their role in demonstrating the history of these lineages. In the past, *Jubula*, *Frullania* and members of the Lejeuneaceae were placed in a single taxonomic group (the subtribe Jubuleae), based largely on the similarities among their sporophytes (e.g. Müller 1915). Verdoorn (1930) argued that based on most characters (e.g., number of archegonia, seta form, and

lobule ontogeny) *Jubula* belongs nearest to *Frullania*, which later lead Schuster (1992, p. 6) to describe *Jubula* as a "*bona-fide* genus of Jubulaceae [= Frullaniaceae]". Mizutani (1961) was the first to propose that, except for the lobule structure, *Jubula* had no alignment with *Frullania*, and subsequently placed *Jubula* into the Lejeuneaceae. However, Asakawa et al. (1979) concluded that chemically, both *Jubula* and *Frullania* are quite different from *Lejeunea* Lib. species. Interestingly, the phylogenetic analysis by Crandall-Stotler and Stotler (2000) of 40 gametophyte and 21 sporophyte characters distributed among 34 liverwort families, resolved *F. asagrayana* Mont. as sister to a clade containing *J. hutchinsiae* (Hook.) Dumort. *subsp. pennsylvanica* (Steph.) Verd. and *L. cavifolia* (Ehrh.) Lindb. However, in the systematic treatment of the same work (Crandall-Stotler and Stotler 2000) Jubulaceae is presented as including both *Jubula* and *Frullania*, whereas the Lejeuneaceae is presented as a separate family, following accepted classifications of the time. The revised version of that classification, incorporating some recent molecular data, presents the Frullaniaceae, Jubulaceae and Lejeuneaceae as three separate families within the suborder Jubulineae (Crandall-Stotler et al. 2008, 2009), which is accepted here but with the transfer of *Neohattoria* from the Frullaniaceae to the Jubulaceae.

Assessing the importance of different morphological characters in circumscribing Frullaniaceae, Jubulaceae and Lejeuneaceae has been a difficult problem, but there are several characters that are consistent with the molecular phylogenetic results presented here. In most Lejeuneaceae a true stylus does not develop, but instead a single, unstalked slime papilla is formed at the junction of the lobule base and the stem, while in *Jubula* and *Neohattoria* there is a one- or two-celled filament terminated by a slime papilla in this position (Crandall-Stotler and Guerke 1980, Stotler and Crandall-Stotler 1987). Both types of structures are clearly different from those of the Frullaniaceae, where the stylus is always formed by more than two cells and is usually very conspicuous. The Jubulaceae and Frullaniaceae can be clearly differentiated from the Lejeuneaceae by the lobule, which is almost free from the larger dorsal lobe, and typically modified into an inflated, balloon-like to helmet-shaped sac whose aperture is directed either toward the shoot base or toward the stem, with the exception of *Nipponolejeunea* which has Lejeuneaceae-like lobules. Guerke (1978) hypothesised that *Jubula* was more advanced than *Frullania* on the basis that *Jubula* has many specialized characteristics e.g., a highly reduced stylus, seta, and foot, and features associated with the sporeling. In contrast, Schuster (1992, p. 9) stated that taxa such as *Amphijubula microcaulis* (Gola) R.M.Schust. (≡ *F. microcaulis* Gola), with a 16 + 4 seriate seta and monogynous gynoecia, diminish the distinctions between the two groups such that he prefers not to attempt a "subfamilial separation" at all. However, revision of the chemical, morphological, and ecological data provided support for the recognition of two subfamilies in the Jubulaceae (Guerke 1978, von Konrat 2004). Alternatively, Asakawa et al. (1979), on the basis of biochemical and morphological evidence, proposed two families: Jubulaceae (*Jubula*, *Neohattoria*) and Frullaniaceae (*Frullania*, *Steerea* S.Hatt., *Amphijubula*, and *Schusterella* S.Hatt.). Hattori (1982, 1984, 1986) and Hattori and Mizutani (1982) also accepted two families. This approach has been adopted in most recent hepatic floras and classifications (Paton 1999, Damsholt 2002, Casas et al. 2009, Crandall-Stotler et al. 2009, Frey and Stech 2009).

Schuster (1980, 1992) questioned the division into two families and argued that only the single family Jubulaceae should be recognized, but commented that this area of classification remains replete with ambiguities and contradictions. Interestingly, he also suggested that there was a possibility that *Neohattoria* might share a closer affinity to Jubulopsidaceae (= Lepidolaenaceae) than to Jubulaceae (Schuster 1996), a view first expressed when Grolle (1966) transferred *Jubula novae-zelandiae* E.A.Hodgs. & S.W.Arnell, which is the generitype of *Jubulopsis* R.M.Schust., to *Neohattoria*. However, recent molecular analyses (e.g., Heinrichs et al. 2005, Forrest et al. 2006) have demonstrated that *Jubulopsis* (= *Lepidolaena*) is far removed from the Jubulaceae.

Morphologically, the monogeneric Frullaniaceae can be differentiated from the Jubulaceae by: (1) plants usually with conspicuous secondary pigmentation, often reddish; (2) initial leaves of branches either trifid or bifid; and (3) spores with rosette-like protrusions. Conversely, in the Jubulaceae the plants are: (1) soft and without secondary pigmentation (thus usually dull green to pale brown); (2) the initial leaves of branches are small, subtriangular, and never tri- or bifid; and (3) the spores without rosette-like protrusions. The first two of these characters support the placement of *Neohattoria* within Jubulaceae rather than Frullaniaceae (spores remain unknown in *Neohattoria*).

Chemically, *Frullania* species in general, produce significant amounts of sesquiterpene lactones, diterpenoids, and bibenzyl derivatives, which are considered important chemosystematic markers of the group (Asakawa et al. 1981, 1983, 1987, Kraut et al. 1994). On the other hand, cyclocolorenone and maalioxide have been isolated as major components of *Jubula hutchinsiae* (Hook.) Dumort. subsp. *japonica* (Steph.) Horik. & Ando (Asakawa et al. 1979); interestingly cyclocolorenone is also widely distributed in the Porellaceae. In contrast, no members of *Jubula* or *Frullania* produce paraffinic hydrocarbons which are characteristic for *Neohattoria* (Inoue et al. 1981).

Interestingly, Schuster (1996) suggested that there was a possibility that *Neohattoria* might share a closer affinity to Jubulopsidaceae (= Lepidolaenaceae) than to Jubulaceae. This view was first expressed when Grolle (1966) transferred *Jubula novae-zelandiae* E.A.Hodgs. & S.W.Arnell, which is the type species of *Jubulopsis* R.M.Schust., to *Neohattoria*. However, preliminary unrooted trees made for this contribution including *Ascidiota* C.Massal., *Gackstroemia* Trevis., *Goebeliella* Steph., *Lepidogyna* R.M.Schust., *Lepidolaena* Dumort. (= *Jubulopsis*) and *Porella* L. together with representatives outside the Porellales, showed *Neohattoria* far away from Lepidolaenaceae but within Jubulaceae (results not depicted). These results are basically the same as the ones observed in recent molecular phylogenies (e.g. Heinrichs et al. 2005, Forrest et al. 2006), demonstrating that these groups are only distantly related to either the Jubulaceae or the Frullaniaceae.

Circumscription and relationships of *Neohattoria*

Our results place *Neohattoria* in the Jubulaceae with strong support, together with *Nipponolejeunea* and *Jubula*. Within the Jubulaceae, *Neohattoria* is resolved as sister to *Nipponolejeunea*, and this latter clade sister to *Jubula*, although this relationship is sen-

sitive to taxon sampling (cf. Figs. 1 and 2), and not strongly supported in the analyses. When describing the genus *Hattoria* (later renamed *Neohattoria*), Kamimura (1961) conceived it as a monotypic genus containing only the Japanese endemic *N. herzogii*. The singularity of this taxon was well described and illustrated, highlighting its closer affinities to *Jubula* instead of *Frullania*, mostly because of its branching pattern and leaf insertion: "[…] *the branch replaces the lobule of leaf in origin and the lobe is inserted partly to the stem and partly to the branch. The first leaf and underleaf of branches are much deformed, being the "Vorblätter" of Verdoorn (1930)*." (Kamimura 1961, p. 94). The characteristic combination of traits that led Kamimura to describe this new genus vanished when Schuster (1963, 1970) added more species in the circumscription of *Neohattoria* as explained above. Schuster (1970) still recognized the taxonomic singularity of *N. herzogii* when placing it in its own subgenus within *Neohattoria*, but failed to see the relationships of this taxon with other *Jubula* species, precisely because of his wide concept of *Neohattoria* that includes members of *F.* subg. *Microfrullania* and *F.* subg. *Diastaloba*.

Oil-bodies in *Neohattoria* are homogenous, usually more than ten per cell, and similar in size to chloroplasts (Hattori et al. 1972, Inoue et al. 1981). Hattori et al. (1972) reported 10–20 oil-bodies per leaf lobe median cell for *N. herzogii* and later Inoue et al. (1981, p. 25) reported a similar number "usually 7–15 per leaf-lobe cell (rarely up to 22)". Hattori et al. (1972) stated that oil-bodies of *Neohattoria* are hyaline and homogenous, and Inoue et al. (1981) recorded in their specimen of *Neohattoria* that the oil-bodies were completely colourless and homogenous. However, they noted that sometimes they were faintly papillose with a few distinct granules; Inoue et al. (1981) were uncertain if this was due to degeneration of the oil-bodies. Reports of oil-body numbers for *Jubula* are ambiguous: although Guerke (1979) and Paton (1999) suggested they range between 3–7 in all *Jubula* taxa, Schuster (1992) stated that the oil-bodies are numerous in the North American material of *J. pennsylvanica* (≡ *J. hutchinsiae* subsp. *pennsylvanica*), ranging from 6–16 per cell, and Mizutani (1961) reported 2–10 for Japanese *Jubula*. All authors agree that the oil-bodies in *Jubula* are faintly granular or homogeneous. In *Nipponolejeunea*, on the other hand, the oil-bodies range between 3–5(7) per cell, are hyaline to somewhat grayish, and are formed by 15–20 internal oil-globules (Mizutani 1961). In *Frullania* the oil-bodies are usually larger, finely to coarsely papillose rather than smooth, and few per cell, with their number generally increasing from the leaf-lobe marginal cells to the basal cells, except in the species that have basal ocelli; however, this number rarely reaches the number of oil-bodies seen in *Neohattoria* or *Jubula*. The average number of oil-bodies from the 22 species studied by von Konrat (2004) is 4.3 per median lobe cell. One remarkable exception is the North American species *F. stylifera* (R.M.Schust.) R.M.Schust., which has up to 16 oil-bodies per median cell (von Konrat 2004). A survey of over sixty species (including literature data) suggests that this is a rare condition in the genus (von Konrat 2004). Schuster (1992) described the oil-bodies of *Frullania* as formed of numerous oil-globules and usually appearing coarsely to finely papillose, the only exception being the oil-bodies of *F.* subg. *Microfrullania*, which are smooth and frequently

appear as almost homogeneous oil-droplets (von Konrat 2004). The oil-bodies of *Neohattoria* then appear closer to the other Jubulaceae genera in appearence (although smooth, homogeneous oil-bodies are also seen in *Frullania* subg. *Microfrullania*) and number, notwithstanding the number reported for *Nipponolejeunea* and some reports of *Jubula* taxa with fewer oil-body numbers.

Nomenclatural novelties

Neohattoria Kamim., Journal of Japanese Botany 37: 218. 1962.
≡ *Frullania* subg. *Dentatilobi* Stotler & Crand.-Stotl., Memoirs of The New York Botanical Garden 45: 542. 1987 ("*Dentatiloba*"). **syn.nov.** – Type: *Frullania herzogii* S.Hatt.

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References

Ahonen I (2004) Molecular phylogeny of liverwort order Porellales (Marchantiophyta, Jungermanniopsida). In: Goffinet B, Hollowell VC, Magill R (Eds) Molecular Systematics of Bryophytes. Monographs in Systematic Botany from the Missouri Botanical Garden 98: 169–188.

Ahonen I (2006) The taxonomic position of the genus *Nipponolejeunea* Hatt. Journal of the Hattori Botanical Laboratory 99: 319–342.

Ahonen I, Muona J, Piippo S (2003) Inferring the phylogeny of the Lejeuneaceae (Jungermannipsida): a first appraisal of molecular data. The Bryologist 106: 297–308. doi: 10.1639/0007-2745(2003)106[0297:ITPOTL]2.0.CO;2

Asakawa Y, Tokunaga N, Toyota M, Takemoto T, Hattori S, Mizutani M, Suire C (1979) Chemosystematics of bryophytes II. The distribution of terpenoids in Hepaticae and Anthocerotae. Journal of the Hattori Botanical Laboratory 46: 67–76.

Asakawa Y, Matsuda R, Toyota M, Hattori S, Ourisson G (1981) Terpenoids and bibenzyls of 25 liverwort *Frullania* species. Phytochemistry 20: 2187–2194. doi: 10.1016/0031-9422(81)80111-2

Asakawa Y, Matsuda R, Toyota M, Takemoto T, Connolly JD, Phillips WR (1983) Sesquiterpenoids from *Chiloscyphus* sp., *Clasmatocolea* sp., and *Frullania* sp. Phytochemistry 22: 961–964. doi: 10.1016/0031-9422(83)85030-4

Asakawa Y, Matsuda R, Cheminat A (1987) Bibenzyl derivatives from *Frullania* species. Phytochemistry 26: 1117–1122. doi: 10.1016/S0031-9422(00)82361-4

Borsch T, Quandt D (2009) Mutational dynamics and phylogenetic utility of noncoding chloroplast DNA. Plant Systematics and Evolution 282: 169–199. doi: 10.1007/s00606-009-0210-8

Casas C, Brugués M, Cros RM, Sérgio C, Infante M (2009) Handbook of liverworts and hornworts of the Iberian Peninsula and the Balearic Islands. Ilustrated keys to genera and species. Institut d'Estudis Catalans, Secció de Ciències Biològiques, Barcelona, 177 pp.

Cooper ED, Shaw AJ, Shaw B, Henwood MJ, Heslewood MM, Brown EA (2011) A multi-locus molecular phylogeny of the Lepidoziaceae: Laying the foundations for a stable classification. Molecular Phylogenetics and Evolution 59: 489–509. doi: 10.1016/j.ympev.2011.02.006

Crandall-Stotler B, Guerke WR (1980) Developmental anatomy of *Jubula* Dum. (Hepaticae). Bryologist 83: 179–201. doi: 10.2307/3242131

Crandall-Stotler B, Stotler RE (2000) Morphology and classification of the Marchantiophyta. In: Shaw AJ, Goffinet B (Eds) Bryophyte biology. Cambridge University Press, Cambridge, 21–70. doi: 10.1017/CBO9781139171304.003

Crandall-Stotler B, Stotler RE, Long DG (2008) Morphology and classification of the Marchantiophyta. In: Goffinet B, Shaw AJ (Eds) Bryophyte biology, second edition. Cambridge University Press, Cambridge, 1–54.

Crandall-Stotler B, Stotler RE, Long DG (2009) Phylogeny and classification of the Marchantiophyta. Edinburgh Journal of Botany 66: 155–198. doi: 10.1017/S0960428609005393

Damsholt K (2002) Illustrated flora of Nordic liverworts and hornworts. Nordic Bryological Society, Lund, 837 pp.

Davis EC (2004) A molecular phylogeny of leafy liverworts (Jungermanniidae: Marchantiophyta). Monographs in Systematic Botany from the Missouri Botanical Garden 98: 87–118.

Engel JJ (1978) A taxonomic and phytogeographic study of Brunswick Peninsula (Strait of Magellan) Hepaticae and Anthocerotae. Fieldiana Botany 41: 1–319. doi: 10.5962/bhl.title.2426

Feldberg K, Schneider H, Stadler T, Schäfer-Verwimp A, Schmidt A, Heinrichs J (2014) Epiphytic leafy liverworts diversified in angiosperm-dominated forests. Scientific Reports 4: 5974. doi: 10.1038/srep05974

Forrest LL, Davis EC, Long DG, Crandall-Stotler BJ, Clark A, Hollingsworth ML (2006) Unraveling the evolutionary history of the liverworts (Marchantiophyta): multiple taxa, genomes

and analyses. The Bryologist 109: 303–334. doi: 10.1639/0007-2745(2006)109[303:UTEHOT]2.0.CO;2

Frey W, Stech M (2009) Marchantiophyta. In: Frey W (Ed.) Syllabus of plant families – A. Engler's Syllabus der Pflanzenfamilien. part 3: Bryophytes and seedless vascular plants. 13th edition, viii, Borntraeger, Berlin/Stuttgart, 13–115.

Gradstein SR, Churchill SP, Salazar-Allen N (2001) Guide to the bryophytes of tropical America. Memoirs of the New York Botanical Garden 86: 1–577.

Grolle R (1966) Miscellanea hepaticologica (51–60). Journal of Japanese Botany 41: 141–147.

Grolle R, Meister K (2004) The liverworts in Baltic and Bitterfeld amber. Weissdorn, Jena, 1–91.

Guerke WR (1978) A monograph of the genus *Jubula* Dumortier. Bryophytorum Biblioteca 17: 1–118.

Hattori S (1955) A remarkable *Frullania* species from northern Japan. Feddes Repertorium Specierum Novarum Regni Vegetabilis 58: 53–54.

Hattori S (1982) A synopsis of New Guinean *Frullania*, Hepaticae. Journal of the Hattori Botanical Laboratory 51: 203–271.

Hattori S (1984) New Caledonian Frullaniaceae. Journal of the Hattori Botanical Laboratory 57: 405–426.

Hattori S (1986) A synopsis of New Caledonian Frullaniaceae. Journal of the Hattori Botanical Laboratory 60: 203–237.

Hattori S, Mizutani M (1982) A status of *Amphijubula* (Hepaticae) with special reference to the seta anatomy. Journal of the Hattori Botanical Laboratory 52: 441–448.

Hattori S, Sharp AJ, Mizutani M (1972) *Schusterella*, a new genus of Jubulaceae (Hepaticae). Journal of Japanese Botany 20: 329–338.

Heinrichs J, Gradstein SR, Wilson R, Schneider H (2005) Towards a natural classification of liverworts (Marchantiophyta) based on the chloroplast gene *rbc*L. Cryptogamie, Bryologie 26: 215–233.

Heinrichs J, Hentschel J, Wilson R, Feldberg K, Schneider H (2007) Evolution of leafy liverworts (Jungermanniidae, Marchantiophyta): estimating divergence times from chloroplast DNA sequences using penalized likelihood with integrated fossil evidence. Taxon 56: 31–44.

Hentschel J, von Konrat MJ, Pócs T, Schäfer-Verwimp A, Shaw AJ, Schneider H, Heinrichs J (2009) Molecular insights into the phylogeny and subgeneric classification of *Frullania* Raddi (Frullaniaceae, Porellales). Molecular Phylogenetics and Evolution 52: 142–156. doi: 10.1016/j.ympev.2008.12.021

Holmgren PK, Holmgren NH, Barnett LC (1990) Index herbariorum. Part I: The herbaria of the world (Regnum Veg. 120), eighth edition. New York Botanical Garden, New York, 693 pp.

Huelsenbeck JP, Ronquist F (2001) MrBayes: Bayesian inference of phylogeny. Bioinformatics 17: 754–755. doi: 10.1093/bioinformatics/17.8.754

Inoue H, Asakawa Y, Gradstein SR (1981) A biosystematic study of *Neohattoria herzogii* (Hatt.) Kamim. Bulletin of the National Science Museum, Tokyo, Series B, 7: 23–30.

Kamimura M (1961) A monograph of Japanese Frullaniaceae. Journal of the Hattori Botanical Laboratory 24: 1–109.

Kamimura M (1962) On the genus *Neohattoria* Kamim. nom. nov. (Hepaticae). Journal of Japanese Botany 37: 26.

Kelchner SA (2000) The evolution of non-coding chloroplast DNA and its application in plant systematics. Annals of the Missouri Botanical Garden 87: 482–498. doi: 10.2307/2666142

Konstantinova NA, Vilnet AA (2011) *Jubula hutchinsiae* subsp. *caucasica* subsp. nov. (Jubulaceae, Marchantiophyta) – a new taxon from the western Caucasus. Arctoa 20: 227–238. doi: 10.15298/arctoa.20.18

Kraut L, Mues R, Sim-Sim M (1994) Sesquiterpene lactones and 3-benzylphthalides from *Frullania muscicola*. Phytochemistry 37: 1337–1346. doi: 10.1016/S0031-9422(00)90409-6

Lanfear R, Calcott B, Ho SYW, Guindon S (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 2: 1695–1701. doi: 10.1093/molbev/mss020

Lanfear R, Calcott B, Kainer D, Mayer C, Stamatakis A (2014) Selecting optimal partitioning schemes for phylogenomic datasets. BMC Evolutionary Biology 14: 82. doi: 10.1186/1471-2148-14-82

Mizutani M (1961) A revision of Japanese Lejeuneaceae. Journal of the Hattori Botanical Laboratory 24: 115–302.

Müller K (1915) Die Lebermoose Deutschlands, Oesterreichs u. d. Schweiz mit Berücksichtigung der übrigen Länder Europas, II. Abteilung. In: Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. 2. Auflage, 6. Band, 24. Lieferung. Eduard Kummer, Leipzig, 593–656.

Olsson S, Buchbender V, Enroth J, Hedenäs L, Huttunen S, Quandt D (2009) Phylogenetic analyses reveal high levels of polyphyly among pleurocarpous lineages as well as novel clades. The Bryologist 112: 447–466. doi: 10.1639/0007-2745-112.3.447

Paton JA (1999) The liverwort flora of the British Isles. Harley Books, Colchester, 626 pp.

Pätsch R, Hentschel J, Linares-Palomino R, Zhu R-L, Heinrichs J (2010) Diversification and taxonomy of the liverwort *Jubula* Dumort. (Jungermanniopsida: Porellales) inferred from nuclear and chloroplast DNA sequences. Systematic Botany 35: 6–12. doi: 10.1600/036364410790862515

Pedersen N, Holyoak DT, Newton AE (2007) Systematics and morphological evolution within the moss family Bryaceae: A comparison between parsimony and Bayesian methods for reconstruction of ancestral character states. Molecular Phylogenetics and Evolution 43: 891–907. doi: 10.1016/j.ympev.2006.10.018

Rambaut A, Drummond AJ (2007) Tracer, version 1.4. http://beast.bio.ed.ac.uk/Tracer

Ronquist F, Huelsenbeck JP (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574. doi: 10.1093/bioinformatics/btg180

Schuster RM (1961) Studies in Lophoziaceae. I. The genera *Anastrophyllum* and *Sphenolobus* and their segregates. Revue Bryologique et Lichénologique 30: 55–73.

Schuster RM (1963) Studies on antipodal Hepaticae. I. Annotated key to the genera of antipodal Hepaticae with special reference to New Zealand and Tasmania. Journal of the Hattori Botanical Laboratory 26: 185–309.

Schuster RM (1970) Studies on antipodal hepaticae, III. *Jubulopsis* Schuster, *Neohattoria* Kamimura and *Amphijubula* Schuster. Journal of the Hattori Botanical Laboratory 33: 266–304.

Schuster RM (1980) New combinations and taxa of Hepaticae, I. Phytologia 45: 415–437.

Schuster RM (1992) The Hepaticae and Anthocerotae of North America east of the hundredth meridan. Volume V. Field Museum of Natural History, Chicago, 854 pp.

Schuster RM (1996) On *Jubulopsis* Schust. (Jungermanniales: Jubulopsidaceae fam. nov.) and its relationships. Journal of Bryology 19: 297–310.

Shaw AJ, Cox CJ, Boles SB (2003) Polarity of peatmoss evolution: who says mosses have no roots? American Journal of Botany 90: 1777–1787. doi: 10.3732/ajb.90.12.1777

Stotler RE, Crandall-Stotler B (1987) A re-evaluation of the genus *Neohattoria* (Jubulaceae). Memoirs of the New York Botanical Garden 45: 535–543.

Stöver BC, Müller KF (2010) TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. BMC Bioinformatics 11: 7. doi: 10.1186/1471-2105-11-7

Sukumaran J, Holder MT (2010) DendroPy: A Python library for phylogenetic computing. Bioinformatics 26: 1569–1571. doi: 10.1093/bioinformatics/btq228

Verdoorn F (1930) Die Frullaniaceae der Indomalesischen Inseln. (De Frullaniaceis VII). Annales Bryologici Supplmentary Volume 1: 1–188. doi: 10.1007/978-94-015-5385-8

von Konrat M (2004) A systematic study of the liverwort genus *Frullania* Raddi: encompassing a worldwide monograph of subg. *Microfrullania* (Schust.) Schust.; a revision of the New Zealand species & study of subsidiary species. PhD dissertation, The University of Auckland, NZ, xxviii + 408 pp.

von Konrat M, Hentschel J, Heinrichs J, Braggins JE, Pócs T (2010) Forty-one degrees below and sixty years in the dark: *Frullania* sect. *Inconditum*, a new section of Australasian *Frullania* species including *F. colliculosa*, sp. nov., *F. hodgsoniae*, nom. and stat. nov., *F. aterrima*, and *F. hattorii* (Frullaniaceae, Marchantiophyta). Nova Hedwigia 91: 471–500. doi: 10.1127/0029-5035/2010/0091-0471

von Konrat M, de Lange P, Greif M, Strozier L, Hentschel J, Heinrichs J (2012) *Frullania knightbridgei*, a new liverwort (Frullaniaceae, Marchantiophyta) species from the deep south of Aotearoa-New Zealand based on an integrated evidence-based approach. PhytoKeys 8: 13–36. doi: 10.3897/phytokeys.8.2496

Wilson R, Gradstein SR, Heinrichs J, Groth H, Ilkiu-Borges AL, Hartmann FA (2004) Phylogeny of Lejeuneaceae: a cladistic analysis of chloroplast *rbc*L sequences and morphology with preliminary comments on the mithocondrial *nad*4–2 spacer region. In: Goffinet B, Hollowell VC, Magill RE (Eds) Molecular Systematics of Bryophytes. Monographs in Systematic Botany from the Missouri Botanical Garden 98: 189–202.

Wilson R, Gradstein SR, Schneider H, Heinrichs J (2007) Unravelling the phylogeny of Lejeuneaceae (Jungermanniopsida): Evidence for four main lineages. Molecular Phylogenetics and Evolution 43: 270–282. doi: 10.1016/j.ympev.2006.10.017

Zwickl DJ (2006) GARLI (Genetic Algorithm for Rapid Likelihood Inference). Version 2.01. http://www.bio.utexas.edu/faculty/antisense/garli/garli.html

Appendix 1

Voucher information for data set 1. Information is presented in the following order: taxon name, collector followed by collection number (herbarium acronyms follow Holmgren et al. 1990), country: region (if known), GenBank accesion numbers (*psb*A/*rbc*L/*rps*3/*nad*1). Lacking sequences are indicated by a dash (—). New sequences generated for this study are marked by an asterisk (*).

Acanthocoleus madagascariensis (Steph.) Kruijt, Pócs 97145/AA (GOET), Uganda, EF011843/DQ983649/—/—; *Blepharolejeunea chimantaensis* van Slageren & Kruijt, Pócs & Rico 00234/A (F), Venezuela, KF851876/—/—/KF852465; *Bryopteris filicina* (Sw.) Nees, Churchill, Magombo & Price 19855 (NY), Bolivia, AY607930/DQ439681/KF851576/KF852481; *Caudalejeunea reniloba* (Gottsche) Steph., Pócs et al. 01090/AB (F), Australia, KF851845/KF852294/KF851541/KF852441; *Ceratolejeunea coarina* (Gottsche) Schiffn., Zartman 1235.1 (DUKE), Brazil, AY607934/AY608026/—/KF852489; *Cololejeunea microscopica* (Taylor) Schiffn., Long & Rothero 37789 (E), Scotland: Wester Ross, KF851954/KF852386/KF851651/KF852552; *Colura conica* (Sande Lac.) K.I.Goebel, Pócs & Streimann 9986/W (F), Australia: Queensland, KM817490*/KM817513*/KM817536*/KM817462*; *Colura imperfecta* Steph., Pócs & Pócs 07019/A (F), Thailand, KF851881/KF852327/—/KF852469; *Drepanolejeunea erecta* (Steph.) Mizut., Long 28691 (E), Bhutan, JF513393/JF513452/KF851515/JF513342; *Frullania albertii* Steph., Davis 295 (DUKE), Ecuador, AY607942/DQ439685/KM817549*/KM817477*; *Frullania atrata* (Sw.) Nees ex Mont., Dauphin 3306 (F), Costa Rica, KM817491*/—/KM817540*/KM817466*; *Frullania caulisequa* (Nees) Mont., Karst, Shaw & Gibbs 022 (DUKE), USA: North Carolina, KM817500*/KM817526*/KM817553*/KM817481*; *Frullania dilatata* (L.) Dumort., Stotler 4666 (SIU), Portugal, KM817502*/KM817528*/KM817555*/KM817482*; *Frullania eboracensis* Lehm., Stotler 80-4354 (ABSH), USA: Illinois, AY688827/AY688779/KM817547*/KM817475*; *Frullania ecklonii* (Spreng.) Spreng. ex Gottsche, Lindenb. & Nees, Pócs 02030/W (F), Kenya, KM817488*/KM817510*/KM817533*/KM817459*; *Frullania ericoides* (Nees) Mont., Long 35167 (E), China: Yunnan, KM817486*/KM817507*/KM817531*/KM817456*; *Frullania falciloba* Taylor ex Lehm., Engel, von Konrat & Braggins 26837 (F), New Zealand, KM817489*/KM817511*/KM817534*/KM817460*; *Frullania moniliata* (Reinw., Blume & Nees) Mont., Mizutani s.n. (ABSH), Japan, AY507484/AY507401/KM817548*/KM817476*; *Frullania nodulosa* (Reinw., Blume & Nees) Nees, Pócs & Pócs 03261/A (F) Fiji, KM817492*/KM817517*/KM817541*/KM817467*; *Frullania parhamii* (R.M.Schust.) R.M.Schust. ex von Konrat, L.Söderstr. & A.Hagborg, von Konrat, Braggins & Naikatini 6/16-5 (F), Fiji, —/KM817516*/KM817539*/KM817465*; *Frullania pycnantha* (Hook.f. & Taylor) Taylor ex Gottsche, Lindenb. & Nees, von Konrat 99/409 (F), New Zealand, KM817499*/KM817525*/—/KM817480*; *Frullania rostrata* (Hook.f. & Taylor) Hook.f. & Taylor ex Gottsche, Lindenb. & Nees, Engel, von Konrat & Braggins 27770 (F), New Zealand, —/KM817512*/KM817535*/KM817461*; *Frullania tamarisci* (L.) Dumort. 1, Stot-

ler 4661 (SIU), Portugal: Sintra, KM817501*/KM817527*/KM817554*/—; *Frullania tamarisci* 2, Long 35371 (E), France, KM817487*/KM817508*/KM817532*/KM817457*; *Frullanoides densifolia* Raddi, Gradstein 10171 (GOET), Ecuador, KF851930/KF852371/KF851634/KF852530; *Fulfordianthus pterobryoides* (Spruce) Gradst., Gradstein & Varon 11069 (GOET), Colombia, KF851931/KF852372/KF851635/KF852531; *Jubula hutchinsiae* (Hook.) Dumort. 1, Long 29077 (E), UK: England, —/KM817509*/—/KM817458*; *Jubula hutchinsiae* 2, Drehwald 3007 (GOET), Portugal, EF011746/AY548101/—/—; *Jubula hutchinsiae* subsp. *bogotensis* (Steph.) Verd., Gradstein s.n. (GOET), Mexico, EF011758/AY548100/—/—; *Jubula hutchinsiae* subsp. *javanica* (Steph.) Verd. 1, Konstantinova & Savchenko K479/1-07 (F), Russia, —/KM817506*/KM817542*/KM817468*; *Jubula hutchinsiae* subsp. *javanica* 2, Kodama s.n. (ABSH), Japan: Wakayama Pref., AY507492/AY507408/KF851585/JF513366; *Jubula hutchinsiae* subsp. *pennsylvanica* (Steph.) Verd., Risk 11005 (DUKE), USA, AY607954/KM817523*/KM817550*/—; *Lejeunea deplanata* Nees var. *deplanata*, Shaw F533 (DUKE), USA: North Carolina, KM817498*/KM817524*/KM817552*/KM817479*; *Lejeunea japonica* Mitt., Bakalin s.n. (F), Russia, —/KM817518*/KM817543*/KM817469*; *Lejeunea tuberculosa* Steph., Long 28596 (E), Bhutan, JF513394/JF513453/KF851518/JF513344; *Leptolejeunea elliptica* (Lehm.) Besch., Yamaguchi s.n. (F), Japan, KM817485*/KM817515*/KM817538*/KM817464*; *Lopholejeunea eulopha* (Taylor) Schiffn., Pócs et al. 08036/U (F), Fiji, KF851868/KF852314/—/—; *Marchesinia mackaii* (Hook.) Gray, Buryova 2181 (DUKE), UK: Wales, —/KF852356/KF851619/KF852515; *Mastigolejeunea auriculata* (Wilson) Steph., Shaw 6222 (DUKE), USA: Alabama, KF851917/KF852359/KF851622/KF852518; *Neohattoria herzogii* (S.Hatt.) Kamim., Furuki 22673 (F), Japan: Honshu, KM817504*/KM817530*/KM817557*/KM817484*; *Nipponolejeunea pilifera* (Steph.) S.Hatt., Ohnishi 5975 (HIRO), Japan, AM396291/AM392293/—/—; *Nipponolejeunea subalpina* (Horik.) S.Hatt., Ohnishi 5611 (GOET), Japan, AM396290/AM392292/—/—; *Odontolejeunea lunulata* (F.Weber) Schiffn., Picon et al. 00227/CE (F), Venezuela, —/KM817514*/KM817537*/KM817463*; *Ptychanthus striatus* (Lehm.) Nees, Pócs & Pócs 03288/O (F), Fiji, KF851872/KF852318/KF851558/KF852460; *Radula buccinifera* (Hook.f. & Taylor) Taylor ex Gottsche, Lindenb. & Nees, Engel, von Konrat & Braggins 23569 (F), New Zealand, KM817495*/KM817521*/KM817545*/KM817472*; *Radula cuspidata* Steph., Engel & von Konrat 23517 (F), New Zealand, KM817496*/—/KM817546*/KM817473*; *Radula grandis* Steph., Engel, von Konrat & Braggins 24847 (F), New Zealand, KM817494*/KM817520*/KM817544*/KM817471*; *Radula lindenbergiana* Gottsche ex C.Hartm., Stotler 4656 (SIU), Portugal, KM817503*/KM817529*/KM817556*/KM817483*; *Radula perrottetii* Gottsche ex Steph., Mizutani 15030 (F), Japan, —/DQ439700/KM817551*/KM817478*; *Radula ratkowskiana* K.Yamada, Engel, von Konrat & Braggins 24365 (F), New Zealand, KM817497*/KM817522*/—/KM817474*; *Radula tasmanica* Steph., Engel, von Konrat & Braggins 24874 (F), New Zealand, KM817493*/KM817519*/—/KM817470*; *Spruceanthus thozetianus* (Gottsche & F.Muell.) B.M.Thiers & Gradst., Pócs 01107/M (GOET), Australia,

AM396273/AM384877/—/—; *Stictolejeunea squamata* (Willd. ex F.Weber) Schiffn., Dauphin & Gonzalez 2134 (GOET), Costa Rica: Alajeula, KF851951/—/—/KF852549; *Thysananthus convolutus* Lindenb., Gradstein 10205 (GOET), Indonesia: Java, KF851953/DQ983737/KF851650/KF852551.

Appendix 2

Voucher information for data set 2. Information is presented in the following order: taxon name, collector followed by collection number (herbarium acronyms follow Holmgren et al. 1990), country: region (if known), GenBank accesion numbers (ITS region/rbcL/trnL-F/psbA). Lacking sequences are indicated by a dash (—). New sequences generated for this study are marked by an asterisk (*).

Frullania kunzei (Lehm.) Lehm. & Lindenb., Costa & Gradstein 3769 (GOET), Brazil, FJ380536/FJ380863/FJ380387/FJ380697; *Frullania nisquallensis* Sull., Doyle 11001 (GOET), USA, FJ380503/FJ380826/FJ380349/FJ380661; *Frullania peruviana* Gottsche, Schaefer-Verwimp & al. 24356 (GOET), Ecuador, FJ380543/FJ380870/FJ380394/FJ380704; *Frullanoides mexicana* van Slageren, Burghardt 4421a, Mexico, DQ987366/DQ983682/DQ987464/EF011851; *Fulfordianthus pterobryoides* (Spruce) Gradst., Dauphin 2518, Costa Rica, AM237145/DQ983684/AM237198/EF011832; *Jubula hutchinsiae* (Hook.) Dumort., Ahonen, Huttunen et Virtanen 3190 (H), Taiwan, AY125350/AY125946/AY144477/—; *Jubula hutchinsiae* subsp. *bogotensis* (Steph.) Verd. 1, Gradstein s.n. (GOET), Mexico: Veracruz, FN396818/—/FN398013/—; *Jubula hutchinsiae* subsp. *bogotensis* 2, Gradstein s.n. (GOET?), Mexico, DQ987273/AY548100/DQ987388/AM396281; *Jubula hutchinsiae* subsp. *bogotensis* 3, Gradstein 9449 (GOET), Costa Rica, FN396817/—/FN398012/—; *Jubula hutchinsiae* subsp. *bogotensis* 4, Frahm et al. 1313 (GOET), Peru, FN396816/—/—/—; *Jubula hutchinsiae* subsp. *caucasica* Konstant. & Vilnet 1, Konstantinova K456-5-07 (KPABG), Russia: Caucasus, JN836964/—/JN836974/—; *Jubula hutchinsiae* subsp. *caucasica* 2, Konstantinova K429-3-08 (KPABG), Russia: Caucasus, JN836961/—/JN836971/—; *Jubula hutchinsiae* subsp. *caucasica* 3, Konstantinova K462-1-08 (KPABG), Russia: Caucasus, JN836960/—/JN836970/—; *Jubula hutchinsiae* subsp. *caucasica* 4, Konstantinova K463-1-07 (KPABG), Russia: Caucasus, JN836962/—/JN836972/—; *Jubula hutchinsiae* subsp. *caucasica* 5, Konstantinova K371-1-08 (KPABG), Russia: Caucasus, JN836958/—/JN836968/—; *Jubula hutchinsiae* subsp. *caucasica* 6, Konstantinova K446-7-08 (KPABG), Russia: Caucasus, JN836959/—/JN836969/—; *Jubula hutchinsiae* subsp. *caucasica* 7, Konstantinova K443-14-08 (KPABG), Russia: Caucasus, JN836963/—/JN836973/—; *Jubula hutchinsiae* subsp. *hutchinsiae* 1, Long 29077 (GOET), UK: Devon, FN396813/—/FN398010/—; *Jubula hutchinsiae* subsp. *hutchinsiae* 2, Long 35296 (GOET), UK: Wales, FN396814/—/FN398011/—; *Jubula hutchinsiae* subsp. *hutchinsiae* 3, Schaefer-Verwimp & Verwimp 25675 (GOET), Portugal: Madeira, FN396811/—/FN397099/—; *Jubula hutchinsiae* subsp. *hutchinsiae* 4, Schaefer-

Verwimp & Verwimp 25796 (GOET), Portugal: Boaventura, FN396812/—/FN398009/—; *Jubula hutchinsiae* subsp. *hutchinsiae* 5, Drehwald & Reiner-Drehwald 3007 (GOET), Portugal, DQ987260/AY548101/DQ987380/AM396282; *Jubula hutchinsiae* subsp. *japonica* (Steph.) Horik. & Ando 1, Koponen et al. 54308 (H), China, AY125342/AY125938/AY144479/—; *Jubula hutchinsiae* subsp. *japonica* 2, Inoue BSE755 (GOET), Japan: Kochi, FN396809/—/—/—; *Jubula hutchinsiae* subsp. *japonica* 3, Gradstein & Mizutani 2958 (GOET), Japan: Miyazaki, FN396810/—/FN397098/—; *Jubula hutchinsiae* subsp. *japonica* 4, Bakalin P-68-10-08 (KPABG), Russia: Primorsky Kray, JN836967/—/JN836977/—; *Jubula hutchinsiae* subsp. *javanica* (Steph.) Verd. 1, Zhu et al. 3361 (HSNU), China: Hainan, FN396800/—/—/—; *Jubula hutchinsiae* subsp. *javanica* 2, Zhu et al. 20050903-7a (HSNU), China: Hainan, FN396801/—/—/—; *Jubula hutchinsiae* subsp. *javanica* 3, Long 34765 (GOET), China: Yunnan, FN396805/—/FN397095/—; *Jubula hutchinsiae* subsp. *javanica* 4, Pocs 98105/C (GOET), Viet Nam: Vin-Phuc, FN396807/—/—/—; *Jubula hutchinsiae* subsp. *javanica* 5, Pocs & Tran Ninh 98103/A2 (GOET), Viet Nam: Vin-Phuc, FN396808/—/FN397097/—; *Jubula hutchinsiae* subsp. *javanica* 6, Schaefer-Verwimp & Verwimp 18870/A (GOET), Malaysia: Pahang, FN396802/—/FN397094/—; *Jubula hutchinsiae* subsp. *javanica* 7, Zhu 555 (HSNU), China: Fujian, FN396806/—/FN397096/—; *Jubula hutchinsiae* subsp. *javanica* 8, Bakalin Kor-12-6-08 (KPABG), South Korea, JN836966/—/JN836976/—; *Jubula hutchinsiae* subsp. *javanica* 9, Schaefer-Verwimp & Verwimp 18935 (GOET), Malaysia: Pahang, FN396803/—/—/—; *Jubula hutchinsiae* subsp. *javanica* 10, Wang 685B (HSNU), China: Yunnan, FN396804/—/—/—; *Jubula hutchinsiae* subsp. *pennsylvanica* (Steph.) Verd. 1, Buck 39060 (H?), USA: West Virginia, AY776308/AY776303/AY776309/—; *Jubula hutchinsiae* subsp. *pennsylvanica* 2, Davison 5045 (UNAF), USA: Alabama, FN396819/—/—/—; *Jubula hutchinsiae* subsp. *pennsylvanica* 3, Davison 5201 (UNAF), USA: West Virginia, FN396821/—/FN398015/—; *Jubula hutchinsiae* subsp. *pennsylvanica* 4, Davison 4707 (UNAF), USA: Alabama, FN396822/—/FN398016/—; *Jubula hutchinsiae* subsp. *pennsylvanica* 5, Davison 3775a (UNAF), USA: Alabama, FN396823/—/FN398017/—; *Jubula hutchinsiae* subsp. *pennsylvanica* 6, Davison & Risk 2537 (UNAF), USA: Kentucky, FN396820/—/FN398014/—; *Jubula hutchinsiae* subsp. *pennsylvanica* 7, Konstantinova ACH-3-92 (KPABG), USA, JN836965/—/JN836975/—; *Jubula hutchinsiae* subsp. *pennsylvanica* 8, Davison 4690 (UNAF), USA, Alabama, FN396824/—/FN398018/—; *Jubula hutchinsiae* subsp. *pennsylvanica* 9, Hyatt 8212 (UNAF), USA: North Carolina, FN396825/—/FN398019/—; *Jubula hutchinsiae* subsp. *pennsylvanica* 10, Davison s.n. (UNAF), USA: North Carolina, FN396826/—/FN398020/—; *Neohattoria herzogii* (S.Hatt.) Kamim., Furuki 22673 (F), Japan: Honshu, KM817455*/KM817530*/KM817505*/KM817504*; *Nipponolejeunea pilifera* (Steph.) S.Hatt. 1, Ohnishi 5975 (HIRO), Japan, —/AM392293/FJ380228/AM396291; *Nipponolejeunea pilifera* 2, Higuchi 41359 (H?), Japan, AY776307/AY776304/AY776310/—; *Nipponolejeunea pilifera* 3, Masuzaki 510 (HIRO), Japan: Yakushima Is., —/AB476588/—/—; *Nipponolejeunea pilifera* 4, Ohnishi s.n. (H), Japan, AY125341/AY125937/AY144478/—; *Nippon-*

olejeunea subalpina (Horik.) S.Hatt. 1, Ohnishi 5611 (HIRO), Japan, DQ987289/AM392292/FJ380227/AM396290; *Nipponolejeunea subalpina* 2, Higuchi 41358 (H?), Japan, AY776306/AY776305/AY776311/—; *Ptychanthus striatus* (Lehm.) Nees, Gradstein 10217, Indonesia: Java, DQ987297/DQ983723/DQ987403/EF011777; *Schiffneriolejeunea nymannii* (Steph.) Gradst. & Terken, Gradstein et al. 10321, Malaysia, DQ987320/DQ983725/DQ987424/EF011801.