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# A new species of *Prunus* subgen. *Cerasus* from Central China

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### Abstract
A new species, *Prunus wangii* Q.L.Gan, Z.Y.Li & S.Z.Xu from western Hubei, Central China is described and illustrated. It is morphologically similar to *P. clarofolia* Schneid. and *P. pseudocerasus* Lindl., but differs in larger height, nearly erect branches, densely and horizontally arranged lenticels, straight lateral veins of leaves, persistent brownish bracts, reflexed and entire calyx lobes, 2-lobed petals with narrowly triangular sinus, earlier flowering and broadly ellipsoid fruits. Furthermore, *P. wangii* blooms in late February and the colour of flower changes with time, which makes it possible to be a new breeding material for ornamental cherry with early spring blooms.

### Keywords
Central China, flowering period, *Prunus wangii*, wild cherry

## Introduction

There are extremely rich germplasm resources of wild *Prunus*, especially for *P.* subgen. *Cerasus* (Mill.) A. Gray, in Central China (Koehne 1912; Yu and Li 1986; Li and Bartholomew 2003). In recent years, field investigations on 15 species of *P.* subgen. *Cerasus* were carried out by Qi-Liang Gan in western Hubei Province including Zhuxi, Zhushan, Badong, Shennongjia, Nanzhang, Danjiangkou and so on. Wild populations of *P. canescens* Bois and some other species which were not recorded by Flora of China (Li and Bartholomew 2003) and the revised checklist (Xia and Tong 2018) have been rediscovered during the fieldwork. In 2021, Gan found an unknown species of wild cherry in Zhangjiashan Village and Tianbaozhaichachang, Zhuxi County. Based on field surveys, morphological and phenological studies and taxonomic literature research, we concluded that this species should be included in *P.* subgen. *Cerasus* (Mill.) A. Gray (Shi et al. 2013), but, as it differed from previously described taxa, we named and described it as a new species herein.

## Materials and methods

Specimens of the putative new species were collected in Zhuxi County of Hubei Province in 2021. Comparisons with its relatives were made by consulting specimens stored in PE or some virtual specimen databases (HIB, CCAU, KUN, IBK, IBSC, CVH, JSTOR). All morphological characters were measured with dissecting microscopes and were described using the terminology presented by Harris and Harris (1994).

## Taxonomic treatment

***Prunus wangii* Q.L.Gan, Z.Y.Li & S.Z.Xu, sp. nov.**
urn:lsid:ipni.org:names:77299024-1
Fig. 1

**Diagnosis.** *Prunus wangii* Q.L.Gan, Z.Y.Li & S.Z.Xu is similar to *P. clarofolia* Schneid. and *P. pseudocerasus* Lindl., but the new species can be easily distinguished from the latter two species by its larger trees, densely and horizontally arranged lenticels, straight lateral veins of leaves, persistent brownish bracts, 2-lobed petals with narrowly triangular sinus and broadly ellipsoid fruits.

**Type.** China, Hubei Province, Zhuxi County, Quanxi Town, Zhangjiashan Village, in mixed forest on hillside, alt. 700 m, 26 February 2021, Q.L. Gan 3237-1 (holotype: PE!; isotype: PE!)

**Description.** Trees, deciduous, to 21 m tall (flowering well even when less than 6 m tall), DBH to 30 cm. Bark dark grey, lenticels distinct, transversely elliptic, densely arranged in horizontal lines; crown ovoid. Branchlets grey or taupe, sparsely pilose when young, later glabrate. Winter buds ovoid, ca. 2.5 mm long, internal bud scales brown, glabrous outside, densely pilose inside. Stipules linear, 6–8 mm long, with laciniate or lacerate and gland-tipped lobes, caducous. Leaves alternate, brownish-green when young; petiole 8–12 mm long, sparsely pubescent, lavender brown adaxially, longitudinally grooved; leaf blade elliptic or obovate, 5–11 cm long, 3–6.4 cm wide, base shallowly cordate, rounded or sometimes obliquely cuneate, base of blade or apical part of petiole with or sometimes without 1–3 purple discoid glands, margin biserrate and uniserrate, serrations acute, with a small apical gland, apex cuspidate or acuminate; adaxial surface deep green, glabrous, abaxial surface pale

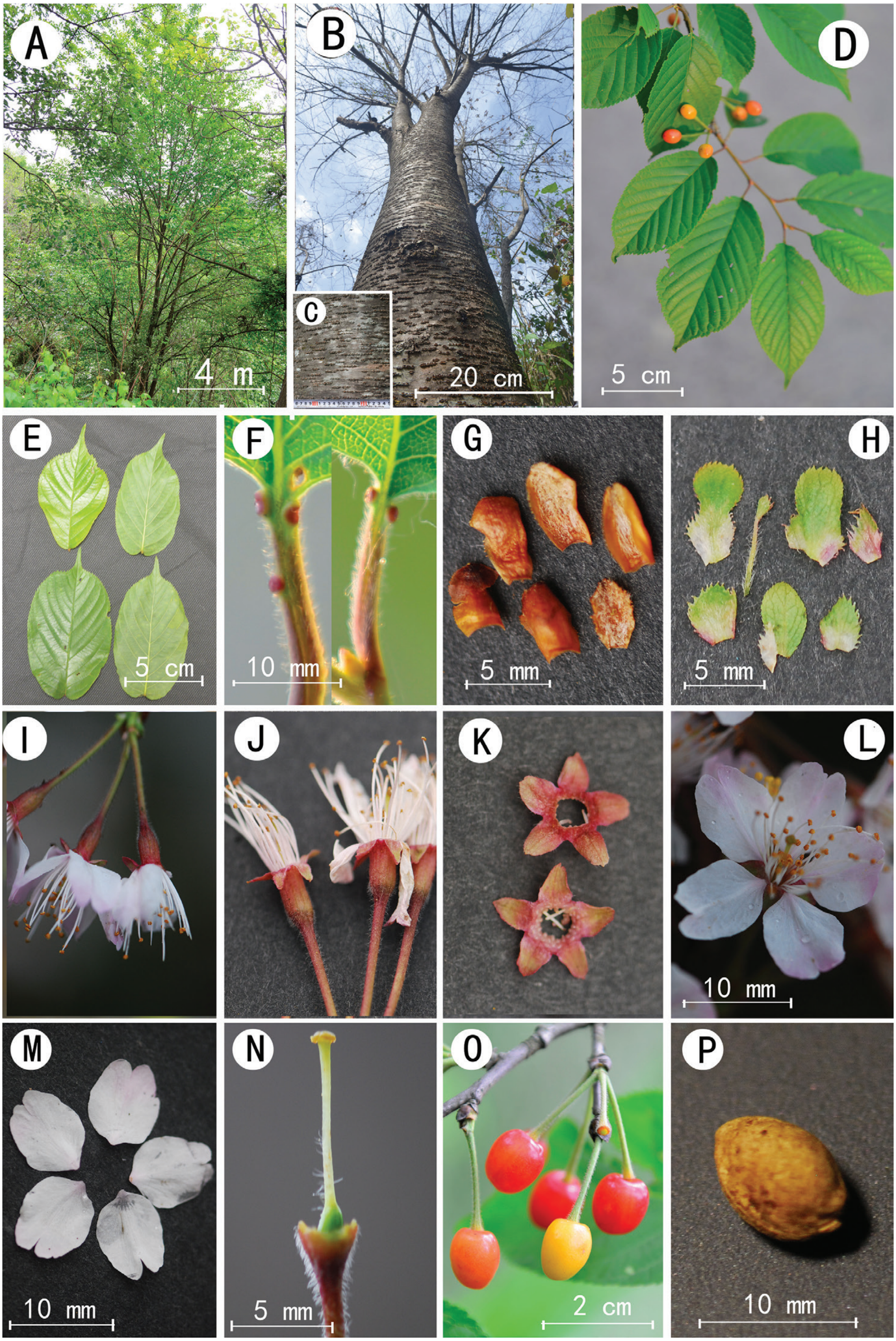


**Figure 1.** *Prunus wangii* sp. nov. **A** crown **B** trunk **C** bark **D** fruiting branches **E** leaf blades **F** petioles and glands **G** internal bud scales **H** involucres and bracts **I** inflorescence **J** pedicels and hypanthia **K** calyces **L** corolla **M** petals **N** ovary and style **O** fruits **P** seed.

green, white pubescent along veins, margin ciliate; lateral veins 6–9 pairs, straight, veins slightly impressed on adaxially surface and raised abaxially. Inflorescences corymbose 4–6-flowered or umbellate 2–3-flowered; involucre green, orbicular-ovate, 2–5 mm long, 2–4 mm wide, abaxially glabrous, adaxially densely pilose; peduncle 2–11 mm long, subglabrous or sparsely white pubescent; bracts green, brownish when dry, fan-shaped, rarely linear, 2–7 mm long, 0.5–3.5 mm wide, proximal one larger, margin glandular-serrate, persistent in fruit. Flowers and leaves opening at same time (coetaneous) or nearly so. Pedicel 0.9–1.2 cm long, to 1.3–2 cm long in fruit, straight, thickened at apex, densely white pilose. Hypanthium campanulate, 5–6 mm long, 2.5–3 mm in diam., pilose outside; calyx lobes triangular, 2.5–3 mm long, margin entire, apex rounded or subacute, glabrous or pilose outside, at first patent, reflexed when flower fully expanded. Petals pink during early blooming, then white or slight pinkish tinged, broadly ovate, 7–11 mm long, 5–9 mm wide, apex 2-lobed, sinus narrowly triangular. Stamens 34–38, as long as or shorter than petals, glabrous, 6–11 mm long; filaments white; anthers dark yellow, broadly ellipsoid, 0.65–0.75 mm long. Ovary green, glabrous; style shorter than stamens, sparsely patent white-pilose below middle. Drupe broadly ellipsoid, 10–12 mm long, 8–10 mm in diam., glabrous, red at maturity, shiny, tasting sweet and sour. Stone flattened ovoid, 8–8.5 mm long, 5–5.5 mm wide, ca. 4 mm thick, fawn, surface almost smooth, ribbed on one side.

**Phenology.** Flowering from late February to late March, flowers and leaves opening at same time (coetaneous) or nearly so; fruiting from April to May.

**Distribution and habitat.** *Prunus wangii* is known from only two populations composed of ca. 20 individuals in Zhangjiashan Village, Quanxi Town and Tianbaozhaichachang, Tianbao Town, Zhuxi County. It grows sparsely in mixed forests on hillsides at elevations from 600 to 800 m. The main companion species include trees: *Populus adenopoda* Maxim., *Liquidambar formosana* Hance, *Castanea seguinii* Dode, *Platycarya strobilacea* Sieb. & Zucc., *Pinus massoniana* Lamb., *Cunninghamia lanceolata* (Lamb.) Hook., *Prunus conradinae* Koehne and *Prunus subhirtella* var. *ascendens* (Maxim.) E.H.Wilson; shrubs: *Coriaria nepalensis* Wall., *Rubus lambertianus* Ser., *Rubus coreanus* Miq., *Lindera glauca* (Sieb. & Zucc.) Bl. and *Rosa banksiae* var. *normalis* Regel; vines: *Hedera nepalensis* var. *sinensis* (Tobl.) Rehd., *Lonicera japonica* Thunb., *Clematis florida* Thunb. and *Pueraria montana* (Lour.) Merr.; herbs: *Chrysanthemum indicum* L., *Miscanthus floridulus* (Lab.) Warb. ex Schum & Laut. and *Senecio scandens* Buch.-Ham. ex D. Don; ferns: *Cyrtomium fortunei* J. Sm., *Athyrium filix-femina* (L.) Roth, *Asplenium varians* Wall. ex Hook. & Grev. and *Pteris cretica* var. *nervosa* (Thunb.) Ching & S. H. Wu.

**Etymology.** The species is named in honour of Professor Wen-Tsai Wang (1926–), a taxonomist at the Institute of Botany, the Chinese Academy of Sciences, who has devoted over 60 years to taxonomic studies of Ranunculaceae, Gesneriaceae, Boraginaceae, Urticaceae and many other families and the floristic research in eastern Asia.

**Vernacular name.** Wen Cai Ying Tao (Chinese).

**Conservation assessment.** We found *Prunus wangii* only in the towns of Quanxi and Tianbao, Hubei Province and estimated the population size to be ca. 20 individuals. The provisional conservation status is Critically Endangered (CR), based on criterion D (number of mature individuals fewer than 50) (IUCN 2022).

**Economic uses.** There are more than 140 species of flowering cherries widely distributed in the Northern Hemisphere, but species blossoming in February are rare. Two species, *P. pseudocerasus* Lindl. and *P. campanulata* Maxim., have been used as important breeding materials of flowering cherries with early spring blooms since their introduction into Japan (Ohwi and Ohta 1973; Ohba 2001; Wang 2014). *Prunus wangii* will provide a new breeding material for early flowering ornamental cherries. The timber of this species is hard and was used to make chopping blocks and furniture by the local people. The mature fruit is red, sweet or slightly bitter and is eaten by the local people.

**Paratypes.** China. Hubei: Zhuxi County, Quanxi Town, Zhangjiashan Village, in mixed forest on hillside, alt. ca. 700 m, 11 March 2021, Qi-Liang Gan 3238 (PE!); the same locality, 21 April 2021, Qi-Liang Gan 3239-1, 3239-2 and 3239-3 (PE!); Zhuxi County, Tianbao Town, Tianbaozhaichachang, in mixed forest on hillside, alt. ca. 750 m, 11 March 2021, Qi-Liang Gan 3240 (PE!).

## Results

*Prunus wangii* is morphologically similar to *P. clarofolia* and wild *P. pseudocerasus*. These three species bear red, sweet fruits known as 'yeyingtao' meaning wild fruit cherries. The diagnostic features of these three species are listed in Table 1.

*Prunus wangii* resembles *P. clarofolia* in the dark grey old bark, green bracts, pilose style, campanulate hypanthium, reflexed calyx lobes, pink or white petals and flowers and leaves opening at the same time. *Prunus wangii* differs from *P. clarofolia* in having lenticels densely arranged in horizontal lines (vs. lenticels usually sparse), straight (vs. curved) lateral veins, hypanthium outside pilose (vs. glabrous), petals 2-lobed at apex, sinus narrowly triangular (vs. entire, crenate or erose), stamens 34–38 (vs. 20–30), flowering from late February to late March (vs. from early April to late May).

*Prunus wangii* can be distinguished from *P. pseudocerasus* in height, up to 21 m tall (vs. less than 8 m), having dark grey (vs. greyish-brown) bark, lenticels densely arranged in horizontal lines (vs. discontinuously arranged in horizontal lines), straight (vs. curved) lateral veins, style pilose below the middle (vs. glabrous), broadly ellipsoid (vs. globose) drupe, flowers and leaves opening at same time (vs. flowers opening before leaves).

Besides, *P. wangii* is also somewhat similar to *P. dielsiana* C. K. Schneid., but the latter can be easily distinguished by the densely yellowish to yellowish-brown pilose twigs, 10–13 pairs of lateral leaf veins, bracts with long stalked glands, calyx lobes ca. 1.5–2 times as long as the hypanthium, flowering from March to April and flowers opening before leaves.

**Table 1.** Morphological comparisons of *Prunus clarofolia*, *P. pseudocerasus* and *P. wangii*.

| Characters | *P. clarofolia* | *P. pseudocerasus* | *P. wangii* |
|---|---|---|---|
| Habit | shrubs or smaller trees, 2.5–8 (–13)* m tall | small trees, rarely shrubs, (2–) 4–8 m tall | trees, up to 21 m tall |
| Bark | dark grey, lenticels usually sparse | grey-brown, lenticels usually discontinuously arranged in horizontal lines | dark grey, lenticels densely arranged in horizontal lines |
| Leaf blades | ovate, ovate-elliptic or obovate-elliptic | ovate, oval or oblong-ovate | elliptic or obovate |
| Lateral veins | 7–12 pairs, curved | 9–11 pairs, curved | 6–9 pairs, straight |
| Flowering (in Zhuxi county) | early April to late May, flowers and leaves opening at same time (coetaneous) | mid-February to late March, flowers opening before leaves (precocious) | late February to late March, flowers and leaves opening at same time (coetaneous) or nearly so |
| Bracts | green, persistent in fruit | greenish, but brownish when dry, deciduous after anthesis | green, but brownish when dry, persistent in fruit |
| Hypanthium | campanulate, glabrous | campanulate to broadly campanulate (some cultivars), outside pilose | campanulate, outside pilose |
| Calyx lobes | reflexed, margin glandular serrate or entire | spreading or scarcely reflexed, entire | reflexed, entire |
| Petals | pink or white, 7–9 × 5–8 mm, entire, crenate or erose | pink or white, 8–13 × 3.5–9 mm, apex emarginate or 2-lobed, sinus triangular | pink during early blooming, then white to slightly pinkish tinge, 7–11 × 5–9 mm, apex 2-lobed, sinus narrowly triangular |
| Stamens | 20–30, shorter to longer than the petals | 30–50, shorter than the petals | 34–38, as long as or shorter than the petals |
| Style | pilose below the middle | glabrous | pilose below the middle |
| Drupe | ellipsoid, 7–9 × 4–5 mm, red, sweet and sour taste | globose, 9–13 mm in diam., red, rarely yellow or white (cultivars), sweet or sweet and sour taste | broadly ellipsoid, 10–12 × 8–9.5 mm, red, sweet and slightly bitter taste |

*Yu & Li (1986, p.54) recorded *P. clarofolia* as 'shrubs or small trees, 2.5–20 m tall'. '20 m' is incongruent with 'small trees' and we think it should be 12 m. Furthermore, based on specimen records and fieldwork, this species is up to 13 m tall.

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# *Indigofera vallicola* (Fabaceae), a new species from Yunnan, southwest China

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### Abstract
*Indigofera vallicola* (Fabaceae), a new species is described and illustrated. This plant is only found from two localities in the central Yunnan Province, southwest China. It is characterized by having the prostrate habit, usually 13–17-foliolate leaves and the relatively small (3–5 mm long) flowers. Morphological comparisons with its closest relatives, *I. rigioclada*, *I. franchetii*, *I. chaetodonta*, and *I. henryi* are also presented.

### Keywords
Dry-hot valley, endemism, *Indigofera rigioclada*, Leguminosae, prostrate shrub

## Introduction

The genus *Indigofera* L., comprising approximately 750 species, is the third largest genus after *Astragalus* and *Acacia* s.l. in the legume family (Fabaceae) (Schrire et al. 2005, 2009), and composes one of the 50 largest genera of angiosperms (Frodin 2004). Species of *Indigofera* are mostly shrubs, except some are small trees or herbaceous perennials or annuals. It has a near worldwide distribution; nevertheless centers of species diversity primarily occur in Africa and Madagascar (ca. 550 species), Asia, especially the temperate Sino-Himalayan region (ca. 105 species), Australia (ca. 50 species), and the New World (ca. 45 species) (Schrire et al. 2009).

China possesses a rich set of species of *Indigofera*, and the highest species diversity was found in the southwest region (Yin et al. 1992). One hundred years ago, Craib

(1913) made the first comprehensive revision of Chinese *Indigofera.* In his treatment, 57 species were recognized from China, 31 species of which were newly named. In the most recent revision by Gao and Schrire (2010) for the "Flora of China", 79 species and 9 varieties have been recognized, including 45 endemics. More recently, two additional new species of *Indigofera* were described from southwest China by Zhao and Gao (2015) and Zhao et al. (2020) respectively; these findings highlight the need for continued field exploration and taxonomical research in this area.

During recent field surveys in Yunnan Province (SW China), we came across an unknown species of *Indigofera* in the Luzhijiang valley. After detailed comparison with its morphologically similar species, it became clear that this plant represents a distinct new species.

## Materials and methods

The study followed the normal practice of plant taxonomic survey and herbarium taxonomy. Morphological studies of the new species were based on observation of living plants and specimens housed at PYU and YUKU. Digital images of type specimens of the genus *Indigofera* available at JSTOR Global Plants (http://plants.jstor.org/), as well as collections housed at CDBI, KUN, PE, PYU and YUKU, were extensively examined and compared with the new species. Pertinent taxonomic literature (e.g. Fang and Zheng 1994; Sun 2006; Gao and Schrire 2009, 2010; Chauhan et al. 2013; Clark et al. 2015) were extensively consulted. Measurements were carried out under a stereomicroscope (Olympus SZX2, Tokyo, Japan) using a ruler and a metric vernier caliper.

## Taxonomy

***Indigofera vallicola* Huan C. Wang & Jin L. Liu, sp. nov.**
urn:lsid:ipni.org:names:77299060-1
Figs 1–4

**Type.** China. Yunnan Province: Yimen County, Luzhi Town, Luzhijiang valley, Xiao Luzhi, 24°24'N, 101°34'E, alt. 1,320 m, 25 September 2021, *Huan-Chong Wang et al. YM15303* (Holotype: YUKU!; isotypes: YUKU!)

**Diagnosis.** *I. vallicola* is most similar to *I. rigioclada* Craib by sharing the procumbent habit, relatively small leaves and the similar flower shape, but it clearly differs from the latter by its usually 13–17-foliolate, flowers 3–5 mm long, calyx teeth triangular-lanceolate, and legumes 1–2 mm in diameter.

**Description.** Dwarf shrubs, usually prostrate, 20–35 cm in height. Stems branched, brown, glabrescent, usually 1–2.5 mm in diameter. Branchlets nearly terete, 10–15 cm long, with dense appressed white and brown medifixed and symmetrically

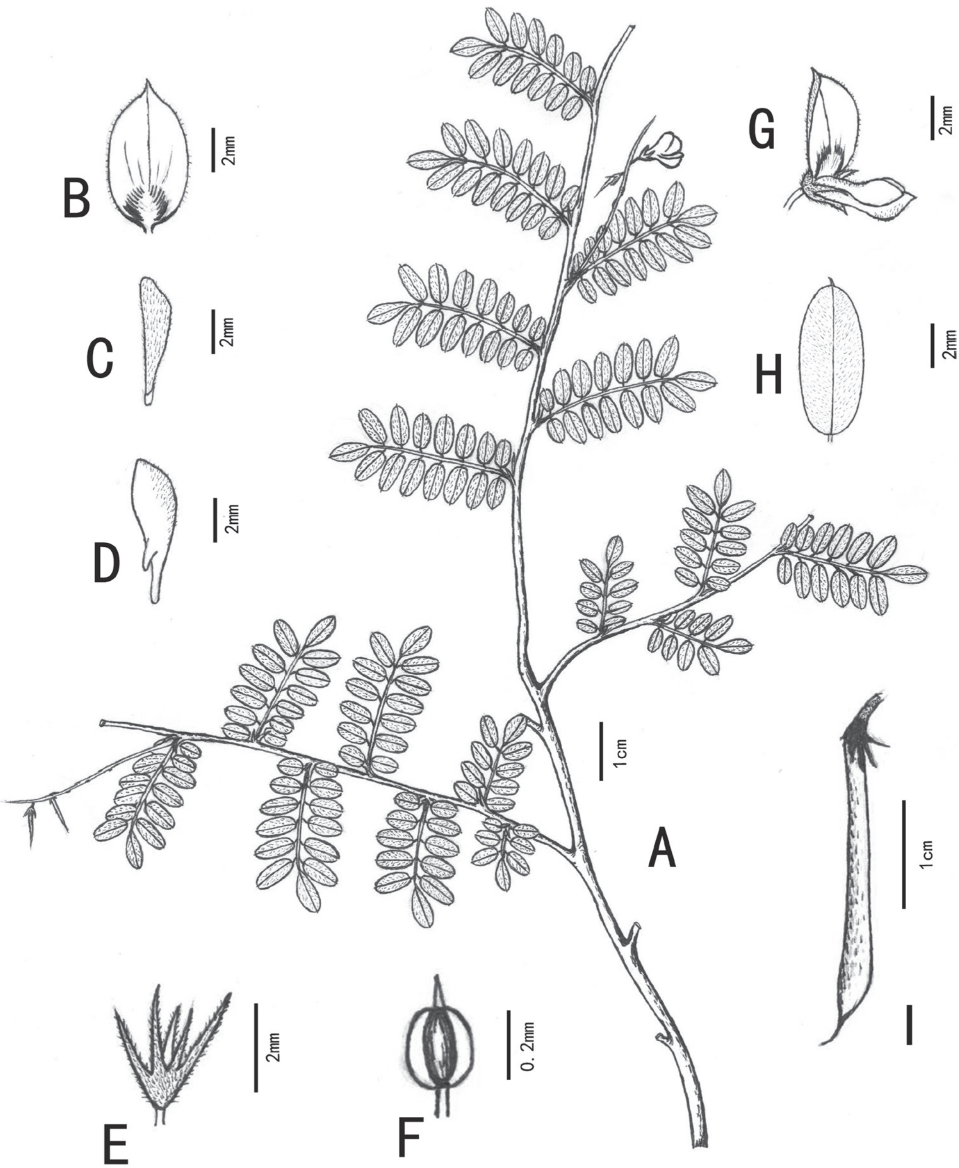


**Figure 1.** *Indigofera vallicola* Huan C. Wang & Jin L. Liu sp. nov. (Drawn by Jin-Li Liu) **A** habit **B** standard **C** wing **D** keel **E** calyx **F** anther **G** flower **H** leaflet **I** legume.

2-branched trichomes. Leaves imparipinnate, 2–5 cm long, 1–2 cm wide, usually (7–)13–17-foliolate. Stipules lanceolate to subulate, 1–2 mm long. Petioles 0.2–0.4 cm long, petioles and rachis subterete, adaxially grooved, with appressed white and brown medifixed symmetrically 2-branched trichomes. Leaflets opposite, 0.2–1.2 cm long, 0.15–0.5 cm wide, adaxially green, abaxially gray, midvein abaxially prominent and adaxially impressed, secondary veins inconspicuous, both surfaces with white and


**Figure 2.** *Indigofera vallicola* Huan C. Wang & Jin L. Liu sp. nov. **A** habit **B** a portion of branchlet showing abaxial surfaces of leaflets **C** plants in fruiting stage **D** stipules **E** a portion of inflorescens **F** calyces **G** legume. Scale bars: 10 cm (**A**); 4 cm (**C**); 1 cm (**B, G**); 4 mm (**E**); 3 mm (**F**); 1 mm (**D**).

brown medifixed symmetrically 2-branched trichomes; terminal leaflets obovate, apex rounded to truncate, and mucronate, base cuneate; lateral leaflets oblong or elliptic, apex rounded to truncate and mucronate, base rounded. Inflorescences racemose, axillary, 2.5–6 cm long. Peduncles 1–1.8 cm long. Bracts caducous, lanceolate to

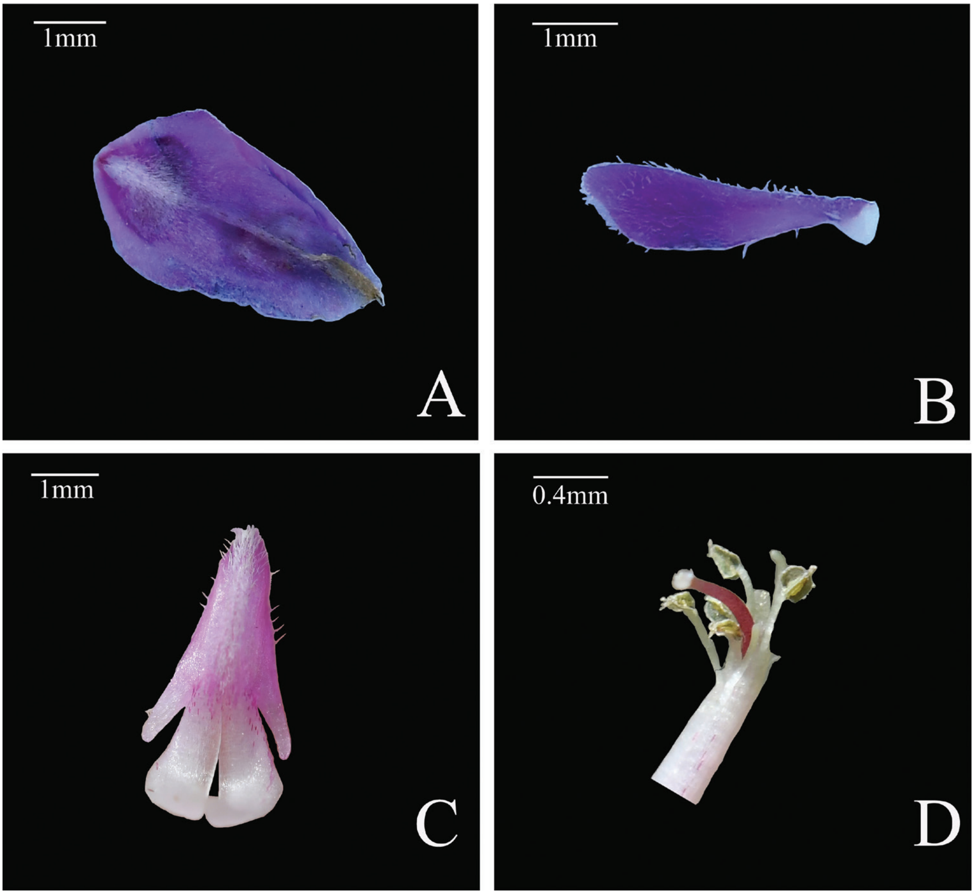


**Figure 3.** *Indigofera vallicola* Huan C. Wang & Jin L. Liu sp. nov. **A** standard **B** wing **C** keel **D** stamens and pistil.

ovate-lanceolate, purple, ca. 0.2 cm long, abaxially with white medifixed trichomes, adaxially glabrous. Pedicels 1–2 mm long. Calyx funnelform, rarely cup-shaped, purple, outside with white and brown medifixed symmetrically 2-branched trichomes, glabrous inside; tube ca. 1 mm long; teeth 5, unequal, triangular-lanceolate, ca. 1 mm long, apex acuminate. Corolla pink; standard obovate, 3–5 mm long, 2–3 mm wide, apex mucronate, outside with white medifixed trichomes; wings spoon-shaped, 2.5–4.0 mm long, ca. 1 mm wide, outside pilose; keels 3–5 mm long, ca. 1 mm wide, outside pilose, with a small lateral spur. Stamens 3–5 mm long, anthers broadly ovoid, apex mucronate. Ovary hairy, style glabrous. Legumes linear, cylindric, 1.5–3.2 cm long, 0.1–0.2 cm in diameter, apex beaked, with white and brown medifixed symmetrically 2-branched trichomes. Seeds usually 6–8, oblong to rectangle, dark-brown, glabrous, 1–2 mm long, ca. 1 mm wide.

**Phenology.** Flowering occurs from September to November, fruiting from October to December.


**Figure 4.** A specimen (YUKU-02024801) of *Indigofera vallicola* Huan C. Wang & Jin L. Liu sp. nov. collected in October 1965 from Ainishan village in Shuangbai County, southwest China.

**Distribution and ecology.** *Indigofera vallicola* is endemic to southwest China, where it has only been collected from two localities (ca. 45 km apart from each other) in central Yunnan to date: Xiao Luzhi (type locality) in Luzhijiang valley and Ainishan village in Shuangbai County. The climate in its habitat is seasonally hot and arid. In the type locality, *I. vallicola* occurs in the xerophilous scrubs or grasslands at elevations of 1200–1800 m, and its association include *Phyllanthus emblica* Linn. (Phyllanthaceae), *Paliurus orientalis* (Franch.) Hemsl. (Rhamnaceae), *Dalbergia yunnanensis* Franch. (Fabaceae), *Symphoricarpos sinensis* Rehd. (Caprifoliaceae), *Duhaldea lachnocephala* Huan C. Wang & Feng Yang (Asteraceae) (an endemic species described by Yang et al. (2022)), *Pterygiella luzhijiangensis* Huan C. Wang (Orobanchaceae), *Silene otodonta* Franch. (Caryophyllaceae), *Spodiopogon sagittifolius* Rendle (Poaceae), *Heteropogon contortus* (Linn.) Beauv. ex Roem. & Schult. (Poaceae) and *Themeda caudata* (Nees ex Hooker & Arnott) A. Camus (Poaceae).

**Etymology.** The specific epithet is taken from the Latin "*vallis*" (valley) and the suffix "*-cola*" (dweller), referring to the habitat where the new species is found.

**Additional specimens examined. China. Yunnan:** Shuangbai County, Ainishan, alt. 1,800 m, 22 October 1965, *W. M. Zhu et al. 04195* (YUKU); Yimen County, Luzhi Town, alt. 1,250 m, 20 October 1965, *W. M. Zhu et al. 4659* (YUKU); *ibid.*, 3 October 2016, *H. C. Wang et al. YM1274* (YUKU); *ibid.*, 12 November 2019, *H. C. Wang et al. YM8322* (YUKU).

**Taxonomic notes.** *Indigofera vallicola* is mainly characterized by having the prostrate habit, usually 13–17-foliolate leaves and relatively small (3–5 mm long) flowers. Morphologically, it is most similar to *I. rigioclada* Craib by sharing the procumbent habit, relatively small leaves and similar flower shape, but it clearly differs from the latter by its usually 13–17-foliolate (vs. 5–13-foliolate in *I. rigioclada*), flowers 3–5 mm (vs. 8–10 mm) long, calyx teeth triangular-lanceolate (vs. triangular), and legumes 1–2 mm (vs. larger than 2 mm) in diameter. *Indigofera vallicola* is also more or less similar to *I. henryi* Franch. in its overall appearance, relatively gracile pedicels and shape of calyx. Nevertheless, *I. henryi* clearly differs from the former in having the linear stipules usually 5 mm long (vs. lanceolate to subulate, 1–2 mm long in *I. vallicola*), leaves larger, 3–10 cm (vs. 2–5 cm) long, rachis of adaxially flattened, slightly winged (vs. grooved and without winged), leaflet blades 1.7–2.3 × 0.5–1.2 cm (vs. 0.2–1.2 × 0.15–0.5 cm), pedicels (2)3–6(–9) mm (vs. 1–2 mm) long, corolla much larger in size, white (vs. pink), with 7–9 × 5–6 mm (vs. 3–5 × 2–3 mm) standard and 7–9 mm (vs. 3–5 mm) long keels.

*Indigofera vallicola* is somewhat close to *I. franchetii* X. F. Gao & Schrire, an endemic species found from the dry-hot valleys of Jinsha River and its tributaries in southwestern China. Nevertheless, *I. franchetii* differs from *I. vallicola* in having 35–50 cm long branchlets, (11–)17–27-foliolate leaves ca. 5–10 cm long, racemes 5.5–11 cm long, peduncles 0.7–3.0 cm long, pedicels 0.5–1.0 mm long, calyces cup-shaped, standards oblong-elliptic, 7–8 mm long, legumes 2.5–4.0 cm long, 1.5–2.5 mm in diameter. The new species shows some similarities with *I. chaetodonta* Franch. in the habit, flower size, and calyx shape. However, *I. chaetodonta* is well differentiated from *I. vallicola* in having (5 or) 7- or 9-foliolate leaves 0.6–1.5 (–2.0) cm long, leaflet blades oblong to oblanceolate, 3.5–6 × 1.5–2.5 mm, adaxially nearly glabrous, standards broadly elliptic, 5–7 × ca. 4 mm, legumes 1.5–2.0 cm long, glabrous or with sparse appressed medifixed trichomes.

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# *Mazus danxiacola* (Mazaceae), a distinct new species endemic to Danxia landform in Jiangxi Province, eastern China

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## Abstract
*Mazus danxiacola*, a new species endemic to Danxia landform in east Jiangxi Province, eastern China, is described and illustrated. The systematic placement of this new species was confirmed by molecular phylogenetic analyses based on four plastid markers (*matK*, *rbcL*, *rps16* and *trnL-trnF*) and nuclear ribosome ITS sequence, and its specific relationships within *Mazus* were discussed. Morphologically, the new species is clearly different from other *Mazus* species by having a series of uncommon traits, i.e., annual habit, without stolons and basal leaves, single, erect and unbranched stems, long petiolate leaves abaxially grayish green to silver gray, truncate to broadly cuneate leaf bases, racemes extremely elongated up to 35 cm long, white corolla, and palate densely covered by conspicuous clavate gland-like hairs. The new species is assigned to Critically Endangered (CR) according to the IUCN Red List Categories and Criteria.

## Keywords
cpDNA, Lamiales, molecular phylogenetics, morphology, nrITS

## Introduction

Mazaceae (Reveal 2011) is a newly established small family that was separated from the traditionally circumscribed Scrophulariaceae (e.g., Von Wettstein 1891; Thieret 1967; Fischer 2004). There are four genera currently recognized in the family: *Dodartia* L., *Lancea* Hook.f. & Thomson, *Mazus* Lour, and *Puchiumazus* Bo Li, D.G. Zhang & C.L. Xiang (Stevens 2001 onwards; Xiang et al. 2021). Among these, *Dodartia*, *Lancea* and *Puchiumazus* contains only sole or two species (Fischer 2004; Deng et al. 2019; Xiang et al. 2021), while *Mazus* includes 37 accepted species which are distributed mainly in Asia to Australasia (POWO 2022). Nearly all species of *Mazus* are annual or perennial herbs (Hong et al. 1998; Deng et al. 2016), except the *M. fruticosus* Bo Li, D.G. Zhang & C.L. Xiang which was recently described as a new species having a shrubby habit (Xiang et al. 2021). *Mazus* is characterized by a combination of morphological characters: a strongly two-lipped corolla (3/2-bilabiatae), a palate with two longitudinal plaits and a capsule enclosed in a persistent calyx (Fischer 2004; Deng et al. 2019). In China, 25 species and three varieties were recorded in the *Flora of China* (*FOC*, Hong et al. 1998), but new species were continuously reported since the publication of the *FOC*, i.e., *M. tainanensis* T.H. Hsieh (Hsieh 2000), *M. sunhangii* D.G. Zhang & T. Deng (Deng et al. 2016), *M. somggangensis* S.S. Ying (Ying 2019), *M. fruticosus* (Xiang et al. 2021), etc., indicating that there is probably a hidden diversity of *Mazus* in China that needs to be revealed.

In 2021, during a special botanical survey for the Danxia landforms in Jiangxi Province, eastern China, the authors encountered two populations of an unusual species of *Mazus* in Guixi City, eastern Jiangxi. The unknown plant is an annual herb having a single erect unbranched stem, no rosulate basal leaves, stem leaves many and alternate with long petioles up to 4.5 cm, abaxial leaf surface grayish green to silver gray, raceme extremely elongated up to 35 cm and densely pubescent and glandular hairs, white corolla with the palate densely covering conspicuous and clavate gland-like hairs (Fig. 1). After checking and comparing the plant with all known congeneric taxa, we conclude that it represents a distinct undescribed new species of *Mazus*, *M. danxiacola*, which is described in the present study.

## Materials and methods

Field investigations were carried out in Danxia mountains of Guixi City, Jiangxi Province from May to October in 2021. Voucher specimens in flowering and fruiting were collected in the field in June and August, respectively. All specimens were deposited in the herbarium of Shanghai Chenshan Botanical Garden (CSH) and voucher photos taken *in situ* were deposited in the "Chinese Field Herbarium" (https://www.cfh.ac.cn/album/ShowSpAlbum.aspx?spid=94285).

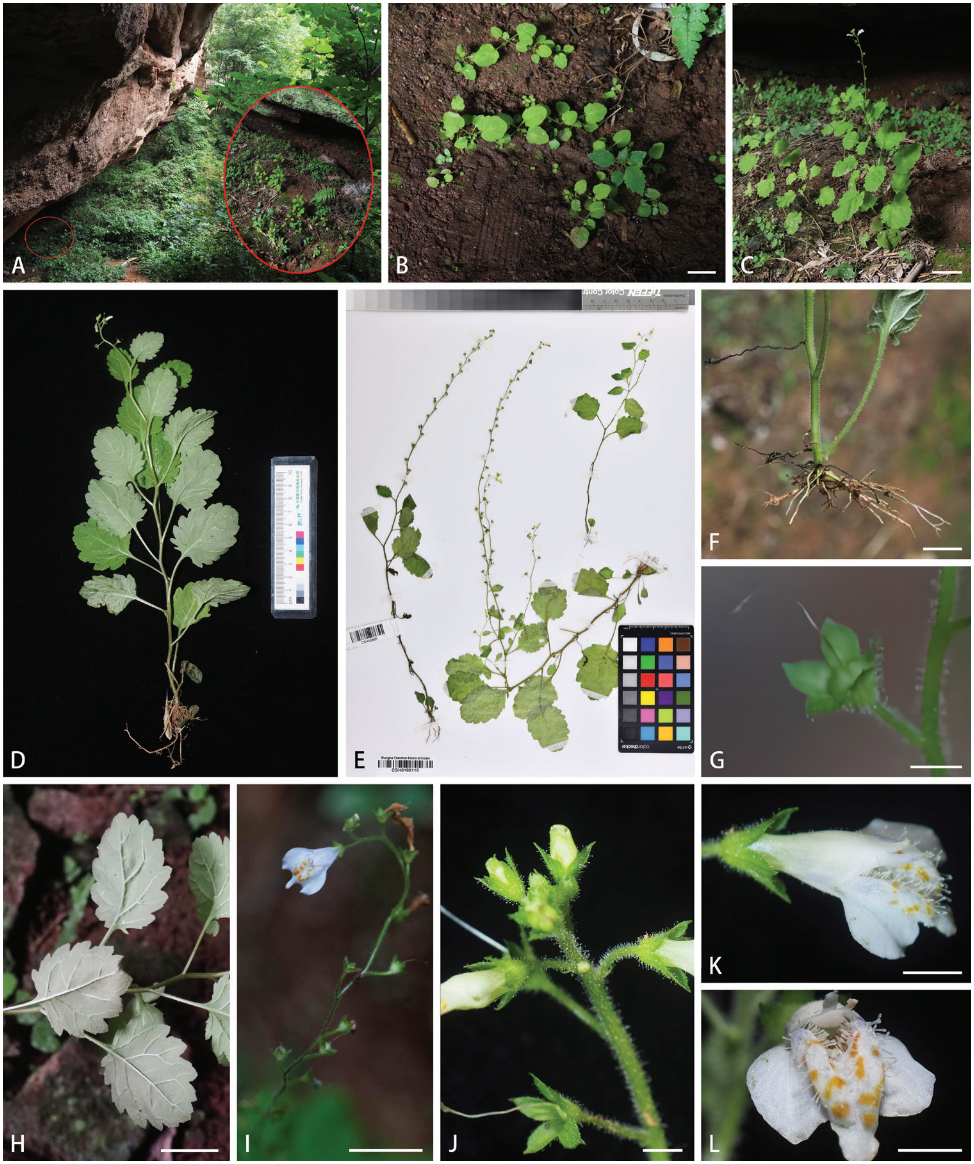


**Figure 1.** Morphology of *Mazus danxiacola* sp. nov. **A** habitat **B** seedlings **C** habit **D** a flowering individual **E** fruiting specimens **F** roots **G** fruit **H** leaves **I** a mature inflorescence with flowers and fruits **J** young inflorescence, showing dense pubescence and glandular hairs **K** flower (lateral view) **L** palate, showing the conspicuously long and clavate gland-like hairs. Scale bars: 2 cm (**B, H**); 5 cm (**C**); 1 cm (**F, I**); 2 mm (**G, J, K, L**).

The morphological description of the putative new species was conducted based on observations and measurements of mature plants in field as well as specimens. Measurements were taken using a ruler and a vernier caliper. Herbarium specimens of other

*Mazus* species in China were examined via the Chinese Virtual Herbarium (https://www.cvh.ac.cn/) and National Specimen Information Infrastructure (http://www.nsii.org.cn/2017/home.php) platforms. High resolution images of the type specimens of *Mazus* were consulted on JSTOR Global Plants (http://about.jstor.org/). The conservation status of the new species was evaluated based on the guidelines of the IUCN Red List categories and criteria (IUCN 2022).

In order to confirm the systematic placement of the putative new species within *Mazus*, molecular phylogenetic analyses were conducted following the procedures presented in Xiang et al. (2021). The combined cpDNA dataset (*matK*, *rbcL*, *rps16* and *trnL-trnF*) and the nrITS dataset used in Xiang et al. (2021) were employed with the addition of two individuals (*B.Chen CB06425* and *B.Chen CB05735*) of the putative new species. The two datasets were simplified and adjusted to set the species of *Mazus* as ingroups (22 and 17 species in cpDNA and nrITS datasets, respectively) and *Dodartia orientalis* L. and *Lancea tibetica* Hook. f. & Thomson were selected as outgroups based on previous phylogenies (Deng et al. 2019; Xiang et al. 2021). Methods of DNA extraction, amplification, sequencing, and phylogenetic analyses using maximum likelihood (ML) and Bayesian inference (BI) follow those presented in Deng et al. (2019) and Xiang et al. (2021). Voucher information and GenBank accession numbers for taxa used in this study are provided in Table 1.

## Results

### Phylogenetic analysis

The combined cpDNA dataset has 25 aligned sequences and comprise 3851 characters (860 bp for *matK*, 1267 bp for *rbcL*, 837 bp for *rps16*, and 887bp for *trnL-trnF*, respectively), of which 327 are variable (8.49%) and 225 are parsimony-informative (5.84%). The nrITS dataset has 20 sequences with the aligned length of 609 bp, of which 176 are variable (28.90%) and 142 are parsimony-informative (23.32%). Phylogenetic analyses based on the two datasets were conducted separately because the taxon sampling is different in these datasets. ML and BI trees generated from each dataset yielded similar topologies, thus only the ML trees are presented (Figs 2, 3). In all analyses, the monophyly of *Mazus* was strongly supported (Figs 2, 3; cpDNA tree: ML-BS=100%, BI-PP=1.00; nrITS tree: ML-BS=100%, BI-PP=1.00; all values reported in this order below), and the two individuals of *M. danxiacola* formed a highly supported clade (99%, 1.00; 99%, 0.99), which was consistently nested within *Mazus* in both cpDNA and nrITS trees. However, specific relationships within the genus were not fully resolved. In the cpDNA tree, *M. danxiacola* was sister to *M. fauriei* Bonati with moderate supports (Fig. 2; 83%, 0.99), while in the nrITS tree, *M. danxiacola* was sister to a clade comprising *M. pumilis* (N.L. Burman) Steenis and *M. gracilis* Hemsl. (100%, 1.00), and they together obtained highly supported values (100%, 1.00).

**Table 1.** Taxa, GenBank accession numbers of DNA sequences, and their vouchers used in this study. Newly sequenced taxa are shown in bold, and missing data are indicated by a dash (-).

| Taxa | matK | Voucher | rbcL | voucher | rps16 | voucher | trnL-F | voucher | ITS | voucher |
|---|---|---|---|---|---|---|---|---|---|---|
| *Dodartia orientalis* L. | MK392230 | *XZ-2008-1* | JQ342984 | *XZ-2008-1* | JQ342982 | *XZ-2008-1* | JQ342981 | *XZ-2008-1* | JQ342980 | *XZ-2008-1* |
| *Lancea tibetica* Hook. f. & Thomson | MF786907 | *Tibet-MacArthur2276* | MF786661 | *Tibet-MacArthur2276* | FJ172699 | *XZ-2007-0525* | FJ172685 | *XZ-2007-0525* | FJ172736 | *XZ-2007-0525* |
| *Mazus alpinus* Masam. | MK266256 | *Sunhang11307* | KX783481 | *Sunhang11307* | KX783501 | *Sunhang11307* | KX783520 | *Sunhang11307* | MK192641 | *Sunhang11307* |
| *M. caducifer* Hance | MK266277 | *KUN35025* | KX783477 | *KUN35025* | KX783497 | *KUN35025* | KX783516 | *KUN35025* | MK192664 | *KUN35025* |
| *M. celsioides* Hand.-Mazz. | – | – | KX783486 | *YIF0093* | MK266366 | *YIF0093* | KX783525 | *YIF0093* | – | – |
| ***M. danxiacola* Bo Li & B. Chen 1** | **ON323563** | ***CB06425*** | **ON323565** | ***CB06425*** | **ON323567** | ***CB06425*** | **ON323569** | ***CB06425*** | **ON286711** | ***CB06425*** |
| ***M. danxiacola* Bo Li & B. Chen 2** | **ON323564** | ***CB05735*** | **ON323566** | ***CB05735*** | **ON323568** | ***CB05735*** | **ON323570** | ***CB05735*** | **ON303604** | ***CB05735*** |
| *M. fauriei* Bonati | – | – | KX783479 | *Sunhang11248* | KX783499 | *Sunhang11248* | KX783518 | *Sunhang11248* | LC034207 | *HUP97* |
| *M. gracilis* Hemsl. | – | – | FJ172729 | *XZ-2007-058* | FJ172701 | *XZ-2007-058* | FJ172687 | *XZ-2007-058* | FJ172738 | *XZ-2007-058* |
| *M. fruticosus* Bo Li, D.G. Zhang & C.L. Xiang | MK266261 | *zdg4447* | KX783470 | *zdg4447* | KX783490 | *zdg4447* | KX783509 | *zdg4447* | MK192660 | *zdg4447* |
| *M. humilis* Hand.-Mazz. | – | – | – | – | MK266367 | *dt149* | MK266421 | *dt149* | MK192667 | *dt149* |
| *M. longipes* Bonati | MK266267 | *Deng1941* | KX783474 | *Deng1941* | KX783494 | *Deng1941* | KX783513 | *Deng1941* | MK192652 | *Deng1941* |
| *M. miquelii* Makino | NC_056339 | *Zeng et al. (2021)* | NC_056339 | *Zeng et al. (2021)* | NC_056339 | *Zeng et al. (2021)* | NC_056339 | *Zeng et al. (2021)* | LC027734 | *Maruyama:sn* |
| *M. novaezeelandiae* W.R. Barker | MK266278 | *dtA68* | KX783469 | *dtA68* | KX783489 | *dtA68* | KX783508 | *dtA68* | MK192676 | *dtA68* |
| *M. omeiensis* H.L. Li | MK266252 | *nie1976* | KX807209 | *nie1976* | KX807203 | *nie1976* | KX807208 | *nie1976* | MK192636 | *nie1976* |
| *M. procumbens* Hemsl. | MK266261 | *zdg6074* | KX783478 | *zdg6074* | KX783498 | *zdg6074* | KX783517 | *zdg6074* | MK192647 | *zdg6074* |
| *M. pulchellus* Hemsl. | – | – | KX783472 | *dt093* | KX783492 | *dt093* | KX783511 | *dt093* | MK192638 | *dt093* |
| *M. pumilio* R. Br. | MK266277 | *Pagest.s.n.2021829* | KX783468 | *Pagest.s.n.2021829* | KX783488 | *Pagest.s.n.2021829* | KX783507 | *Pagest.s.n.2021829* | MK192671 | *Pagest.s.n.2021829* |
| *M. pumilus* (Burm. f.) Steenis | MK266259 | *XZ-2007-051* | FJ172728 | *XZ-2007-051* | FJ172700 | *XZ-2007-051* | FJ172686 | *XZ-2007-051* | FJ172737 | *XZ-2007-051* |
| *M. pumilus var. delavayi* (Bonati) T.L. Chin ex D.Y. Hong | MK266257 | *Sunhang11459* | KX783482 | *Sunhang11459* | KX783502 | *Sunhang11459* | KX783521 | *Sunhang11459* | – | – |
| *M. radicans* Cheesman | – | – | KT626738 | *CHR618785* | MK266381 | *CHR618785* | – | – | MK192635 | *CHR618785* |
| *M. spicatus* Vaniot | MK266251 | *XZ-2007-0514* | FJ172730 | *XZ-2007-0514* | FJ172703 | *XZ-2007-0514* | FJ172689 | *XZ-2007-0514* | FJ172740 | *XZ-2007-0514* |
| *M. sunhangii* D.G. Zhang & T. Deng | – | – | KX783484 | *zdg4142* | KX783504 | *zdg4142* | KX783523 | *zdg4142* | – | – |
| *M. surculosus* D. Don | – | – | KX783473 | *KUN0472212* | KX783493 | *KUN0472212* | KX783512 | *KUN0472212* | – | – |
| *M. xiuningensis* X.H. Guo & X.L. Liu | NC_056340 | *Zeng et al. (2021)* | NC_056340 | *Zeng et al. (2021)* | NC_056340 | *Zeng et al. (2021)* | NC_056340 | *Zeng et al. (2021)* | – | – |

## Taxonomic treatment

### *Mazus danxiacola* Bo Li & B. Chen, sp. nov.

urn:lsid:ipni.org:names:77299061-1
Fig. 1

**Diagnosis.** This species is distinct from all currently known congeneric species and could be easily distinguishable by its annual habit, single, erect and unbranched stems, long petiolate leaves with truncate to broadly cuneate base and grayish green to silver gray lower surface, terminal racemes up to 35 cm long, white corolla with the palate densely covering conspicuous clavate gland-like hairs and having no stolons and basal leaves.

**Type.** China. Jiangxi Province: Guixi City, Liukou town, under the cliffs of Danxia mountains, alt. 75m a.s.l., 12 June 2021, *Bin Chen CB05735* (holotype CSH!, barcode CSH0186434; isotypes CSH!, barcode CSH0186431, CSH0186433, CSH0118470); in the same location of holotype, 24 August 2021, *Xingui Le & Lin Xu CSH42465* (paratype CSH!, barcode CSH0188116).

**Description.** Annual herbs, 15–65 cm tall, without stolons. Primary roots thick and strong; adventitious roots numerous, shotting from the stem base, white and slightly freshy. Stems single, erect, unbranched, terete; old stems purplish brown, sparsely puberulent; young stems grayish green, densely villous and sparsely glandular hairy. Leaves all cauline, numerous, alternate, long petiolate, larger at middle of stem; petioles densely puberulent to subglabrous, 1.5–4.5 cm long; leaf blade broadly ovate to suborbicular, membranous, 2.5–5.3 × 2.3–4.8 cm, adaxially green, subglabrous to sparsely puberulent, abaxially grayish green to silver gray, subglabrous, densely villous on veins, apex obtuse to rounded, base truncate to broadly cuneate, margin crenate, teeth apices callous, sometimes with 1 or 2 pairs of lobes near base; veins conspicuous on both surface, elevated abaxially, fluted adaxially. Racemes terminal or occasionally axillary on the top 1–3 nodes, shortened when young but elongated up to 35 cm long when fruiting, lax, multiflowered; pedicels slender, 0.8–2.5 cm long, densely villous and glandular hairy. Calyces broadly campanulate, 3.0–4.0 mm long, 5-veined, densely villous and glandular hairy outside, subglabrous inside; lobes 5, ovate-triangular, longer than the tube, apex acute, midrib conspicuous, lateral veins inconspicuous. Corolla white, dotted yellow on palate, 0.9–1.2 cm long, sparsely minutely puberulent to glabrous outside, tube cylindric, 0.4–0.6 cm long, exserted from calyx; limb 2-lipped, upper lip bilobed, upwarp, lobes lanceolate; lower lip trilobed, middle lobe narrowly ovate, ca. 1.5 mm long, smaller than lateral lobes, lateral lobes spreading away from middle lobes, broadly ovate to rectangular; palate comprising 2 longitudinal elevations extending from point of filament fusion to base of lower lobes, densely covered by gland-like hairs, hairs clavate and conspicuous, ca. 0.7 mm long, white to transparent. Stamens 4, didynamous, glabrous, inserted at the same level in distal part of tube, included; anterior pair longer, curved, appressed to corolla tube, posterior pair spreading; anthers bithecal, positioned adjacent to corolla tube on upper lip; filaments filiform, glabrous. Styles 0.4–0.5 cm long, included, exserted beyond anthers, stigma 2-lamellate. Capsule globose, ca. 2.5 mm in diam, apex rounded, included by persistent calyx.

**Phenology.** Flowering was observed from early June to late August and fruiting from June to late September.

**Distribution and habitat.** The species is currently known only from the type locality of Danxia mountains in Liukou Town of Guixi City, eastern Jiangxi Province, China (Fig. 4), and grows under shaded cliffs and near the edges of subtropical evergreen broad-leaved forests, at an elevation about 75 m a.s.l. (Figs 1A, 5).

**Etymology.** The specific epithet "*danxiacola*" refers to the species inhabiting in Danxia landform.

**Vernacular name.** Simplified Chinese: 丹霞通泉草; Chinese pinyin: Dān Xiá Tōng Quán Cǎo.

**Provisional conservation status.** Based on our special botanical surveys for Danxia landforms in Jiangxi Province in 2021, *M. danxiacola* has been discovered only from one single locality so far in Liukou Town of Guixi City in Jiangxi Province, China, and 2 populations were found in the locality, which totally occupied ca. 200 m$^2$. In these populations, a total of ca. 80 fruiting individuals were counted in August 2021 and there were a lot of seedlings in each of the population when we firstly encountered


**Figure 2.** Maximum Likelihood phylogram of *Mazus* as inferred from analysis of combined dataset of *matK*, *rbcL*, *rps16* and *trnL-trnF*. Support values ≥ 50% BS or 0.90 PP are displayed above and below the branches, respectively.

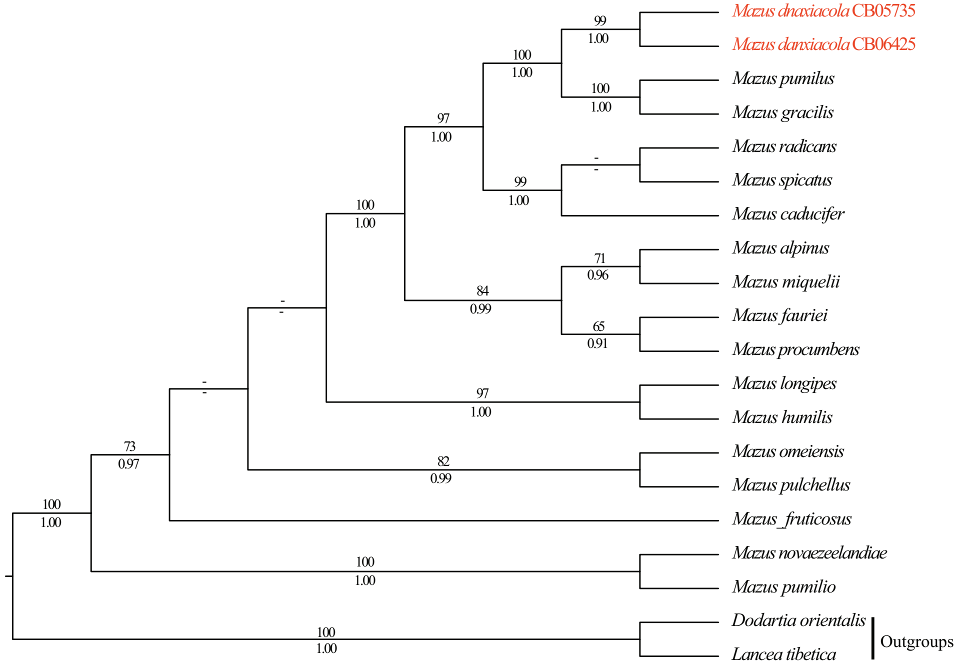


**Figure 3.** Maximum Likelihood phylogram of *Mazus* as inferred from analysis of nrITS dataset. Support values ≥ 50% BS or 0.90 PP are displayed above and below the branches, respectively.

the species in June 2021 (Fig. 1B, C), indicating that the species has a well-developed reproductive strategy in the habitat of Danxia landform. However, the locality is close to downtown of Guixi City, has not been projected to a nature reserve yet and all populations are obviously facing man-made interferences, such as deforestation, touring and grazing, we thus propose to categorize the species as critically endangered (CR) under criteria B and D following IUCN Red List Categories (IUCN 2022).

**Taxonomic note.** Morphologically, *M. danxiacola* bears a series of rare traits which are not common in *Mazus*, such as annual habit, single erect unbranched stems, without basal leaves, stem leaves many and alternate, extremely long petioles up to 4.5 cm, abaxial leaf surface grayish green to silver gray, and palate of corolla densely covered by conspicuously clavate gland-like hairs. The combination of these traits makes *M. danxiacola* distinct from all other congeneric taxa. Our molecular phylogenetic analyses based on cpDNA dataset indicated that *M. fauriei* may be closely related to *M. danxiacola* (Fig. 2), but *M. fauriei* is a perennial herb with all leaves basal and rosulate and petioles broadly winged (Hong et al. 1998), which is apparently different from *M. danxiacola* that has only cauline leaves and long unwinged petioles. In the nrITS trees, *M. pumilis* and *M. gracilis* were shown as possible alliances of *M. danxiacola*, however, cauline leaves of the former two species are always opposite, and their basal and cauline leaves are all decurrent to form short

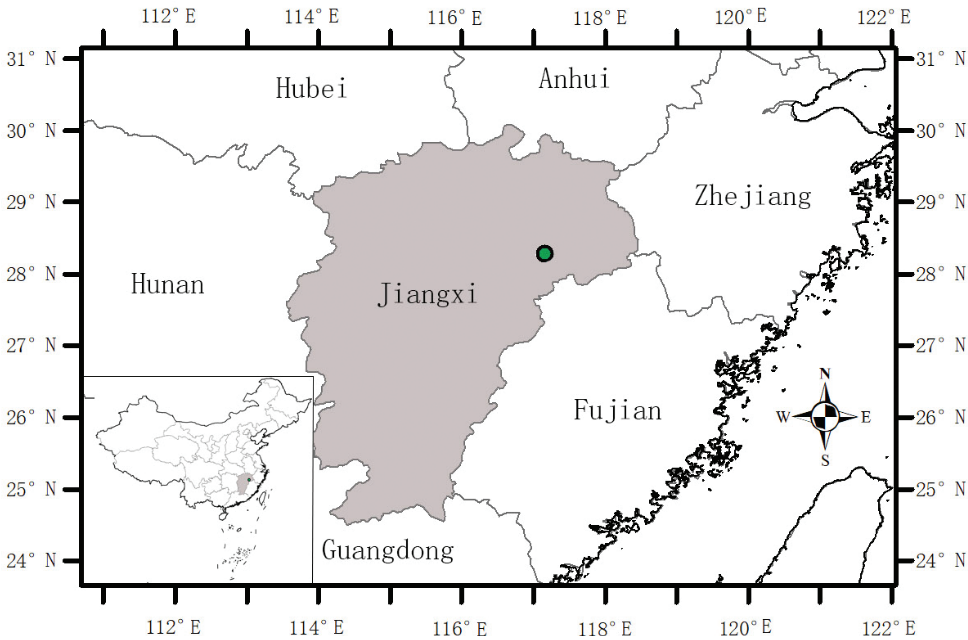


**Figure 4.** Distribution map of *Mazus danxiacola* sp. nov.

petioles (Hong et al. 1998), clearly differing from those alternate and long petiolate leaves of *M. danxiacola*. It is worth mentioning that there are obvious conflicts between the cpDNA and nrITS phylogenies which have been discovered and discussed in a previous study (Xiang et al. 2021). In fact, the available molecular data of *Mazus* were not sufficient enough to represent all known species of the genus, thus it is hard to definitely confirm the closest relatives of *M. danxiacola* at the moment through molecular phylogenetics. Future molecular studies including more species at population level and using more DNA markers may shed light on the determination of specific relationships within *Mazus*.

So far, *M. danxiacola* is the first species of *Mazus* that was found to be endemic to Danxia landform. Danxia landform is a unique type of petrographic geomorphology found in southeast, southwest, and northwest China with a high level of floral endemism (Liu et al. 1999; Liu and Liu 2003; Luo et al. 2010). In southeast China, Danxia landforms are well developed in Guangdong, Fujian, Jiangxi, and Hunan provinces, and the special environment, including deep valleys, grooves, moist caves, cliffy rocks, dry cliff-tops and shaded rock bottoms (Fig. 5), has significant effects on the growth of special plants (Chen et al. 2008). Just in the last ten years, a lot of new taxa have been continuously discovered from Danxia mountains of these provinces, i.e., *Danxiaorchis* J.W. Zhai, F.W. Xing & Z.J. Liu (Zhai et al. 2013), *Spiradiclis danxiashanensis* R.J. Wang (Wang et al. 2015), *Viola hybanthoides* W.B. Liao & Q. Fan (Fan et al. 2015), *Begonia danxiaensis* D.K. Tian & X.L. Yu (Tian et al. 2019),

**Figure 5.** Danxia landform of the type locality of *Mazus danxiacola* sp. nov. (left) and the habitat of the new species under a cliff (right). Arrows show where the population could be found.

*Phyllostachys danxiashanensis* N.H. Xia & X.R. Zheng (Zheng et al. 2019), *Semiaquilegia danxiashanensis* L. Wu, J.J. Zhou, Qiang Zhang & W.S. Deng (Zhou et al. 2019), *Lespedeza danxiaensis* Q. Fan, W.Y. Zhao & K.W. Jiang (Zhao et al. 2021), *Asplenium danxiaense* K.W. Xu et al. (2022), etc., indicating that it is valuable to strengthen the flora investigations in Danxia landforms and uncover the biodiversity.

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# An updated checklist of liverworts and hornworts of Malaysia

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**Abstract**

An updated checklist of the liverworts and hornworts of Malaysia accepts 773 species and 31 infraspecific taxa of liverworts, in 120 genera and 40 families, and 7 species of hornworts (6 genera, 3 families). The largest family is Lejeuneaceae with 312 species in 30 genera, accounting for 40% of the total number of species. The largest genera are *Cololejeunea*, *Bazzania* and *Frullania* with 90, 61 and 55 species, respectively. The greatest number of species has been recorded from Sabah with 568 species, followed by Pahang and Sarawak with 338 and 265 species, respectively.

**Keywords**

Bryophytes, checklist, hornworts, liverworts, Malaysia, species

## Introduction

The country of Malaysia consists of two separate regions, Peninsular Malaysia in the West, being part of the Asian mainland, and the states of Sabah and Sarawak on the island of Borneo in the East. Physiogeographically, the two regions are characterized by hills and mountain ranges. On Peninsular Malaysia, mountain ranges cover about one-third of the total land surface, running parallel to the long axis of the peninsula. They include Titiwangsa Range (the main range), Bintang Range, Nakawan Range, Kedah-Singgora Range, Keledang Range, Benom Range, Tahan Range and Pantai Timur Range. Many of them rise to 2000 m and about 23% of the land lies above 300 m (Wyatt-Smith, 1963; Mohamed and Tan 1988). Mount Tahan (2189 m) in Titiwangsa Range, at the border with Thailand, is the highest peak on the peninsula. The rest of the area consists of coastal plains and alluvial terraces, usually extending 15 to 65 km inland from the coast, as well as riverine flood plains.

Sabah's highlands include Crocker Range, Trus Madi Range, Witti Range, Maitland Range and Brassey Range. Among these, Crocker Range is the longest and highest mountain range, rising to 4095 m on Mt Kinabalu, being the highest mountain of Malaysia and of Southeast Asia. Those of Sarawak are Tama Abu Range, Iran Mountains, Hose Mountains, Kapuas Hulu Range and Kelinkang Range. The physiographies of these two states are somewhat different. Only a small proportion of the land of Sabah consists of lowland, including coastal plains and river valleys. Sarawak, in contrast, has more low-lying, flat lands and swampy coastal areas. Both states, however, have steep undulating hills and mountains in the interior parts, acting as a barrier against inland penetration.

## Climate

Malaysia is located near the Equator and experiences a humid tropical climate with constant temperatures, high humidity and copious rainfall. Rainfall distribution is usually seasonal dependent on wind flow patterns and physiogeography (Malaysian Meteorological 2021). Generally, the East Coast states of Peninsular Malaysia receive high rainfall almost throughout the year with June and July being the driest months. The remaining states (except for the southwest coastal region) have two maximum rainfall periods (October-November and April-May) that are separated by drier periods (Malaysian Meteorological 2021). The country is subjected to four monsoonal seasons each year: northeast monsoon, southwest monsoon and two shorter inter-monsoon periods. The northeast monsoon normally occurs from November to March and the southwest monsoon during May or early June to September.

## Vegetation and flora

The vegetation of Malaysia can be classified into different types based on climate and soil. Climatic vegetation types include evergreen and semi-evergreen lowland rainforest, lower montane forest and the upper montane forest, while the edaphic types include heath vegetation, limestone forest, beach vegetation, mangrove forest, brackish water vegetation, peat swamp forest, freshwater swamp forest and riparian vegetation (Symington 2004). In lowland and hill areas, dipterocarp forests are the most prominent forest type (Ashton 1995; Saw 2010). Malaysia has a very rich flora that is made up of Sundaic and mainland Asiatic floristic elements in Peninsular Malaysia and of Sundaic elements with many local endemics on the island of Borneo (Saw and Chung 2015).

The Malaysian rainforests stand out by their very high species diversity (e.g., Austin et al. 1973; Baillie and Ashton 1983; Baillie et al. 1987; Saw and Chung 2015), as well as by intricate stratification and regeneration dynamics patterns that have been the subject of numerous major studies by specialists from all over the world (e.g., Burgess 1961, 1975; Denslow 1987; Ashton and Hall 1992; Manokaran et al. 1992; Saiful and Latiff 2017).

### Malaysian liverwort and hornwort flora

The first checklist of liverworts and hornworts of Malaysia, recognizing 727 species and 37 infraspecific taxa in 127 genera and 39 families, was published by Chuah-Petiot (2011). Lee et al. (2018) presented a review of the history of liverwort exploration in Malaysia and the more recent papers on Malaysian liverworts, and further additions to the liverwort flora were published by Pócs et al. (2020), Pesiu et al. (2021) and Sarimi et al. (2021). A manual of the genera of liverworts and hornworts of Malaysia has been prepared by Lee and Gradstein (2021). The present paper provides an updated checklist of liverworts and hornworts of Malaysia based on a compilation of the published literature and a critical revision of the nomenclature of the taxa and new synonymy, resulting from taxonomic revisions. The updated checklist accepts 773 species and 31 infraspecific taxa in 120 genera in 40 families of liverworts, and 7 species (3 families, 6 genera) of hornworts. The largest family is Lejeuneaceae with 312 species in 30 genera, accounting for 40% of the total number of liverwort species. The largest genera are *Cololejeunea*, *Bazzania* and *Frullania* with 90, 61 and 55 species, respectively. Genera with more than ten species include *Lejeunea* (40), *Plagiochila* (35), *Radula* (34), *Colura* (27), *Drepanolejeunea* (26), *Cheilolejeunea* (24), *Riccardia* (19), *Lepidozia* (18), *Acromastigum* (16), *Leptolejeunea* (16), *Thysananthus* (16), *Solenostoma* (15), *Lopholejeunea* (12), *Heteroscyphus* (13) and *Anastrophyllum* (10). Forty eight genera have fewer than 10 species (e.g., *Acrolejeunea*, *Andrewsianthus*, *Cephalozia*, *Ceratolejeunea*, *Diplasiolejeunea*, *Kurzia*, *Marchantia*, *Microlejeunea*, *Metzgeria*, *Odontoschisma*, *Schistochila*, *Syzygiella*, *Trichocolea* and *Tricholepidozia*) and 54 are represented only by a single species, such as *Acroscyphella*, *Balantiopsis*, *Conoscyphus*, *Eotrichocolea*, *Haplomitrium*, *Jubula*, *Kymatocalyx*, *Mastigopelma*, *Metalejeunea*, *Mesoptygia*, *Nardia*, *Pictolejeunea*, *Soella*, *Southbya*, *Treubia*, *Triandrophyllum*, *Tritomaria* and the five genera of hornworts. Sabah has the largest number of species with 568 recorded species, followed by Pahang and Sarawak with 338, 265, respectively (Table 1).

## An updated checklist of liverworts and hornworts of Malaysia

The nomenclature follows Söderström et al. (2016) with updates. For explanation of some of the new nomenclature, see Lee and Gradstein (2021). In taxon authorities, only the name of the validating author is cited and “ex” authors are omitted for brevity and because their citation is not obligatory. Reports from Malaysia that are only based on secondary information (= papers dealing with liverworts of other regions (not Malaysia) and citing 'Malaya', 'Malaysia', 'Malay Peninsular', 'Malacca' etc. in the section on species distribution) and are not supported by direct evidence, are omitted. Similarly, records based on doubtful identifications ("cf.", "aff.") are not taken into account. Furthermore, we have omitted all reports citing only "Borneo" unless there is evidence that the record was from Malaysia (Sarawak, Sabah). For example, species reported by Stephani from Borneo based on material collected by Everett (e.g., *Bazzania fleischeri* (Steph.) Abeyw., *B. inaequitexta* Steph., *Plagiochila borneensis* Steph., *P. kuhliana* Sande Lac.) are included in the checklist because these Everett collections are presumably from Sarawak (Menzel 1988).

**Table 1.** The number of recorded species of liverworts and hornworts per state in Malaysia.

| State | Number of species | | |
|---|---|---|---|
| | Liverworts | Hornworts | Total |
| Sabah | 565 | 3 | 568 |
| Pahang | 334 | 4 | 338 |
| Sarawak | 263 | 2 | 265 |
| Penang | 95 | – | 95 |
| Perak | 82 | 1 | 83 |
| Johor | 81 | – | 81 |
| Terengganu | 62 | – | 62 |
| Kedah including Langkawi | 59 | 1 | 60 |
| Selangor | 48 | – | 48 |
| Negeri Sembilan | 44 | – | 44 |
| Kelantan | 35 | – | 35 |
| Malacca | 11 | – | 11 |
| Perlis | 5 | – | 5 |

## Liverworts (Marchantiophyta)

***Acrobolbus ciliatus*** (Mitt.) Schiffn. – Kodama and Narita (1974). Sabah.

***Acrobolbus saccatus*** (Hook.) Briscoe – Kitagawa and Kodama (1974 as *Tylimanthus saccatus*). Sabah.

***Acrolejeunea arcuata*** (Nees) Grolle et Gradst. – Kodama and Kitagawa (1974 as *Ptychocoleus coroniformis*), Gradstein (1975), Kürschner (1990), Lee et al. (2013), Renner (2013), Wang et al. (2014b), Cheah (2017). Pahang, Sabah.

***Acrolejeunea crassicaulis*** (Steph.) J.Wang bis et Gradst. – Mizutani (1989 as *Trocholejeunea crassicaulis*), Gradstein et al. (2002 as *T. crassicaulis*), Wang et al. (2014a). Sabah.

***Acrolejeunea fertilis*** (Reinw., Blume et Nees) Schiffn. – Verdoorn (1933 as *Ptychocoleus wichurae*, 1934a as *P. fertilis*), Mizutani (1969 as *P. fertilis*), Gradstein (1975), Lee et al. (2013). Penang, Perak, Pahang, Sabah.

***Acrolejeunea pycnoclada*** (Taylor) Schiffn. – Schiffner (1898), Verdoorn (1933, 1934a both as *Ptychocoleus pycnocladus*), Mizutani (1969 as *P. pycnocladus*), Kitagawa

(1971 as *P. pycnocladus*), Kamimura (1974 as *P. pycnocladus*), Gradstein (1975), Lee et al. (2013), Wang et al. (2016). Penang, Perak, Malacca, Sarawak, Sabah.

***Acrolejeunea tjibodensis*** (Verd.) Grolle et Gradst. – Kamimura (1974 as *Ptychocoleus tjibodensis*), Gradstein (1975), Lee et al. (2013). Pahang, Sabah.

***Acromastigum aurescens*** A.Evans – Evans (1934). Johor.

***Acromastigum bancanum*** (Sande Lac.) A.Evans – De Notaris (1874 as *Mastigobryum bancanum*), Schiffner (1898 as *Bazzania bancana*), Evans (1934, also as *A. bidenticulatum*), Herzog (1950), Kitagawa and Kodama (1973), Tixier (1974 as *A. bidenticulatum*), Kürschner (1990), Pócs et al. (2020). Kedah, Johor, Sarawak, Sabah.

***Acromastigum bifidum*** (Steph.) A.Evans – Evans (1934 as *A. denticulatum*), Herzog (1950), Grolle (1978). Sarawak.

***Acromastigum brotheri*** (Steph.) A.Evans – Stephani (1909 as *Mastigobryum brotheri*), Evans (1934), Kitagawa and Kodama (1973). Sarawak, Sabah.

***Acromastigum curtilobum*** A.Evans – Kitagawa and Kodama (1973), Kürschner (1990). Sabah.

***Acromastigum divaricatum*** (Nees) Reimers – Evans (1934), Kitagawa and Kodama (1973). Johor, Sabah.

***Acromastigum echinatiforme*** (De Not.) A.Evans – De Notaris (1874 as *Mastigobryum echinatiforme*), Schiffner (1898 as *Bazzania echinatiformis*), Evans (1934), Herzog (1950), Kitagawa and Kodama (1973), Grolle (1978), Kürschner (1990), Cheah (2017). Pahang, Sarawak, Sabah.

***Acromastigum echinatum*** (Gottsche) A.Evans – Evans (1934), Herzog (1950), Kitagawa and Kodama (1973), Tixier (1974). Kedah, Johor, Sarawak, Sabah.

***Acromastigum fimbriatum*** (Steph.) A.Evans – Stephani (1909 as *Mastigobryum fimbriatum*), Evans (1934), Herzog (1950). Sarawak.

***Acromastigum herzogii*** Grolle – Grolle (1964), Kürschner (1990). Sarawak, Sabah.

***Acromastigum inaequilaterum*** (Lehm. et Lindenb.) A.Evans – De Notaris (1874 as *Mastigobryum elegantulum*), Schiffner (1898 as *Bazzania notarisii*), Stephani (1909 as *M. notarisii*), Evans (1934), Herzog (1950), Kitagawa (1969c), Kitagawa and Kodama (1973), Kürschner (1990), Wolseley et al. (1996). Penang, Negeri Sembilan, Johor, Sarawak, Sabah.

***Acromastigum laevigatum*** A.Evans – Evans (1934), Tixier (1974). Kedah, Sarawak.

***Acromastigum leptophyllum*** Herzog – Herzog (1950). Sarawak.

***Acromastigum linganum*** (De Not.) A.Evans – De Notaris (1874 as *Mastigobryum linganum*), Schiffner (1898 as *Bazzania lingana*), Stephani (1909 as *M. linganum*), Evans (1934). Sarawak.

***Acromastigum lobuliferum*** A.Evans – Grolle (1978). Sabah.

***Acromastigum obliquatum*** (Mitt.) A.Evans – Kitagawa and Kodama (1973 as *A. gemmiferum*), Grolle (1978). Sabah.

***Acroscyphella tjiwideiensis*** (Sande Lac.) N.Kitag. et Grolle – Cheah (2017). Pahang.

***Allorgella semperiana*** (Steph.) Bechteler, G.E.Lee, Schäf.-Verw. et Heinrichs – Tixier (1980b as *A. changiana*), Grolle (1985 as *Otolejeunea semperiana*), Zhu and So (2001 as *O. semperiana*), Schäfer-Verwimp (2006 as *O. semperiana*). Kedah, Perak, Pahang.

***Anastrophyllum assimile*** (Mitt.) Steph. – Kitagawa (1970), Gradstein and Váňa (1987), Váňa and Piippo (1989), Váňa (1991c). Sabah.

***Anastrophyllum auritum*** (Lehm.) Steph. – Kitagawa (1970 as *A. appendiculatum*), Váňa and Piippo (1989), Váňa (1991c). Sabah.

***Anastrophyllum bidens*** (Reinw., Blume et Nees) Steph. – Inoue (1967a, 1968b), Kitagawa (1970), Kitagawa and Kodama (1973), Kürschner (1990), Váňa (1991c). Pahang, Sarawak, Sabah.

***Anastrophyllum bidens*** var. ***aristatum*** N.Kitag. – Herzog (1950), Kitagawa (1970), Kitagawa and Kodama (1973), Kürschner (1990), Váňa (1991c). Sarawak, Sabah.

***Anastrophyllum borneense*** Herzog – Herzog (1950), Inoue (1967a,b, 1968b all as *A. malayense*), Kitagawa (1970), Váňa (1991c). Pahang, Sarawak, Sabah.

***Anastrophyllum fissum*** Steph. – Herzog (1950 as *A. divergens*), Váňa (1991c as *A. divergens*). Sarawak, Sabah.

***Anastrophyllum obtusum*** Herzog – Herzog (1950), Váňa (1991c). Sabah.

***Anastrophyllum piligerum*** (Nees) Steph. – De Notaris (1874 as *Jungermannia piligera* [‘*pilifera*’]), Schiffner (1898, also as *A. imbricatum*), Herzog (1950, also as *A. imbricatum*), Inoue (1967a), Kitagawa (1969c, 1970), Kitagawa and Kodama (1973), Kürschner (1990), Váňa (1991c), Álvaro-A (2011). Penang, Pahang, Johor (“Mt. Ophir” (Gunung Ledang) was mistakenly listed as in Malacca), Sarawak, Sabah.

***Anastrophyllum prionophyllum*** S.Hatt. – Kitagawa (1970), Váňa (1991c). Sabah.

***Anastrophyllum revolutum*** Steph. – Kitagawa (1970), Váňa (1991c), Cheah (2017). Pahang, Sabah.

***Anastrophyllum squarrosum*** Herzog – Kitagawa (1970), Váňa (1991c), Cheah (2017). Pahang, Sabah.

***Andrewsianthus bidens*** (Steph.) R.M.Schust. – Cheah (2017). Pahang.

***Andrewsianthus chimbuensis*** R.M.Schust. – Kürschner (1990), Váňa (1991c). Sabah.

***Andrewsianthus kinabaluensis*** N.Kitag. – Kitagawa (1970), Váňa (1974, 1991c). Sabah.

***Andrewsianthus mizutanii*** N.Kitag. – Amakawa (1969a as *Jamesoniella minutissima*), Kitagawa (1969d), Váňa (1974, 1991c). Sabah.

***Andrewsianthus papillosus*** N.Kitag. – Kitagawa (1970), Kitagawa and Kodama (1973), Váňa (1974, 1991c). Sabah.

***Andrewsianthus puniceus*** (Nees) Grolle – Kitagawa (1970), Pocock et al. (1984), Váňa (1991c). Pahang, Sabah.

***Andrewsianthus recurvifolius*** (Nees) R.M.Schust. – Váňa (1991c). Sabah.

***Aneura maxima*** (Schiffn.) Steph. – Kitagawa and Kodama (1974). Sabah.

***Aneura pinguis*** (L.) Dumort. – Johnson (1972 as *Riccardia pinguis*). Pahang.

***Aphanotropis saxicola*** Herzog – Herzog (1952a). Sarawak. (synonym of *Colura*?, see Gradstein and Benitez 2014, Lee and Gradstein 2021).

***Asterella limbata*** D.G.Long et Grolle – Long and Grolle (1994), Long (2006). Sabah.

***Balantiopsis ciliaris*** S.Hatt. – Hattori (1966), Kitagawa and Kodama (1973). Sabah.

***Bazzania albifolia*** Horik. – Cheah and Yong (2016). Pahang.

***Bazzania angustistipula*** N.Kitag. – Cheah and Yong (2016). Pahang.

***Bazzania asymmetrica*** (Steph.) N.Kitag. – Cheah and Yong (2016). Pahang.

***Bazzania bicrenata*** N.Kitag. – Cheah and Yong (2016). Pahang.

***Bazzania bidentula*** (Steph.) Yasuda – Cheah and Yong (2016). Pahang.

***Bazzania bilobata*** N.Kitag. – Pócs et al. (2014). Pahang.

***Bazzania borneensis*** N.Kitag. – Stephani (1908 as as *Mastigobryum borneense*), Kitagawa (1973). Sarawak.

***Bazzania calcarata*** (Sande Lac.) Schiffn. – Stephani (1908 as *Mastigobryum calcaratum*), Herzog (1950 as *B. richardsii*), Meijer (1960), Tixier (1971). Pahang, Sarawak.

***Bazzania caudata*** (Steph.) Herzog – Stephani (1908 as *Mastigobryum caudatum*), Herzog (1950), Tixier (1971), Kitagawa and Kodama (1973). Penang, Pahang, Sarawak, Sabah.

***Bazzania ceylanica*** (Mitt.) Steph. – Kamimura (1975). Sabah.

***Bazzania cincinnata*** (De Not.) Trevis. – De Notaris (1874 as *Mastigobryum cincinnatum*), Schiffner (1898), Stephani (1908 as *M. cincinnatum*), Kamimura (1975). Sarawak, Sabah.

***Bazzania commutata*** (Lindenb. et Gottsche) Schiffn. – Tixier (1971). Pahang.

***Bazzania confertifolia*** (Steph.) Herzog – Herzog (1950). Sarawak.

***Bazzania conophylla*** (Sande Lac.) Schiffn. – Kitagawa and Kodama (1973), Kitagawa (1973). Sabah.

***Bazzania densa*** (Sande Lac.) Schiffn. – Kitagawa (1971), Kitagawa and Kodama (1973), Kürschner (1990). Penang, Sabah.

***Bazzania diminuta*** Herzog – Herzog (1950). Sarawak.

***Bazzania distans*** (Nees) Trevis. – Johnson (1972). Pahang.

***Bazzania drepanophylla*** Herzog – Herzog (1950). Sarawak.

***Bazzania dulitensis*** Herzog – Herzog (1950), Kitagawa and Kodama (1973), Kürschner (1990). Sarawak, Sabah.

***Bazzania erosa*** (Reinw., Blume et Nees) Trevis. – De Notaris (1874 as *Mastigobryum vagum*), Schiffner (1898), Stephani (1908 as *M. vagum*), Herzog (1950 as *B. vaga* and *B. serrulata*), Kitagawa and Kodama (1973), Kitagawa (1977), Cheah and Yong (2016). Penang, Pahang, Sarawak, Sabah.

***Bazzania erosa*** var. ***pulopenangensis*** (Lindenb. et Gottsche) Schiffn. – Lindenberg and Gottsche (1851 as *Mastigobryum erosum* δ *pulopenangense*), Schiffner (1898). Penang.

***Bazzania fallax*** (Sande Lac.) Schiffn. – De Notaris (1874 as *Mastigobryum borneense*), Schiffner (1898), Herzog (1950 as *B. fallax* f. *fissa*), Meijer (1960). Sarawak.

***Bazzania fleischeri*** (Steph.) Abeyw. – Stephani (1908, 1909 both as *Mastigobryum fleischeri*). Sarawak.

***Bazzania friabilis*** N.Kitag. et T.Kodama – Kitagawa and Kodama (1973, 1975), Kürschner (1990), Cheah and Yong (2016). Pahang, Sabah.

***Bazzania grandiretis*** (Steph.) Herzog – Herzog (1950), Kitagawa and Kodama (1973). Sarawak, Sabah.

***Bazzania harpago*** (De Not.) Schiffn. – De Notaris (1874 as *Mastigobryum ferox* and *M. harpago*), Schiffner (1898), Stephani (1908 as *M. harpago*), Herzog (1950, 1952b), Kitagawa (1972), Kitagawa and Kodama (1973), Kamimura (1975, also as *B. ferox*), Kürschner (1990), Ludwiczuk and Asakawa (2010), Ng et al. (2021). Sarawak, Sabah.

***Bazzania herzogiana*** Meijer – Herzog (1950 as *B. remotifolia*). Sarawak.

***Bazzania horridula*** Schiffn. – Herzog (1932 as *Mastigobryum muricatulum*, 1950), Kitagawa and Kodama (1973), Kürschner (1990), Cheah and Yong (2016). Pahang, Sarawak, Sabah.

***Bazzania inaequitexta*** Steph. – Stephani (1908, 1909 both as *Mastigobryum inaequitextum*). Sarawak.

***Bazzania indica*** (Gottsche et Lindenb.) Trevis. – Kamimura (1975), Kürschner (1990). Sabah.

***Bazzania insignis*** (De Not.) Trevis. – De Notaris (1874 as *Mastigobryum insigne*), Schiffner (1898), Evans (1932), Kamimura (1975). Sarawak, Sabah.

***Bazzania intermedia*** (Gottsche et Lindenb.) Trevis. – De Notaris (1874 as *Mastigobryum concinnum*), Schiffner (1898 as *B. concinna*), Stephani (1908 as *M. concinnum*), Herzog (1950 as *B. concinna*), Meijer (1960), Kitagawa (1969c), Tixier (1971), Kitagawa and Kodama (1973), Kamimura (1975), Grolle (1987). Penang, Pahang, Sarawak, Sabah.

***Bazzania intermedia*** var. ***sarawakiana*** (De Not.) Schiffn. – De Notaris (1874 as *Mastigobryum intermedium* var. *sarawakianum*), Schiffner (1898). Sarawak.

***Bazzania involutiformis*** (De Not.) Trevis. – De Notaris (1874 as *Mastigobryum duplex* and *M. involutiforme*), Schiffner (1898), Herzog (1950, 1952b), Kitagawa (1972), Kitagawa and Kodama (1973), Kamimura (1975), Kürschner (1990). Sarawak, Sabah.

***Bazzania kokawana*** N.Kitag. et T.Kodama – Kitagawa and Kodama (1973). Sabah.

***Bazzania linearis*** Herzog – Herzog (1950). Sarawak.

***Bazzania linguiformis*** (Sande Lac.) Trevis. – Stephani (1908 as *Mastigobryum linguiforme* [‘*linguaeforme*’]). Penang.

***Bazzania longicaulis*** (Sande Lac.) Schiffn. – Herzog (1950), Johnson (1972), Kitagawa and Kodama (1973), Kitagawa (1977), Kürschner (1990). Pahang, Sarawak, Sabah.

***Bazzania loricata*** (Reinw., Blume et Nees) Trevis. – Stephani (1908 as *Mastigobryum loricatum*), Herzog (1950), Inoue (1967a, 1968b), Pocock et al. (1984). Pahang, Sarawak.

***Bazzania lowii*** (Steph.) Schiffn. – Stephani (1886, 1908 both as *Mastigobryum lowii*), Schiffner (1898), Evans (1932 as *M. lowii*). Sabah.

***Bazzania malaccensis*** (Steph.) Tixier – Stephani (1908 as *Mastigobryum malaccense*), Tixier (1971, 1974). Kedah, Perak, Pahang.

***Bazzania manillana*** (Steph.) Steph. – Stephani (1917 as *Mastigobryum crenatistipulum*), Kamimura (1975), Mizutani (1967a). Penang, Sabah.

***Bazzania marginella*** (Herzog) N.Kitag. et T.Kodama – Kitagawa and Kodama (1973). Sabah.

***Bazzania menzelii*** E.D.Cooper – Herzog (1950 as *Acromastigum emarginatum*). Sarawak.

***Bazzania paradoxa*** (Sande Lac.) Steph. – Stephani (1908 as *Mastigobryum natunense*), Meijer (1960), Kitagawa and Kodama (1973). Pahang, Sarawak, Sabah.

***Bazzania parvitexta*** Steph. – Kitagawa (1979a). Sabah.

***Bazzania patentistipa*** (Sande Lac.) Schiffn. – Kitagawa and Kodama (1973 ['*patentistipula*']). Sabah.

***Bazzania pectinata*** (Lindenb. et Gottsche) Schiffn. – Herzog (1950, 1952b), Tixier (1971), Kitagawa and Kodama (1973), Pocock et al (1984). Pahang, Sarawak, Sabah.

***Bazzania praerupta*** (Reinw., Blume et Nees) Trevis. – Kitagawa and Kodama (1973), Kürschner (1990), Ludwiczuk and Asakawa (2010). Sabah.

***Bazzania pseudovittata*** N.Kitag. et T.Kodama – Kitagawa and Kodama (1973, 1975), Kürschner (1990), Cheah and Yong (2016). Pahang, Sabah.

***Bazzania recurva*** (Mont.) Trevis. – Montagne (1843 as *Herpetium recurvum*, 1856 as *Mastigobryum recurvum*), Gottsche et al. (1845 as *M. recurvum*), Lindenberg and Gottsche (1851 as *M. recurvum*), De Notaris (1874 as *M. recurvum* var. *pallens*), Schiffner (1898 as *B. recurva* var. *pallens*), Stephani (1908 as *M. recurvum*), Inoue (1968b). Penang, Pahang, Sarawak.

***Bazzania revoluta*** (Steph.) N.Kitag. – Kamimura (1975 as *B. recurvolimbata*). Sabah.

***Bazzania serpentina*** (Nees) Trevis. – Cheah and Yong (2016). Pahang.

***Bazzania sikkimensis*** Schiffn. – Kamimura (1975). Sabah.

***Bazzania spiralis*** (Reinw., Blume et Nees) Meijer – Meijer (1960), Kitagawa and Kodama (1973), Tixier (1971, 1974), Kamimura (1975), Kürschner (1990), Ludwiczuk and Asakawa (2010). Kedah, Pahang, Sarawak, Sabah.

***Bazzania subtilis*** (Sande Lac.) Trevis. – De Notaris (1874 as *Mastigobryum subtile*), Stephani (1917 as *M. repandistipulum*), Meijer (1960), Kitagawa and Kodama (1973), Kitagawa (1977, 1979 as *B. palmatifida*), Kürschner (1990), Wolseley et al. (1996). Negeri Sembilan, Sarawak, Sabah.

***Bazzania sumbavensis*** (Steph.) Steph. – Kamimura (1975). Sabah.

***Bazzania tridens*** (Reinw., Blume et Nees) Trevis. – Schiffner (1898 as *B. australis*), Herzog (1950, also as *B. coreana*), Kitagawa (1969c, 1972, also as *B. australis*), Tixier (1971), Kitagawa and Kodama (1973, also as *B. australis*), Kamimura (1975, also as *B. tridens* f. *minutissima*), Kürschner (1990). Penang, Pahang, Sarawak, Sabah.

***Bazzania tridens*** var. ***assamica*** (Steph.) Pócs – Kamimura (1975), Pócs et al. (2014 as *B. assamica*). Pahang, Sabah.

***Bazzania uncigera*** (Reinw., Blume et Nees) Trevis. – Herzog (1950), Kitagawa and Kodama (1973), Kürschner (1990), Cheah and Yong (2016). Pahang, Sarawak, Sabah.

***Bazzania uncigera*** var. ***brevifolia*** Herzog – Herzog (1950). Sarawak.

***Bazzania undulata*** Herzog – Herzog (1950). Sarawak.

***Bazzania vittata*** (Gottsche) Trevis. – Herzog (1950), Inoue (1967a), Kitagawa and Kodama (1973), Kürschner (1990). Pahang, Sarawak, Sabah.

***Bazzania vittata*** var. ***luxurians*** (De Not.) Schiffn. – De Notaris (1874 as *Mastigobryum vittatum* var. *luxurians*), Schiffner (1898). Sarawak.

***Bazzania wiltensii*** (Steph.) Schiffn. – Pocock et al. (1984). Pahang.

***Bazzania zollingeri*** (Lindenb.) Trevis. – De Notaris (1874 as *Mastigobryum zollingeri*). Sarawak.

***Blepharostoma trichophyllum*** (L.) Dumort. – Akiyama et al. (2001). Sabah.

***Calypogeia apiculata*** (Steph.) Steph. – Kitagawa and Kodama (1973). Sabah.

***Calypogeia arguta*** Nees et Mont – Wolseley et al. (1996), Bisang et al. (2003). Pahang, Negeri Sembilan.

***Caudalejeunea cristiloba*** (Steph.) Gradst. – Verdoorn (1934a, 1937 both as *C. circinata*), Mizutani (1966, 1969 both as *C. circinata*, 1988), Kitagawa and Kodama (1974 as *C. circinata*). Johor, Sarawak, Sabah.

***Caudalejeunea reniloba*** (Gottsche) Steph. – Stephani (1912 as *C. serrata*), Verdoorn (1934a), Herzog (1952b), Mizutani (1966, 1969, also as *C. stephanii*, 1988, also as *C. recurvistipula*), Tixier (1971 as *C. stephanii*, 1980a), Kitagawa and Kodama (1974), Thiers (1985), Pócs et al. (2020), Pesiu et al. (2021, in press). Penang, Perak, Selangor, Pahang, Malacca, Terengganu, Johor, Sarawak, Sabah.

***Cephalolejeunea parvilobula*** Mizut. – Mizutani (1979b). Sabah.

***Cephalozia acuminata*** (Herzog) Váňa – Herzog (1950 as *Metahygrobiella acuminata*), Váňa (1993 as *M. acuminata*). Sarawak.

***Cephalozia acutiloba*** (Inoue) Váňa – Inoue (1967a,b, both as *Metahygrobiella acutiloba*). Pahang.

***Cephalozia hamatiloba*** Steph. – Müller and Schäfer-Verwimp (1999), Cheah (2017). Pahang.

***Cephalozia mollusca*** (De Not.) Váňa – De Notaris (1874 as *Jungermannia mollusca*), Schiffner (1898 as *Hygrobiella mollusca*), Stephani (1908 as *H. mollusca*), Herzog (1950 as *Metahygrobiella mollusca*), Kitagawa and Kodama (1974 as *M. mollusca*), Váňa (1993 as *M. mollusca*). Sarawak, Sabah.

***Cephalozia stolonacea*** (Herzog) Váňa – Herzog (1950 as *Metahygrobiella stolonacea* and *Hygrobiella mollusca* f. *subintegerrima*), Grolle (1963 as *M. stolonacea*), Váňa (1993 as *M. stolonacea*). Sarawak.

***Cephaloziella capillaris*** (Steph.) Douin – Inoue (1967a), Inoue and Miller (1967). Pahang.

***Cephaloziella kiaeri*** (Austin) Douin – Kitagawa and Kodama (1974 as *C. willisana*), Váňa (1992). Sabah.

***Cephaloziella microphylla*** (Steph.) Douin – Kitagawa (1969c). Penang.

***Ceratolejeunea aliena*** Herzog – Herzog (1952b), Kitagawa and Kodama (1974), Mizutani (1981a). Sarawak, Sabah.

***Ceratolejeunea belangeriana*** (Gottsche) Steph. – Kitagawa and Kodama (1974, also as *C. ryukyuensis*), Mizutani (1981a as *C. oceanica*), Zhu et al. (2005), Cheah (2017). Pahang, Johor, Sabah.

***Ceratolejeunea cornuta*** (Lindenb.) Steph. – Inoue (1967a as *C. tahitensis*). Pahang.

***Ceratolejeunea minor*** Mizut. – Mizutani (1981a), Zhu et al. (2005), Sarimi et al. (2021). Terengganu, Sabah.

***Ceratolejeunea moniliata*** Herzog – Herzog (1952b), Mizutani (1970, 1981a), Pesiu et al. (in press). Terengganu, Johor, Sarawak, Sabah.

***Ceratolejeunea singapurensis*** (Lindenb.) Steph. – Herzog (1952b), Cheah (2017), Sarimi et al. (2021). Pahang, Terengganu, Sarawak.

***Ceratolejeunea spinistipula*** (Herzog) R.L.Zhu, L.Shu, Xiong He et Y.M.Wei – Herzog (1948 as *Drepanolejeunea spinistipula*), Pócs et al. (1995 as *Acantholejeunea spinistipula*), Zhu et al. (2018a as *D. spinistipula*). Johor, Sarawak, Sabah.

***Cheilolejeunea adnata*** (Lehm.) Grolle var. ***autoica*** Gradst. et Ilk.-Borg. – Shu et al. (2015 as *C. larsenii*). Penang.

***Cheilolejeunea ceylanica*** (Gottsche) R.M.Schust. et Kachroo – Schiffner (1898 as *Pycnolejeunea ceylanica*), Mizutani (1966, 1970, 1980), Tixier (1972, 1974 both as *P. arietina*, 1980a as *Xenolejeunea ceylanica*), Kitagawa and Kodama (1974), Grolle (1979), Kürschner (1990), Wolseley et al. (1996), Zhu and So (2001), Pócs et al. (2020), Pesiu et al. (2021). Kedah, Penang, Pahang, Negeri Sembilan, Malacca, Terengganu, Sabah.

***Cheilolejeunea decursiva*** (Sande Lac.) R.M.Schust. – Mizutani (1970 as *C. spathulata*), Grolle (1977), Zhu and Lai (2005), Shu et al. (2014), Cheah (2017). Pahang, Sabah.

***Cheilolejeunea falsinervis*** (Sande Lac.) R.M.Schust. et Kachroo – Mizutani (1966, 1970), Kitagawa and Kodama (1974), Tixier (1974 as *Xenolejeunea falsinervis*), Thiers (1986), Kürschner (1990), Wolseley et al. (1996). Kedah, Negeri Sembilan, Sabah.

***Cheilolejeunea gigantea*** (Steph.) R.M.Schust. et Kachroo – Herzog (1950 as *Pycnolejeunea gigantea*). Sarawak.

***Cheilolejeunea incisa*** (Gottsche) R.M.Schust. et Kachroo – Hoffmann (1935 as *Pycnolejeunea excisula*), Mizutani (1970 as *C. excisula*), Tixier (1971 as *P. excisula*), Kamimura (1974 as *C. excisula*), Kitagawa and Kodama (1974 as *C. excisula*), Grolle and Piippo (1990 as *C. excisula*). Pahang, Johor, Sabah.

***Cheilolejeunea insignis*** Jovet-Ast et Tixier – Kitagawa and Kodama (1974). Sabah.

***Cheilolejeunea intertexta*** (Lindenb.) Steph. – Mizutani (1967b, 1970), Kitagawa (1971), Grolle (1979), Kürschner (1990), Pócs et al. (2020). Penang, Sarawak, Sabah.

***Cheilolejeunea krakakammae*** (Lindenb.) R.M.Schust. – Cheah (2017). Pahang.

***Cheilolejeunea lindenbergii*** (Gottsche) Mizut. – Herzog (1950 as *Hygrolejeunea lindenbergii* and *Euosmolejeunea luerssenii*), Inoue (1967 as *C. luerssenii* [‘*luersonii*’]), Kitagawa (1969a as *C. luerssenii*, 1971), Mizutani (1970), Kitagawa and Kodama (1974), Kürschner (1990), Cheah (2017). Penang, Pahang, Sarawak, Sabah.

***Cheilolejeunea loriana*** (Steph.) W.Ye et R.L.Zhu – Mizutani (1970 as *Leucolejeunea loriana*). Sabah.

***Cheilolejeunea malaccensis*** (G.Hoffm.) Xiao L.He – Hoffmann (1935 as *Pycnolejeunea malaccensis*), Thiers (1986 as *P. malaccensis*), He (1996). Penang.

***Cheilolejeunea micholitzii*** (Steph.) R.M.Schust. et Kachroo – Hoffman (1935 as *Pycnolejeunea micholitzii*). Johor.

***Cheilolejeunea mizutanii*** W.Ye et R.L.Zhu – Mizutani (1976 as *Leucolejeunea decurrens*), Grolle and Piippo (1990 as *L. decurrens*). Sabah.

***Cheilolejeunea nipponica*** (S.Hatt.) S.Hatt. – Pócs and Lee (2016). Selangor.

***Cheilolejeunea occlusa*** (Herzog) T.Kodama et N.Kitag. – Herzog (1950 as *Strepsilejeunea occlusa*), Kitagawa and Kodama (1974), Mizutani (1980), Wolseley et al. (1996), Pócs et al. (2020). Negeri Sembilan, Sarawak, Sabah.

***Cheilolejeunea orientalis*** (Gottsche) Mizut. – Kitagawa and Kodama (1974). Sabah.

***Cheilolejeunea serpentina*** (Mitt.) Mizut. – Hashimoto et al. (1993), Cheah (2017). Langkawi, Pahang.

***Cheilolejeunea streimannii*** Pócs et Ninh – Pócs and Lee (2016). Pahang.

***Cheilolejeunea trapezia*** (Nees) R.M.Schust. et Kachroo – Stephani (1890 as *Lejeunea imbricata*), Hoffmann (1935 as *Pycnolejeunea imbricata*, *P. meyeniana* and its var. *ligulata*, *C. longiloba*), Herzog (1948 as *Placolejeunea subarrhyncha*), Mizutani (1966, 1970 both as *C. imbricata*, 1980 as *C. longiloba*), Inoue (1967a as *C. imbricata*), Kitagawa (1971 as *C. imbricata*), Tixier (1971, 1974, 1980a as *Xenolejeunea longiloba* and *X. meyeniana*), Kitagawa and Kodama (1974 as *C. imbricata* and *C. meyeniana*), Grolle (1979), Thiers (1986 as *C. meyeniana*), Kürschner (1990 as *C. imbricata*), Cheah (2017 as *C. imbricata*), Pócs et al. (2020, also as *C. meyeniana*), Pesiu et al. (2021). Kedah, Penang, Pahang, Terengganu, Johor, Sarawak, Sabah.

***Cheilolejeunea trifaria*** (Reinw., Blume et Nees) Mizut. – Inoue (1967a as *C. viridula*), Mizutani (1970, 1982), Kamimura (1974), Kitagawa and Kodama (1974), Hashimoto et al. (1993), Lee et al. (2013), Pócs et al. (2020), Pesiu et al. (2021). Langkawi, Perak, Pahang, Terengganu, Sabah.

***Cheilolejeunea ventricosa*** (P.Syd.) Xiao L.He – Hoffman (1935 as *Pycnolejeunea ventricosa*), Mizutani (1970 as *P. ventricosa*), Hattori and Kamimura (1971 as *P. ventricosa*), Zhu and Lai (2005), Pócs et al. (2020). Penang, Sabah.

***Cheilolejeunea verrucosa*** Steph. – Tixier (1974), Mizutani (1979b). Kedah, Sabah.

***Cheilolejeunea vittata*** (G.Hoffm.) R.M.Schust. et Kachroo – Mizutani (1970, 1980), Kürschner (1990), Wolseley et al. (1996), Pócs et al. (2020). Negeri Sembilan, Sabah.

***Cheilolejeunea xanthocarpa*** (Lehm. et Lindenb.) Malombe – Verdoorn (1934a as *Leucolejeunea xanthocarpa*), Inoue (1967a as *L. xanthocarpa*), Tixier (1971 as *L. xanthocarpa*), Kamimura (1975 as *L. xanthocarpa*). Pahang, Sabah.

***Chiastocaulon braunianum*** (Nees) S.D.F.Patzak, M.A.M Renner, Schäf.-Verw. et Heinrichs – Kitagawa and Kodama (1974 as *Plagiochilion braunianum*), Akiyama et al. (2001 as *P. braunianum*). Sabah.

***Chiastocaulon dendroides*** (Nees) Carl – De Notaris (1874 as *Plagiochila dendroides*), Schiffner (1898 as *P. dendroides*), Herzog (1950 as *P. dendroides*), Kitagawa and Kodama (1974 as *P. dendroides*), Inoue (1967a, 1968b, 1984 as *P. dendroides*), Kürschner (1990 as *P. dendroides*), So (2001 as *P. dendroides*), Akiyama et al. (2001 as *P. dendroides*). Pahang, Sarawak, Sabah.

***Chiastocaulon oppositum*** (Reinw., Blume et Nees) S.D.F.Patzak, M.A.M Renner, Schäf.-Verw. et Heinrichs – Stephani (1904 as *Plagiochila opposita*), Hattori (1942a as *Plagiochila opposita*, 1950), Inoue (1964, 1967a both as *Plagiochilion oppositum*), Kitagawa and Kodama (1974 as *Plagiochilion oppositum*), Kamimura (1975 as *Plagiochilion oppositum*), Kürschner (1990 as *Plagiochilion oppositum*). Perak, Pahang, Sarawak, Sabah.

***Chiastocaulon pachycephalum*** (De Not.) Herzog – De Notaris (1874 as *Plagiochila pachycephala*), Schiffner (1898 as *Plagiochila pachycephala*), Herzog (1950 as *Plagiochilion pachycephalum*), Inoue (1964 as *Plagiochilion pachycephalum*), So and Grolle (2000 as *Plagiochilion pachycephalum*), So (2001 as *Plagiochila pachycephala*). Sarawak.

***Chiastocaulon theriotianum*** (Steph.) S.D.F.Patzak, M.A.M Renner, Schäf.-Verw. et Heinrichs – Inoue (1964 as *Plagiochilion theriotianum*). Sarawak.
***Cololejeunea abnormis*** Mizut. – Mizutani (1970), Tixier (1985). Penang, Sabah.
***Cololejeunea acuminata*** Mizut. – Mizutani (1970), Wolseley et al. (1996), Pócs et al. (2020). Negeri Sembilan, Sabah.
***Cololejeunea aequabilis*** (Sande Lac.) Schiffn. – Benedix (1953 as *C. yulensis*), Mizutani (1966 as *C. yulensis*), Kitagawa and Kodama (1974 as *C. yulensis*), Pesiu et al. (2021). Terengganu, Johor, Sarawak, Sabah.
***Cololejeunea amphibola*** B.M.Thiers – Eggers et al. (1998), Pócs and Lee (2016). Selangor, Kelantan, Pahang, Sarawak.
***Cololejeunea angulata*** (Steph.) Mizut. – Kitagawa (1969a, 1969c), Wolseley et al. (1996), Mizutani (1966). Penang, Negeri Sembilan, Sabah.
***Cololejeunea angustiflora*** (Steph.) Mizut. – Mizutani (1966, 1970 both as *C. javanica* and *C. crenulata*), Kitagawa and Kodama (1974 as *C. crenulata*), Tixier (1985 as *C. javanica*), Zhu and So (2000a as *C. mackeeana*, 2002). Penang, Sarawak, Sabah.
***Cololejeunea appressa*** (A.Evans) Benedix – Mizutani (1966, 1970), Sarimi et al. (2021). Terengganu, Sabah.
***Cololejeunea bidentula*** (Steph.) E.W.Jones – Pócs and Lee (2016). Selangor.
***Cololejeunea ceatocarpa*** (Ångstr.) Steph – Pócs and Lee (2016). Kelantan, Pahang.
***Cololejeunea ceratilobula*** (P.C.Chen) R.M.Schust. – Mizutani (1966, 1970 both as *C. formosana*), Pesiu et al. (in press). Terengganu, Sabah.
***Cololejeunea chamlongiana*** Tixier – Tixier (1985). Perak.
***Cololejeunea chinii*** Tixier – Tixier (1973b), Kitagawa (1981). Selangor, Kelantan.
***Cololejeunea cordiflora*** Steph. – Tixier (1971 as *C. karstenii*, 1985). Perak, Penang, Pahang.
***Cololejeunea decliviloba*** Steph. – Tixier (1980a). Pahang.
***Cololejeunea desciscens*** Steph. – Eggers et al. (1998). Sarawak.
***Cololejeunea diaphana*** A.Evans – Eggers et al. (1998 as *Aphanolejeunea proboscoidea*), Pócs and Lee (2016). Kelantan, Sarawak.
***Cololejeunea dilatata*** (Steph.) Mizut. – Mizutani (1966, 1970). Sabah.
***Cololejeunea dozyana*** (Sande Lac.) Schiffn. – Benedix (1953), Tixier (1980a), Pócs et al. (2020). Pahang, Sabah.
***Cololejeunea ensifera*** Tixier – Pócs et al. (2020), Sarimi et al. (2021). Sabah.
***Cololejeunea equialbi*** Tixier – Pócs et al. (2020), Sarimi et al. (2021), Pesiu et al (in press). Terengganu, Sabah.
***Cololejeunea falcata*** (Horik.) Benedix – Mizutani (1966, 1970 both as *C. falcatoides*), Tixier (1971, 1974 both as *C. falcatoides*, 1978, 1980a), Kitagawa and Kodama (1974 as *C. falcatoides*), Pesiu et al. (2021, in press). Kedah, Perak, Penang, Pahang, Terengganu, Sabah.
***Cololejeunea filidens*** Benedix – Tixier (1985). Perak, Selangor.
***Cololejeunea fissilobula*** Herzog – Herzog (1950). Sarawak.
***Cololejeunea floccosa*** (Lehm. et Lindenb.) Schiffn. – Benedix (1953), Kitagawa (1969c), Mizutani (1966, 1970, 1984a), Tixier (1971, 1974, 1978), Kitagawa and

Kodama (1974), Wolseley et al. (1996), Pesiu et al. (2021, in press). Kedah, Penang, Perak, Pahang, Negeri Sembilan, Terengganu, Sarawak, Sabah.

***Cololejeunea floccosa*** var. ***amoena*** (Benedix) Pócs – Benedix (1953 as *C. amoena*), Mizutani (1966, 1970, both as *C. amoena*). Johor, Sabah.

***Cololejeunea floccosa*** var. ***aurita*** Benedix – Benedix (1953), Tixier (1978). Kedah, Penang, Perak, Johor.

***Cololejeunea floccosa*** var. ***trivittata*** Tixier – Eggers et al. (1998 as *C. floccosa* var. *vittata*), Crosby and Engel (2006). Pahang, Sarawak.

***Cololejeunea fructumarginata*** Tixier – Tixier (1985). Penang.

***Cololejeunea georgiana*** Tixier – Tixier (1985). Penang.

***Cololejeunea gottschei*** (Steph.) Pandé, K.P.Srivast. et Ahmad – Mizutani (1966 as *C. paroica*), Pócs et al. (2020), Sarimi et al. (2021), Pesiu et al. (in press). Kelantan, Terengganu, Sabah.

***Cololejeunea gradsteinii*** M.J.Lai et R.L.Zhu – Tixier (1971 as *C. pusilla*). Pahang.

***Cololejeunea gynophthalma*** Benedix – Tixier (1971, 1978), Mizutani (1966, 1970). Penang, Pahang, Sabah.

***Cololejeunea haskarliana*** (Lehm.) Schiffn. – Benedix (1953), Mizutani (1966, 1970, 1986a), Kitagawa (1971), Kitagawa and Kodama (1974), Tixier (1980a, 1985), Wolseley et al. (1996), Pócs et al. (2020). Penang, Perak, Pahang, Negeri Sembilan, Johor, Sarawak, Sabah.

***Cololejeunea hattoriana*** Mizut. et Pócs – Mizutani (1966 as *Campylolejeunea pusilla*). Sabah.

***Cololejeunea hildebrandii*** (Austin) Steph. – Tixier (1980a as *C. filicaulis*, 1985), Pócs et al. (2014, 2020). Penang, Perak, Selangor, Pahang, Sabah.

***Cololejeunea hirta*** Steph. – Tixier (1985). Perak, Pahang.

***Cololejeunea indica*** Pandé et R.N.Misra – Tixier (1985 as *C. planiflora*). Penang.

***Cololejeunea inflata*** Steph. – Benedix (1953 as *C. oshimensis*), Mizutani (1966, 1970 both as *C. oshimensis*), Tixier (1971, 1974 both as *C. oshimensis*, 1978, 1980a), Kitagawa and Kodama (1974 as *C. oshimensis*), Pesiu et al. (2021). Kedah, Pahang, Terengganu, Johor, Sabah.

***Cololejeunea inflectens*** (Mitt.) Benedix – Benedix (1953 as *C. ciliatilobula* and *C. peculiaris*), Mizutani (1970 as *Campylolejeunea peculiaris*), Tixier (1971 as *C. ciliatilobula*, 1974 as *Campylolejeunea peculiaris*, 1980a as *C. inflectidens*), Pesiu et al. (2021). Kedah, Pahang, Terengganu, Johor, Sarawak, Sabah.

***Cololejeunea johannis-winkleri*** (Herzog) R.L.Zhu – Zhu et al. (2004). Sabah.

***Cololejeunea kulenensis*** Tixier – Tixier (1985). Johor.

***Cololejeunea lacinulata*** Benedix – Benedix (1953). Sabah.

***Cololejeunea lanciloba*** Steph. – Mizutani (1966, 1984b), Kitagawa (1971), Tixier (1971 as *C. pahangiana*, 1985 as *C. bolombensis*), Kitagawa and Kodama (1974), Pócs et al. (2020), Pesiu et al. (2021, in press). Penang, Pahang, Terengganu, Johor, Sabah.

***Cololejeunea latilobula*** (Herzog) Tixier – Pócs and Lee (2016). Kelantan.

***Cololejeunea longifolia*** (Mitt.) Mizut. – Tixier (1984, 1985), Pócs et al. (2020). Penang, Johor, Sabah.

***Cololejeunea macounii*** (Spruce) A.Evans – Mizutani (1966, 1970 both as *C. kinabalensis*), Pócs et al. (2020). Sabah.

***Cololejeunea madothecoides*** (Steph.) Benedix. – Benedix (1953). Sarawak.

***Cololejeunea magnilobula*** (Horik.) S.Hatt. – Pócs et al. (2020). Sabah.

***Cololejeunea magnilobula*** var. ***falcidentata*** Pócs et G.E.Lee – Pócs and Lee (2016). Kelantan.

***Cololejeunea malaccensis*** Tixier – Tixier (1985). Johor.

***Cololejeunea malayana*** Tixier – Tixier (1980a, 1985), Eggers (2006). Perak, Pahang.

***Cololejeunea maritima*** Tixier – Tixier (1979, 1985). Perak, Johor.

***Cololejeunea metzgeriopsis*** (K.I.Goebel) Gradst., R.Wilson, Ilk.-Borg. et Heinrichs – Mizutani (1966 as *Metzgeriopsis pusilla*), Kitagawa (1969b as *M. pusilla*), Kitagawa and Kodama (1974 as *M. pusilla*), Tixier (1980a as *M. pusilla*), Akiyama et al. (2001 as *M. pusilla*), Gradstein et al. (2006), Pócs and Piippo (2011), Pócs et al. (2020), Pesiu et al. (2021). Perak, Pahang, Terengganu, Sabah.

***Cololejeunea mutabilis*** Benedix – Benedix (1953 as *C. mutabilis* f. *borneensis*), Tixier (1978 as *C. mutabilis* f. *borneensis*, f. *floccodoides* and f. *subfalcata*), Mizutani (1966), Pócs et al. (2020). Perak, Sabah.

***Cololejeunea obliqua*** (Nees et Mont.) Schiffn. – Benedix (1953 as *C. androgyna*, *C. nymannii*), Mizutani (1966 as *C. jelinekii* and *C. nymannii*, 1970 as *C. nymannii*), Tixier (1971 as *C. jelinekii*, 1980a, 1985 both as *C. scabriflora*), Kitagawa and Kodama (1974 as *C. nymannii*), Asthana and Srivastava (2003 as *C. jelinekii*), Pócs et al. (2020), Pesiu et al. (2021). Penang, Perak, Pahang, Terengganu, Sarawak, Sabah.

***Cololejeunea ocellata*** (Horik.) Benedix – Pócs and Lee (2016). Pahang.

***Cololejeunea ocelloides*** (Horik.) Mizut. – Benedix (1953 as *C. leonidens* and its var. *saccata*), Mizutani (1966, 1970 both as *C. leonidens*, 1984a), Inoue (1967a as *C. leonidens*), Tixier (1969 as *C. meijeri*, 1971, 1978, 1980a all as *C. leonidens*), Kitagawa and Kodama (1974 as *C. leonidens*), Pesiu et al. (2021). Perak, Pahang, Terengganu, Sabah.

***Cololejeunea pacifica*** Pócs – Pócs and Lee (2016). Kelantan.

***Cololejeunea papillosa*** (K.I.Goebel) Mizut. – Herzog (1950 as *Aphanolejeunea microscopica* var. *borneensis*), Mizutani (1966), Pócs and Piippo (1999 as *A. borneensis*), Pócs and Bernecker (2009), Pócs and Lee (2016), Pócs et al. (2020). Pahang, Sarawak, Sabah.

***Cololejeunea peponiformis*** Mizut. – Mizutani (1970), Pócs et al. (2020). Sabah.

***Cololejeunea peraffinis*** (Schiffn.) Schiffn. – Herzog (1952b as *Taeniolejeunea peraffinis*), Benedix (1953), Mizutani (1966, 1970, 1984a), Kitagawa (1969a), Kitagawa and Kodama (1974), Tixier (1978 as *C. peraffinis* var. *elegans*, 1980a). Penang, Pahang, Johor, Sarawak, Sabah.

***Cololejeunea perakensis*** Tixier – Tixier (1985). Perak.

***Cololejeunea planissima*** (Mitt.) Abeyw. – Mizutani (1970, 1984b), Kitagawa (1971), Kitagawa and Kodama (1974), Tixier (1985), Asthana and Srivastava (2003), Pócs et al. (2020), Pesiu et al. (2021). Penang, Perak, Terengganu, Johor, Sabah.

***Cololejeunea platyneura*** (Spruce) A.Evans – Mizutani (1966 as *C. astyla*), Zhu and So (1998b, 2001), Cheah (2017). Pahang, Sabah

***Cololejeunea pretiosa*** Benedix – Kitagawa and Kodama (1974). Sabah.

***Cololejeunea pseudofloccosa*** (Horik.) Benedix – Benedix (1953), Mizutani (1966, 1970), Kitagawa and Kodama (1974), Tixier (1980a). Pahang, Sabah.

***Cololejeunea pseudoschmidtii*** Tixier – Tixier (1985). Penang.

***Cololejeunea pseudostephanii*** Tixier – Pócs and Lee (2016). Pahang.

***Cololejeunea pseudostipulata*** P.Syd. – Mizutani (1970). Sabah.

***Cololejeunea raduliloba*** Steph. – Mizutani (1966), Pócs et al. (2020). Sabah.

***Cololejeunea reineckeana*** Steph. – Tixier (1985). Perak.

***Cololejeunea rosellata*** Mizut. – Mizutani (1966), Kitagawa and Kodama (1974), Tixier (1985). Sabah.

***Cololejeunea schmidtii*** Steph. – Mizutani (1966, 1970 as *C. benedixii*), Kitagawa and Kodama (1974), Cheah (2017), Sarimi et al. (2021), Pesiu et al. (in press). Pahang, Terengganu, Sabah.

***Cololejeunea selangorensis*** Tixier – Tixier (1985). Selangor.

***Cololejeunea serrulata*** Steph. – Kitagawa (1971). Penang.

***Cololejeunea setosa*** Mizut. – Mizutani (1966), Eggers et al. (1998). Sarawak, Sabah.

***Cololejeunea shimizui*** N.Kitag. – Kitagawa (1969c, 1981). Kelantan.

***Cololejeunea siamensis*** Steph. – Benedix (1953 as *C. pluriplicata*, orth. var. of *C. pluripunctata*), Mizutani (1966, 1970 both as *C. pluripunctata*), Tixier (1978), Wolseley et al. (1996). Penang, Negeri Sembilan, Johor, Sabah.

***Cololejeunea sigmoidea*** Jovet-Ast et Tixier – Mizutani (1966), Kitagawa (1969c), Tixier (1971, 1980a), Kitagawa and Kodama (1974), Bernecker-Lücking and Morales (1999), Pesiu et al. (2021). Penang, Pahang, Terengganu, Sabah.

***Cololejeunea sigmoidea*** var. ***dubia*** Tixier – Tixier (1985). Perak.

***Cololejeunea smitinandii*** Tixier – Pócs and Lee (2016). Kelantan.

***Cololejeunea spathulifolia*** (Steph.) H.A.Mill. – Pócs and Lee (2016). Kelantan.

***Cololejeunea sphaerodonta*** Mizut. – Mizutani (1966), Zhu (1995), Zhu and So (2001), Pócs et al. (2020). Sabah.

***Cololejeunea stephanii*** Benedix – Benedix (1953), Mizutani (1966, 1970), Kitagawa and Kodama (1974), Tixier (1974, 1978, 1980a), Zhu (1995), Eggers et al. (1998), Pócs et al. (2020), Pesiu et al. (2021, in press). Kedah, Perak, Pahang, Terengganu, Johor, Sarawak, Sabah.

***Cololejeunea stoniana*** Tixier – Tixier (1976, 1985), Eggers et al. (1998). Johor, Sarawak.

***Cololejeunea stylosa*** Steph. – Tixier (1985), Pócs and Lee (2016), Pócs et al. (2020). Penang, Kelantan, Sabah.

***Cololejeunea tenella*** Benedix – Benedix (1953), Tixier (1974, 1978, 1985 the latter two as *C. tenella* var. *vittata*), Wolseley et al. (1996), Pócs et al. (2020). Kedah, Penang, Perak, Negeri Sembilan, Johor, Sabah.

***Cololejeunea thailandensis*** Tixier – Tixier (1985). Penang.

***Cololejeunea triapiculata*** (Herzog) Tixier – Tixier (1971, 1980a, 1985). Pahang.

***Cololejeunea trichomanis*** (Gottsche) Besch. – Mizutani (1966, 1970 both as *C. goebelii*), Kitagawa (1971 as *C. goebelii*), Kitagawa and Kodama (1974 as *C. goebelii*), Tixier (1974, 1985 as *C. balansae* and *C. goebelii*), Asthana and Srivastava (2003). Kedah, Penang, Perak, Sabah.

***Cololejeunea tridentata*** Tixier – Tixier (1985), Eggers et al. (1998). Johor, Sarawak.

***Cololejeunea uchimae*** Amakawa – Tixier (1985 as *C. pakseana*). Selangor.

***Cololejeunea veillonii*** Tixier – Pócs and Lee (2016). Pahang.

***Cololejeunea verrucosa*** Steph. – Benedix (1953), Pesiu et al. (2021, in press). Terengganu, Johor.

***Cololejeunea verrucosa*** var. ***rectispina*** (Herzog) Benedix – Benedix (1953), Kitagawa and Kodama (1974). Sarawak, Sabah.

***Cololejeunea wightii*** Steph. – Stephani (1895), Kitagawa (1971, 1972), Tixier (1971, 1985). Penang, Pahang.

***Colura acroloba*** (Prantl) Jovet-Ast – Jovet-Ast (1954, 1967, 1976), Mizutani (1966, 1970), Kitagawa (1969a), Tixier (1971, 1980a), Kitagawa and Kodama (1974), Wolseley et al. (1996), Pócs et al. (2020), Pesiu et al. (2021, in press). Kedah, Selangor, Pahang, Negeri Sembilan, Terengganu, Johor, Sarawak, Sabah.

***Colura ari*** (Steph.) Steph. – Herzog (1952b as *C. javanica*), Jovet-Ast (1976), Mizutani (1966, 1970), Sarimi et al. (2021), Pesiu et al. (in press). Perak, Terengganu, Sarawak, Sabah.

***Colura bisvoluta*** Herzog et Jovet-Ast – Jovet-Ast (1954). Malacca.

***Colura brevistyla*** Herzog – Pócs and Lee (2016). Kelantan.

***Colura clementis*** Grolle – Jovet-Ast (1967). Sabah.

***Colura conica*** (Sande Lac.) K.I.Goebel – Jovet-Ast (1958, 1967), Mizutani (1966, 1970 both as *C. acutifolia*), Kitagawa (1969a as *C. acutifolia*), Kitagawa and Kodama (1974), Wolseley et al. (1996), Pócs et al. (2020), Pesiu et al. (2021, in press). Penang, Negeri Sembilan, Terengganu, Sarawak, Sabah.

***Colura corynophora*** (Nees, Lindenb. et Gottsche) Trevis. – Herzog (1952b as *C. trialata*), Mizutani (1966, 1970), Jovet-Ast (1954, 1958, 1967, 1976), Kitagawa (1969c), Wolseley et al. (1996), Pócs et al. (2020), Pesiu et al. (2021, in press). Penang, Perak, Negeri Sembilan, Terengganu, Johor, Sarawak, Sabah.

***Colura crenulata*** Grolle – Jovet-Ast (1967). Sabah.

***Colura cristata*** Jovet-Ast – Jovet-Ast (1976), Sangrattanaprasert et al. (2019), Pócs et al. (2020). Penang, Sabah.

***Colura cymbalifera*** Herzog et Jovet-Ast – Jovet-Ast (1954). Peninsular Malaysia (type locality).

***Colura galeata*** Jovet-Ast – Jovet-Ast (1967). Sabah.

***Colura imperfecta*** Steph. – Jovet-Ast (1954), Eggers et al. (1998). Pahang, Sarawak.

***Colura inflata*** K.I.Goebel – Müller and Schäfer-Verwimp (1999). Perak.

***Colura inuii*** Horik. – Cheah (2017), Sarimi et al. (2021), Pesiu et al. (in press). Terengganu, Pahang.

***Colura karstenii*** K.I.Goebel – Jovet-Ast (1954), Lee et al. (2013), Sangrattanaprasert et al. (2018). Kedah, Pahang, Johor, Sabah.

***Colura leratii*** (Steph.) Steph. – Jovet-Ast (1967 as *C. apiculata*). Sabah.

***Colura maxima*** Jovet-Ast – Pócs et al. (2020). Sabah.

***Colura mosenii*** Steph. – Pócs and Lee (2016). Kelantan.

***Colura ornata*** K.I.Goebel – Schiffner (1893 as *Lejeunea ornata*,1898 as *Colurolejeunea ornata*), Jovet-Ast (1954, 1967), Mizutani (1966), Kitagawa and Kodama (1974), Wolseley et al. (1996), Pócs et al. (2020). Penang, Pahang, Negeri Sembilan, Sarawak, Sabah.

***Colura pluridentata*** Jovet-Ast – Mizutani (1970). Sabah.

***Colura sigmoidea*** Sangratt., Chantanaorr. et R.L.Zhu – Sangrattanaprasert et al. (2019). Pahang.

***Colura speciosa*** Jovet-Ast – Pócs and Lee (2016). Kelantan.

***Colura strophiolata*** Jovet-Ast – Jovet-Ast (1976). Kedah.

***Colura superba*** (Mont.) Steph. – Jovet-Ast (1967), Pócs et al. (2020). Sabah.

***Colura tenuicornis*** (A.Evans) Steph. – Jovet-Ast (1954, 1976), Mizutani (1970), Tixier (1980a), Pócs et al. (2020). Pahang, Johor, Sabah.

***Colura valida*** Jovet-Ast – Sangrattanaprasert et al. (2019). Pahang.

***Colura verdoornii*** Herzog et Jovet-Ast – Jovet-Ast (1954, 1976), Tixier (1980a), Sangrattanaprasert et al. (2019), Pócs et al. (2020). Kedah, Pahang, Johor, Sabah.

***Conoscyphus trapezioides*** (Sande Lac.) Schiffn. – De Notaris (1874 as *Diploscyphus borneensis*), Herzog (1950 as *C. inflexifolius*), Inoue (1967a), Kitagawa and Kodama (1974), Piippo (1989), Piippo et al. (2014). Pahang, Malacca, Sarawak, Sabah.

***Cryptolophocolea ciliolata*** (Nees) L.Söderstr., Crand.-Stotl., Stotler et Váňa – Kitagawa and Kodama (1974 as *Lophocolea ciliolata*), Piippo (1989 as *Chiloscyphus ciliolatus*), Inoue (1967a, 1968b both as *L. ciliolata*), Cheah (2017 as *C. ciliolatus*). Pahang, Sabah.

***Cryptolophocolea costata*** (Nees) L.Söderstr. – Herzog (1950 as *Lophocolea costata*), Inoue (1967a as *L. costata*), Kitagawa and Kodama (1974 as *L. costata*), Piippo (1989 as *Chiloscyphus costatus*), Akiyama et al. (2001 as *L. costata*). Pahang, Sarawak, Sabah.

***Cryptolophocolea levieri*** (Schiffn.) L.Söderstr. – Piippo (1989 as *Chiloscyphus paroicus*). Sabah.

***Cryptolophocolea massalongoana*** (Schiffn.) L.Söderstr. – Pocock et al. (1984 as *Lophocolea massalongoana*). Pahang.

***Cyathodium foetidissimum*** Schiffn. – Lang (1905). Perak.

***Cyathodium cavernarum*** Kunze – Lee and Gradstein (2021). Kelantan.

***Cylindrocolea tagawae*** (N.Kitag.) R.M.Schust. – Kitagawa (1971 as *Cephaloziella tagawae*). Penang.

***Dactylophorella muricata*** (Gottsche) R.M.Schust. – Mizutani (1970 as *Drepanolejeunea muricata*), Yong and Chan (2017). Perak, Sabah.

***Denotarisia linguifolia*** (De Not.) Grolle – De Notaris (1874 as *Plagiochila linguifolia*), Inoue (1968b as *Jamesoniella ovifolia*), Amakawa (1969a as *J. flexicaulis* f. *affinis*), Kitagawa (1970 as *J. pulchra*), Grolle (1971), Kitagawa and Kodama (1973), Kürschner (1990), Váňa (1991c), Akiyama et al. (2001). Pahang, Sarawak, Sabah.

***Dinckleria singularis*** (Schiffn.) M.A.M.Renner, Schäf.-Verw. et Heinrichs – Inoue (1989 as *Plagiochila singularis*), Cheah (2017 as *P. singularis*). Pahang, Sabah.

***Diplasiolejeunea cavifolia*** Steph. – Tixier (1971 as *D. brachyclada*, 1980a as *D. javanica*), Mizutani (1966 as *D. javanica*, 1970 as *D. brachyclada*), Kitagawa and Kodama (1974), Dong et al. (2012), Pócs et al. (2020). Perak, Pahang, Sabah.

***Diplasiolejeunea cobrensis*** Steph. – Mizutani (1970 as *D. incurvata*). Sabah.

***Diplasiolejeunea jovet-astiae*** Grolle – Grolle (1966), Kitagawa and Kodama (1974), Tixier (1980a), Dong et al. (2012), Pócs et al. (2020). Pahang, Sarawak, Sabah.

***Diplasiolejeunea longilobula*** Herzog – Herzog (1950). Sarawak.

***Diplasiolejeunea patelligera*** Herzog – Mizutani (1970 as *D. neobrachyclada*), Tixier (1980a, also as *D. neobrachyclada*), Dong et al. (2012). Pahang, Sabah.

***Diplasiolejeunea unidentata*** (Lehm. et Lindenb.) Schiffn. – Pócs and Lee (2016 as *D. rudolphiana*). Kelantan.

***Diplophyllum kinabaluense*** Furuki et Suleiman – Furuki and Suleiman (2016). Sabah.

***Diplophyllum nanum*** Herzog – Müller and Schäfer-Verwimp (1999). Pahang.

***Drepanolejeunea angustifolia*** (Mitt.) Grolle – Herzog (1950 as *D. tenuis*), Tixier (1971 as *D. tenuis*), Kamimura (1974 as *D. tenuis*). Pahang, Sarawak, Sabah.

***Drepanolejeunea bischlerae*** (Grolle) Grolle et R.L.Zhu – Grolle and Zhu (2000). Sabah.

***Drepanolejeunea ciliata*** Mizut. – Mizutani (1970), Kamimura (1974). Sabah.

***Drepanolejeunea cyclops*** (Sande Lac.) Grolle et R.L.Zhu – Herzog (1943 as *Rhaphidolejeunea cyclops*), Mizutani (1966, 1970 both as *R. cyclops*), Bischler (1968 as *R. cyclops*). Selangor, Sarawak, Sabah.

***Drepanolejeunea dactylophora*** (Nees, Lindenb. et Gottsche) J.B.Jack et Steph. – Herzog (1934, 1950), Mizutani (1966, 1970), Kamimura (1974), Kitagawa and Kodama (1974), Pócs et al. (2020), Pesiu et al. (2021). Terengganu, Johor, Sarawak, Sabah.

***Drepanolejeunea elegans*** Herzog – Herzog (1936). Sabah.

***Drepanolejeunea fissicornua*** Steph. – Mizutani (1990), Pócs et al. (2014, 2020), Pócs and Lee (2016). Kelantan, Pahang, Selangor, Sabah.

***Drepanolejeunea foliicola*** Horik. – Eggers (2006). Pahang.

***Drepanolejeunea intermedia*** Zwickel – Grolle (1976). Sabah.

***Drepanolejeunea levicornua*** Steph. – Tixier (1971 [‘*laevicornua*’]), Mizutani (1990), Eggers et al. (1998), Pócs et al. (2014), Pesiu et al. (2021, in press). Selangor, Pahang, Terengganu, Sarawak.

***Drepanolejeunea longicornua*** (Herzog) Mizut. – Mizutani (1970 as *D. levicornua* var. *longicornua*, 1990), Kitagawa and Kodama (1974 as *D. levicornua* var. *longicornua*), Pócs et al. (2020), Pesiu et al. (2021). Penang, Terengganu, Sarawak, Sabah.

***Drepanolejeunea longicruris*** (Steph.) Grolle et R.L.Zhu – Herzog (1943 as *Rhaphidolejeunea longicruris*), Bischler (1968 as *R. longicruris*), Kitagawa and Kodama (1974 as *R. longicruris*), Grolle and Zhu (2000). Sabah.

***Drepanolejeunea nymanii*** Steph. – Mizutani (1990). Sabah.

***Drepanolejeunea obliqua*** Steph. – Herzog (1939), Mizutani (1970). Johor, Sabah.

***Drepanolejeunea obtriangulata*** T.Kodama – Kodama (1976), Pócs et al. (2014). Selangor, Sabah.

***Drepanolejeunea pentadactyla*** (Mont.) Steph. – Herzog (1934 as *D. micholitzii* and its var. *angustissima*), Tixier (1974 as *D. micholitzii*, 1980a as *D. micholitzii* var. *brevifolia*), Mizutani (1966, 1970 both as *D. micholitzii*), Kitagawa and Kodama (1974 as *D. micholitzii*), Pócs et al. (2014, 2020), Pesiu et al. (2021, in press). Kedah, Selangor, Pahang, Terengganu, Johor, Sarawak, Sabah.

***Drepanolejeunea pentadactyla*** var. ***dactylophoroides*** (Herzog) Pócs – Herzog (1934 as *D. micholitzii* var. *dactylophoroides*). Sabah.

***Drepanolejeunea pleiodictya*** Herzog – Tixier (1980a). Pahang.

***Drepanolejeunea serricalyx*** Herzog – Pócs et al. (2020). Sabah.

***Drepanolejeunea spicata*** (Steph.) Grolle et R.L.Zhu – Mizutani (1966 as *Rhaphidolejeunea spicata*), Bischler (1968 as *R. spicata*), Grolle and Zhu (2000), Pócs et al. (2014), Pesiu et al. (2021, in press). Pahang, Terengganu, Sarawak, Sabah.

***Drepanolejeunea spinosocornuta*** Steph. – Tixier (1980a). Pahang.

***Drepanolejeunea tenera*** K.I.Goebel – Herzog (1934 as *D. tenera* var. *genuina* and f. *goebelii*, 1952b), Mizutani (1966, 1970), Tixier (1971, 1974, 1980a as *D. tenera* f. *goebelii*). Kitagawa and Kodama (1974), Pócs et al. (2020). Kedah, Pahang, Sarawak, Sabah.

***Drepanolejeunea ternatensis*** (Gottsche) Schiffn. – Herzog (1950, also as *D. ternatensis* var. *lancispina*), Mizutani (1966, 1970), Kamimura (1974), Cheah (2017), Pócs et al. (2020), Pesiu et al. (2021, in press). Pahang, Terengganu, Sarawak, Sabah.

***Drepanolejeunea teysmannii*** (Gottsche) Steph. – Herzog (1950), Mizutani (1966, 1970), Inoue (1968b), Kamimura (1974, 1975), Kitagawa and Kodama (1974), Kürschner (1990), Pócs et al. (2020). Pahang, Sarawak, Sabah.

***Drepanolejeunea thwaitesiana*** (Mitt.) Steph. – Goebel (1930 [‘*Thwaitesii*’]), Mizutani (1966, 1970, 1990), Tixier (1971, 1974, 1980a), Kitagawa and Kodama (1974), Pócs et al. (2020), Pesiu et al. (2021, in press). Kedah, Perak, Selangor, Pahang, Terengganu, Sabah.

***Drepanolejeunea thwaitesiana*** var. ***zhengii*** R.L.Zhu – Zhu and So (2001). Pahang.

***Drepanolejeunea tricornua*** Herzog – Mizutani (1970, 1990), Pócs et al. (2014, 2020). Selangor, Pahang, Sarawak, Sabah.

***Drepanolejeunea vesiculosa*** (Mitt.) Steph. – Herzog (1950 as *D. vesiculosa* f. *robusta*), Inoue (1967a, 1968b), Mizutani (1966, 1970), Kamimura (1974), Kitagawa and Kodama (1974), Kürschner (1990), Lee et al. (2013), Pócs et al. (2020). Perak, Pahang, Sarawak, Sabah.

***Dumortiera hirsuta*** (Sw.) Nees – Johnson (1958), Akiyama et al. (2001), Ludwiczuk and Asakawa (2010). Pahang, Sabah.

***Dumortiera hirsuta*** subsp. ***nepalensis*** (Taylor) R.M.Schust. – Campbell (1915 as *D. trichocephala*, 1918 as *D. calcicola*), Evans (1919 as *D. nepalensis*), Kitagawa and Kodama (1974 as *D. nepalensis*). Perak, Selangor, Sarawak, Sabah.

***Eotrichocolea furukii*** T.Katag. – Katagiri et al. (2012). Sabah.

***Frullania alstonii*** Verd. – Verdoorn (1932b), Hattori (1976). Johor, Sabah.

***Frullania apiculata*** (Reinw., Blume et Nees) Nees – Verdoorn (1932a), Herzog (1950), Inoue (1967a, 1968b), Tixier (1974, 1980a), Kamimura (1974, 1975), Kitagawa and Kodama (1974), Hattori (1975c, 1976), Kodama (1976), Pócs et al. (2020), Pesiu et al. (2021). Kedah, Terengganu, Pahang, Selangor, Sarawak, Sabah.

***Frullania apiculata*** var. ***goebelii*** Schiffn. – Verdoorn (1934b), Herzog (1950), Tixier (1971). Pahang, Sarawak, Sabah.

***Frullania armatifolia*** Verd. – Hattori (1976 as *F. altemammillata*). Sabah.

***Frullania armitiana*** Steph. – Kamimura (1974). Sabah.

***Frullania benjaminiana*** Inoue – Inoue (1967a,b), Hattori (1975a). Pahang.

***Frullania berthoumieui*** Steph. – Hattori (1976). Sabah.

***Frullania brotheri*** Steph. – Stephani (1894), Schiffner (1898), Bonner (1965), Hattori (1975a,c, 1976, 1980), Kürschner (1990), Sukkharak (2018). Perlis, Perak, Selangor, Pahang, Malacca, Johor, Sabah.

***Frullania claviloba*** Steph. – Verdoorn (1930, 1932b), Herzog (1950), Kamimura (1974), Kitagawa and Kodama (1974), Hattori (1974b, 1975b,c, 1976). Selangor, Johor, Sarawak, Sabah.

***Frullania clemensiana*** Verd. – Verdoorn (1932a), Hattori and Kamimura (1971 as *Steerea mastigophoroides*), Hattori (1976 as *S. clemensiana*). Sabah.

***Frullania cordistipula*** (Reinw., Blume et Nees) Nees – Kamimura (1974, 1975). Sabah.

***Frullania ericoides*** (Nees) Mont. – Verdoorn (1929 as *F. squarrosa*), Hattori (1975a, 1976). Penang, Pahang, Sabah.

***Frullania fallax*** Gottsche – Verdoorn (1930). Pahang.

***Frullania gaudichaudii*** (Nees et Mont.) Nees et Mont. – Verdoorn (1930, 1932a), Herzog (1950), Kitagawa and Kodama (1974), Hattori (1975c, 1976), Cheah (2017). Selangor, Pahang, Sarawak, Sabah.

***Frullania gracilis*** (Reinw., Blume et Nees) Nees – Verdoorn (1932a as *F. minor*), Herzog (1950), Kamimura (1974, 1975), Kitagawa and Kodama (1974), Hattori (1975a, 1975c as *F. minor*, 1976), Kürschner (1990). Selangor, Pahang, Malacca, Johor, Sarawak, Sabah.

***Frullania grandistipula*** Lindenb. – Verdoorn (1932a), Tixier (1971), Hattori (1976). Pahang, Sabah.

***Frullania hasskarliana*** Lindenb. – Verdoorn (1932a), Hattori (1973, 1975a, 1976 as *F. hasskarliana* var. *integribracteata*), Kitagawa and Kodama (1974). Pahang, Sabah.

***Frullania hottana*** S.Hatt. – Hattori (1976, 1986). Sarawak.

***Frullania hypoleuca*** Nees – Hattori (1976), Kamimura (1974). Sarawak, Sabah.

***Frullania integristipula*** (Nees) Nees – Verdoorn (1930, 1932a), Herzog (1950), Kamimura (1974), Kitagawa and Kodama (1974), Tixier (1974, 1980a), Hattori (1976, 1980). Kedah, Pahang, Johor, Sarawak, Sabah.

***Frullania intermedia*** (Reinw., Blume et Nees) Nees – Verdoorn (1930, 1934b), Herzog (1950), Kitagawa and Kodama (1974), Hattori (1975c, 1976 as *F. intermedia* var. *submorokensis* and *F. intermedia* f. *billardieriana*, 1980), Wolseley et al. (1996). Penang, Perak, Kelantan, Negeri Sembilan, Johor, Sarawak, Sabah.

***Frullania junghuhniana*** Gottsche – Verdoorn (1932a, 1934b), Hattori (1974c, 1976), Kürschner (1990). Sabah.

***Frullania junghuhniana*** var. ***bisexualis*** S.Hatt. – Hattori (1976), Kodama (1976). Sabah.

***Frullania junghuhniana*** var. ***tenella*** (Sande Lac.) Grolle et S.Hatt. – Kamimura (1974 as *F. perversa*), Tixier (1974 as *Neohattoria perversa*), Hattori (1975a, 1976 as *F. junghuhniana* var. *minutissima* and *F. perminuta*). Kedah, Pahang, Sabah.

***Frullania meijeri*** S.Hatt. – Hattori (1974c, 1976). Sabah.

***Frullania meyeniana*** Lindenb. – Verdoorn (1934b), Tixier (1971), Hattori (1975c). Pahang, Sabah.

***Frullania mizutanii*** Kamim. et S.Hatt. – Hattori and Kamimura (1973), Kamimura (1974), Hattori (1976, 1978), Kodama (1976). Sabah.

***Frullania moniliata*** (Reinw., Blume et Nees) Mont. – Verdoorn (1932a as *F. moniliata* subsp. *breviramea*), Hattori (1972, 1976 both as *F. tamarisci* var. *breviramea*). Sabah.

***Frullania monocera*** (Hook.f. et Taylor) Gottsche, Lindenb. et Nees – Hattori (1976 as *F. hampeana*). Sabah.

***Frullania nepalensis*** (Spreng.) Lehm. et Lindenb. – Verdoorn (1932b). Pahang.

***Frullania nigricaulis*** (Reinw., Blume et Nees) Nees – Verdoorn (1930, 1932a), Hattori (1975a). Pahang, Sabah.

***Frullania nodulosa*** (Reinw., Blume et Nees) Nees – Verdoorn (1930, 1932a, 1934b), Herzog (1950), Inoue (1968b), Kitagawa and Kodama (1974), Hattori (1975c, 1980). Perak, Selangor, Pahang, Johor, Sarawak, Sabah.

***Frullania notarisii*** Steph. – Verdoorn (1934b), Hattori (1974c, 1976), Kitagawa and Kodama (1974), Tixier (1974). Kedah, Sarawak, Sabah.

***Frullania obscura*** (Sw.) Mont. – Hattori (1975a as *F. wallichiana*). Pahang.

***Frullania ocellata*** S.Hatt. et Kamim. – Hattori and Kamimura (1973), Kamimura (1974). Sabah.

***Frullania orientalis*** Sande Lac. – Verdoorn (1937), Hattori (1976). Pahang, Sabah.

***Frullania ornithocephala*** (Reinw., Blume et Nees) Nees – Verdoorn (1934b), Hattori (1975a, 1976 as *F. ornithocephala* f. *magnilobula* and f. *retusa*, 1980). Pahang, Sabah.

***Frullania papillata*** Steph. – Kamimura (1974, 1975). Sabah.

***Frullania papillilobula*** S.Hatt. – Hattori (1975b, 1976). Sabah.

***Frullania polyptera*** Taylor – Hattori (1975a). Pahang.

***Frullania pullei*** Verd. – Tixier (1974). Kedah.

***Frullania ramuligera*** (Nees) Mont. – Verdoorn (1932a, 1934b), Hattori (1972), Pócs et al. (2020). Sabah.

***Frullania recurvistipula*** S.Hatt. – Hattori (1975a, 1986). Pahang.

***Frullania reflexistipula*** Sande Lac. – Verdoorn (1932a), Hattori (1975a as *F. philippinensis*, 1976). Pahang, Sabah.

***Frullania repandistipula*** Sande Lac. subsp. ***spinibractea*** S.Hatt. – Hattori (1975c, 1976 as *F. repandistipula* subsp. *spinifera*), Pesiu et al. (in press). Terengganu, Sabah.

***Frullania sabahana*** S.Hatt. – Hattori (1976, 1980). Sarawak, Sabah.

***Frullania sarawakensis*** S.Hatt. – Hattori (1976, 1980). Sarawak.

***Frullania serrata*** Gottsche – Verdoorn (1932b, 1934b), Herzog (1950), Kamimura (1974, 1975), Kitagawa and Kodama (1974), Hattori (1975a, 1976 as *F. serrata* f. *crispulodentata*), Ludwiczuk and Asakawa (2010). Pahang, Johor, Sarawak, Sabah.

***Frullania sinuata*** Sande Lac. – Verdoorn (1932b, 1934b), Hattori (1975a, 1980). Johor, Pahang.

***Frullania sublignosa*** Steph. – Stephani (1910 as *F. borneensis*), Verdoorn (1930), Hattori (1976). Sarawak.

***Frullania subnigricaulis*** S.Hatt. – Hattori (1974b, 1975a, 1976). Pahang, Sabah.

***Frullania subocellata*** S.Hatt. – Pócs et al. (2014). Pahang.

***Frullania ternatensis*** Gottsche – Verdoorn (1930, 1932a, 1934b), Herzog (1950), Tixier (1971, 1974), Kamimura (1974, 1975), Kitagawa and Kodama (1974), Hattori (1975c). Kedah, Pahang, Sarawak, Sabah.

***Frullania ternatensis*** var. ***nonappendiculata*** S.Hatt. – Hattori (1976). Sarawak, Sabah.

***Frullania togashiana*** S.Hatt. – Hattori (1975a). Pahang.

***Frullania tricarinata*** Sande Lac. – Kamimura (1974). Sabah.

***Frullania trichodes*** Mitt. – Verdoorn (1930, 1934b as *F. picta*, *F. tenuicaulis* and *F. vethii*), Herzog (1950 as *F. picta*, *F. tenuicaulis* and *F. vethii*), Kitagawa (1969c as *F. picta*), Kamimura (1974, 1975 both as *F. tenuicaulis*), Kitagawa and Kodama (1974 as *F. tenuicaulis*), Tixier (1974 as *F. picta*), Hattori (1976 as *F. vethii* f. *acutiloba*), Pócs et al. (2014), Cheah (2017). Kedah, Penang, Pahang, Johor, Sarawak, Sabah.

***Frullania vaginata*** (Sw.) Nees – Hattori (1975a). Pahang.

***Frullania venusta*** S.Hatt. – Hattori (1974b, 1976). Sabah.

***Gottschelia schizopleura*** (Spruce) Grolle – Inoue (1967a as *Jamesoniella microphylla*), Amakawa (1969a as *J. microphylla*), Váňa (1991c). Pahang, Sabah.

***Gymnomitrion incompletum*** (Gottsche) Váňa – Kitagawa (1973 as *G. laceratum* var. *borneense*), Kitagawa and Kodama (1973 as *G. laceratum* var. *borneense*), Váňa (1991a). Sabah.

***Gymnomitrion revolutum*** (Nees) H.Philib. – Kitagawa (1967 as *Marsupella revoluta*), Kitagawa and Kodama (1973 as *M. revoluta*), Váňa (1991a as *M. revoluta*), Akiyama et al. (2001 as *M. revoluta*). Sabah.

***Gymnomitrion subintegrum*** (S.W.Arnell) Váňa – Kitagawa (1967 as *Marsupella integra*), Váňa (1991a *M. subintegra*). Sabah.

***Haplomitrium blumei*** (Nees) R.M.Schust. – Bartholomew-Began (1991). Pahang.

***Herbertus aduncus*** (Dicks.) Gray – Kürschner (1990 as *H. dicranus* [‘*dicrananus*’]), Juslén (2006 as *H. dicranus* and *H. longispinus*), Cheah (2017 as *H. dicranus*). Pahang, Sabah.

***Herbertus ceylanicus*** (Steph.) Abeyw. – Juslén (2006). Pahang.

***Herbertus pilifer*** (Steph.) H.A.Mill. – Juslén (2006). Sarawak.

***Herbertus ramosus*** (Steph.) H.A.Mill. – Kamimura (1975 [‘*Herberta ramosa*’]). Sabah.

***Herbertus sendtneri*** (Nees) Lindb. – Kürschner (1990 as *H. armitanus* and *H. circinatus*), Akiyama et al. (2001 as *H. armitanus*), Juslén (2006 as *H. circinatus*), Cheah (2017 as *H. armitanus*). Pahang, Sabah.

***Heteroscyphus acutangulus*** (Schiffn.) Schiffn. – Inoue (1968b as *Chiloscyphus acutangulus*). Pahang.

***Heteroscyphus argutus*** (Reinw., Blume et Nees) Schiffn. – Herzog (1950 as *Chiloscyphus argutus*), Kitagawa (1969c), Tixier (1971 as *C. argutus*), Kitagawa and Kodama (1974 as *C. argutus*), Inoue (1981), Piippo (1989), Wolseley et al. (1996). Penang, Pahang, Negeri Sembilan, Sarawak, Sabah.

***Heteroscyphus aselliformis*** (Reinw., Blume et Nees) Schiffn. – Mitten and Wright (1894 as *Chiloscyphus aselliformis*), Herzog (1950 as *C. aselliformis* var. *neesii*), Inoue (1967a as *C. aselliformis*), Kitagawa and Kodama (1974), Piippo (1989), Kürschner (1990 as *C. aselliformis*), Ludwiczuk and Asakawa (2010). Pahang, Sarawak, Sabah.

***Heteroscyphus balnetii*** (Herzog) Grolle – Piippo (1989). Sabah.

***Heteroscyphus coalitus*** (Hook.) Schiffn. – Herzog (1950 as *Chiloscyphus communis*), Inoue (1967a, 1968b both as *C. communis*), Kitagawa (1971 as *H. communis*), Tixier (1971 as *C. communis*), Kitagawa and Kodama (1974 as *C. communis*), Kamimura (1975 as *H. bescherellei*), Piippo (1989). Penang, Pahang, Sarawak, Sabah.

***Heteroscyphus diestianus*** (Sande Lac.) Piippo – Kitagawa and Kodama (1974 as *Chiloscyphus diestianus*), Piippo (1989), Akiyama et al. (2001). Sarawak, Sabah.

***Heteroscyphus integerrimus*** **(**Schiffn.) Gradst. et G.E.Lee – Pócs et al. (2014 as *Chiloscyphus integerrimus*). Pahang.

***Heteroscyphus iwatsukii*** (S.Hatt.) Piippo – Hattori (1964 as *Saccogynidium iwatsukii*), Piippo (1989). Sabah.

***Heteroscyphus parvulus*** (Schiffn.) Schiffn. – Kitagawa and Kodama (1974 as *Chiloscyphus parvulus*). Sabah.

***Heteroscyphus splendens*** (Lehm. et Lindenb.) Grolle – De Notaris (1874 as *Chiloscyphus decurrens* and *C. densifolius*), Herzog (1950, 1952b both as *C. decurrens*), Inoue (1967a, 1968b, both as *C. decurrens*), Kitagawa (1969c as *C. decurrens*), Kitagawa and Kodama (1974 as *C. decurrens*), Tixier (1974 as *C. decurrens*), Piippo (1989), Kürschner (1990), Akiyama et al. (2001). Kedah, Penang, Pahang, Sarawak, Sabah.

***Heteroscyphus succulentus*** (Gottsche) Schiffn. – De Notaris (1874 as *Chiloscyphus concinnus*), Stephani (1907 as *C. succulentus*), Herzog (1950 as *C. succulentus*), Kitagawa (1973 as *C. succulentus*), Kitagawa and Kodama (1974 as *C. succulentus*), Piippo (1989). Penang, Sarawak, Sabah.

***Heteroscyphus tridentatus*** (Sande Lac.) Grolle – Cheah (2017). Pahang.

***Heteroscyphus wettsteinii*** (Schiffn.) Schiffn. – Kitagawa and Kodama (1974 as *Chiloscyphus wettsteinii*), Müller and Schäfer-Verwimp (1999), Cheah (2017). Perak, Pahang, Sabah.

***Hygrolembidium boschianum*** (Sande Lac.) R.M.Schust. – Grolle (1967). Malacca.

***Isotachis japonica*** Steph. – Inoue (1967a). Pahang.

***Jackiella angustifolia*** Herzog – Herzog (1950, 1952a), Váňa (1992). Sarawak, Sabah.

***Jackiella javanica*** Schiffn. – Herzog (1950), Inoue (1967a), Kitagawa (1971), Váňa (1992). Penang, Pahang, Sarawak, Sabah.

***Jackiella singapurensis*** Schiffn. – Kitagawa (1969c, 1981). Penang.

***Jensenia decipiens*** (Mitt.) Grolle – Herzog (1950 as *Makednothallus obtusidens*), Kitagawa and Kodama (1974 as *J. zollingeri*), Grolle and Piippo (1986), Akiyama et al. (2001), Forrest et al. (2005). Sarawak, Sabah.

***Jubula javanica*** Steph. – Herzog (1950 as *J. hutchinsiae* subsp. *javanica*), Kitagawa and Kodama (1974 as *J. hutchinsiae* subsp. *javanica*), Váňa and Piippo (1989b as *J. hutchinsiae* subsp. *javanica*), Pätsch et al. (2010 as *J. hutchinsiae* subsp. *javanica*). Pahang, Sarawak, Sabah.

***Kurzia abbreviata*** Mizut. – Mizutani (1974), Hürlimann (1985), Cheah (2017). Pahang, Sarawak, Sabah.

***Kurzia abietinella*** (Herzog) Grolle – Herzog (1950 as *Lepidozia abietinella*), Kitagawa and Kodama (1973), Mizutani (1974), Kürschner (1990), Cheah (2017). Pahang, Sarawak, Sabah.

***Kurzia borneensis*** Mizut. – Mizutani (1974), Kamimura (1975), Akiyama et al. (2001), Cheah (2017). Pahang, Sabah.

***Kurzia geniculata*** Mizut. – Mizutani (1974), Cheah (2017). Pahang, Sabah.

***Kurzia gonyotricha*** (Sande Lac.) Grolle – Herzog (1952b as *Lepidozia gonyotricha*), Kitagawa (1969c), Mizutani (1974), Akiyama et al. (2001). Penang, Sarawak, Sabah.

***Kurzia lineariloba*** Mizut. – Mizutani (1974), Kürschner (1990), Cheah (2017). Pahang, Sabah.

***Kymatocalyx rhizomaticus*** (Herzog) Gradst. et Váňa – Herzog (1950, 1952a both as *Stenorrhipis rhizomatica*), Váňa (1991c as *S. rhizomatica*). Sarawak.

***Leiomitra merrillana*** (Steph.) T.Katag. – Kitagawa (1973 as *Trichocolea merrillana*), Akiyama et al. (2001 as *T. merrillana*), Katagiri and Deguchi (2012). Pahang, Sabah.

***Lejeunea adpressa*** Nees – Inoue (1968b as *L. boninensis*), Kitagawa (1971 as *L. borneensis*), Mizutani (1978 as *L. borneensis*), Wolseley et al. (1996 as *L. caespitosa*), Zhu and So (2001 as *L. anisophylla*), Lee (2013 as *L. anisophylla*), Pesiu et al. (2021, in press). Perlis, Langkawi, Perak, Penang, Selangor, Kuala Lumpur, Pahang, Negeri Sembilan, Terengganu, Johor, Sarawak, Sabah.

***Lejeunea alata*** Gottsche – Mizutani (1970 as *L. mitracalyx*), Kitagawa and Kodama (1974 as *L. mitracalyx*), Lee (2013). Pahang, Sabah.

***Lejeunea albescens*** (Steph.) Mizut. – Eifrig (1937 as *Taxilejeunea albescens*), Inoue (1967a as *T. albescens*), Mizutani (1970), Hattori and Kamimura (1971), Lee (2013). Pahang, Sabah.

***Lejeunea apiculata*** Sande Lac. – Mizutani (1966 as *Prionolejeunea ungulata*, 1970 as *Stenolejeunea apiculata*), Tixier (1971 as *S. apiculata*), Kitagawa and Kodama (1974 as *P. ungulata*), Lee (2013), Cheah (2017). Pahang, Sabah.

***Lejeunea cocoes*** Mitt. – Mizutani (1963), Kamimura (1974), Lee (2013), Pesiu et al. (in press). Perlis, Pahang, Terengganu, Sarawak, Sabah.

***Lejeunea compacta*** (Steph.) Steph. – Lee (2013). Sabah.

***Lejeunea compressiuscula*** (Steph.) G.E.Lee et Heinrichs – Eifrig (1937 as *Taxilejeunea compressiuscula*), Tixier (1971 as *T. compressiuscula*). Pahang, Johor.

***Lejeunea contracta*** Mizut. – Mizutani (1970), Kitagawa and Kodama (1974), Lee (2013). Sabah.

***Lejeunea convexiloba*** M.L.So et R.L.Zhu – Sarimi et al. (2021). Sabah.

***Lejeunea dimorpha*** Kodama – Kodama (1976), Lee (2013), Pócs et al. (2014). Selangor, Kelantan, Pahang, Sabah.

***Lejeunea dipterota*** (Eifrig) G.E.Lee – Lee (2013). Sabah.

***Lejeunea discreta*** Lindenb. – Mizutani (1970), Kitagawa and Kodama (1974), Tixier (1980a as *Xylolejeunea longiloba*), Lee et al. (2011b), Lee (2013). Perlis, Perak, Pahang, Sabah.

***Lejeunea eifrigii*** Mizut. – Mizutani (1970), Lee et al. (2011b), Lee (2013). Pahang, Sabah.

***Lejeunea exilis*** (Reinw., Blume et Nees) Grolle – Mizutani (1970), Pócs et al. (2020). Sabah.

***Lejeunea exilis*** var. ***abnormis*** (Herzog) G.E.Lee – Lee (2013). Kelantan, Pahang.

***Lejeunea flava*** (Sw.) Nees – Inoue (1967a), Mizutani (1970), Kitagawa and Kodama (1974), Lee (2013), Pócs et al. (2020). Kedah, Penang, Perak, Selangor, Kelantan, Pahang, Sabah.

***Lejeunea flavida*** Mitt. – Kamimura (1974 as *Pycnolejeunea flavida*), Inoue (1967a as *P. flavida*). Pahang, Sabah.

***Lejeunea fleischeri*** (Steph.) Mizut. – Lee (2013). Perak, Pahang.

***Lejeunea gradsteinii*** G.E.Lee, Damanhuri et Latiff – Lee et al. (2011a), Lee (2013), Pócs and Lee (2016). Pahang, Sabah.

***Lejeunea kinabalensis*** Mizut. – Mizutani (1970), Lee (2013). Sabah.

***Lejeunea leratii*** (Steph.) Mizut. – Eifrig (1937 as *Taxilejeunea patersonii*). Sabah.

***Lejeunea lumbricoides*** (Nees) Nees – Eifrig (1937 as *Taxilejeunea lumbricoides*), Mizutani (1970), Kitagawa and Kodama (1974), Tixier (1980a), Lee (2013). Pahang, Sabah.

***Lejeunea malaysiana*** G.E.Lee et Pócs - Lee et al. (in press). Pahang.

***Lejeunea micholitzii*** Mizut. – Mizutani (1970), Lee (2013), Pócs et al. (2014, 2020), Pesiu et al. (2021). Langkawi, Selangor, Pahang, Negeri Sembilan, Kelantan, Terengganu, Sarawak, Sabah.

***Lejeunea microloba*** Taylor – Mizutani (1970 as *L. chalmersii*), Lee (2013). Sabah.

***Lejeunea mimula*** Hürl. – Tixier (1971 as *Taxilejeunea luteola*), Mizutani (1970 as *L. luteola*), Kitagawa and Kodama (1974 as *L. luteola*), Lee (2013). Pahang, Sabah.

***Lejeunea mizutanii*** Grolle – Mizutani (1970 as *L. zollingeri*), Lee (2013). Sabah.

***Lejeunea papilionacea*** Prantl – Mizutani (1966 as *L. infestans* and *L. pterota*, 1970 as *L. herzogii* and *L. infestans*, 1972b as *L. diversitexta*), Kitagawa and Kodama (1974 as *L. diversitexta*), Zhu and Grolle (2001), Lee (2013), Pócs et al. (2020). Kedah, Langkawi, Selangor, Kelantan, Pahang, Sarawak, Sabah.

***Lejeunea patersonii*** (Steph.) Steph. – Inoue (1967a), Lee (2013). Kuala Lumpur, Kelantan, Pahang, Johor.

***Lejeunea patriciae*** Schäf.-Verw. – Tixier (1971 as *L. pilifera*), Schäfer-Verwimp (2001, 2006), Lee (2013). Penang, Perak, Kelantan, Pahang.

***Lejeunea pectinella*** Mizut. – Mizutani (1970), Lee (2013). Sabah.

***Lejeunea pulchriflora*** (Pearson) G.E.Lee, Bechteler, Pócs, Schäf.-Verw. et Heinrichs – Lee (2013 as *L. tamaspocsii*), Lee and Gradstein (2013 as *L. tamaspocsii*), Lee et al. (2016). Kelantan, Pahang, Sabah.

***Lejeunea sordida*** (Nees) Nees – Eifrig (1937 as *Taxilejeunea sordida*), Mizutani (1970), Lee et al. (2011a, 2011b), Lee (2013). Perlis, Langkawi, Kedah, Penang, Perak, Selangor, Kelantan, Pahang, Johor, Sarawak, Sabah.

***Lejeunea stenodentata*** M.A.M.Renner et Pócs – Herzog (1950 as *Crossotolejeunea borneensis*). Mizutani (1966, 1970 both as *C. borneensis*, 1972a as *Drepanolejeunea dentata*). Sarawak, Sabah.

***Lejeunea stephaniana*** Mizut. – Mizutani (1966, 1970), Lee (2013). Sabah.

***Lejeunea thallophora*** (Eifrig) Gradst. – Zhu et al. (2018b). Sabah.

***Lejeunea trinitensis*** Lindenb. – Reiner-Drehwald and Grolle (2012). Johor.

***Lejeunea tuberculosa*** Steph. – Lee (2013). Kedah, Penang, Perak, Selangor, Pahang, Sabah.

***Lejeunea umbilicata*** (Nees) Nees – Herzog (1950 as *Taxilejeunea umbilicata*), Mizutani (1970), Kitagawa and Kodama (1974), Tixier (1980a), Grolle (1988 as *L. cuculliflora*), Lee (2013). Perak, Selangor, Kelantan, Pahang, Johor, Sarawak, Sabah.

***Lejeunea utriculata*** (Steph.) Mizut. – Mizutani (1966 as *Pycnolejeunea utriculata*, 1970), Lee (2013). Sabah.

***Lejeunea wightii*** Steph. – Mizutani (1966, 1970). Sabah.

***Lepicolea rara*** (Steph.) Grolle – Inoue (1967a, 1968b both as *L. loriana*), Kitagawa (1978 as *L. loriana*), Pocock et al. (1984 as *L. loriana*), Kürschner (1990), Cheah (2017). Pahang, Sabah.

***Lepicolea yakusimensis*** (S.Hatt.) S.Hatt. – Inoue (1967a), Kitagawa and Kodama (1973), Akiyama et al. (2001). Pahang, Sabah.

***Lepidolejeunea bidentula*** (Steph.) R.M.Schust – Hoffman (1935 as *Pycnolejeunea corticola* and *P. decurvifolia*), Herzog (1950 as *P. badia* f. *parvistipa*, 1952b as *P. corticola* and *P. nicobarica*), Mizutani (1966, 1970 as *P. bidentula*, *P. punctata* and *P. nicobarica*), Inoue (1967a as *P. bidentula*), Kitagawa (1969c as *P. nicobarica*), Kitagawa and Kodama (1974 as *P. bidentula* and *P. nicobarica*), Piippo (1986), Wolseley et al. (1996), Pócs et al. (2020), Pesiu et al. (2021). Penang, Selangor, Pahang, Negeri Sembilan, Terengganu, Johor, Sarawak, Sabah.

***Lepidolejeunea integristipula*** (J.B.Jack et Steph.) R.M.Schust. – Mizutani (1970, 1972b both as *Pycnolejeunea integristipula*), Kitagawa and Kodama (1974 as *P. integristipula*), Piippo (1986), Cheah (2017). Pahang, Sabah.

***Lepidozia ambigua*** De Not. – De Notaris (1874), Schiffner (1898), Stephani (1909). Sarawak.

***Lepidozia borneensis*** Steph. – Herzog (1950), Kitagawa and Kodama (1973), Mizutani (1974), Kamimura (1975), Ludwiczuk and Asakawa (2010). Sarawak, Sabah.

***Lepidozia brotheri*** Steph. – Kürschner (1990). Sabah.

***Lepidozia cladorhiza*** (Reinw., Blume et Nees) Nees – Mitten and Wright (1894), Herzog (1950 as *L. cladorhiza* var. *macgregorii*), Kitagawa and Kodama (1973), Mizutani (1974), Kürschner (1990), Akiyama et al. (2001). Sarawak, Sabah.

***Lepidozia everettii*** Steph. – Stephani (1909), Herzog (1950), Mizutani (1968). Sarawak.

***Lepidozia fauriana*** Steph. – Mizutani (1974), Ludwiczuk and Asakawa (2010). Sabah.

***Lepidozia ferdinandi-muelleri*** Steph. – Kitagawa and Kodama (1973), Mizutani (1974). Sabah.

***Lepidozia haskarliana*** (Gottsche, Lindenb. et Nees) Steph. – Mizutani (1974). Sabah.

***Lepidozia holorhiza*** (Reinw., Blume et Nees) Nees – Mitten and Wright (1894), Inoue (1968b). Pahang, Sabah.

***Lepidozia kinabaluensis*** Mizut. – Mizutani (1974). Sabah.

***Lepidozia lacerifolia*** Steph. – Herzog (1950). Sarawak.

***Lepidozia miqueliana*** Sande Lac. – De Notaris (1874), Schiffner (1898), Herzog (1950). Sarawak.

***Lepidozia reptans*** (L.) Dumort. – Mizutani (1974). Sabah.

***Lepidozia richardsii*** Herzog – Herzog (1950). Sarawak.

***Lepidozia squamifolia*** Steph. – Mizutani (1968, 1974). Sarawak, Sabah.

***Lepidozia subintegra*** Lindenb. – Mitten and Wright (1894), Herzog (1950). Sarawak, Sabah.

***Lepidozia supradecomposita*** Lindenb. – Kitagawa and Kodama (1973), Mizutani (1974), Akiyama et al. (2001). Sabah.

***Lepidozia trichodes*** (Reinw., Blume et Nees) Nees – Mitten and Wright (1894), Herzog (1950), Inoue (1967a), Kitagawa (1969c), Kitagawa and Kodama (1973), Mizutani (1974), Kamimura (1975), Pocock et al. (1984), Kürschner (1990). Penang, Pahang, Sarawak, Sabah.

***Leptolejeunea amphiophthalma*** Zwickel – Mizutani (1966 as *L. picta*), Kitagawa and Kodama (1974 as *L. picta*), Tixier (1974 as *L. picta*), Grolle (1988), Pócs et al. (2020), Pesiu et al. (2021). Kedah, Terengganu, Sarawak, Sabah.

***Leptolejeunea apiculata*** (Horik.) S.Hatt. – Pócs and Lee (2016). Pahang.

***Leptolejeunea balansae*** Steph. – Dürhammer and Schäfer-Verwimp (1995). Perak.

***Leptolejeunea borneensis*** Herzog – Herzog (1942), Mizutani (1966). Sabah.

***Leptolejeunea dentistipula*** Steph. – Herzog (1942). Sarawak.

***Leptolejeunea epiphylla*** (Mitt.) Steph. – Herzog (1942), Mizutani (1966), Kitagawa (1969c), Kitagawa and Kodama (1974), Tixier (1974), Thiers (1986), Wolseley et al. (1996), Pócs et al. (2020), Pesiu et al. (2021, in press). Kedah, Penang, Selangor, Pahang, Negeri Sembilan, Terengganu, Sabah.

***Leptolejeunea foliicola*** Steph. – Herzog (1942), Tixier (1971, 1974). Kedah, Pahang, Johor.

***Leptolejeunea ligulata*** Herzog – Herzog (1942), Pócs et al. (2020). Pahang, Sabah.

***Leptolejeunea maculata*** (Mitt.) Schiffn. – Herzog (1942 as *L. schiffneri* f. *latifolia*, f. *angustifolia* and var. *subintegerrima*), Tixier (1974, 1980a both as *L. radiata*), Kitagawa and Kodama (1974 as *L. schiffneri*), Mizutani (1966, 1970 both as *L. schiffneri*, 1975), Dürhammer and Schäfer-Verwimp (1995), Wolseley et al. (1996 as *L. schiffneri*), Pócs et al. (2020), Pesiu et al. (2021, in press). Kedah, Perak, Pahang, Negeri Sembilan, Terengganu, Johor, Sarawak, Sabah.

***Leptolejeunea massartiana*** Herzog – Tixier (1971). Pahang.

***Leptolejeunea renneri*** Herzog – Shu et al. (2021). Kelantan.

***Leptolejeunea subacuta*** A.Evans – Herzog (1942), Mizutani (1966, also as *L. elliptica*), Tixier (1971), Kitagawa and Kodama (1974 as *L. elliptica*), Wolseley et al. (1996 as

*L. elliptica* subsp. *subacuta*), Pócs et al. (2020 as *L. elliptica*), Pesiu et al. (2021, in press). Perak, Pahang, Negeri Sembilan, Terengganu, Johor, Sabah.

***Leptolejeunea subdentata*** Herzog – Herzog (1942), Mizutani (1966), Pócs et al. (2020). Johor, Sarawak, Sabah.

***Leptolejeunea subrotundifolia*** Herzog – Shu et al. (2021). Kelantan, Pahang.

***Leptolejeunea tripuncta*** (Mitt.) Steph. – Herzog (1942 as *L. serrulata*), Inoue (1967a as *L. serrulata*), Kitagawa (1969c as *L. serrulata*), Thiers (1986 as *L. serrulata*), Pócs et al. (2020), Shu et al. (2021). Penang, Selangor, Pahang, Sabah.

***Leptolejeunea vitrea*** (Nees) Schiffn. – Herzog (1942), Mizutani (1966), Kitagawa (1969c), Tixier (1971, 1974, 1980a), Kitagawa and Kodama (1974), Wolseley et al. (1996), Pócs et al. (2020), Pesiu et al. (2021, in press). Kedah, Penang, Perak, Pahang, Negeri Sembilan, Terengganu, Johor, Sabah.

***Lobatiriccardia coronopus*** (De Not.) Furuki – Herzog (1950 as *Riccardia lobata* and f. *gigantea*), Furuki (1996 as *L. lobata*). Pahang, Sarawak, Sabah.

***Lophocolea bidentata*** (L.) Dumort. – Piippo (1989 as *Chiloscyphus latifolius*), Cheah (2017 as *C. coadunatus* and *C. cuspidatus*). Pahang, Sabah.

***Lophocolea kurzii*** Sande Lac. – Kitagawa and Kodama (1974), Piippo (1989 as *Chiloscyphus kurzii*). Sabah.

***Lophocolea mollis*** (Nees) Nees – Inoue (1967a). Pahang.

***Lophocolea muricata*** (Lehm.) Nees – Kitagawa and Kodama (1974), Piippo (1989 as *Chiloscyphus muricatus*), Müller and Schäfer-Verwimp (1999), Cheah (2017 as *C. muricatus*). Pahang, Sabah.

***Lophocolea sikkimensis*** (Steph.) Herzog et Grolle – Piippo (1989 as *Chiloscyphus sikkimensis*). Sabah.

***Lophocolea steetziae*** De Not. – De Notaris (1874), Schiffner (1898), Piippo (1989 as *Chiloscyphus steetziae*).

***Lopholejeunea applanata*** (Reinw., Blume et Nees) Schiffn. – Verdoorn (1934a), Mizutani (1969), Kitagawa and Kodama (1974), Zhu and Gradstein (2005). Perak, Sabah.

***Lopholejeunea borneensis*** (Steph.) Verd. – Verdoorn (1934a), Zhu and Gradstein (2005). Sarawak, Sabah.

***Lopholejeunea ceylanica*** Steph. – Mizutani (1985), Zhu and Gradstein (2005), Cheah (2017), Pesiu et al. (in press). Pahang, Terengganu, Sabah.

***Lopholejeunea eulopha*** (Taylor) Schiffn. – Stephani (1912 as *L. cranstonii*), Verdoorn (1934a), Kitagawa (1969a), Mizutani (1969, 1979b), Kitagawa and Kodama (1974), Zhu and Gradstein (2005), Lee et al. (2013), Cheah (2017 as *L. nicobarica*), Pócs et al. (2020), Pesiu et al. (in press). Penang, Perak, Pahang, Terengganu, Johor, Sarawak, Sabah.

***Lopholejeunea herzogiana*** Verd. – Verdoorn (1934a), Mizutani (1969, 1985), Kitagawa and Kodama (1974), Tixier (1974), Thiers (1983), Zhu and Gradstein (2005). Kedah, Pahang, Sabah.

***Lopholejeunea horticola*** Schiffn. – Mizutani (1985). Sabah.

***Lopholejeunea magna*** Mizut. – Mizutani (1969), Kitagawa and Kodama (1974), Zhu and Gradstein (2005). Sabah.

***Lopholejeunea nigricans*** (Lindenb.) Schiffn. – Mizutani (1969, 1985 as *L. javanica*), Kitagawa and Kodama (1974), Zhu and Gradstein (2005), Lee et al. (2013), Cheah (2017), Pócs et al. (2020), Pesiu et al. (in press). Perak, Pahang, Terengganu, Sarawak, Sabah.

***Lopholejeunea recurvata*** Mizut. – Zhu and Gradstein (2005). Pahang.

***Lopholejeunea subfusca*** (Nees) Schiffn. – Verdoorn (1934a), Herzog (1950), Mizutani (1966, 1969), Kitagawa (1969a), Tixier (1971, 1980a), Kamimura (1974), Kitagawa and Kodama (1974), Kürschner (1990), Wolseley et al. (1996), Zhu and Gradstein (2005), Lee et al. (2013), Pócs et al. (2020). Perak, Penang, Pahang, Negeri Sembilan, Sarawak, Sabah.

***Lopholejeunea wiltensii*** Steph. – Mizutani (1979a), Akiyama et al. (2001), Zhu and Gradstein (2005). Pahang, Sabah.

***Lopholejeunea zollingeri*** (Steph.) Schiffn. – Verdoorn (1934a), Mizutani (1969, also as *L. nipponica*, 1981b), Kitagawa and Kodama (1974), Zhu and Gradstein (2005), Cheah (2017 as *L. latialata*). Pahang, Sabah.

***Marchantia acaulis*** Steph. – Tixier (1971), Bischler-Causse (1989). Perak, Pahang, Sarawak, Sabah.

***Marchantia emarginata*** Reinw., Blume et Nees – Bischler-Causse (1989), Gepp (1914). Selangor, Sarawak, Sabah.

***Marchantia geminata*** Reinw., Blume et Nees – Johnson (1958), Bischler-Causse (1989). Perak, Pahang, Selangor.

***Marchantia novoguineensis*** Bischl. – Bischler-Causse (1989). Sabah.

***Marchantia polymorpha*** L. – Johnson (1958), Kitagawa and Kodama (1974), Bischler-Causse (1989). Perak, Sabah.

***Marchantia streimannii*** Bischl. – Bischler-Causse (1989). Sabah.

***Marchantia subgeminata*** Steph. – Bischler-Causse (1989). Sabah.

***Marsupella emarginata*** (Ehrh.) Dumort. – Kitagawa (1967), Gradstein and Váňa (1987), Váňa (1991a). Sabah.

***Marsupella stoloniformis*** N.Kitag. – Kitagawa (1967), Váňa (1991a). Sabah.

***Marsupella vermiformis*** (R.M.Schust.) Bakalin et Fedosov. – Bakalin et al. (2021). Sabah.

***Mastigopelma pulvinulatum*** (De Not.) Grolle – De Notaris (1874 as *Mastigobryum pulvinulatum*), Schiffner (1898 as *Bazzania pulvinulata*), Herzog (1950 as *M. bilobum*). Sarawak.

***Mastigophora diclados*** (F.Weber) Nees – De Notaris (1874 as *Sendtnera diclados* var. *borneensis*), Verdoorn (1932c), Herzog (1950, 1952b), Johnson (1958), Inoue (1967a, 1968b), Tixier (1971), Kitagawa and Kodama (1973), Kamimura (1975), Kodama (1976), Kürschner (1990), Ludwiczuk and Asakawa (2010), Ng et al. (2017). Kedah, Pahang, Johor, Sarawak, Sabah.

***Mastigophora diclados*** var. ***borneensis*** (De Not.) Schiffn. – Schiffner (1898). Sarawak.

***Mastigophora diclados*** var. ***ramentifissa*** Herzog – Herzog (1950). Sarawak.

***Mastigophora diclados*** var. ***villosa*** Herzog – Herzog (1950). Sarawak.

***Mesoptychia subcrispa*** (Herzog) L.Söderstr. et Váňa – Cheah (2017 as *Hattoriella subcrispa*). Pahang.

***Metalejeunea cucullata*** (Reinw., Blume et Nees) Grolle – Herzog (1950 as *Microlejeunea sundaica*), Mizutani (1966, 1970 both as *Lejeunea cucullata*), Hattori and Kamimura (1971), Tixier (1971, 1974, 1980a as *M. cucullata*), Kitagawa and Kodama (1974 as *L. cucullata*), Kürschner (1990 as *L. cucullata*), Wolseley et al. (1996 as *M. cucullata*), Pócs et al. (2020), Pesiu et al. (2021). Kedah, Pahang, Negeri Sembilan, Terengganu, Sarawak, Sabah.

***Metzgeria ciliata*** Raddi – Kuwahara (1965 as *M. decipiens*), Kürschner (1990 as *M. decipiens*), Cheah (2017). Pahang, Sabah.

***Metzgeria foliicola*** Schiffn. – Kuwahara (1965), Kitagawa and Kodama (1974). Sabah.

***Metzgeria francana*** Steph. – Kuwahara (1965 as *Austrometzgeria francana*). Sabah.

***Metzgeria furcata*** (L.) Corda – Kuwahara (1965 as *M. molokaiensis*), Tixier (1971). Pahang, Sabah.

***Metzgeria kinabaluensis*** (Kuwah.) Masuzaki – Kuwahara (1965 as *Apometzgeria pubescens* var. *kinabaluensis*), Kitagawa and Kodama (1974 as *A. pubescens* var. *kinabaluensis*), Kürschner (1990 as *A. pubescens* var. *kinabaluensis*), Akiyama et al. (2001 as *A. pubescens* var. *kinabaluensis*), Masuzaki (2011). Sabah.

***Metzgeria leptoneura*** Spruce – Herzog (1950 as *M. hamata*), Kuwahara (1965 as *M. borneensis*, *M. hamata* and *M. sandei*, 1976 as *M. thomeensis* and *M. papulosa*, 1984 as *M. sharpii*), Johnson (1972 as *M. hamata*), Kitagawa and Kodama (1974 as *M. hamata*), So (2003a). Pahang, Sarawak, Sabah.

***Metzgeria lindbergii*** Schiffn. – Kuwahara (1965 as *M. conjugata* subsp. *japonica* and *M. pectinata*), So (2003a), Cheah (2017). Pahang, Sabah.

***Metzgeria scobina*** Mitt. – Mitten (1886), Schiffner (1898), Kitagawa (1969c), Thiers (1983), So (2003a). Penang, Selangor, Sarawak.

***Microlejeunea constricta*** (Grolle) Grolle – Mizutani (1973 as *Harpalejeunea constricta*), Pócs et al. (2020). Sabah.

***Microlejeunea filicuspis*** (Steph.) Heinrichs, Schäf.-Verw., Pócs et S.Dong – Mizutani (1970 as *Drepanolejeunea filicuspis*, 1973 as *Harpalejeunea filicuspis* and *H.riddleana*), Pócs and Lee (2016), Cheah (2017 as *H. filicuspis*), Pócs et al. (2020). Kelantan, Pahang, Sabah.

***Microlejeunea kinabaluensis*** (Mizut.) Grolle – Mizutani (1973 as *Harpalejeunea kinabaluensis*), Grolle and Reiner-Drehwald (1999). Sabah.

***Microlejeunea lunulatiloba*** Horik. – Bischler et al. (1962 as *M. gracillima*), Pócs et al. (2020). Malacca, Sabah.

***Microlejeunea mammillosa*** (Mizut.) Grolle – Mizutani (1973 as *Harpalejeunea mammillosa*), Grolle and Reiner-Drehwald (1999). Sabah.

***Microlejeunea minutissima*** (Mizut.) Grolle – Mizutani (1973 as *Harpalejeunea minutissima*), Grolle and Reiner-Drehwald (1999). Sabah.

***Microlejeunea punctiformis*** (Taylor) Steph. – Kamimura (1974 as *Lejeunea punctiformis*), Pócs and Lee (2016), Pócs et al. (2020), Pesiu et al. (2021, in press). Kelantan, Terengganu, Sabah.

***Microlejeunea spinosa*** (Mizut.) Grolle – Mizutani (1973 as *Harpalejeunea spinosa*), Grolle and Reiner-Drehwald (1999). Sabah.

***Mizutania riccardioides*** Furuki et Z.Iwats. – Furuki and Iwatsuki (1989), Masuzaki et al. (2010). Pahang, Johor, Sarawak, Sabah.

***Mnioloma fuscum*** (Lehm.) R.M.Schust. – Grolle (1965 as *Calypogeia baldwinii*), Bisang et al. (2003 as *C. fusca*), Cheah (2017). Pahang, Sarawak.

***Mohamedia borneensis*** (Steph.) R.L.Zhu et L.Shu – Mizutani (1972b as *Pycnolejeunea borneensis*), Piippo (1986 as *Lepidolejeunea borneensis*), Zhu et al. (2019). Sarawak, Sabah.

***Mohamedia brunnea*** (Mizut.) R.L.Zhu et L.Shu – Mizutani (1970 as *Drepanolejeunea brunnea*), Pócs and Lee (2016 as *D. brunnea*), Zhu et al. (2019). Pahang, Sabah.

***Myriocoleopsis minutissima*** (Sm.) R.L.Zhu, Y.Yu et Pócs – Pócs et al. (2020). Sabah.

***Nardia assamica*** (Mitt.) Amakawa – Váňa (1991b). Sabah.

***Neolepidozia longitudinalis*** (Herzog) E.D.Cooper – Herzog (1950 as *Lepidozia longitudinalis*), Engel and Merrill (2004 as *Telaranea longitudinalis*). Sarawak.

***Neolepidozia mamillosa*** (Schiffn.) E.D.Cooper – Grolle (1967 as *Lepidozia mamillosa*), Mizutani (1974b as *L. mamillosa*). Sabah.

***Neolepidozia ophiria*** (Gottsche) E.D.Cooper – Stephani (1909 as *Lepidozia ophiria*), Mizutani (1974b as *L. ophiria*), Pocock et al. (1984 as *L. ophiria*), Engel and Merrill (2004 as *Telaranea ophiria*). Pahang, Johor ("Mt. Ophir" (Gunung Ledang) was mistakenly listed as in Malacca), Sabah.

***Neolepidozia papulosa*** (Steph.) Fulford et J.Taylor – Kitagawa (1973 as *Lepidozia papulosa*), Kitagawa and Kodama (1973 as *L. papulosa*). Sarawak, Sabah.

***Neolepidozia wallichiana*** (Gottsche) Fulford et J.Taylor – De Notaris (1874 as *Lepidozia wallichiana*), Mitten and Wright (1894 as *L. wallichiana*), Herzog (1950 as *L. wallichiana*), Kitagawa and Kodama (1973 as *L. wallichiana*), Mizutani (1974 as *L. wallichiana*), Kamimura (1975 as *L. wallichiana*), Pocock et al. (1984 as *L. wallichiana*), Kürschner (1990 as *L. wallichiana*), Wolseley et al. (1996 as *L. wallichiana*), Bisang et al. (2003 as *L. wallichiana*). Penang, Pahang, Negeri Sembilan, Sarawak, Sabah.

***Notoscyphus lutescens*** (Lehm. et Lindenb.) Mitt. – Herzog (1950 as *N. paroicus*), Inoue (1967a), Kitagawa (1969c as *N. paroicus*), Kitagawa and Kodama (1973 as *N. paroicus*). Penang, Pahang, Sarawak, Sabah.

***Nowellia borneensis*** (De Not.) Schiffn. – De Notaris (1874 as *Jungermannia curvifolia* var. *borneensis*), Schiffner (1898), Herzog (1950), Grolle (1968), Kitagawa and Kodama (1974), Akiyama et al. (2001), Cheah (2017). Pahang, Sarawak, Sabah.

***Nowellia curvifolia*** (Dicks.) Mitt. – Grolle (1968), Váňa (1993). Johor, Sabah.

***Nowellia langii*** Pearson – Pearson (1922), Grolle (1968), Kitagawa and Kodama (1974), Váňa (1993). Perak, Johor, Sabah.

***Odontoschisma denudatum*** (Mart.) Dumort. subsp. ***naviculare*** (Steph.) Gradst., S.C.Aranda et Vanderp. – Kitagawa and Kodama (1974 as *O. denudatum*), Gradstein and Váňa (1987 as *O. denudatum*), So (2004 as *O. denudatum*), Gradstein and Ilkiu-Borges (2015). Pahang, Johor, Sabah.

***Odontoschisma jishibae*** (Steph.) L.Söderstr. et Váňa – Kitagawa (1964 as *Iwatsukia exigua*), Kürschner (1990 as *I. exigua*), Váňa (1993 as *I. exigua*), Gradstein and Ilkiu-Borges (2015). Sabah.

***Odontoschisma purpuratum*** Herzog – Herzog (1950, 1952b), So (2004), Gradstein and Ilkiu-Borges (2015). Pahang, Sarawak, Sabah.

***Pallavicinia ambigua*** (Mitt.) Steph. – Kitagawa and Kodama (1974 as *P. fistulosa*), Grolle and Piippo (1986). Sabah.

***Pallavicinia indica*** Schiffn. – Herzog (1950), Grolle (1969), Kitagawa (1971), Johnson (1972). Penang, Pahang, Sarawak, Sabah.

***Pallavicinia levieri*** Schiffn. – Johnson (1972), Grolle and Piippo (1986). Pahang, Sabah.

***Pallavicinia lyellii*** (Hook.) Gray – Grolle and Piippo (1986). Sarawak.

***Pedinophyllum autoicum*** (Steph.) Inoue – Kamimura (1975). Sabah.

***Pictolejeunea mizutanii*** Grolle – Mizutani (1970 as *Cheilolejeunea picta*), Kitagawa and Kodama (1974 as *C. picta*), Grolle (1977), Thiers (1986), Wolseley et al. (1996), Bi et al. (2019). Negeri Sembilan, Sarawak, Sabah.

***Plagiochila abietina*** (Nees) Mont. et Nees – Herzog (1950), Inoue (1984). Sarawak, Sabah.

***Plagiochila arbuscula*** (Lehm. et Lindenb.) Lindenb. – Kitagawa and Kodama (1974), Kamimura (1975), Inoue (1984, 1989), Kürschner (1990). Pahang, Terengganu, Sabah.

***Plagiochila bantamensis*** (Reinw., Blume et Nees) Mont. – De Notaris (1874 as *P. mutabilis*), Herzog (1950 as *P. mutabilis* and *P. richardsii*), Inoue (1967a as *P. lobulata*, 1984, 1989), Kitagawa and Kodama (1974), Wolseley et al. (1996), So and Grolle (2000), So (2001), Pesiu et al. (in press). Perak, Pahang, Negeri Sembilan, Terengganu, Sarawak, Sabah.

***Plagiochila bicornuta*** Steph. – Stephani (1903 as *P. laxissima*), Inoue (1989 as *P. laxissima*). Cheah (2017). Pahang, Sarawak, Sabah.

***Plagiochila blepharophora*** (Nees) Lindenb. – Herzog (1950 as *P. estipulata* and *P. elegantissima*), Inoue (1984, 1989), So and Grolle (2000), So (2001), Cheah (2017). Pahang, Sarawak, Sabah.

***Plagiochila borneensis*** Steph. – Stephani (1918). Sarawak.

***Plagiochila chauviniana*** Mont. – Herzog (1950 as *P. vanikorensis*). Sarawak.

***Plagiochila clavatosaccata*** Steph. – Inoue (1984), So and Grolle (2000 as *P. longifolia*), So (2001). Perak, Sabah.

***Plagiochila denigrata*** Inoue – Inoue (1989), So and Grolle (2000). Sabah.

***Plagiochila dolichoblasta*** – Herzog (1950), So and Grolle (2000). Sarawak.

***Plagiochila frondescens*** (Nees) Lindenb. – De Notaris (1874), Herzog (1950), Kitagawa and Kodama (1974), Kamimura (1975), Inoue (1967a, 1984, 1989). Pahang, Sarawak, Sabah.

***Plagiochila gymnoclada*** Sande Lac. – Inoue (1984, 1989), Kürschner (1990), So and Grolle (2000), So (2001). Sabah.

***Plagiochila hampeana*** Gottsche – Inoue (1968b, 1969, 1984 all as *P. cameronensis*, 1989), Kürschner (1990). Pahang, Sabah.

***Plagiochila integrilobula*** Schiffn. – Inoue (1989). Sabah.

***Plagiochila javanica*** (Sw.) Nees et Mont – Inoue (1989, also as *P. infirma*), Kamimura (1975), Cheah (2017). Pahang, Sabah.

***Plagiochila junghuhniana*** Sande Lac. – Kitagawa and Kodama (1974), Kamimura (1975), Cheah (2017). Pahang, Sabah.

***Plagiochila korthalsiana*** Molk. – Kitagawa and Kodama (1974 as *P. accedens*), Inoue (1989), So (2000). Sabah.

***Plagiochila kuhliana*** Sande Lac. – Stephani (1903, 1906). Sarawak.

***Plagiochila kurzii*** Steph. – Kitagawa and Kodama (1974 as *P. sambusana*), Inoue (1984), Wolseley et al. (1996), So and Grolle (2000), So (2001). Negeri Sembilan, Sarawak, Sabah.

***Plagiochila massalongoana*** Schiffn. – Kitagawa and Kodama (1974), Inoue (1984). Pahang, Sabah.

***Plagiochila nitens*** Inoue – Inoue (1989), So and Grolle (2000), So (2001). Sabah.

***Plagiochila nobilis*** Gottsche – Inoue (1989). Sabah.

***Plagiochila obtusa*** Lindenb. – Inoue (1968b). Pahang.

***Plagiochila peculiaris*** Schiffn. – Inoue (1984, 1989), Kürschner (1990), Renner (2018). Pahang, Sarawak, Sabah.

***Plagiochila perserrata*** Herzog – Inoue (1975, 1984 both as *P. hottae*), So and Grolle (2000), So (2001). Sabah.

***Plagiochila philippinensis*** Steph. – Inoue (1989). Sabah.

***Plagiochila propinqua*** Sande Lac. – De Notaris (1874), Schiffner (1898), Stephani (1903), Herzog (1950), Inoue (1984, 1989). Perak, Sarawak, Sabah.

***Plagiochila renitens*** (Nees) Lindenb. – Inoue (1967a, 1984, 1989), Kürschner (1990). Pahang, Sabah.

***Plagiochila sandei*** Dozy – De Notaris (1874), Schiffner (1898), Herzog (1950 as *P. sandei* f. *remotidens*), Kitagawa and Kodama (1974), Kamimura (1975), Inoue (1984, 1989), Müller and Schäfer-Verwimp (1999), Cheah (2017), Renner (2018). Pahang, Sarawak, Sabah.

***Plagiochila sciophila*** Nees – Inoue (1984, 1989), So (2001), Cheah (2017). Pahang, Sarawak, Sabah.

***Plagiochila spathulifolia*** Mitt. – Kitagawa and Kodama (1974), Inoue (1984, 1989). Sarawak, Sabah.

***Plagiochila sumatrana*** Schiffn. – Inoue (1989). Sabah.

***Plagiochila teysmannii*** Sande Lac. – Kitagawa and Kodama (1974), Inoue (1984, 1989), Grolle and So (1999 as *P. fraseri*). Perak, Sabah.

***Plagiochila trapezoidea*** Lindenb. – Inoue (1989). Sabah.

***Plagiochila ungarangana*** Sande Lac. – Stephani (1917 as *P. tridens*), Inoue (1975 as *P. tsutomui*, 1984), So and Grolle (2000). Perak, Sabah.

***Pleurozia acinosa*** (Mitt.) Trevis. – De Notaris (1874 as *Physiotium myriangium*), Schiffner (1898), Inoue (1967a), Kitagawa (1979b), Thiers (1993). Selangor, Pahang, Sarawak, Sabah.

***Pleurozia articulata*** (Lindb.) Lindb. et Lackström – Kürschner (1990). Sabah.

***Pleurozia conchifolia*** (Hook. et Arn.) Austin – Herzog (1950), Kitagawa and Kodama (1974), Kürschner (1990), Thiers (1993), Akiyama et al. (2001). Sarawak, Sabah.

***Pleurozia gigantea*** (F.Weber) Lindb. – De Notaris (1874 as *P. gigantea* var. *borneensis*), Herzog (1950 as *Eopleurozia simplicissima*), Inoue (1967a, 1968b), Kitagawa and Kodama (1974 also as *E. simplicissima*), Tixier (1974), Kürschner (1990), Thiers (1993), Akiyama et al. (2001), Ludwiczuk and Asakawa (2010). Kedah, Pahang, Malacca, Johor, Sarawak, Sabah.

***Pleurozia johannis-winkleri*** Herzog – Thiers (1993), Akiyama et al. (2001). Sabah.

***Pleurozia subinflata*** (Austin) Austin – Kamada et al. (2020). Sabah.

***Plicanthus hirtellus*** (F.Weber) R.M.Schust. – Herzog (1950 as *Chandonanthus hirtellus*), Kitagawa (1970 as *C. hirtellus*), Kitagawa and Kodama (1973 as *C. hirtellus*), Kürschner (1990 as *C. hirtellus*), Akiyama et al. (2001 as *C. hirtellus*), Ludwiczuk and Asakawa (2010 as *C. hirtellus*), Cheah (2017 as *C. hirtellus*). Pahang, Sarawak, Sabah.

***Podomitrium malaccense*** (Steph.) Campb. – Kitagawa (1969c), Kitagawa and Kodama (1974), Grolle and Piippo (1986), Campbell (1915), Wolseley et al. (1996). Penang, Negeri Sembilan, Johor, Sarawak, Sabah.

***Porella acutifolia*** (Lehm. et Lindenb.) Trevis. – Kitagawa and Kodama (1974 as *P. acutifolia* var. *elbertii*), Hattori (1967 as *P. johannis-winkleri*, 1969 as *P. acutifolia* var. *johannis-winkleri*). Sarawak, Sabah.

***Porella caespitans*** (Steph.) S.Hatt. subsp. ***latior*** (S.Hatt.) S.Hatt. – Hattori (1969 as *P. acutifolia* subsp. *latior*). Pahang.

***Porella japonica*** (Sande Lac.) Mitt. – Hattori (1967). Sabah.

***Porella javanica*** (Gottsche) Inoue – Inoue (1967a). Pahang.

***Pseudolepicolea andoi*** (R.M.Schust.) Inoue – Hattori and Mizutani (1968 as *P. trollii* subsp. *andoi*). Sabah.

***Pseudolepicolea trollii*** (Herzog) Grolle et Ando – Hattori (1966). Sabah.

***Pseudomarsupidium borneensis*** (Grolle) Váňa, L.Söderstr., A.Hagborg et von Konrat – Grolle (1972 as *Adelanthus borneensis*), Kitagawa and Kodama (1974 as *A. borneensis*). Sabah.

***Psiloclada clandestina*** Mitt. – Herzog (1950), Kitagawa and Kodama (1973), Mizutani (1974), Pocock et al. (1984), Kürschner (1990), Akiyama et al. (2001), Cheah (2017). Pahang, Sarawak, Sabah.

***Ptychanthus striatus*** (Lehm. et Lindenb.) Nees – Verdoorn (1934a), Herzog (1950), Mizutani (1969), Tixier (1971), Kamimura (1974, 1975), Kitagawa and Kodama (1974). Pahang, Sarawak, Sabah.

***Pycnolejeunea cavistipula*** (Steph.) Mizut. – Mizutani (1970 as *P. molaris*), Kitagawa and Kodama (1974), Kürschner (1990). Sabah.

***Pycnolejeunea contigua*** (Nees) Grolle – Mizutani (1970 as *P. bancana*), Kürschner (1990 as *P. bancana*), He (1999). Sabah.

***Pycnolejeunea grandiocellata*** Steph. – Kürschner (1990), Wolseley et al. (1996), He (1999), Schäfer-Verwimp (2006). Pahang, Negeri Sembilan, Sarawak.

***Pycnolejeunea grossiloba*** Steph. – Hoffmann (1935). Johor.

***Pycnolejeunea sphaeroides*** (Sande Lac.) J.B.Jack et Steph. – Kodama (1976 as *P. kinabaluensis*), He (1999), Schäfer-Verwimp (2006). Pahang, Sabah.

***Radula acuminata*** Steph. – Yamada (1973, 1979, 1989), Wolseley et al. (1996), Pesiu et al. (2021, in press). Selangor, Negeri Sembilan, Terengganu, Sabah.

***Radula amentulosa*** Mitt. – Herzog (1950), Yamada (1979, 1989), Cheah (2017). Pahang, Sarawak, Sabah.

***Radula amoena*** Herzog – Yamada (1979), Yamada and Piippo (1989). Sarawak, Sabah.

***Radula anceps*** Sande Lac. – De Notaris (1874), Schiffner (1898), Herzog (1950 as *R. laciniata*), Castle (1961), Inoue and Miller (1965), Yamada (1973, also as *R. apiculata*, 1979, 1989), Kitagawa and Kodama (1974), Wolseley et al. (1996), Cheah (2017 as *R. apiculata*). Perak, Pahang, Negeri Sembilan, Sarawak, Sabah.

***Radula assamica*** Steph. – Pócs et al. (2014), Pesiu et al. (2021, in press). Selangor, Pahang, Terengganu.

***Radula borneensis*** Steph. – Inoue (1967a), Castle (1936), Yamada (1979, 1989). Pahang, Sarawak, Sabah.

***Radula caduca*** K.Yamada – Cheah (2017). Pahang.

***Radula campanigera*** Mont. – Castle (1936), Yamada (1973, 1979, 1989). Perak, Sabah.

***Radula cavifolia*** Gottsche, Lindenb. et Nees – Yamada (1973, 1979, 1989). Sabah.

***Radula ceylanica*** K.Yamada – Yamada (1979). Pahang.

***Radula densifolia*** Castle – Yamada (1973, 1979, 1989). Sabah.

***Radula falcata*** Steph. – Cheah (2017). Pahang.

***Radula formosa*** (Spreng.) Nees – Inoue (1967a as *R. novae-guineae*), Yamada (1973 as *R. novae-guineae*, 1979, 1989), Kitagawa and Kodama (1974), Tixier (1974). Kedah, Pahang, Sabah.

***Radula gedena*** Gottsche – Yamada (1973, 1979, 1989). Sabah.

***Radula grandilobula*** Promma et Chantanaorr. – Sarimi et al. (2021), Zhang et al. (2021), Pesiu et al. (in press). Terengganu, Sarawak.

***Radula iwatsukii*** K.Yamada – Yamada (1979, 1989), Yamada and Piippo (1989). Sabah.

***Radula javanica*** Gottsche – De Notaris (1874), Schiffner (1898), Herzog (1950), Yamada (1973, 1979 also as *R. yangii*, 1989), Kitagawa and Kodama (1974), Wolseley et al. (1996), Pesiu et al. (in press). Selangor, Pahang, Negeri Sembilan, Terengganu, Sarawak, Sabah.

***Radula kinabaluensis*** K.Yamada – Yamada (1979, 1989). Sabah.

***Radula lacerata*** Steph. – Castle (1961), Yamada (1979, 1989), Wolseley et al. (1996). Negeri Sembilan, Sarawak, Sabah.

***Radula lingulata*** Gottsche – Cheah (2017). Pahang.

***Radula madagascariensis*** Gottsche – Yamada (1979, 1989). Sabah.

***Radula mizutanii*** K.Yamada – Yamada (1973, 1979, 1989), Yamada and Piippo (1989). Sabah.

***Radula morobeana*** K.Yamada et Piippo – Kürschner (1990). Sabah.

***Radula multiflora*** Schiffn. – Yamada (1979, 1989). Sabah.

***Radula nymannii*** Steph. – Tixier (1971, 1980a), Yamada (1973, 1979, 1989), Kitagawa and Kodama (1974), Pesiu et al. (2021, in press). Pahang, Terengganu, Sabah.

***Radula obscura*** Mitt. – Yamada (1973, 1979, 1989). Sabah.

***Radula philippinensis*** K.Yamada – Yamada (1979). Selangor.

***Radula protensa*** Lindenb. – Herzog (1952b), Wolseley et al. (1996). Negeri Sembilan, Sarawak.

***Radula retroflexa*** Taylor – Inoue (1968b as *R. miqueliana*), Tixier (1974 as *R. miqueliana*). Yamada (1979, also as *R. retroflexa* var. *fauciloba*, 1989). Kedah, Selangor, Pahang, Terengganu, Sabah.

***Radula sumatrana*** Steph. – Kamimura (1975), Yamada (1979, 1989). Sarawak, Sabah.

***Radula tabularis*** Steph. – Yamada (1973 as *R. indica*, 1979, 1989), Cheah (2017). Pahang, Sabah.

***Radula tjibodensis*** K.I.Goebel – Kitagawa (1969c), Yamada (1973, 1979, 1989), Kamimura (1975), Kitagawa and Kodama (1974), Pócs et al. (2020), Pesiu et al. (2021, in press). Penang, Pahang, Terengganu, Sabah.

***Radula ventricosa*** Steph. – Yamada (1973, 1979, 1989 all as *R. subpallens*), Kitagawa and Kodama (1974 as *R. subpallens*). Sarawak, Sabah.

***Radula vrieseana*** Sande Lac. – Kitagawa and Kodama (1974), Yamada (1979, 1989), Wolseley et al. (1996). Negeri Sembilan, Sarawak, Sabah.

***Reboulia hemisphaerica*** (L.) Raddi subsp. ***australis*** R.M.Schust. – Gepp (1914 as *R. hemisphaerica* var. *javanica*). Sabah.

***Riccardia albomarginata*** (Steph.) Schiffn. – Furuki (1995), Cheah (2017). Pahang, Sabah.

***Riccardia aspera*** (Steph.) Grolle – Furuki (1998). Sabah.

***Riccardia baumannii*** Hürl. – Furuki (1994). Sabah.

***Riccardia crassa*** (Schwägr.) C.Massal. – Herzog (1950 as *R. scabra*), Johnson (1958 as *R. scabra*), Kitagawa and Kodama (1974 as *R. scabra*). Pahang, Sarawak, Sabah.

***Riccardia crassiretis*** Schiffn. – Furuki (2001). Pahang, Sabah.

***Riccardia crenulata*** Schiffn. – Furuki (2001). Sabah.

***Riccardia deguchii*** Furuki et K.T.Yong – Furuki et al. (2013). Pahang.

***Riccardia elata*** (Steph.) Schiffn. – Herzog (1950 also as *R. ridleyi*), Cheah (2017). Pahang, Sarawak.

***Riccardia fruticosa*** (Steph.) Furuki – Furuki (1998), Cheah (2017). Pahang, Sabah.

***Riccardia grollei*** Furuki – Furuki (1999), Cheah (2017). Pahang, Sabah.

***Riccardia grossitexta*** (Steph.) Furuki – Furuki (1994). Johor, Sarawak, Sabah.

***Riccardia hattorii*** Furuki – Furuki (1994). Sabah.

***Riccardia heteroclada*** Schiffn. – Herzog (1950), Furuki (1998), Cheah (2017). Pahang, Sarawak.

***Riccardia inconspicua*** (Steph.) Reeb et Bardat – Furuki (1994 as *R. tenuicostata*). Johor, Sarawak, Sabah.

***Riccardia jackii*** Schiffn. – Johnson (1958). Pahang.

***Riccardia nobilis*** (Steph.) Schiffn. – Stephani (1893, 1900), Schiffner (1898). Sarawak.

***Riccardia parvula*** Schiffn. – Johnson (1958, 1972), Furuki (2001 as *Aneura subcrenulata*). Perak, Pahang, Sarawak, Sabah.

***Riccardia pindensis*** Hewson – Furuki (1995). Sabah.

***Riccardia planiflora*** (Steph.) S.Hatt. var. ***aequatorialis*** Furuki – Furuki (1997), Cheah (2017). Pahang, Sabah.

***Riccardia sumatrana*** Schiffn. – Herzog (1950). Sarawak.

***Riccia fluitans*** L. – Gepp (1914). Sabah.

***Ricciocarpos natans*** (L.) Corda – Gepp (1914). Sabah.

***Saccogynidium goebelii*** (Herzog) Grolle – Inoue (1967a, 1968b). Pahang.

***Saccogynidium muricellum*** (De Not.) Grolle – De Notaris (1874 as *Chiloscyphus muricellus*), Schiffner (1898), Mitten and Wright (1894 as *Saccogyna muricella*), Schiffner (1898 as *C. muricellus*), Kitagawa and Kodama (1974), Piippo (1989). Sarawak, Sabah.

***Saccogynidium rigidulum*** (Nees) Grolle – Herzog (1950 as *Saccogyna rigidula*), Grolle (1960, 1963 both as *Saccgynidium jugatum*), Inoue (1967a). Perak, Pahang, Johor, Sarawak, Sabah.

***Sandeothallus radiculosus*** (Schiffn.) R.M.Schust. – Campbell and Williams (1914), Pocock et al. (1984), Crandall-Stotler and Stotler (2007). Perak, Pahang, Sabah.

***Scapania javanica*** Gottsche – Herzog (1950 as *S. javanica* f. *amplifolia*), Schäfer-Verwimp (2009), Ludwiczuk and Asakawa (2010). Pahang, Sarawak, Sabah.

***Scapania lepida*** Mitt. – Mitten and Wright (1894), Hattori (1964), Kitagawa and Kodama (1973), Akiyama et al. (2001). Sabah.

***Scapania ornithopodioides*** (With.) Waddell. – Kodama and Narita (1974). Sabah.

***Schiffneria hyalina*** Steph. – Kitagawa (1973), Kitagawa and Kodama (1974), Grolle and Piippo (1984). Pahang, Sabah.

***Schiffneriolejeunea cumingiana*** (Mont.) Gradst. – Lee et al. (2013). Perak.

***Schiffneriolejeunea nymannii*** (Steph.) Gradst. et Terken. – Stephani (1912 as *Ptychocoleus longispicus*), Verdoorn (1934a as *P. longispicus*), Gradstein and Terken (1981). Sarawak.

***Schiffneriolejeunea omphalanthoides*** Verd. – Gradstein (2015). Sabah.

***Schiffneriolejeunea pulopenangensis*** (Gottsche) Gradst. – Gottsche et al. (1845 as *Phragmicoma pulopenangensis*), Stephani (1890 as *P. pulopenangensis*, 1912 as *Ptychocoleus cranstonii* and *P. tridens*), Schiffner (1898 as *Acrolejeunea pulopenangensis*), Verdoorn (1934a as *Ptychocoleus pulopenangensis*), Herzog (1950 as *Ptychocoleus pulopenangensis*), Kitagawa (1969a as *P. pulopenangensis*), Mizutani (1969 as *Ptychocoleus pulopenangensis*), Thiers and Gradstein (1989), Haerida et al. (2010), Lee et al. (2013). Penang, Pahang, Sarawak, Sabah.

***Schiffneriolejeunea tumida*** (Nees) Gradst. – Nees (1838 as *Ptychanthus tumidus*), Stephani (1890 as *Phragmicoma tumida*, 1912 as *Ptychocoleus sarawakensis* and *P. squarrosifolius*), Schiffner (1898 as *Acrolejeunea tumida*), Verdoorn (1933 as *Phragmicoma tumida*, 1934a as, *Ptychocoleus sarawakensis*), Inoue (1967a as *Ptychocoleus sarawakensis*), Mizutani (1969 as *Ptychocoleus sarawakensis* and *P. haskarlianus*), Kitagawa (1971 as *Ptychocoleus sarawakensis*), Gradstein and Terken (1981), Lee et al. (2013), Gradstein (2015), Pócs et al. (2020). Penang, Perak, Pahang, Sarawak, Sabah.

***Schistochila acuminata*** Steph. – Herzog (1950), Kitagawa and Kodama (1973 as *S. wrayana*), So (2003b), Ng et al. (2016). Perak, Sarawak, Sabah.

***Schistochila aligera*** (Nees et Blume) J.B.Jack et Steph. – De Notaris (1874 as *Gottschea aligera*, *G. aligeriformis* and *G. philippinensis*), Schiffner (1898 as *G. gaudichaudii* and *S. aligeriformis*), Herzog (1950 also as *S. philippinensis*), Kitagawa (1969c as *S. philippinensis*, 1973), Kitagawa and Kodama (1973, also as *S. philippinensis*), So (2003b). Penang, Selangor, Pahang, Johor, Sarawak, Sabah.

***Schistochila beccariana*** (De Not.) Trevis. – De Notaris (1874 as *Gottschea beccariana*), Schiffner (1898), So (2003b). Sarawak, Sabah.

***Schistochila blumei*** (Nees) Trevis. – Gepp (1914 as *S. wallisii*), Inoue (1967a), Kitagawa and Kodama (1973), So (2003b). Perak, Kelantan, Pahang, Sarawak, Sabah.

***Schistochila doriae*** (De Not) Trevis. – De Notaris (1874 as *Gottschea doriae*), Schiffner (1898), So (2003b). Pahang, Sarawak, Sabah.

***Schistochila reinwardtii*** (Nees) Schiffn. – So (2003b), Cheah (2017). Pahang, Sabah.

***Schistochila rubriseta*** Steph. – Kürschner (1990). Sabah.

***Schistochila sciurea*** (Nees) Schiffn. – De Notaris (1874 as *Gottschea sciurea*), Schiffner (1898), Herzog (1950), Inoue (1967a, 1968b), Kitagawa and Kodama (1973), Kürschner (1990), So (2003b). Perak, Pahang, Sarawak, Sabah.

***Soella spinistipula*** (Mizut.) R.L.Zhu et L.Shu – Mizutani (1970 as *Pycnolejeunea spinistipula*), Bi et al. (2019 as *Leptolejeunea spinistipula*), Shu et al. (2021). Sarawak, Sabah.

***Solenostoma appressifolium*** (Mitt.) Váňa et D.G.Long – Amakawa (1969b as *Jungermannia kinabalensis* and *J. decolyana*), Váňa (1991b as *J. appressifolia*). Sabah.

***Solenostoma ariadne*** (Taylor) Váňa et D.G.Long – Inoue (1967a as *Jungermannia ariadne*), Amakawa (1968 as *J. ariadne*), Kitagawa and Kodama (1973 as *J. ariadne*), Váňa (1991b, 1972 both as *J. ariadne*). Penang, Perak, Pahang, Negeri Sembilan, Sabah.

***Solenostoma borneense*** (Amakawa) Váňa, Hentschel et Heinrichs – Amakawa (1970 as *Jungermannia borneensis*), Váňa (1991b as *J. borneensis*). Sabah.

***Solenostoma comatum*** (Nees) C.Gao – Inoue (1967a as *Jungermannia comata*). Pahang.

***Solenostoma haskarlianum*** (Nees) Váňa et D.G.Long – Váňa (1972, 1975, 1991b all as *J. haskarliana*). Perak, Pahang, Sarawak, Sabah.

***Solenostoma javanicum*** (Schiffn.) Steph. – Váňa (1991b as *Jungermannia herzogiana*). Sabah.

***Solenostoma pseudocyclops*** (Inoue) Váňa et D.G.Long – Amakawa (1969b as *Jungermannia pseudocyclops*). Sabah.

***Solenostoma riclefii*** Váňa et D.G.Long – Amakawa (1969b as *Jungermannia grollei*), Váňa (1991b as *J. grollei*). Sabah.

***Solenostoma sphaerocarpum*** (Hook.) Steph. – Gradstein and Váňa (1987 as *Jungermannia sphaerocarpa*), Váňa (1991b as *J. sphaerocarpa*). Sabah.

***Solenostoma stephanii*** (Schiffn.) Steph. – Amakawa (1969b as *Jungermannia stephanii* and *J. mizutanii*), Váňa (1991b as *J. stephanii*). Sabah.

***Solenostoma strictum*** (Schiffn.) Váňa, Hentschel et Heinrichs – Amakawa (1969b as *Jungermannia stricta*), Váňa (1991b as *J. stricta*). Sabah.

***Solenostoma tetragonum*** (Lindenb.) Váňa et D.G.Long – Herzog (1950 as *Plectocolea parabolica*), Váňa (1991b as *Jungermannia tetragona*). Sarawak, Sabah.

***Solenostoma truncatum*** (Nees) Váňa et D.G.Long – Stephani (1901 as *Jungermannia polyrhiza*), Horikawa (1943 as *Aplozia polyrhiza*), Herzog (1950 as *Plectocolea truncata*), Amakawa (1972 as *J. truncata*), Váňa (1991 as *J. truncata*). Penang, Sarawak, Sabah.

***Solenostoma tuberculiferum*** (Herzog) Váňa, Hentschel et Heinrichs – Váňa (1991b as *Jungermannia tuberculifera*). Sabah.

***Solenostoma virgatum*** (Mitt.) Váňa et D.G.Long – Váňa (1991b as *Jungermannia virgata*). Sabah.

***Southbya organensis*** Herzog – Kodama and Narita (1974 as *S. grollei*). Sabah.

***Sphenolobopsis pearsonii*** (Spruce) R.M.Schust. – Kitagawa (1970 as *Cephalozia pearsonii*), Kodama and Narita (1974), Kürschner (1990 as *S. kitagawae*), Váňa (1991c). Sabah.

***Sphenolobus minutus*** (Schreb.) Berggr. – Kitagawa (1970 as *Anastrophyllum minutum*), Kitagawa and Kodama (1973 as *A. minutum*), Váňa (1991c as *A. minutum*). Sabah.

***Spruceanthus planiusculus*** (Mitt.) X.Q.Shi, Gradst. et R.L.Zhu – Verdoorn (1934a as *Archilejeunea mariana* and *Spruceanthus marianus*), Mizutani (1969 as *S. marianus*), Kitagawa and Kodama (1974 as *S. marianus*), Lee et al. (2013 as *A. planiuscula*). Penang, Sarawak, Sabah.

***Spruceanthus polymorphus*** (Sande Lac.) Verd. – Verdoorn (1934a), Mizutani (1969), Kitagawa and Kodama (1974), Wolseley et al. (1996), Lee et al. (2013). Perak, Pahang, Negeri Sembilan, Sabah.

***Spruceanthus semirepandus*** (Nees) Verd. – Verdoorn (1934a), Sun et al. (2018). Kedah, Sabah.

***Spruceanthus sulcatus*** (Nees) Gradst. – Verdoorn (1934a as *Ptychanthus sulcatus*), Mizutani (1969 as *P. sulcatus*). Sabah.

***Stictolejeunea balfourii*** (Mitt.) E.W.Jones – Herzog (1950 as *S. richardsii*), Mizutani (1969 as *S. richardsii*), Gradstein (1985), Thiers and Gradstein (1989). Sarawak, Sabah.

***Symphyogynopsis gottscheana*** (Mont. et Nees) Grolle – Grolle and Piippo (1986 as *S. filicum*), Cheah (2017). Perak, Pahang.

***Syzygiella autumnalis*** (DC.) K.Feldberg, Váňa, Hentschel et Heinrichs – Akiyama et al. (2001 as *Jamesoniella autumnalis*). Sabah.

***Syzygiella contracta*** (Reinw., Blume et Nees) Gradst. et G.E.Lee – Kitagawa (1970 as *Cuspidatula contracta*), Váňa (1991c as *Jamesoniella contracta*). Sabah.

***Syzygiella flaccida*** (Steph.) Gradst. et G.E.Lee – Grolle (1971 as *Anomacaulis flaccidus*), Váňa (1991c as *A. flaccidus*). Sabah.

***Syzygiella flexicaulis*** (Nees) Gradst. et G.E.Lee – Inoue (1967a as *Jamesoniella flexicaulis*), Amakawa (1969a as *J. flexicaulis* var. *mizutanii*), Grolle (1971 as *J. flexicaulis*), Kürschner (1990 as *J. flexicaulis*), Váňa (1991c as *J. flexicaulis*). Pahang, Sabah.

***Syzygiella nipponica*** (S.Hatt.) K.Feldberg, Váňa, Hentschel et Heinrichs – Amakawa (1969a as *Jamesoniella perverrucosa*), Grolle (1971 as *J. nipponica*), Kürschner (1990 as *J. nipponica*), Váňa (1991c as *J. nipponica*). Sabah.

***Syzygiella ovalifolia*** Inoue – Váňa (1991c). Sabah.

***Syzygiella securifolia*** (Nees) Inoue – Inoue (1966, 1967a, 1968b all as *S. variegata*), Kitagawa and Kodama (1974 as *S. variegata*). Pahang, Sabah.

***Syzygiella sonderi*** (Gottsche) K.Feldberg, Váňa, Hentschel et Heinrichs – Amakawa (1969b as *Jungermannia iwatsukii*), Kitagawa and Kodama (1973 as *J. iwatsukii*), Váňa (1991c as *Cryptochila grandiflora*). Sabah.

***Syzygiella subintegerrima*** (Reinw., Blume et Nees) Spruce – Inoue (1966, 1967a, 1968a), Kitagawa and Kodama (1974), Váňa (1991c). Pahang, Sabah.

***Telaranea major*** (Herzog) J.J.Engel et G.L.Merr – Herzog (1950 as *Arachniopsis major*), Kitagawa and Kodama (1973 as *A. major*), Mizutani (1974b as *A. major*), Manuel (1981 as *A. major*), Engel and Merrill (2004). Pahang, Sarawak, Sabah.

***Telaranea monocera*** (R.M.Schust. et Grolle) J.J.Engel et G.L.Merr. – Piippo (1985 as *Arachniopsis monocera*), Engel and Merrill (2004). Johor ["Mt. Ophir" (Gunung Ledang)].

***Telaranea papulosa*** (Steph.) J.J.Engel et G.L.Merr. – Cheah (2017). Pahang.

***Temnoma setigerum*** (Lindenb.) R.M.Schust. – Kitagawa and Kodama (1973). Sabah.

***Tetralophozia filiformis*** (Steph.) Urmi – Kitagawa (1973 as *Chandonanthus filiformis*), Kitagawa and Kodama (1973 as *C. filiformis*), Kodama and Narita (1974 as *C. filiformis*). Sabah.

***Tetralophozia pilifera*** (Steph.) R.M.Schust. – Kürschner (1990 as *Chandonanthus pilifer* ['*piliferus*']). Sabah.

***Thiersianthus silamensis*** R.L.Zhu et L.Shu – Zhu et al. (2017). Sabah.

***Thysananthus aculeatus*** Herzog – Verdoorn (1934a as *T. richardsianus*), Herzog (1950 as *T. richardsianus*), Inoue (1967a, 1968b), Mizutani (1969), Kamimura (1974), Thiers (1985), Sukkharak (2015). Pahang, Sarawak, Sabah.

***Thysananthus ciliaris*** (Sande Lac.) Sukkharak – Sukkharak (2015). Perak.

***Thysananthus comosus*** Lindenb. – Lehmann (1844), Stephani (1890), Schiffner (1898), Mizutani (1977), Sukkharak et al. (2011), Sukkharak (2015). Kedah, Penang, Perak, Selangor, Johor, Sarawak, Sabah.

***Thysananthus convolutus*** Lindenb. – Stephani (1912 as *T. laceratus*), Verdoorn (1934a), Herzog (1950), Kamimura (1974), Kitagawa and Kodama (1974), Sukkharak et al. (2011), Sukkharak (2015). Penang, Selangor, Kelantan, Pahang, Johor, Sarawak, Sabah.

***Thysananthus convolutus*** var. ***laceratus*** (Steph.) Sukkharak – Sukkharak (2015). Sabah.

***Thysananthus fruticosus*** (Lindenb. et Gottsche) Schiffn. – Verdoorn (1934a), Herzog (1950 as *T. fruticosus* f. *pendulus*), Mizutani (1969, 1987), Kitagawa and Kodama (1974), Kürschner (1990), Wolseley et al. (1996), Sukkharak (2015). Pahang, Selangor, Negeri Sembilan, Johor, Sarawak, Sabah.

***Thysananthus gottschei*** (J.B.Jack et Steph.) Steph. – Stephani (1912 as *T. borneensis*), Verdoorn (1934a), Kamimura (1974), Kitagawa and Kodama (1974), Thiers (1985), Sukkharak (2015). Penang, Pahang, Sarawak, Sabah.

***Thysananthus gottschei*** var. ***continuus*** Sukkharak – Sukkharak (2015). Sarawak.

***Thysananthus gradsteinii*** (Sukkharak) Sukkharak et Gradst. – Sukkharak and Gradstein (2014 as *Mastigolejeunea gradsteinii*). Kelantan, Pahang.

***Thysananthus humilis*** (Gottsche) Sukkharak et Gradst. – Mizutani (1969 as *Mastigolejeunea humilis*, 1986b as *M. recurvifolia*), Kitagawa (1971 as *M. humilis*), Kamimura (1974 as *M. humilis*), Sukkharak and Gradstein (2014 as *M. humilis*), Cheah (2017 as *M. humilis*). Penang, Pahang, Sarawak, Sabah.

***Thysananthus indicus*** (Steph.) Sukkharak et Gradst. – Sukkharak and Gradstein (2014 as *M. indica*). Kedah.

***Thysananthus ligulatus*** (Lehm. et Lindenb.) Sukkharak et Gradst. – Stephani (1890 as *Phragmicoma ligulata*), Schiffner (1898 as *Mastigolejeunea ligulata*), Verdoorn (1934a as *M. ligulata*), Mizutani (1969 as *M. ligulata*), Kitagawa and Kodama (1974 as *M. ligulata*), Thiers and Gradstein (1989 as *M. ligulata*), Kürschner (1990), Gradstein et al. (2002 as *M. ligulata*), Lee et al. (2013 as *M. ligulata*), Sukkharak and Gradstein (2014 as *M. ligulata*). Penang, Pahang, Sarawak, Sabah.

***Thysananthus reconditus*** (Steph.) Sukkharak et Gradst. – Mizutani (1969 as *Mastigolejeunea recondita*), Sukkharak and Gradstein (2014 as *M. recondita*), Sun et al. (2018). Pahang, Sarawak, Sabah.

***Thysananthus repletus*** (Taylor) Sukkharak et Gradst. – Mizutani (1969 as *Mastigolejeunea atypos*, 1986b as *M. repleta*), Sukkharak and Gradstein (2014 as *M. repleta*). Kedah, Selangor, Sabah.

***Thysananthus retusus*** (Reinw., Blume et Nees) B.M.Thiers et Gradst. – Mizutani (1969, 1987 both as *T. planus*), Tixier (1971). Pahang, Sabah.

***Thysananthus spathulistipus*** (Reinw., Blume et Nees) Lindenb. – Verdoorn (1934a), Herzog (1950 as *T. spathulistipus* f. *borneensis*), Inoue (1967a, 1968b), Tixier (1971, 1974), Kamimura (1974), Kitagawa and Kodama (1974), Kodama (1976), Thiers (1985), Kürschner (1990), Sukkharak (2015), Cheah (2017 as *T. minor*). Kedah, Penang, Perak, Kelantan, Pahang, Negeri Sembilan, Malacca, Johor, Sarawak, Sabah.

***Thysananthus truncatus*** (Mizut.) Sukkharak et Gradst. – Mizutani (1986b as *Mastigolejeunea truncata*), Sukkharak and Gradstein (2014 as *M. truncata*). Sabah.

***Thysananthus virens*** Ångstr. – Mizutani (1986b as *Mastigolejeunea virens*), Sukkharak and Gradstein (2014 as *M. virens*). Penang, Sabah.

***Treubia insignis*** K.I.Goebel – Akiyama et al. (2001). Sabah.

***Triandrophyllum heterophyllum*** (Steph.) Grolle – Cheah (2017). Pahang.

***Trichocolea magna*** T.Katag. – Katagiri et al. (2013). Sarawak.

***Trichocolea mollissima*** (Hook.f et Taylor) Gottsche – Katagiri et al. (2013). Sabah.

***Trichocolea pluma*** (Reinw., Blume et Nees) Mont. – De Notaris (1874), Herzog (1950), Inoue (1965), Kitagawa (1971, 1973), Kitagawa and Kodama (1973), Tixier (1974), Pocock et al. (1984), Kürschner (1990), Akiyama et al. (2001), Ludwiczuk and Asakawa (2010), Katagiri et al. (2013). Kedah, Penang, Pahang, Sarawak, Sabah.

***Trichocolea rudimentaris*** Steph. – Katagiri et al. (2013). Pahang.

***Trichocolea tomentella*** (Ehrh.) Dumort. – Gottsche et al. (1845 as *T. tomentella* f. *javanica*), Johnson (1972), Katagiri et al. (2013). Penang, Pahang, Sabah.

***Tricholepidozia neesii*** (Lindenb.) E.D.Cooper – De Notaris (1874), Herzog (1950 as *Lepidozia neesii*), Inoue (1967a, 1968b both as *Telaranea neesii*), Kitagawa and Kodama

(1973), Mizutani (1974 as *Telaranea neesii*), Akiyama et al. (2001 as *Telaranea neesii*), Engel and Merrill (2004 as *Telaranea neesii*). Pahang, Sarawak, Sabah.

***Tricholepidozia octoloba*** (Del Ros.) E.D.Cooper – Shi and Zhu (2008 as *Telaranea octoloba*). Johor.

***Tricholepidozia quadriseta*** (Steph.) E.D.Cooper – Pócs et al. (2014 as *Telaranea quadriseta*). Pahang.

***Tricholepidozia semperiana*** (Steph.) E.D.Cooper – Mizutani (1974b as *Telaranea semperiana*). Sabah.

***Tricholepidozia trichocoleoides*** (Herzog) E.D.Cooper – Herzog (1950 as *Lepidozia trichocoleoides*), Kitagawa and Kodama (1973 as *L. trichocoleoides*), Engel and Merrill (2004 as *Telaranea trichocoleoides*). Sarawak, Sabah.

***Tritomaria exsecta*** (Schmidel) Loeske – Kitagawa (1970). Sabah.

***Tuyamaella angulistipa*** (Steph.) R.M.Schust. et Kachroo – Stephani (1896 as *Pycnolejeunea angulistipa*), Schiffner (1898 as *P. angulistipa*), Mizutani (1966, 1970), Tixier (1971, 1973a), Zhu and So (2000b). Perak, Pahang, Johor, Sabah.

***Tuyamaella borneensis*** Tixier – Tixier (1973a). Sabah.

***Tuyamaella molischii*** (Schiffn.) S.Hatt. – Tixier (1973a), Pesiu et al. (2021). Kedah, Terengganu.

***Tuyamaella serratistipa*** S.Hatt. – Herzog (1951 as *Pycnolejeunea appendiculata*), Mizutani (1966), Tixier (1973a), Kitagawa and Kodama (1974), Zhu and So (1998a, 2000c), Pócs et al. (2020). Sarawak, Sabah.

***Wiesnerella denudata*** (Mitt.) Steph. – Akiyama et al. (2001), Ludwiczuk and Asakawa (2010). Sabah.

***Zoopsis liukiuensis*** Horik. – Herzog (1950 as *Z. argentea*), Kitagawa and Kodama (1973), Manuel (1981), Grolle and Piippo (1984), Pocock et al. (1984), Mizutani and Chang (1986), Bisang et al. (2003). Pahang, Sarawak, Sabah.

***Zoopsis setigera*** K.I.Goebel – Kitagawa and Kodama (1973 as *Z. rigida*), Schuster (1999). Sarawak, Sabah.

## Hornworts (Anthocerotophyta)

***Anthoceros angustus*** Steph. – Mohamed and Yong (2005 as *A. formosae*), Mohamed et al. (2005 as *A. formosae*), Lee and Gradstein (2021). Langkawi.

***Dendroceros cavernosus*** J.Haseg. – Hasegawa (1980). Sabah.

***Dendroceros difficilis*** Steph. – Chantanaorrapint et al. (2014). Pahang.

***Folioceros glandulosus*** (Lehm. et Lindenb.) D.C.Bharadwaj – Meijer (1957 as *Anthoceros grandulosus*), Tixier (1971 as *A. grandulosus*). Pahang, Sarawak.

***Megaceros flagellaris*** (Mitt.) Steph. – Herzog (1950 as *M. celebensis*), Hasegawa (1983), Lee and Gradstein (2021). Pahang, Sarawak, Sabah.

***Phaeoceros carolinianus*** (Michx.) Prosk. – Johnson (1958 as *Anthoceros validus*). Perak, Pahang.

***Phaeomegaceros foveatus*** (J.Haseg.) J.C.Villarreal – Hasegawa (2001 as *Phaeoceros foveatus*). Sabah.

## Further records

The following records from Malaysia (Genting Highlands, Pahang; Cheah 2017) need verification.

*Cololejeunea denticulata* (Horik.) S.Hatt.
*Cololejeunea dinghuiana* R.L.Zhu et Y.F.Wang
*Cololejeunea drepanolejeuneoides* (Horik.) R.M.Schust.
*Cololejeunea grossepapillosa* (Horik.) N.Kitag.
*Cololejeunea plagiophylla* Benedix
*Cololejeunea spinosa* (Horik.) Pandé et R.N.Misra
*Plagiochila fusca* Sande Lac.
*Plagiochila gracilis* Lindenb. et Gottsche
*Plagiochila salacensis* Gottsche
*Plagiochila stephanii* Schiffn.
*Riccardia diminuta* Schiffn.
*Riccardia hattorii* Furuki
*Riccardia multifida* (L.) Gray
*Riccardia multifidoides* Schiffn.
*Riccardia pumila* Furuki
*Riccardia singapurensis* Schiffn.

## Doubtful records

*Anastrophyllum piligerum* f. *denticalyx* – Reported from Sarawak (Herzog 1950); status unclear.

*Aspiromitus vesiculosus* var. *latifrons* Herzog – Reported from Sarawak (Herzog 1950), but its status is unclear. *Aspiromitus* is now a synonym of *Anthoceros*.

*Bazzania everettii* (Steph.) Meijer nom. inval. (ICN Art. 41.5) – Reported from Sarawak (Stephani 1908 as *Mastigobryum everettii*); status unclear.

*Bazzania karcharias* Herzog, nom. inval. (ICN 38.1) – Sarawak (Herzog 1950).

*Bazzania stonii* Inoue nom. inval. (ICN Art. 38.1(a) – Reported from Pahang (Inoue 1968b); the record should be checked.

*Bazzania subhyalina* (Steph.) Chuah-Pet. nom. inval. (ICN Art. 41.5) – Reported from Sarawak (Stephani 1924 as *Mastigobryum subhyalinum*); status unclear.

*Cephaloziella stephanii* Douin – Reported from Pahang (Cheah 2017); the record should be checked.

*Chiloscyphus ceylanicus* Tixier nom. inval. (ICN Art. 38.1a) – Reported from Kedah (Tixier 1974); the record should be checked.

*Chiloscyphus schiffneri* J.J.Engel et R.M.Schust. nom illeg. – Synonym of *Lophocolea javanica* Schiffn., its occurrence in Pahang (Cheah 2017) is doubtful.

*Chiloscyphus flaccidens* Steph. – Reported from Kedah (Tixier 1974); the record should be checked.

*Drepanolejeunea blumei* var. *angulistipa* Herzog nom inval. (ICN Art. 39.1) – Reported from Sabah (Herzog 1936); the record should be checked.

*Drepanolejeunea malayana* Tixier ("Grolle") nom. inval. – Reported from Kedah (Tixier 1974); the record should be checked.

*Drepanolejeunea vesiculosa* subsp. *propagulifera* Herzog nom. inval. (ICN Art. 39.1) – Reported from Negeri Sembilan (Wolseley et al. 1996) and Pahang (Inoue 1967a); the record should be checked.

*Frullania ornithocephala* f. *magnilobula* and f. *retusa* – Reported from Sabah (Hattori 1976), but their status is unclear.

*Gottschea integerrima* (Steph.) Grolle et Zijlstra – Accepted name: *Schistochila integerrima* Steph., only known from Vanuatu and New Caledonia (Thouvenot 2021). Its occurrence in Pahang (Cheah 2017) is doubtful and the record is most likely *S. nuda* Horik., known from Thailand and Southeast Asia.

*Radula kurzii* Steph. – Reported from Pahang (Cheah 2017); not known in tropical Southeast Asia and very similar to the widespread Asian *R. javanica* Gottsche.

*Symphyogyna similis* Grolle – Reported from Pahang (Cheah 2017); the record should be checked, only known from the Huon Peninsula and Java (Grolle and Piippo 1986).

*Telaranea wallichiana* var. *remotifolia* Herzog – Reported from Sarawak (Herzog 1950), but its status is unclear.

## Excluded and erroneous records (See Menzel 1988 for further excluded records)

*Acrolejeunea aulacophora* (Mont.) Steph. – The record from Sabah (Mizutani 1969 as *Ptychocoleus aulacophorus*) is doubtful.

*Acrolejeunea borneensis* Bonner, nom. inval. from Sarawak (Bonner 1962) is a *Schiffneriolejeunea* sp. fide Gradstein (1975).

*Acrolejeunea sandvicensis* (Gottsche) J.Wang et Gradst. – The record from Malaysia (Tixier (1975 as *Brachiolejeunea sandvicensis*) belongs to *Thysananthus reconditus* (Sun et al. 2018).

*Bazzania tricrenata* (Wahlenb.) Lindb. – This is a Holarctic species, not known in tropical Southeast Asia, and its occurence in Malaysia (Pahang; Cheah 2017) is considered erroneous. Also reported from Sabah by Sande Lacoste (1864 as *Mastigobryum deflexum*).

*Cheilolejeunea parvidens* B.M.Thiers – The record from Sabah (Pócs et al. 2020) belongs to *C. intertexta.*

*Chiloscyphus minor* (Nees) J.J.Engel et R.M.Schust. – This is a Holarctic species, not known in tropical Southeast Asia, and its occurence in Malaysia (Pahang; Cheah 2017) is considered erroneous.

*Frullania integristipula* var. *emarginata* Verd. – Reported from Sabah by Chuah-Petiot (2011) based on Hattori (1982), but the latter author did not report this variety from Malaysia.

*Frullania pulogensis* Steph. – Reported from Sabah by Verdoorn (1932a) but it was rejected by Hattori (1978) due to the scarcity of the specimen. No material of *F. pulogensis* but fragmental shoots of *F. mizutanii* are present.

*Kurzia mauiensis* (H.A.Mill.) H.A.Mill. – Reported from Pahang (Cheah 2017). Only known from the Pacific Islands and its occurrence in Malaysia needs verification.

*Lejeunea dentata* Mitt. – Reported from Pahang (Cheah 2017). Synonym of *Radula cuspidata* Steph., only known in New Zealand.

*Lejeunea ulicina* (Taylor) Gottsche, Lindenb. et Nees – Accepted name: *Microlejeunea ulicina* (Taylor) Steph., a Holarctic species, not known in tropical Southeast Asia. Its occurrence in Malaysia (Pahang; Cheah 2017) is considered erroneous.

*Metacalypogeia alternifolia* (Nees) Grolle – Reported from Sarawak by Herzog (1950 as *Calypogeia alternifolia*). According to Grolle (1964), this record is erroneous.

*Metzgeria albinea* Spruce – This is a Neotropical species according to So (2002), and its occurrence in Malaysia (Pahang; Cheah 2017) needs verification.

*Mnioloma stamatotonum* M.A.M.Renner et E.A.Br. – Reported from Pahang (Cheah 2017); an Australasian species, not known in tropical Southeast Asia.

*Riccia treubiana* Steph. – Reported from Peninsular Malaysia by Chuah Petiot (2011) based on Meijer (1958) but the latter author reported this species from Singapore. *Riccia treubiana* is a common species and often found in gardens, recreational parks and secondary forests. Its occurrence in Malaysia is to be expected.

*Odontoschisma denudatum* (Nees) Dumort. – Reported from Sabah by various authors (see Chuah-Petiot 2011), but the material belongs to *O. denudatum* subsp. *navicular*e (see Gradstein and Ilkiu-Borges 2015).

*Odontoschisma sphagni* (Dicks.) Dumort. – Reported from Sabah by Mitten and Wright (1894), but the record is considered erroneous (Váňa 1993). According to Gradstein and Ilkiu-Borges (2015) *O. sphagni* is a species from Europe and North America that does not occur in Asia.

*Saccogynidium irregularospinum* C.Gao, T.Cao et M.J.Lai – Reported from Pahang (Cheah 2017); a temperate Asiatic species from Sikkim and China, not known in tropical Southeast Asia.

*Schistochila nyamanii* – Reported from Pahang (Cheah 2017), but the species name does not exist.

*Solenostoma obliquifolium* (Schiffn.) Váňa, Hentschel et Heinrichs – Reported from Sabah by Chuah-Petiot (2011) based on Váňa (1991b as *Jungermannia obliquifolia*) but the latter author did not report this species in Sabah.

*Telaranea granulata* J.J.Engel et G.L.Merr. – Reported from Pahang (Cheah 2017); endemic to New Zealand, not known in tropical Southeast Asia.

*Telaranea patentissima* (Hook.f et Taylor) E.A.Hodgs. – Reported from Pahang (Cheah 2017); an Australasian species from Australia and New Zealand, not known in tropical Southeast Asia.

*Thysananthus auriculatus* (Wilson et Hook.) Sukkharak et Gradst. – Reported from Pahang by Lee et al. (2013 as *Mastigolejeunea auriculata*). According to Sukkharak and Gradstein (2014, 2017) *T. auriculatus* is an Afro-American species; Asiatic records of this species belong to *T. humilis*.

*Wettsteinia inversa* (Sande Lac.) Schiffn. – Reported from Sabah by Frahm et al. (1990) and Chuah-Petiot (2011) based on Menzel (1988), but the latter author reported this species only from Kalimantan Selatan (leg. Korthals, paratype of *Plagiochila scabra* Sande Lac.). *Wettsteinia inversa* is a widespread Malesian species (see Piippo 1984) and its occurrence in Malaysia is to be expected.

## Synonyms

New synonymy published after the appearance of World Checklist (Söderström et al. 2016) is provided with a reference.

*Acantholejeunea spinistipula* (Herzog) R.M.Schust. ≡ *Ceratolejeunea spinistipula* (Herzog) R.L.Zhu, L.Shu, Qiong He et Y.M.Wei

*Acrolejeunea pulopenangensis* (Gottsche) Schiffn. ≡ *Schiffneriolejeunea pulopenangensis* (Gottsche) Gradst.

*Acrolejeunea tumida* (Nees) Steph. ≡ *Schiffneriolejeunea tumida* (Nees) Gradst.

*Acromastigum bidenticulatum* A.Evans = *A. bancanum* (Sande Lac.) A.Evans

*Acromastigum denticulatum* A.Evans = *A. bifidum* (Steph.) A.Evans

*Acromastigum emarginatum* Herzog ≡ *Bazzania menzelii* E.D.Cooper

*Acromastigum gemmiferum* N.Kitag. et T.Kodama = *A. obliquatum* (Mitt.) A.Evans

*Adelanthus borneensis* Grolle ≡ *Pseudomarsupidium borneensis* (Grolle) Váňa, L.Söderstr., A.Hagborg et von Konrat

*Allorgella changiana* Tixier = *Otolejeunea semperiana* (Steph.) Grolle

*Anastrophyllum appendiculatum* N.Kitag = *A. auritum* (Lehm.) Steph.

*Anastrophyllum divergens* Herzog = *A. fissum* Steph.

*Anastrophyllum imbricatum* (Gottsche, Lindenb. et Nees) Steph. = *A. piligerum* (Nees) Steph.

*Anastrophyllum minutum* (Schreb.) R.M.Schust. ≡ *Sphenolobus minutus* (Schreb.) Berggr.

*Aneura subcrenulata* Herzog = *Riccardia parvula* Schiffn.

*Anomacaulis flaccidus* (Steph.) Grolle ≡ *Syzygiella flaccida* (Steph.) Gradst. et G.E.Lee (Lee and Gradstein 2021)

*Anthoceros formosae* Steph. = *A. angustus* Steph.

*Anthoceros glandulosus* Lehm. et Lindenb. ≡ *Folioceros glandulosus* (Lehm. et Lindenb.) Bhardwaj

*Anthoceros validus* Steph. = *Phaeoceros carolinianus* (Michx.) Prosk.

*Aplozia polyrhiza* (Hook.) Horik. = *Solenostoma truncatum* (Nees) Váňa et D.G.Long

*Apometzgeria pubescens* var. *kinabaluensis* Kuwah. = *Metzgeria kinabaluensis* (Kuwah.) Masuzaki

*Aphanolejeunea borneensis* (Herzog) Pócs = *Cololejeunea papillosa* (K.I.Goebel) Mizut.

*Aphanolejeunea microscopica* var. *borneensis* Herzog = *Cololejeunea papillosa* (K.I.Goebel) Mizut.

*Aphanolejeunea proboscoidea* (K.I.Goebel) R.M.Schust. = *Cololejeunea diaphana* A.Evans

*Arachniopsis major* Herzog ≡ *Telaranea major* (Herzog) J.J.Engel et G.L.Merr.

*Arachniopsis monocera* R.M.Schust. et Grolle ≡ *Telaranea monocera* J.J.Engel et G.L.Merr.
*Archilejeunea mariana* auct. (non (Gottsche) Steph.) = *Spruceanthus planiusculus* (Mitt.) X.Q.Shi, R.L.Zhu et Gradst. (Shi et al. 2015)
*Archilejeunea planiuscula* (Mitt.) Steph. ≡ *Spruceanthus planiusculus* (Mitt.) X.Q.Shi, R.L.Zhu et Gradst. (Shi et al. 2015)
*Austrometzgeria francana* (Steph.) Kuwah. ≡ *Metzgeria francana* Steph.
*Bazzania assamica* (Steph.) S.Hatt. = *B. tridens* var. *assamica* (Steph.) Pócs
*Bazzania australis* Gottsche, Lindenb. et Nees = *B. tridens* (Reinw., Blume et Nees) Trevis.
*Bazzania bancana* (Sande Lac.) Trevis. ≡ *Acromastigum bancanum* (Sande Lac.) A.Evans
*Bazzania concinna* (De Not.) Trevis. = *B. intermedia* (Gottsche et Lindenb.) Trevis.
*Bazzania coreana* Herzog = *B. tridens* (Reinw., Blume et Nees) Trevis.
*Bazzania echinatiformis* (De Not.) Trevis. ≡ *Acromastigum echinatiforme* (De Not.) A Evans
*Bazzania ferox* (De Not.) Trevis. = *B. harpago* (De Not.) Schiffn.
*Bazzania remotifolia* Herzog nom. illeg. ≡ *B. herzogiana* Meijer
*Bazzania palmatifida* (Steph.) Grolle = *B. subtilis* (Sande Lac.) Trevis.
*Bazzania fallax* f. *fissa* Herzog = *B. fallax* (Sande Lac.) Schiffn.
*Bazzania lingana* (De Not.) Trevis. ≡ *Acromastigum linganum* (De Not.) A.Evans
*Bazzania notarisii* (Steph.) Schiffn. = *Acromastigum inaequilaterum* (Lehm. et Lindenb.) A.Evans
*Bazzania pulvinulata* (De Not.) Schiffn. ≡ *Mastigopelma pulvinulatum* (De Not.) Grolle
*Bazzania recurva* var. *pallens* (De Not.) Schiffn. = *B. recurva* (Mont.) Trevis.
*Bazzania recurvolimbata* (Steph.) N.Kitag. = *B. revoluta* (Steph.) N.Kitag.
*Bazzania richardsii* Herzog = *B. calcarata* (Sande Lac.) Schiffn.
*Bazzania serrulata* (Mitt.) Steph. = *B. erosa* (Reinw., Blume et Nees) Trevis.
*Bazzania tridens* f. *minutissima* (Kamim.) Pócs = *B. tridens* (Reinw., Blume et Nees) Trevis.
*Bazzania vaga* (De Not.) Trevis. = *B. erosa* (Reinw., Blume et Nees) Trevis.
*Calypogeia baldwinii* Austin = *Mnioloma fuscum* (Lehm.) R.M.Schust.
*Calypogeia fusca* (Lehm.) Steph. ≡ *Mnioloma fuscum* (Lehm.) R.M.Schust.
*Campylolejeunea peculiaris* (Herzog) Amakawa = *Cololejeunea inflectens* (Mitt.) Benedix
*Campylolejeunea pusilla* Mizut. ≡ *Cololejeunea hattoriana* Mizut. et Pócs
*Caudalejeunea circinata* Steph. = *C. cristiloba* (Steph.) Gradst.
*Caudalejeunea serrata* Steph. = *C. reniloba* (Gottsche) Steph.
*Caudalejeunea recurvistipula* (Gottsche) Schiffn. = *C. reniloba* (Gottsche) Steph.
*Caudalejeunea stephanii* Steph. nom. inval. = *C. reniloba* (Gottsche) Steph.
*Cephalozia pearsonii* (Spruce) Steph. ≡ *Sphenolobopsis pearsonii* (Spruce) R.M.Schust.
*Cephaloziella tagawae* N.Kitag. = *Cylindrocolea tagawae* (N.Kitag.) R.M.Schust.
*Cephaloziella willisana* (Steph.) N.Kitag. = *Cylindrocolea kiaeri* (Austin) Douin
*Ceratolejeunea oceanica* (Mitt.) Steph. = *C. belangeriana* (Gottsche) Steph.
*Ceratolejeunea ryukyuensis* Amakawa = *C. belangeriana* (Gottsche) Steph.
*Ceratolejeunea tahitensis* Steph. = *C. cornuta* (Lindenb.) Steph.
*Chandonanthus filiformis* Steph. ≡ *Tetralophozia filiformis* (Steph.) Urmi
*Chandonanthus hirtellus* (F.Weber) Mitt. ≡ *Plicanthus hirtellus* (F.Weber) R.M.Schust.

*Chandonanthus pilifer* Steph. ≡ *Tetralophozia pilifera* (Steph.) R.M.Schust.
*Cheilolejeunea excisula* (Steph.) Mizut. = *C. incisa* (Gottsche) R.M.Schust.
*Cheilolejeunea imbricata* (Nees) S.Hatt. = *C. trapezia* (Nees) R.M.Schust. et Kachroo
*Cheilolejeunea larsenii* Mizut. = *C. adnata* var. *autoica* Gradst. et Ilk.-Borg. (Bastos and Gradstein 2020).
*Cheilolejeunea longiloba* (G.Hoffm.) R.M.Schust. = *C. trapezia* (Nees) R.M.Schust. et Kachroo
*Cheilolejeunea luerssenii* (Steph.) Mizut. = *C. lindenbergii* (Gottsche) Mizut.
*Cheilolejeunea meyeniana* (Nees, Lindenb. et Gottsche) R.M.Schust. et Kachroo = *C. trapezia* (Nees) R.M.Schust. et Kachroo
*Cheilolejeunea picta* Mizut. ≡ *Pictolejeunea mizutanii* Grolle
*Cheilolejeunea spathulata* Mizut. = *C. decursiva* (Sande Lac.) R.M.Schust.
*Cheilolejeunea viridula* (Herzog) Mizut. = *C. trifaria* (Reinw., Blume et Nees) Mizut.
*Chiloscyphus acutangulus* Schiffn. ≡ *Heteroscyphus acutangulus* (Schiffn.) Schiffn.
*Chiloscyphus argutus* (Reinw., Blume et Nees) Nees ≡ *Heteroscyphus argutus* (Reinw., Blume et Nees) Schiffn.
*Chiloscyphus aselliformis* (Reinw., Blume et Nees) Nees ≡ *Heteroscyphus aselliformis* (Reinw., Blume et Nees) Schiffn.
*Chiloscyphus aselliformis* var. *neesii* Schiffn. = *Heteroscyphus aselliformis* (Reinw., Blume et Nees) Schiffn.
*Chiloscyphus ciliolatus* (Nees) J.J.Engel et R.M.Schust. ≡ *Cryptolophocolea ciliolata* (Nees) L.Söderstr., Crand.-Stotl., Stotler et Váňa
*Chiloscyphus coadunatus* (Sw.) J.J.Engel et R.M.Schust. = *Lophocolea bidentata* (L.) Dumort.
*Chiloscyphus communis* Steph. = *Heteroscyphus coalitus* (Hook.) Schiffn.
*Chiloscyphus concinnus* De Not. = *Heteroscyphus succulentus* (Gottsche) Schiffn.
*Chiloscyphus costatus* (Nees) J.J.Engel et R.M.Schust. ≡ *Cryptolophocolea costata* (Nees) L.Söderstr.
*Chiloscyphus cuspidatus* (Nees) J.J.Engel et R.M.Schust. = *Lophocolea bidentata* (L.) Dumort.
*Chiloscyphus decurrens* (Reinw., Blume et Nees) Nees = *Heteroscyphus splendens* (Lehm. et Lindenb.) Grolle
*Chiloscyphus densifolius* De Not. = *Heteroscyphus splendens* (Lehm. et Lindenb.) Grolle
*Chiloscyphus diestianus* Sande Lac. ≡ *Heteroscyphus diestianus* (Sande Lac.) Piippo
*Chiloscyphus integerrimus* Schiffn. ≡ *Heteroscyphus integerrimus* (Schiffn.) Gradst. et G.E.Lee (Lee and Gradstein 2021).
*Chiloscyphus kurzii* (Sande Lac.) J.J.Engel et R.M.Schust. ≡ *Lophocolea kurzii* Sande Lac.
*Chiloscyphus latifolius* (Nees) J.J.Engel et R.M.Schust. = *Lophocolea bidentata* (L.) Dumort.
*Chiloscyphus muricatus* (Lehm.) J.J.Engel et R.M.Schust. ≡ *Lophocolea muricata* (Lehm.) Nees
*Chiloscyphus muricellus* De Not. ≡ *Saccogynidium muricellum* (De Not.) Grolle
*Chiloscyphus paroicus* J.J.Engel et R.M.Schust. ≡ *Cryptolophocolea levieri* (Schiffn.) L.Söderstr.
*Chiloscyphus parvulus* Schiffn. ≡ *Heteroscyphus parvulus* (Schiffn.) Schiffn.

*Chiloscyphus sikkimensis* (Steph.) J.J.Engel et R.M.Schust. ≡ *Lophocolea sikkimensis* (Steph.) Herzog et Grolle
*Chiloscyphus steetziae* (De Not.) J.J.Engel et R.M.Schust. ≡ *Lophocolea steetziae* De Not.
*Chiloscyphus succulentus* Gottsche ≡ *Heteroscyphus succulentus* (Gottsche) Schiffn.
*Chiloscyphus wettsteinii* Schiffn. ≡ *Heteroscyphus wettsteinii* (Schiffn.) Schiffn.
*Chiloscyphus zollingeri* var. *borneensis* Herzog = *Heteroscyphus zollingeri* (Gottsche) Schiffn.
*Cololejeunea androgyna* Benedix = *C. obliqua* (Nees et Mont.) Schiffn.
*Cololejeunea amoena* Benedix ≡ *C. floccosa* var. *amoena* (Benedix) Pócs
*Cololejeunea astyla* Mizut. = *C. platyneura* (Spruce) A.Evans
*Cololejeunea balansae* (Steph.) Mizut. = *C. trichomanis* (Gottsche) Steph.
*Cololejeunea benedixii* Tixier = *C. schmidtii* Steph.
*Cololejeunea bolombensis* (Steph.) Vanden Berghen = *C. lanciloba* Steph.
*Cololejeunea ciliatilobula* (Schiffn.) Schiffn. = *C. inflectens* (Mitt.) Benedix
*Cololejeunea crenulata* (Pearson) H.A.Mill. = *C. angustiflora* (Steph.) Mizut.
*Cololejeunea falcatoides* Benedix = *C. falcata* (Horik.) Benedix
*Cololejeunea filicaulis* Steph. = *C. hildebrandii* (Austin) Steph.
*Cololejeunea formosana* Mizut. = *C. ceratilobula* (P.C.Chen) R.M.Schust.
*Cololejeunea goebelii* (Schiffn.) Schiffn. = *C. trichomanis* (Gottsche) Steph.
*Cololejeunea inflectidens* (Mitt.) Benedix nom. inval. ≡ *C. inflectens* (Mitt.) Benedix
*Cololejeunea javanica* (Steph.) Mizut. = *C. angustiflora* (Steph.) Mizut.
*Cololejeunea jelinekii* Steph. = *C. obliqua* (Nees et Mont.) Schiffn.
*Cololejeunea karstenii* K.I.Goebel = *C. cordiflora* Steph.
*Cololejeunea kinabalensis* Mizut. = *C. macounii* (Underw.) A.Evans
*Cololejeunea leonidens* Benedix = *C. ocelloides* (Horik.) Mizut.
*Cololejeunea leonidens* var. *saccata* Benedix = *C. ocelloides* (Horik.) Mizut.
*Cololejeunea mackeeana* Tixier = *C. angustiflora* (Steph.) Mizut.
*Cololejeunea meijeri* Tixier = *C. ocelloides* (Horik.) Mizut.
*Cololejeunea mutabilis* f. *borneensis* Benedix = *C. mutabilis* Benedix
*Cololejeunea mutabilis* f. *floccodoides* Tixier = *C. mutabilis* Benedix
*Cololejeunea mutabilis* f. *subfalcata* Tixier = *C. mutabilis* Benedix
*Cololejeunea nymannii* (Steph.) Benedix = *C. obliqua* (Nees et Mont.) Schiffn.
*Cololejeunea oshimensis* (Horik.) Benedix = *C. inflata* Steph.
*Cololejeunea pahangiana* Tixier = *C. lanciloba* Steph.
*Cololejeunea pakseana* Tixier = *C. uchimae* Amakawa
*Cololejeunea paroica* Mizut. = *C. gottschei* (Steph.) Mizut.
*Cololejeunea peculiaris* (Herzog) Benedix = *C. inflectens* (Mitt.) Benedix
*Cololejeunea peraffinis* var. *elegans* Benedix = *C. peraffinis* (Schiffn.) Schiffn.
*Cololejeunea planiflora* Benedix = *Cololejeunea indica* Pandé et R.N.Misra
*Cololejeunea pluripunctata* Benedix = *C. siamensis* Steph.
*Cololejeunea pusilla* Steph. = *C. gradsteinii* M.J.Lai et R.L.Zhu
*Cololejeunea scabriflora* Steph = *C. obliqua* (Nees et Mont.) Schiffn.
*Cololejeunea tenella* var. *vittata* Tixier = *C. tenella* Benedix
*Cololejeunea trichomanis* subsp. *cordiflora* (Steph.) Pócs ≡ *C. cordiflora* Steph.
*Cololejeunea yulensis* (Steph.) Benedix = *C. aequabilis* (Sande Lac) Schiffn.

*Colura acutifolia* Jovet-Ast = *C. conica* (Sande Lac.) K.I.Goebel
*Colura apiculata* (Schiffn.) Steph. = *C. leratii* (Steph.) Steph.
*Colura javanica* Steph. = *C. ari* (Steph.) Steph.
*Colura trialata* (Steph.) Herzog et Zwickel = *C. corynophora* (Nees, Lindenb. et Gottsche) Trevis.
*Colurolejeunea ornata* A.Evans ≡ *Colura ornata* K.I.Goebel
*Conoscyphus inflexifolius* Mitt. = *C. trapezioides* (Sande Lac.) Schiffn.
*Crossotolejeunea borneensis* Herzog = *Lejeunea stenodentata* M.A.M.Renner et Pócs
*Cryptochila grandiflora* (Lindenb. et Gottsche) Grolle = *Syzygiella sonderi* (Gottsche) K.Feldberg, Váňa, Hentschel et Heinrichs
*Cuspidatula contracta* (Reinw., Blume et Nees) Steph. ≡ *Syzygiella contracta* (Reinw., Blume et Nees) Gradst. et G.E.Lee (Lee and Gradstein 2021)
*Cylindrocolea kiaeri* (Austin) Váňa ≡ *Cephaloziella kiaeri* (Austin) Douin (Lee and Gradstein 2021)
*Diplasiolejeunea brachyclada* A.Evans = *D. cavifolia* Steph.
*Diplasiolejeunea incurvata* Ast et Tixier = *D. cobrensis* Steph.
*Diplasiolejeunea javanica* Steph. = *D. cavifolia* Steph.
*Diplasiolejeunea neobrachyclada* S.Hatt = *D. patelligera* Herzog
*Diplasiolejeunea rudolphiana* Steph. = *D. unidentata* (Lehm. et Lindenb.) Schiffn.
*Diploscyphus borneensis* De Not. = *Conoscyphus trapezioides* (Sande Lac.) Schiffn.
*Drepanolejeunea brunnea* Mizut. ≡ *Mohamedia brunnea* (Mizut.) R.L.Zhu et L.Shu
*Drepanolejeunea dentata* Steph. ≡ *Lejeunea stenodentata* M.A.M.Renner et Pócs
*Drepanolejeunea filicuspis* (Steph.) Mizut. ≡ *Microlejeunea filicuspis* (Steph.) Heinrichs, Schäf.-Verw., Pócs et S.Dong
*Drepanolejeunea levicornua* var. *longicornua* Herzog = *D. longicornua* (Herzog) Mizut.
*Drepanolejeunea micholitzii* Steph. = *D. pentadactyla* (Mont.) Steph.
*Drepanolejeunea micholitzii* var. *angustissima* Herzog = *D. pentadactyla* (Mont.) Steph.
*Drepanolejeunea micholitzii* var. *brevifolia* Herzog = *D. pentadactyla* (Mont.) Steph.
*Drepanolejeunea micholitzii* var. *dactylophoroides* Herzog ≡ *D. pentadactyla* var. *dactylophoroides* (Herzog) Pócs
*Drepanolejeunea muricata* (Gottsche) Schiffn. ≡ *Dactylophorella muricata* (Gottsche) R.M.Schust.
*Drepanolejeunea spinistipula* Herzog ≡ *Ceratolejeunea spinistipula* (Herzog) R.L.Zhu, L.Shu, Qiong He et Y.M.Wei
*Drepanolejeunea tenera* f. *goebelii* Herzog = *D. tenera* K.I.Goebel
*Drepanolejeunea tenera* var. *genuina* Herzog nom. illeg. = *D. tenera* K.I.Goebel
*Drepanolejeunea tenuis* (Nees) Schiffn. = *D. angustifolia* (Mitt.) Grolle
*Drepanolejeunea ternatensis* var. *lancispina* Herzog = *D. ternatensis* (Gottsche) Schiffn.
*Drepanolejeunea vesiculosa* f. *robusta* Herzog = *D. vesiculosa* (Mitt.) Steph.
*Dumortiera calcicola* Campb. = *D. hirsuta* subsp. *nepalensis* (Taylor) R.M.Schust.
*Dumortiera nepalensis* (Taylor) Nees ≡ *D. hirsuta* subsp. *nepalensis* (Taylor) R.M.Schust.
*Dumortiera trichocephala* (Hook.) Nees = *D. hirsuta* subsp. *nepalensis* (Taylor) R.M.Schust.
*Eopleurozia simplicissima* (Herzog) R.M.Schust. = *Pleurozia gigantea* (F.Weber) Lindb.

*Euosmolejeunea luerssenii* Steph. = *Cheilolejeunea lindenbergii* (Gottsche) Mizut.
*Frullania altemammillata* S.Hatt = *F. armatifolia* Verd.
*Frullania borneensis* Steph. = *F. sublignosa* Steph.
*Frullania hampeana* Nees = *F. monocera* (Hook.f. et Taylor) Gottsche, Lindenb. et Nees
*Frullania hasskarliana* var. *integribracteata* (Verd.) S.Hatt. = *F. hasskarliana* Lindenb.
*Frullania intermedia* f. *billardieriana* (Nees et Mont.) Verd. = *F. intermedia* (Reinw., Blume et Nees) Nees
*Frullania intermedia* var. *submorokensis* S.Hatt = *F. intermedia* (Reinw., Blume et Nees) Nees
*Frullania junghuhniana* var. *minutissima* Verd. = *F. junghuhniana* var. *tenella* (Sande Lac.) Grolle et S.Hatt.
*Frullania minor* Sande Lac. = *F. gracilis* (Reinw., Blume et Nees) Nees
*Frullania moniliata* subsp. *breviramea* (Steph.) Verd. = *F. moniliata* (Reinw., Blume et Nees) Mont.
*Frullania ornithocephala* f. *magnilobula* S.Hatt. = *F. ornithocephala* (Reinw., Blume et Nees) Nees
*Frullania ornithocephala* f. *retusa* S.Hatt. = *F. ornithocephala* (Reinw., Blume et Nees) Nees
*Frullania perminuta* S.Hatt. = *F. junghuhniana* var. *tenella* (Sande Lac.) Grolle et S.Hatt.
*Frullania perversa* Steph. = *F. junghuhniana* var. *tenella* (Sande Lac.) Grolle et S.Hatt.
*Frullania philippinensis* Steph. = *F. reflexistipula* Sande Lac.
*Frullania picta* Steph. = *F. trichodes* Mitt.
*Frullania repandistipula* subsp. *spinifera* S.Hatt. nom. inval. = *F. repandistipula* subsp. *spinibractea* S.Hatt.
*Frullania serrata* f. *crispulodentata* Verd. = *F. serrata* Gottsche
*Frullania squarrosa* (Mont.) Nees = *F. ericoides* (Nees) Mont.
*Frullania tamarisci* var. *breviramea* (Steph.) S.Hatt. = *F. moniliata* (Reinw., Blume et Nees) Mont.
*Frullania tenuicaulis* Mitt. = *F. trichodes* Mitt.
*Frullania vethii* Sande Lac. = *F. trichodes* Mitt.
*Frullania vethii* f. *acutiloba* S.Hatt. = *F. trichodes* Mitt.
*Frullania wallichiana* Mitt = *F. obscura* (Sw.) Mont.
*Gottschea aligera* (Nees et Blume) Nees ≡ *Schistochila aligera* (Nees et Blume) J.B.Jack et Steph.
*Gottschea aligeriformis* De Not. = *Schistochila aligera* (Nees et Blume) J.B.Jack et Steph.
*Gottschea beccariana* De Not. ≡ *Schistochila beccariana* (De Not.) Trevis.
*Gottschea doriae* De Not. ≡ *Schistochila doriae* De Not) Trevis.
*Gottschea gaudichaudii* Gottsche = *Schistochila aligera* (Nees et Blume) J.B.Jack et Steph.
*Gottschea philippinensis* Mont. = *Schistochila aligera* (Nees et Blume) J.B.Jack et Steph.
*Gottschea sciurea* (Nees) Sande Lac. ≡ *Schistochila sciurea* (Nees) Schiffn.
*Gymnomitrion laceratum* var. *borneense* N.Kitag. = *G. incompletum* (Gottsche) Váňa
*Harpalejeunea constricta* Grolle ≡ *Microlejeunea constricta* (Grolle) Grolle
*Harpalejeunea filicuspis* (Steph.) Mizut. ≡ *Microlejeunea filicuspis* (Steph.) Heinrichs, Schäf.-Verw., Pócs et S.Dong
*Harpalejeunea kinabaluensis* Mizut. ≡ *Microlejeunea kinabaluensis* (Mizut.) Grolle

*Harpalejeunea mammillosa* Mizut. ≡ *Microlejeunea mammillosa* (Mizut.) Grolle
*Harpalejeunea minutissima* Mizut. ≡ *Microlejeunea minutissima* (Mizut.) Grolle
*Harpalejeunea riddleana* (Steph.) Mizut. = *Microlejeunea filicuspis* (Steph.) Heinrichs, Schäf.-Verw., Pócs et S.Dong
*Harpalejeunea spinosa* Mizut. ≡ *Microlejeunea spinosa* (Mizut.) Grolle
*Hattoriella subcrispa* (Herzog) Bakalin ≡ *Mesoptychia subcrispa* (Herzog) L.Söderstr. et Váňa
*Herbertus armitanus* (Steph.) H.A.Mill. = *H. sendtneri* (Nees) Lindb.
*Herbertus circinatus* (Steph.) H.A.Mill. = *H. sendtneri* (Nees) Lindb.
*Herbertus dicranus* (Taylor) Trevis. = *H. aduncus* (Dicks.) Gray
*Herbertus longispinus* J.B.Jack et Steph. = *H. aduncus* (Dicks.) Gray
*Herpetium recurvum* Mont. ≡ *Bazzania recurva* (Mont.) Trevis.
*Heteroscyphus bescherellei* (Steph.) S.Hatt. = *H. coalitus* (Hook.) Schiffn.
*Heteroscyphus communis* (Steph.) Schiffn. = *H. coalitus* (Hook.) Schiffn.
*Hygrobiella mollusca* (De Not.) Steph. ≡ *Cephalozia mollusca* (De Not.) Váňa
*Hygrobiella mollusca* f. *subintegerrima* Herzog = *Cephalozia stolonacea* (Herzog) R.M.Schust.
*Hygrolejeunea lindenbergii* (Gottsche) Steph. ≡ *Cheilolejeunea lindenbergii* (Gottsche) Mizut.
*Iwatsukia exigua* N.Kitag. = *Odontoschisma jishibae* (Steph.) L.Söderstr. et Váňa
*Jamesoniella autumnalis* (DC.) Steph. ≡ *Syzygiella autumnalis* (DC.) K.Feldberg, Váňa, Hentschel et Heinrichs
*Jamesoniella contracta* (Reinw., Blume et Nees) N.Kitag. ≡ *Syzygiella contracta* (Reinw., Blume et Nees) Gradst. et G.E.Lee (Lee and Gradstein 2021)
*Jamesoniella flexicaulis* (Nees) Schiffn. ≡ *Syzygiella flexicaulis* (Nees) Gradst. et G.E.Lee (Lee and Gradstein 2021)
*Jamesoniella flexicaulis* f. *affinis* (Schiffn.) Amakawa = *Denotarisia linguifolia* (De Not.) Grolle
*Jamesoniella flexicaulis* var. *mizutanii* Amakawa = *Syzygiella flexicaulis* (Nees) Gradst. et G.E.Lee (Lee and Gradstein 2021)
*Jamesoniella microphylla* (Gottsche, Lindenb. et Nees) Schiffn. = *Gottschelia schizopleura* (Spruce) Grolle
*Jamesoniella minutissima* Amakawa = *Andrewsianthus mizutanii* N.Kitag.
*Jamesoniella nipponica* S.Hatt. ≡ *Syzygiella nipponica* (S.Hatt.) K.Feldberg, Váňa, Hentschel et Heinrichs
*Jamesoniella ovifolia* (Schiffn.) Schiffn. = *Denotarisia linguifolia* (De Not.) Grolle
*Jamesoniella perverrucosa* Amakawa = *Syzygiella nipponica* (S.Hatt.) K.Feldberg, Váňa, Hentschel et Heinrichs
*Jamesoniella pulchra* N.Kitag. = *Denotarisia linguifolia* (De Not.) Grolle
*Jensenia zollingeri* (Gottsche) Grolle = *J. decipiens* (Mitt.) Grolle
*Jubula hutchinsiae* subsp. *javanica* (Steph.) Verd. = *J. javanica* Steph.
*Jungermannia appressifolia* Mitt. ≡ *Solenostoma appressifolium* (Mitt.) Váňa
*Jungermannia ariadne* Taylor ≡ *Solenostoma ariadne* (Taylor) Váňa et D.G.Long
*Jungermannia borneensis* Amakawa ≡ *Solenostoma borneense* (Amakawa) Váňa, Hentschel et Heinrichs

*Jungermannia comata* Nees ≡ *Solenostoma comatum* (Nees) C.Gao
*Jungermannia curvifolia* var. *borneensis* De Not. ≡ *Nowellia borneensis* (De Not.) Schiffn.
*Jungermannia decolyana* Steph. = *Solenostoma appressifolium* (Mitt.) Váňa
*Jungermannia grollei* Amakawa = *Solenostoma riclefii* Váňa et D.G.Long
*Jungermannia haskarliana* (Nees) Mitt. ≡ *Solenostoma haskarlianum* (Nees) Váňa et D.G.Long
*Jungermannia herzogiana* Váňa ≡ *Solenostoma javanicum* (Schiffn.) Steph.
*Jungermannia iwatsukii* Amakawa = *Syzygiella sonderi* (Gottsche) K.Feldberg, Váňa, Hentschel et Heinrichs
*Jungermannia kinabalensis* Amakawa = *Solenostoma appressifolium* (Mitt.) Váňa
*Jungermannia mizutanii* Amakawa = *Solenostoma stephanii* (Schiffn.) Steph.
*Jungermannia mollusca* De Not. ≡ *Cephalozia mollusca* (De Not.) Váňa
*Jungermannia piligera* Nees ≡ *Anastrophyllum piligerum* (Nees) Steph.
*Jungermannia polyrhiza* Lehm. et Lindenb. = *Solenostoma truncatum* (Nees) Váňa et D.G.Long
*Jungermannia pseudocyclops* Inoue ≡ *Solenostoma pseudocyclops* (Inoue) Váňa et D.G.Long
*Jungermannia sphaerocarpa* Hook. ≡ *Solenostoma sphaerocarpum* (Hook.) Steph.
*Jungermannia stephanii* (Schiffn.) Amakawa ≡ *Solenostoma stephanii* (Schiffn.) Steph.
*Jungermannia stricta* (Schiffn.) Steph. ≡ *Solenostoma strictum* (Schiffn.) Váňa, Hentschel et Heinrichs
*Jungermannia tetragona* Lindenb. ≡ *Solenostoma tetragonum* (Lindenb.) Váňa et D.G.Long
*Jungermannia truncata* Nees ≡ *Solenostoma truncatum* (Nees) Váňa et D.G.Long
*Jungermannia tuberculifera* (Herzog) Váňa ≡ *Solenostoma tuberculiferum* (Herzog) Váňa, Hentschel et Heinrichs
*Jungermannia virgata* (Mitt.) Steph. ≡ *Solenostoma virgatum* (Mitt.) Váňa et D.G.Long
*Lejeunea anisophylla* Mont. = *L. adpressa* Nees (Gradstein 2021)
*Lejeunea boninensis* Horik. = *L. adpressa* Nees (Gradstein 2021)
*Lejeunea borneensis* Steph. = *L. adpressa* Nees (Gradstein 2021)
*Lejeunea caespitosa* Lindenb. = *L. adpressa* Nees (Gradstein 2021)
*Lejeunea chalmersii* (Steph.) Mizut. = *L. microloba* Taylor
*Lejeunea comosa* (Lindenb.) Mitt. = *Thysananthus comosus* Lindenb.
*Lejeunea cucullata* (Reinw., Blume et Nees) Nees ≡ *Metalejeunea cucullata* (Reinw., Blume et Nees) Grolle
*Lejeunea cuculliflora* (Steph.) Mizut. = *L. umbilicata* (Nees) Nees
*Lejeunea diversitexta* (Steph.) Mizut. nom illeg. = *L. papilionacea* Prantl
*Lejeunea goebelii* Schiffn. = *Cololejeunea trichomanis* (Gottsche) Steph.
*Lejeunea herzogii* Mizut. = *L. papilionacea* Prantl
*Lejeunea imbricata* (Nees) Nees = *Cheilolejeunea trapezia* (Nees) R.M.Schust. et Kachroo
*Lejeunea infestans* (Steph.) Mizut. = *L. papilionacea* Prantl
*Lejeunea luteola* (Steph.) Mizut. nom. illeg. ≡ *L. mimula* Hürl.
*Lejeunea mitracalyx* (Eifrig) Mizut. = *L. alata* Gottsche

*Lejeunea ornata* (K.I.Goebel) Schiffn. ≡ *Colura ornata* K.I.Goebel
*Lejeunea pilifera* Tixier nom.illeg. ≡ *L. patriciae* Schäf.-Verw.
*Lejeunea pseudostipulata* Schiffn. ≡ *Cololejeunea pseudostipulata* (Schiffn.) Benedix
*Lejeunea pterota* (Herzog) Mizut. = *L. papilionacea* Prantl
*Lejeunea punctiformis* Taylor ≡ *Microlejeunea punctiformis* (Taylor) Steph.
*Lejeunea tamaspocsii* G.E.Lee = *L. pulchriflora* (Pearson) G.E.Lee, Bechteler, Pócs, Schäf.-Verw. et Heinrichs
*Lejeunea zollingeri* (Steph.) Mizut. ≡ *L. mizutanii* Grolle
*Lepicolea loriana* Steph. = *L. rara* (Steph.) Grolle
*Lepidolejeunea borneensis* (Steph.) R.M.Schust. ≡ *Mohamedia borneensis* (Steph.) R.L.Zhu et L.Shu (Zhu et al. 2019)
*Lepidozia abietinella* Herzog ≡ *Kurzia abietinella* (Herzog) Grolle
*Lepidozia cladorhiza* var. *macgregorii* (Steph.) Herzog = *L. cladorhiza* (Reinw., Blume et Nees) Nees
*Lepidozia gonyotricha* Sande Lac. ≡ *Kurzia gonyotricha* (Sande Lac.) Grolle
*Lepidozia longitudinalis* Herzog ≡ *Neolepidozia longitudinalis* (Herzog) E.D.Cooper
*Lepidozia mamillosa* Schiffn. ≡ *Neolepidozia mamillosa* (Schiffn.) E.D.Cooper
*Lepidozia neesii* Lindenb. ≡ *Tricholepidozia neesii* (Lindenb.) E.D.Cooper
*Lepidozia ophiria* Steph. ≡ *Neolepidozia ophiria* (Steph.) E.D.Cooper
*Lepidozia papulosa* Steph. ≡ *Neolepidozia papulosa* (Steph.) Fulford et J.Taylor
*Lepidozia trichocoleoides* Herzog ≡ *Tricholepidozia trichocoleoides* (Herzog) R.M.Schust.
*Lepidozia wallichiana* Gottsche ≡ *Neolepidozia wallichiana* (Gottsche) Fulford et J Taylor
*Leptolejeunea elliptica* auct. (Asian plants; non typus) = *L. subacuta* A.Evans (Bechteler et al. 2017, Shu et al. 2021)
*Leptolejeunea elliptica* subsp. *subacuta* (A.Evans) R.M.Schust. ≡ *L. subacuta* A.Evans
*Leptolejeunea picta* Herzog = *L. amphiophthalma* Zwickel
*Leptolejeunea radiata* (Mitt.) Steph. = *L. maculata* (Mitt.) Schiffn.
*Leptolejeunea schiffneri* (Schiffn.) Steph. = *L. maculata* (Mitt.) Schiffn.
*Leptolejeunea schiffneri* f. *angustifolia* Herzog = *L. maculata* (Mitt.) Schiffn.
*Leptolejeunea schiffneri* f. *latifolia* Herzog = *L. maculata* (Mitt.) Schiffn.
*Leptolejeunea schiffneri* var. *subintegerrima* Herzog = *L. maculata* (Mitt.) Schiffn.
*Leptolejeunea serrulata* Herzog = *L. tripuncta* (Mitt.) Steph. (Shu et al. 2016).
*Leptolejeunea spinistipula* (Mizut.) Xiao L.He ≡ *Soella spinistipula* (Mizut.) R.L.Zhu et L.Shu (Shu et al. 2021)
*Leucolejeunea decurrens* (Steph.) Mizut. ≡ *Cheilolejeunea mizutanii* W.Ye et R.L.Zhu
*Leucolejeunea loriana* (Steph.) Mizut. ≡ *Cheilolejeunea loriana* (Steph.) W.Ye et R.L.Zhu
*Leucolejeunea xanthocarpa* (Lehm. et Lindenb.) A.Evans ≡ *Cheilolejeunea xanthocarpa* (Lehm. et Lindenb.) Malombe
*Lobatiriccardia lobata* (Schiffn.) Furuki = *L. coronopus* (Steph.) Furuki
*Lophocolea ciliolata* (Nees) L.Söderstr. ≡ *Cryptolophocolea ciliolata* (Nees) L.Söderstr.
*Lophocolea costata* (Nees) L.Söderstr. ≡ *Cryptolophocolea costata* (Nees) L.Söderstr.
*Lophocolea massalongoana* Schiffn. ≡ *Cryptolophocolea massalongoana* (Schiffn.) L.Söderstr.

*Lopholejeunea cranstonii* Steph. = *L. eulopha* (Taylor) Schiffn.
*Lopholejeunea javanica* (Nees) Schiffn. = *L. nigricans* (Lindenb.) Schiffn.
*Lopholejeunea latialata* Mizut. = *L. zollingeri* (Steph.) Schiffn.
*Lopholejeunea nicobarica* Steph. = *L. eulopha* (Taylor) Schifnn.
*Lopholejeunea nipponica* Horik = *L. zollingeri* (Steph.) Schiffn.
*Makednothallus obtusidens* Herzog = *Jensenia decipiens* (Mitt.) Grolle
*Marsupella integra* N.Kitag. = *Gymnomitrion subintegrum* (S.W.Arnell) Váňa
*Marsupella revoluta* (Nees) Dumort. ≡ *Gymnomitrion revolutum* (Nees) H.Philib.
*Marsupella subintegra* S.W.Arnell ≡ *Gymnomitrion subintegrum* (S.W.Arnell) Váňa
*Mastigobryum bancanum* Sande Lac. ≡ *Acromastigum bancanum* (Sande Lac.) A.Evans
*Mastigobryum borneense* De Not. = *Bazzania fallax* (Sande Lac.) Schiffn.
*Mastigobryum brotheri* Steph. ≡ *Acromastigum brotheri* (Steph.) A.Evans
*Mastigobryum calcaratum* Sande Lac. ≡ *Bazzania calcarata* (Sande Lac.) Schiffn.
*Mastigobryum cincinnatum* De Not. ≡ *Bazzania cincinnata* (De Not.) Trevis.
*Mastigobryum concinnum* De Not. = *Bazzania intermedia* (Gottsche et Lindenb.) Trevis.
*Mastigobryum crenatistipulum* Steph. = *Bazzania manillana* (Steph.) Steph.
*Mastigobryum duplex* De Not. = *Bazzania involutiformis* (De Not.) Trevis.
*Mastigobryum echinatiforme* De Not. ≡ *Acromastigum echinatiforme* (De Not.) A.Evans
*Mastigobryum elegantulum* De Not. = *Acromastigum inaequilaterum* (Lehm. et Lindenb.) A.Evans
*Mastigobryum erosum* δ *pulopenangense* Lindenb. et Gottsche ≡ *Bazzania erosa* var. *pulopenangensis* (Lindenb. et Gottsche) Schiffn.
*Mastigobryum ferox* De Not. = *Bazzania harpago* (De Not.) Schiffn.
*Mastigobryum fimbriatum* Steph. ≡ *Acromastigum fimbriatum* (Steph.) A.Evans
*Mastigobryum fleischeri* Steph. ≡ *Bazzania fleischeri* (Steph.) Abeyw.
*Mastigobryum harpago* De Not. ≡ *Bazzania harpago* (De Not.) Schiffn.
*Mastigobryum inaequitextum* (Steph.) Steph. ≡ *Bazzania inaequitexta* Steph.
*Mastigobryum insigne* De Not. ≡ *Bazzania insignis* (De Not.) Trevis.
*Mastigobryum intermedium* var. *sarawakianum* De Not. ≡ *Bazzania intermedia* var. *sarawakiana* (De Not.) Schiffn.
*Mastigobryum involutiforme* De Not. ≡ *Bazzania involutiformis* (De Not.) Trevis.
*Mastigobryum linganum* De Not. ≡ *Acromastigum linganum* (De Not.) A.Evans
*Mastigobryum linguiforme* Sande Lac. ≡ *Bazzania linguiformis* (Sande Lac.) Trevis.
*Mastigobryum loricatum* (Reinw., Blume et Nees) Gottsche, Lindenb. et Nees ≡ *Bazzania loricata* (Reinw., Blume et Nees) Trevis.
*Mastigobryum lowii* Sande Lac. ex Steph. ≡ *Bazzania lowii* (Steph.) Schiffn.
*Mastigobryum malaccense* Steph. ≡ *Bazzania malaccensis* (Steph.) Tixier
*Mastigobryum muricatulum* Herzog = *Bazzania horridula* Schiffn.
*Mastigobryum natunense* Steph. = *Bazzania paradoxa* (Sande Lac.) Steph.
*Mastigobryum notarisii* (De Not.) Steph. nom. illeg. = *Acromastigum inaequilaterum* (Lehm. et Lindenb.) A.Evans
*Mastigobryum pulvinulatum* De Not. ≡ *Mastigopelma pulvinulatum* (De Not.) Grolle
*Mastigobryum recurvum* (Mont.) Lindenb. ≡ *Bazzania recurva* (Mont.) Trevis.
*Mastigobryum recurvum* var. *pallens* De Not. = *Bazzania recurva* (Mont.) Trevis.

*Mastigobryum repandistipulum* Steph. = *Bazzania tridens* (Reinw., Blume et Nees) Trevis.
*Mastigobryum subtile* Sande Lac. ≡ *Bazzania subtilis* (Sande Lac.) Trevis.
*Mastigobryum vagum* De Not. = *Bazzania erosa* (Reinw., Blume et Nees) Trevis.
*Mastigobryum vittatum* var. *luxurians* De Not. ≡ *Bazzania vittata* var. *luxurians* (De Not.) Schiffn.
*Mastigobryum zollingeri* Lindenb. ≡ *Bazzania zollingeri* (Lindenb.) Trevis.
*Mastigolejeunea atypos* Sydow = *Thysananthus repletus* (Taylor) Sukkharak et Gradst.
*Mastigolejeunea auriculata* auct. (Asian plants; non typus) = *Thysananthus humilis* (Steph.) Sukkharak et Gradst.
*Mastigolejeunea gradsteinii* Sukkharak ≡ *Thysananthus gradsteinii* (Sukkharak) Sukkharak et Gradst.
*Mastigolejeunea humilis* (Gottsche) Schiffn. ≡ *Thysananthus humilis* (Gottsche) Sukkharak et Gradst.
*Mastigolejeunea indica* Steph. ≡ *Thysananthus indicus* (Steph.) Sukkharak et Gradst.
*Mastigolejeunea ligulata* (Lehm. et Lindenb.) Schiffn. ≡ *Thysananthus ligulatus* (Lehm. et Lindenb.) Sukkharak et Gradst.
*Mastigolejeunea recondita* (Steph.) Mizut. ≡ *Thysananthus reconditus* (Steph.) Sukkharak et Gradst.
*Mastigolejeunea recurvifolia* Mizut. ≡ *Thysananthus humilis* (Gottsche) Sukkharak et Gradst.
*Mastigolejeunea repleta* (Taylor) A.Evans ≡ *Thysananthus repletus* (Taylor) Sukkharak et Gradst.
*Mastigolejeunea truncata* Mizut. ≡ *Thysananthus truncatus* (Mizut.) Sukkharak et Gradst.
*Mastigolejeunea virens* (Ångstr.) Steph. ≡ *Thysananthus virens* (Ångstr.) Sukkharak et Gradst.
*Mastigopelma bilobum* Herzog = *Mastigopelma pulvinulatum* (De Not.) Grolle
*Megaceros celebensis* Steph. = *Megaceros flagellaris* (Mitt.) Steph.
*Metahygrobiella acuminata* (Herzog) R.M.Schust. ≡ *Cephalozia acuminata* (Herzog) R.M.Schust.
*Metahygrobiella acutiloba* Inoue ≡ *Cephalozia acutiloba* Inoue
*Metahygrobiella mollusca* (De Not.) R.M.Schust. ≡ *Cephalozia mollusca* (De Not.) R.M.Schust.
*Metahygrobiella stolonacea* (Herzog) R.M.Schust. ≡ *Cephalozia stolonacea* (Herzog) R.M.Schust.
*Metzgeria borneensis* Kuwah. = *M. leptoneura* Spruce
*Metzgeria conjugata* subsp. *japonica* (S.Hatt.) Kuwah. = *M. lindbergii* Schiffn.
*Metzgeria decipiens* (C.Massal.) Schiffn. = *M. ciliata* Raddi
*Metzgeria hamata* Lindb. = *M. leptoneura* Spruce
*Metzgeria molokaiensis* Kuwah. = *M. furcata* (L.) Corda
*Metzgeria papulosa* Steph. = *M. leptoneura* Spruce
*Metzgeria pectinata* Steph. = *M. lindbergii* Schiffn.
*Metzgeria sandei* Schiffn. = *M. leptoneura* Spruce
*Metzgeria sharpii* Kuwah. = *M. leptoneura* Spruce
*Metzgeria thomeensis* Steph. = *M. leptoneura* Spruce
*Metzgeriopsis pusilla* K.I.Goebel = *Cololejeunea metzgeriopsis* (K.I.Goebel) Gradst., R.Wilson, Ilk.-Borg. et Heinrichs

*Microlejeunea cucullata* (Reinw., Blume et Nees) J.B.Jack et Steph. ≡ *Metalejeunea cucullata* (Reinw., Blume et Nees) Grolle
*Microlejeunea gracillima* (Mitt.) Steph. = *M. lunulatiloba* Horik.
*Microlejeunea sundaica* Steph. = *Metalejeunea cucullata* (Reinw., Blume et Nees) Grolle
*Neohattoria perversa* (Steph.) R.M.Schust. = *Frullania junghuhniana* var. *tenella* (Sande Lac.) Grolle et S.Hatt.
*Notoscyphus paroicus* Schiffn. = *N. lutescens* (Lehm. et Lindenb.) Mitt.
*Otolejeunea semperiana* (Steph.) Grolle ≡ *Allorgella semperiana* (Steph.) Bechteler, G.E.Lee, Schäf.-Verw. et Heinrichs
*Pallavicinia fistulosa* Steph. = *Pallavicinia ambigua* (Mitt.) Steph.
*Phaeoceros foveatus* J.Haseg. ≡ *Phaeomegaceros foveatus* (J.Haseg.) J.C.Villarreal
*Phragmicoma ligulata* (Lehm. et Lindenb.) Gottsche, Lindenb. et Nees ≡ *Thysananthus ligulatus* (Lehm. et Lindenb.) Sukkharak et Gradst.
*Phragmicoma pulopenangensis* Gottsche ≡ *Schiffneriolejeunea pulopenangensis* (Gottsche) Gradst.
*Phragmicoma tumida* (Nees) Nees et Mont. ≡ *Schiffneriolejeunea tumida* (Nees) Gradst.
*Physiotium myriangium* De Not. = *Pleurozia acinosa* (Mitt.) Trevis.
*Placolejeunea subarrhyncha* Herzog = *Cheilolejeunea trapezia* (Nees) R.M.Schust. et Kachroo
*Plagiochila accedens* Steph. = *P. korthalsiana* Molk.
*Plagiochila cameronensis* Inoue = *P. hampeana* Gottsche
*Plagiochila dendroides* (Nees) Lindenb. ≡ *Chiastocaulon dendroides* (Nees) Carl
*Plagiochila elegantissima* Herzog nom. illeg. = *P. blepharophora* (Nees) Lindenb.
*Plagiochila estipulata* Steph. = *P. blepharophora* (Nees) Lindenb.
*Plagiochila fraseri* Steph. = *P. teysmannii* Sande Lac.
*Plagiochila hottae* Inoue = *P. perserrata* Herzog
*Plagiochila infirma* (Sande Lac.) Sande Lac. = *P. javanica* (Sw.) Nees et Mont
*Plagiochila laxissima* Schiffn. = *P. bicornuta* Steph.
*Plagiochila linguifolia* De Not. ≡ *Denotarisia linguifolia* (De Not.) Grolle
*Plagiochila lobulata* Schiffn. = *P. bantamensis* (Reinw., Blume et Nees) Mont
*Plagiochila longifolia* Steph. = *P. clavatosaccata* Steph.
*Plagiochila mutabilis* De Not. = *P. bantamensis* (Reinw., Blume et Nees) Mont
*Plagiochila opposita* Dumort. ≡ *Chiastocaulon oppositum* (Reinw., Blume et Nees) S.D.F.Patzak, M.A.M Renner, Schäf.-Verw. et Heinrichs
*Plagiochila pachycephala* De Not. ≡ *Chiastocaulon pachycephalum* (De Not.) Herzog
*Plagiochila richardsii* Herzog = *P. bantamensis* (Reinw., Blume et Nees) Mont.
*Plagiochila sambusana* (Steph.) Beauverd = *P. kurzii* Steph.
*Plagiochila sandei* f. *remotidens* Herzog = *P. sandei* Dozy
*Plagiochila singularis* Schiffn. ≡ *Dinckleria singularis* (Schiffn.) M.A.M.Renner, Schäf.-Verw. et Heinrichs
*Plagiochila tridens* Steph. = *P. ungarangana* Sande Lac.
*Plagiochila tsutomui* Inoue = *P. ungarangana* Sande Lac.
*Plagiochila vanikorensis* Steph. = *P. bantamensis* (Reinw., Blume et Nees) Mont
*Plagiochilion braunianum* (Nees) S.Hatt. ≡ *Chiastocaulon braunianum* (Nees) S.D.F.Patzak, M.A.M Renner, Schäf.-Verw. et Heinrichs

*Plagiochilion oppositum* (Reinw., Blume et Nees) S.Hatt. ≡ *Chiastocaulon oppositum* (Reinw., Blume et Nees) S.D.F.Patzak, M.A.M Renner, Schäf.-Verw. et Heinrichs
*Plagiochilion pachycephalum* (De Not.) Inoue ≡ *Chiastocaulon pachycephalum* (De Not.) Herzog
*Plagiochilion theriotianum* (Steph.) Inoue ≡ *Chiastocaulon theriotianum* (Steph.) S.D.F.Patzak, M.A.M Renner, Schäf.-Verw. et Heinrichs
*Plectocolea parabolica* Herzog = *Solenostoma tetragonum* (Lindenb.) Váňa et D.G.Long
*Plectocolea truncata* (Nees) Herzog ≡ *Solenostoma truncatum* (Nees) Váňa et D.G.Long
*Pleurozia gigantea* var. *borneensis* (De Not.) Schiffn. = *P. gigantea* (F.Weber) Lindb.
*Porella acutifolia* subsp. *latior* S.Hatt. = *P. caespitans* subsp. *latior* (S.Hatt.) S.Hatt.
*Porella acutifolia* var. *elbertii* (Steph.) S.Hatt. = *P. acutifolia* (Lehm. et Lindenb.) Trevis.
*Porella acutifolia* var. *johannis-winkleri* (Herzog) S.Hatt. = *P. acutifolia* (Lehm. et Lindenb.) Trevis.
*Porella johannis-winkleri* (Herzog) S.Hatt. = *P. acutifolia* (Lehm. et Lindenb.) Trevis.
*Prionolejeunea ungulata* Herzog = *Lejeunea apiculata* Sande Lac.
*Pseudolepicolea trollii* subsp. *andoi* (R.M.Schust.) S.Hatt. et Mizut. = *P. andoi* (R.M.Schust.) S.Hatt. et Mizut.
*Ptychanthus pycnocladus* Taylor ≡ *Acrolejeunea pycnoclada* (Taylor) Schiffn.
*Ptychanthus sulcatus* (Nees) Nees ≡ *Spruceanthus sulcatus* (Nees) Gradst.
*Ptychanthus tumidus* Nees ≡ *Schiffneriolejeunea tumida* (Nees) Gradst.
*Ptychocoleus coroniformis* T.Kodama et N.Kitag. = *Acrolejeunea arcuata* (Nees) Grolle et Gradst.
*Ptychocoleus cranstonii* Steph. = *Schiffneriolejeunea pulopenangensis* (Gottsche) Gradst.
*Ptychocoleus fertilis* (Reinw., Blume et Nees) Trevis. ≡ *Acrolejeunea fertilis* (Reinw., Blume et Nees) Schiffn.
*Ptychocoleus haskarlianus* (Gottsche) Steph. = *Schiffneriolejeunea tumida* (Nees) Gradst.
*Ptychocoleus longispicus* Steph. = *Schiffneriolejeunea nymannii* (Steph.) Gradst. et Terken.
*Ptychocoleus pulopenangensis* (Gottsche) Trevis. ≡ *Schiffneriolejeunea pulopenangensis* (Gottsche) Gradst.
*Ptychocoleus pycnocladus* (Taylor) Steph. ≡ *Acrolejeunea pycnoclada* (Taylor) Schiffn.
*Ptychocoleus sarawakensis* Steph. = *Schiffneriolejeunea tumida* (Nees) Gradst.
*Ptychocoleus squarrosifolius* Steph. = *Schiffneriolejeunea tumida* (Nees) Gradst.
*Ptychocoleus tjibodensis* Verd. ≡ *Acrolejeunea tjibodensis* (Verd.) Grolle et Gradst.
*Ptychocoleus tridens* Steph. = *Schiffneriolejeunea pulopenangensis* (Gottsche) Gradst.
*Ptychocoleus wichurae* (Schiffn.) Steph. = *Acrolejeunea fertilis* (Reinw., Blume et Nees) Schiffn.
*Pycnolejeunea angulistipa* Steph. ≡ *Tuyamaella angulistipa* (Steph.) R.M.Schust. et Kachroo
*Pycnolejeunea appendiculata* Herzog = *Tuyamaella serratistipa* S.Hatt.
*Pycnolejeunea arietina* Tixier = *Cheilolejeunea ceylanica* (Gottsche) R.M.Schust. et Kachroo
*Pycnolejeunea badia* f. *parvistipa* Herzog = *Lepidolejeunea bidentula* (Steph.) R.M.Schust.
*Pycnolejeunea bancana* Steph. = *P. contigua* (Nees) Grolle

*Pycnolejeunea bidentula* Steph. ≡ *Lepidolejeunea bidentula* (Steph.) R.M.Schust.
*Pycnolejeunea borneensis* Steph. ≡ *Mohamedia borneensis* (Steph.) R.L.Zhu et L.Shu (Zhu et al. 2019).
*Pycnolejeunea ceylanica* (Gottsche) Schiffn. = *Cheilolejeunea ceylanica* (Gottsche) R.M.Schust. et Kachroo
*Pycnolejeunea corticola* Steph. = *Lepidolejeunea bidentula* (Steph.) R.M.Schust.
*Pycnolejeunea decurvifolia* (Steph.) Steph. = *Lepidolejeunea bidentula* (Steph.) R.M.Schust.
*Pycnolejeunea excisula* Steph. = *Cheilolejeunea incisa* (Gottsche) R.M.Schust.
*Pycnolejeunea flavida* (Mitt.) Steph. ≡ *Lejeunea flavida* Mitt.
*Pycnolejeunea gigantea* Steph. ≡ *Cheilolejeunea gigantea* (Steph.) R.M.Schust. et Kachroo
*Pycnolejeunea imbricata* (Nees) Schiffn. = *Cheilolejeunea trapezia* (Nees) R.M.Schust. et Kachroo
*Pycnolejeunea integristipula* J.B.Jack et Steph. ≡ *Lepidolejeunea integristipula* (J.B.Jack et Steph.) R.M.Schust.
*Pycnolejeunea kinabaluensis* T.Kodama = *P. sphaeroides* (Sande Lac.) J.B.Jack et Steph.
*Pycnolejeunea malaccensis* G.Hoffm. ≡ *Cheilolejeunea malaccensis* (G.Hoffm.) Xiao L.He
*Pycnolejeunea meyeniana* (Nees, Lindenb. et Gottsche) Steph. = *Cheilolejeunea trapezia* (Nees) R.M.Schust. et Kachroo
*Pycnolejeunea meyeniana* var. *ligulata* G.Hoffm. = *Cheilolejeunea trapezia* (Nees) R.M.Schust. et Kachroo
*Pycnolejeunea micholitzii* Steph. ≡ *Cheilolejeunea micholitzii* (Steph.) R.M.Schust. et Kachroo
*Pycnolejeunea molaris* Mizut. = *P. cavistipula* (Steph.) Mizut.
*Pycnolejeunea nicobarica* Steph. = *Lepidolejeunea bidentula* (Steph.) R.M.Schust.
*Pycnolejeunea punctata* Steph. = *Lepidolejeunea bidentula* (Steph.) R.M.Schust.
*Pycnolejeunea spinistipula* Mizut. ≡ *Soella spinistipula* (Mizut.) R.L.Zhu et L.Shu (Shu et al. 2021)
*Pycnolejeunea utriculata* Steph. ≡ *Lejeunea utriculata* (Steph.) Mizut.
*Pycnolejeunea ventricosa* (Schiffn.) P.Syd. ≡ *Cheilolejeunea ventricosa* (Schiffn.) Xiao L.He
*Radula apiculata* Steph. = *R. anceps* Sande Lac.
*Radula indica* Steph. = *R. tabularis* Steph.
*Radula laciniata* Herzog = *R. anceps* Sande Lac.
*Radula miqueliana* Taylor = *R. retroflexa* Taylor
*Radula novae-guineae* Steph. = *R. formosa* (Spreng.) Nees
*Radula retroflexa* var. *fauciloba* (Steph.) K.Yamada = *R. retroflexa* Taylor
*Radula subpallens* Steph. = *R. ventricosa* Steph.
*Radula yangii* (B.Y.Yang) K.Yamada = *R. javanica* Gottsche
*Reboulia hemisphaerica* var. *javanica* (Nees) Schiffn. = *R. hemisphaerica* subsp. *australis* R.M.Schust.
*Rhaphidolejeunea cyclops* (Sande Lac.) Herzog ≡ *Drepanolejeunea cyclops* (Sande Lac.) Grolle et R.L.Zhu
*Rhaphidolejeunea longicruris* (Steph.) Herzog ≡ *Drepanolejeunea longicruris* (Steph.) Grolle et R.L.Zhu

*Rhaphidolejeunea spicata* (Steph.) Grolle ≡ *Drepanolejeunea spicata* (Steph.) Grolle et R.L.Zhu
*Riccardia lobata* Schiffn. = *Lobatiriccardia coronopus* (Steph.) Furuki
*Riccardia lobata* f. *gigantea* Herzog nom. inval. = *Lobatiriccardia coronopus* (Steph.) Furuki
*Riccardia pinguis* (L.) Gray ≡ *Aneura pinguis* (L.) Dumort.
*Riccardia ridleyi* Schiffn. = *R. elata* (Steph.) Schiffn.
*Riccardia scabra* Schiffn. = *R. crassa* (Schwägr.) C.Massal.
*Riccardia tenuicostata* Schiffn. = *R. inconspicua* (Steph.) Reeb et Bardat
*Saccogyna muricella* (De Not.) Mitt. ≡ *Saccogynidium muricellum* (De Not.) Grolle
*Saccogyna rigidula* (Nees) Schiffn. ≡ *Saccogynidium rigidulum* (Nees) Grolle
*Saccogynidium iwatsukii* S.Hatt. ≡ *Heteroscyphus iwatsukii* (S.Hatt.) Piippo
*Saccogynidium jugatum* (Mitt.) Grolle = *S. rigidulum* (Nees) Grolle
*Scapania javanica* f. *amplifolia* Herzog nom. inval. = *S. javanica* Gottsche
*Schistochila aligeriformis* (De Not.) Schiffn. = *S. aligera* (Nees et Blume) J.B.Jack et Steph.
*Schistochila philippinensis* (Mont.) Steph. = *S. aligera* (Nees et Blume) J.B.Jack et Steph.
*Schistochila wallisii* J.B.Jack et Gottsche = *S. blumei* (Nees) Trevis.
*Schistochila wrayana* Steph. = *S. acuminata* Steph.
*Sendtnera diclados* var. *borneensis* De Not. = *Mastigophora diclados* (F.Weber) Nees
*Southbya grollei* N.Kitag. = *S. organensis* Herzog
*Sphenolobopsis kitagawae* R.M.Schust. = *Sphenolobopsis pearsonii* (Spruce) R.M.Schust.
*Spruceanthus marianus* sensu Mizut. (non typus) = *S. planiuscula* (Mitt.) X.Q.Shi, R.L.Zhu et Gradst. (Shi et al. 2015).
*Steerea clemensiana* (Verd.) S.Hatt. ≡ *Frullania clemensiana* Verd.
*Steerea mastigophoroides* S.Hatt. et Kamim. = *Frullania clemensiana* Verd.
*Stenolejeunea apiculata* (Sande Lac.) R.M.Schust. ≡ *Lejeunea apiculata* Sande Lac.
*Stenorrhipis rhizomatica* Herzog = *Kymatocalyx rhizomaticus* (Herzog) Gradst. et Váňa
*Stictolejeunea richardsii* Herzog = *S. balfourii* (Mitt.) E.W.Jones
*Strepsilejeunea occlusa* Herzog ≡ *Cheilolejeunea occlusa* (Herzog) T.Kodama et N.Kitag.
*Symphyogynopsis filicum* (Nadeaud) Grolle = *S. gottscheana* (Mont. et Nees) Grolle
*Syzygiella variegata* (Lindenb.) Spruce = *S. securifolia* (Nees) Inoue
*Taeniolejeunea peraffinis* (Schiffn.) Zwickel ≡ *Cololejeunea peraffinis* (Schiffn.) Schiffn.
*Taxilejeunea albescens* Steph. ≡ *Lejeunea albescens* (Steph.) Mizut.
*Taxilejeunea compressiuscula* Steph. ≡ *Lejeunea compressiuscula* Steph. (Lee et al. 2018)
*Taxilejeunea lumbricoides* (Nees) Steph. ≡ *Lejeunea lumbricoides* (Nees) Nees
*Taxilejeunea luteola* (Steph.) Eifrig ≡ *Lejeunea mimula* Hürl.
*Taxilejeunea patersonii* (Steph.) Eifrig = *Lejeunea leratii* (Steph.) Mizut.
*Taxilejeunea sordida* (Nees) Eifrig ≡ *Lejeunea sordida* (Nees) Nees
*Taxilejeunea umbilicata* (Nees) J.B.Jack et Steph. ≡ *Lejeunea umbilicata* (Nees) Nees
*Telaranea longitudinalis* (Herzog) R.M.Schust. ≡ *Neolepidozia longitudinalis* (Herzog) E.D.Cooper
*Telaranea neesii* (Lindenb.) Fulford ≡ *Tricholepidozia neesii* (Lindenb.) E.D.Cooper
*Telaranea octoloba* Del Ros. ≡ *Tricholepidozia octoloba* (Del Ros.) E.D.Cooper

*Telaranea ophiria* (Gottsche) J.J.Engel et G.L.Merr. ≡ *Neolepidozia ophiria* (Gottsche) E.D.Cooper
*Telaranea quadriseta* (Steph.) J.J.Engel et G.L.Merr. ≡ *Tricholepidozia quadriseta* (Steph.) E.D.Cooper
*Telaranea semperiana* (Steph.) Del Ros. ≡ *Tricholepidozia semperiana* (Steph.) E.D.Cooper
*Telaranea trichocoleoides* (Herzog) R.M.Schust. ≡ *Tricholepidozia trichocoleoides* (Herzog) R.M.Schust.
*Thysananthus borneensis* Steph. = *T. gottschei* (J.B.Jack et Steph.) Steph.
*Thysananthus fruticosus* f. *pendulus* Herzog = *T. fruticosus* (Lindenb. et Gottsche) Schiffn.
*Thysananthus laceratus* Steph. = *T. convolutus* Lindenb.
*Thysananthus minor* Verd. = *T. spathulistipus* (Reinw., Blume et Nees) Lindenb.
*Thysananthus planus* Sande Lac. = *T. retusus* (Reinw., Blume et Nees) B.M.Thiers et Gradst.
*Thysananthus richardsianus* Verd. = *T. aculeatus* Herzog
*Thysananthus spathulistipus* f. *borneensis* (Herzog) Herzog = *T. spathulistipus* (Reinw., Blume et Nees) Lindenb.
*Trichocolea merrillana* Steph. ≡ *Leiomitra merrillana* (Steph.) T.Katag.
*Trocholejeunea crassicaulis* (Steph.) Mizut. ≡ *Acrolejeunea crassicaulis* (Steph.) J.Wang bis et Gradst.
*Tylimanthus saccatus* (Hook.) Carrington et Pearson ≡ *Acrobolbus saccatus* (Hook.) Briscoe
*Xenolejeunea ceylanica* (Steph.) Tixier nom. inval. ≡ *Cheilolejeunea ceylanica* (Gottsche) R.M.Schust. et Kachroo
*Xenolejeunea falsinervis* (Sande Lac.) Tixier nom. inval. ≡ *Cheilolejeunea falsinervis* (Sande Lac.) R.M.Schust. et Kachroo
*Xenolejeunea longiloba* (Steph.) Tixier nom. inval. = *Cheilolejeunea trapezia* (Nees) R.M.Schust. et Kachroo
*Xenolejeunea meyeniana* (Steph.) Tixier nom. inval. ≡ *Cheilolejeunea trapezia* (Nees) R.M.Schust. et Kachroo
*Zoopsis argentea* (Hook.f. et Taylor) Gottsche, Lindenb. et Nees = *Z. liukiuensis* Horik.
*Zoopsis rigida* Pearson = *Z. setigera* K.I.Goebel

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RESEARCH ARTICLE

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# Molecular, chromosomal, and morphological evidence reveals a new allotetraploid fern species of *Asplenium* (Aspleniaceae) from southern Jiangxi, China

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## Abstract

*Asplenium jiulianshanense*, a new tetraploid fern species of the *A. normale* complex (Aspleniaceae) from Jiulianshan National Nature Reserve, southern Jiangxi, China is described and illustrated. We inferred the phylogenetic position of the new species based on sequences from seven plastid markers (*atpB*, *rbcL*, *rps4*, *rps4-trnS*, *trnL*, *trnL-F*, and *trnG*) and one low-copy nuclear gene, *pgiC*. The plastid phylogeny supported a close relationship among the new species *A. jiulianshanense*, *A. minutifolium*, and *A. kiangsuense*, while the nuclear phylogeny differed in topology from the plastid tree. The new species may be due to hybridization between *A. kiangsuense* and *A. boreale*. Morphologically, the new species can easily be distinguished from other members of the *A. normale* complex by rachises bearing a gemma near the apex, pinna margins entire to sparsely crenate, and (1−)3−4(−6) sori per pinna.

## Keywords

Black-stemmed spleenworts, conservation, new taxon, species complex, taxonomy

* These authors contributed equally to this work.

## Introduction

*Asplenium* L. (Aspleniaceae) is one of the largest fern genera, comprising more than 700 species (Xu et al. 2020). Hybridization and polyploidization events tend to occur in the genus and hence generate a great number of species complexes (Schneider et al. 2017; Chang et al. 2018). *Asplenium normale* D. Don and its affinities constitute a taxonomically challenging species complex in the genus (Chang et al. 2013, 2018). Species delimitation in the *A. normale* complex was poorly understood until an integrative taxonomic approach using cytological, morphological, and DNA sequence data was employed to delimit species in the complex (Chang et al. 2013, 2018; Fujiwara et al. 2017, 2020; Chang et al. 2020).

Members of the *A. normale* complex are widely distributed in south and southeast Asia, tropical east Africa, and tropical Pacific islands (Lin and Viane 2013). Previous floristic treatments tended to use a broadly defined species circumscription including a single widespread species *A. normale* (Lin and Viane 2013) and a few narrowly distributed species such as the Chinese endemic *A. kiangsuense* Ching & Y.X.Jin (Lin and Viane 2013), the Japanese endemic *A. oligophlebium* Bak. (Matsumoto et al. 2003), and the Hawaiian endemic *A. hobdyi* W.H.Wagner (Ranker et al. 2019). However, recent studies revealed that the broadly defined species circumscription overlooked some cryptic species in the complex and was inappropriate (Chang et al. 2013, 2018; Fujiwara et al. 2017). Some cryptic species and subspecies have been recognized and described consequently based on morphological, cytological, and molecular evidence in recent studies (Li et al. 2016; Chang et al. 2018, 2020; Fujiwara et al. 2020).

In 2020, we collected a peculiar specimen of the *A. normale* complex from the Jiulianshan National Nature Reserve, China. It usually has one gemma near each rachis apex, pinna margins entire to sparsely crenate, and each pinna has (1−)3−4(−6) sori (Figs 1, 2). It could not be identified and assigned to any currently recognized species in the *A. normale* complex based on its gross morphology. Our further phylogenetic analyses, however, revealed that this specimen is closely related to, but distinct from, *A. kiangsuense* (Figs 3, 4). Further examination of scale and spore morphology suggested that this entity represents a distinct species new to science. Therefore, we described and illustrated the new species of the *A. normale* complex and provided a key to all related species in the complex.

## Materials and methods

### Fieldwork and morphological study

Under the cooperative project with Jiulianshan National Nature Reserve (#202102220001), several botanical explorations were made to the Jiulianshan National Nature Reserve and extensive field investigations of the new species were conducted from 2020 to 2021 by us. The gross morphology of the new species was photographed and the quantitative characters were measured when conducting field investigations. Herbarium specimens

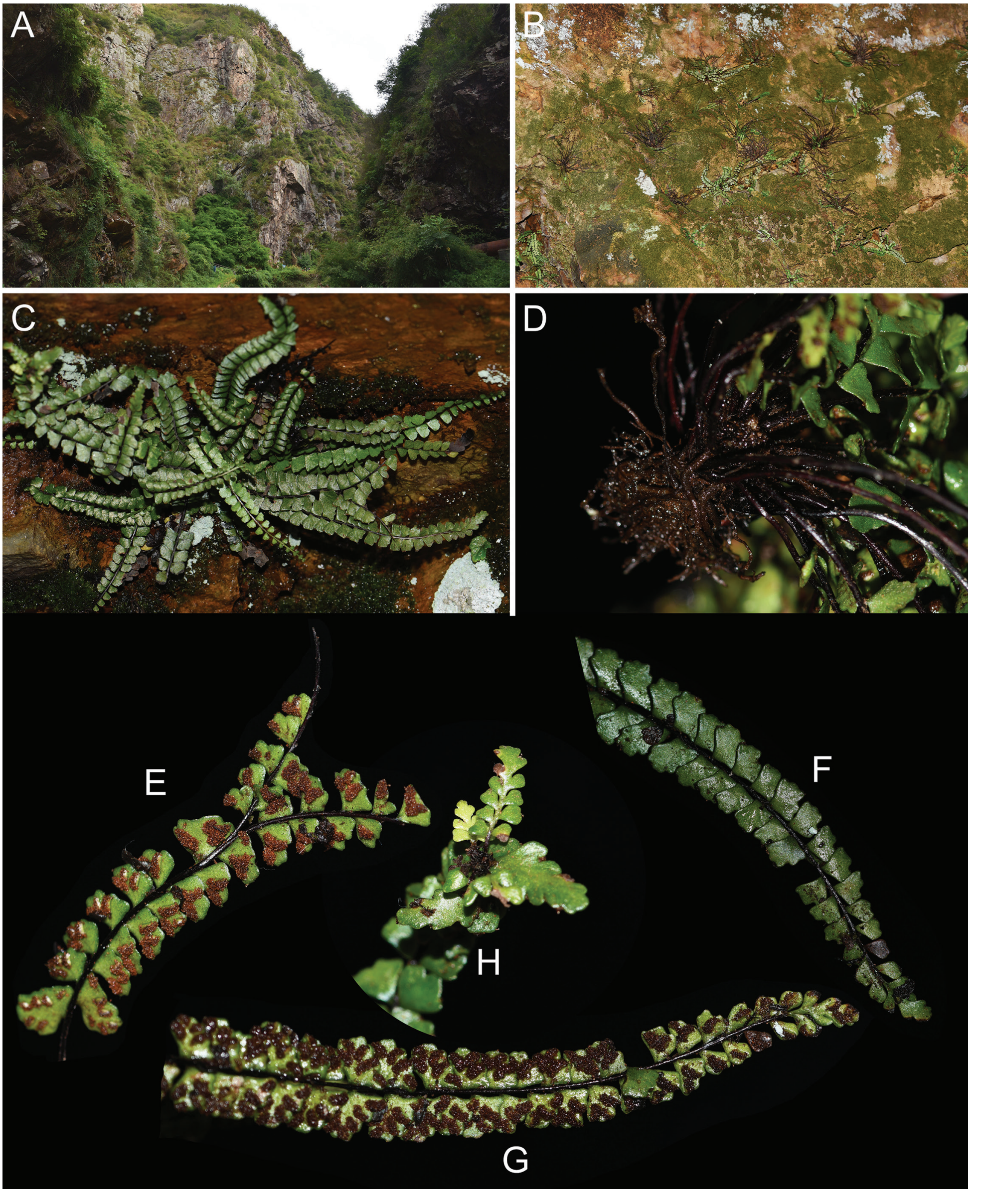


**Figure 1.** *Asplenium jiulianshanense* K.W.Xu & G.L.Xu **A, B** habitat where the new species was discovered **C** habit **D** rhizome and roots **E** irregular branch of lamina **F** adaxial view of portion of lamina **G** abaxial view of portion of fertile lamina **H** frond with a gemma at the distal end of the rachis.

were collected and deposited in the herbaria NF and SYS. Herbarium abbreviations follow Thiers (2020). A systematic examination of online digital images of the *A. normale* complex available on CVH (https://www.cvh.ac.cn/) and GBIF (https://www.gbif.org/) was carried out. Scanning Electron Microscope (SEM) was used to take spore images of the new species. Mature spores obtained from herbarium specimen were mounted on specimen tabs and then coated with platinum in a sputter coater. Observations were conducted using an ESEM-Quanta 200 (FEI, Hillsboro, Oregon, US) with 15 Kv at Nanjing Forestry University, Nanjing, China. ImageJ software (Rasband 1997–2017) was used to measure the morphological data and the SEM micrographs.

## Cytological study

The young root tips of the new species were pretreated with a mixture of 2mM 8-hydroxyquinoline solution and 0.2% colchicine solution (volume ratio = 1: 1) for 3 h and then fixed in Carnoy's solution for 5 h. The tips were then macerated in 1 N HCl at 60 °C for 10 minutes and then squashed in 2% aceto-orcein. The chromosomes of the two samples of the new species were counted and photographed using a light microscope (Olympus, Japan).

## Phylogenetic study

Phylogenetic analyses of the *A. normale* complex were performed to study the interspecific relationships among the new species and other members in the complex based on sequences of seven plastid markers (*atpB*, *rbcL*, *rps4*, *rps4-trnS*, *trnL*, *trnL-F*, and *trnG*; with *trnL* and *trnL-F* combined and *rps4* and *rps4-trnS* combined) and one low-copy nuclear gene, *pgiC*. Total genomic DNA was extracted from silica gel-dried leaves using the modified 2 ×CTAB procedure of Doyle and Doyle (1987). Primers and PCR protocols followed Chang et al. (2018) and Xu et al. (2020). For the nuclear gene *pgiC*, the purified nuclear DNA products were ligated into a pUCm-T Vector (Sangon, Shanghai, China). Ten positive clones for each individual were randomly selected for sequencing. Except for the new species, all other DNA sequences of the *A. normale* complex used in this study were downloaded from NCBI (https://www.ncbi.nlm.nih.gov/) following Chang et al. (2018) and Xu et al. (2020). Voucher information and GenBank accession numbers are provided in Suppl. material 1.

The newly generated sequences were assembled and edited using Sequencher V.4.14 (GeneCodes Corporation, Ann Arbor, Michigan). All sequences of each gene were initially aligned with MAFFT v.7 (Katoh and Standley 2013) and manually adjusted in BioEdit (Hall 1999). The aligned sequences of seven plastid genes were then concatenated using PhyloSuite (Zhang et al. 2020). Independent phylogenetic analyses of the plastid and nuclear datasets were conducted using RAxML (Stamatakis 2006) and MrBayes v. 3.2.7a (Ronquist and Huelsenbeck 2003) on the Cipres web server (Miller et al. 2010), respectively. The maximum likelihood (ML) tree searches were performed using RAxML-HPC2 on XSEDE with 1000 bootstrap replicates. The models of nucleotide substitution for the combined plastid DNA dataset (TIM2+I+G) and the nuclear *pgiC* (F81+I+G) were selected independently under the Akaike Information Criterion (AIC) using jModelTest v. 3.7 (Darriba et al. 2012). The temperature parameter of Bayesian inference (BI) set to 0.2, and other priors set to their default values. Two independent runs, each with four chains (one cold, three heated), were conducted, each beginning with a random tree and sampling one tree every 1000 generations of 10 000 000 generations. Convergence among runs and stationarity was assessed using TRACER v.1.4 (Rambaut and Drummond 2007), and the first 25% was discarded as burnin. The remaining trees were used to calculate a 50% majority-rule consensus topology and posterior probabilities (PP).

## Results

### Ploidy analyses

The spores of the new species *Asplenium jiulianshanense* were well-developed (Fig. 5A). We counted the spore number per sporangium under a light microscope and found that each sporangium contains 64 spores. Therefore, we assumed that it is sexually reproducing. Spore size is considered a good indicator of ploidy level when compared with close relatives in the *A. normale* complex (Chang et al. 2013, 2018). We measured the spore size of the new species (37−43 μm, Fig. 5) and calculated the mean spore size (39.8 μm) based on 20 mature spores using ImageJ. It has a larger spore size than most members of the complex, indicating polyploidy (Fujiwara et al. 2017; Chang et al. 2018). In addition, our cytological study confirmed that the chromosome number of the new species is $2n = 144$ (Fig. 6), which indicates that it is a tetraploid species.

### Plastid gene phylogenetic analyses

The 98 aligned plastid gene sequences are 5,583 bp in length, with 382 parsimony informative sites in total. The tree topologies by the ML and BI analyses were generally concordant when using the concatenated plastid dataset. The major clades of the phylogeny reconstructed in this study were also congruent with those of previous studies (Chang et al. 2018, 2020; Xu et al. 2020). Owing to only one gene region of *rbcL* with 525 bp being available from NCBI for *A. minutifolium* Kanem. & Tagane, four collections of the new species and one collection of *A. minutifolium* together formed a well-supported clade nested within clade III, and this well-supported clade was resolved as sister to *A. kiangsuense* (Fig. 3).

### Low-copy nuclear gene phylogenetic analyses

The nuclear dataset included 54 aligned sequences in total. The total alignment was 851 bp in length, with 98 parsimony informative sites. All the three *pgiC* alleles of the new species were nested within clade A. Within clade A, one allele of the new species was well resolved as sister to *A. kiangsuense*, while the other two alleles were closely related to some alleles of *A. boreale* (Ohwi ex Sa. Kurata) Nakaike (Fig. 4).

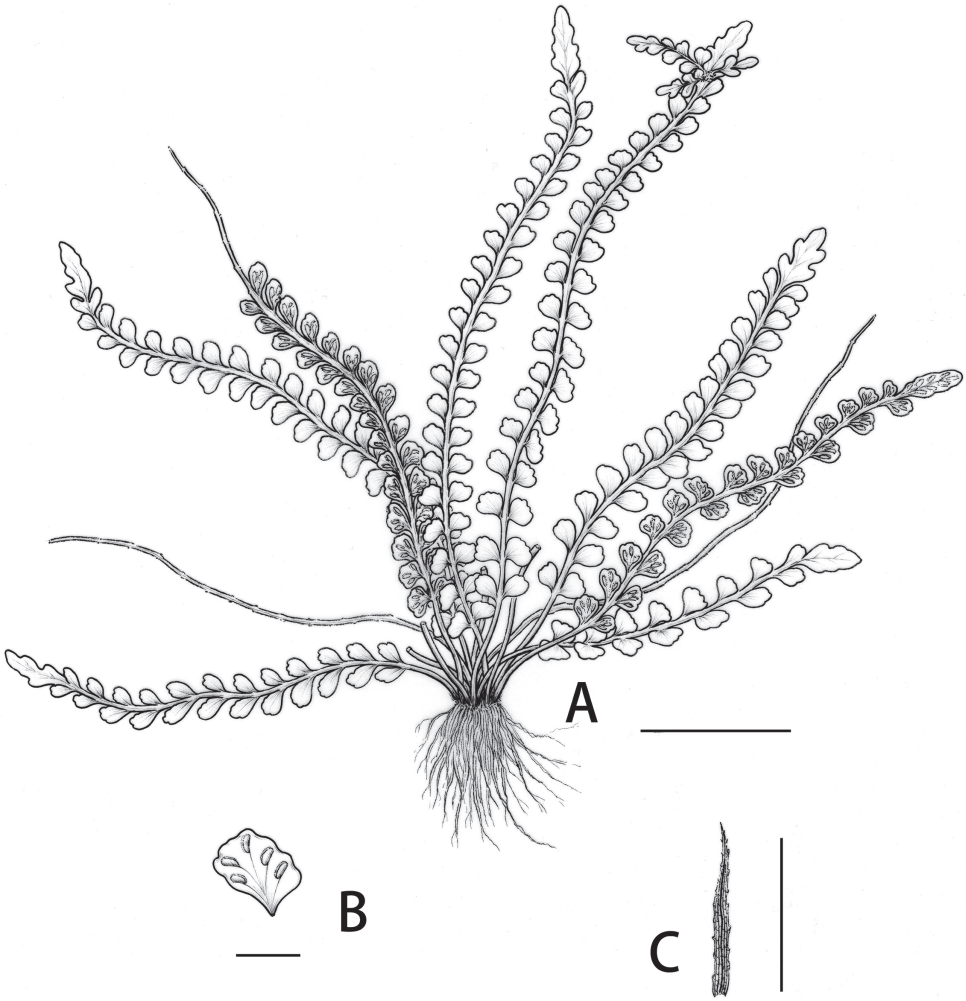


**Figure 2.** *Asplenium jiulianshanense* K.W.Xu & G.L.Xu **A** habit **B** pinna showing the venation and the distribution of sori **C** rhizome scale. Scale bars: 2 cm (**A**); 5 mm (**B**); 2 mm (**C**).

## Taxonomic treatment

***Asplenium jiulianshanense* K.W.Xu & G.L.Xu, sp. nov.**
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Figs 1, 2, 5

**Diagnosis.** *Asplenium jiulianshanense* somewhat resembles *A. kiangsuense* by its small size, rachises adaxially without a deep furrow, pinnae elliptic to trapeziform-oblong, sori 3–4 per pinna in the middle part of frond. However, the former has rachises with only one gemma near apex, pinnae (15−)20−35 pairs, pinna margins entire to sparsely crenate,

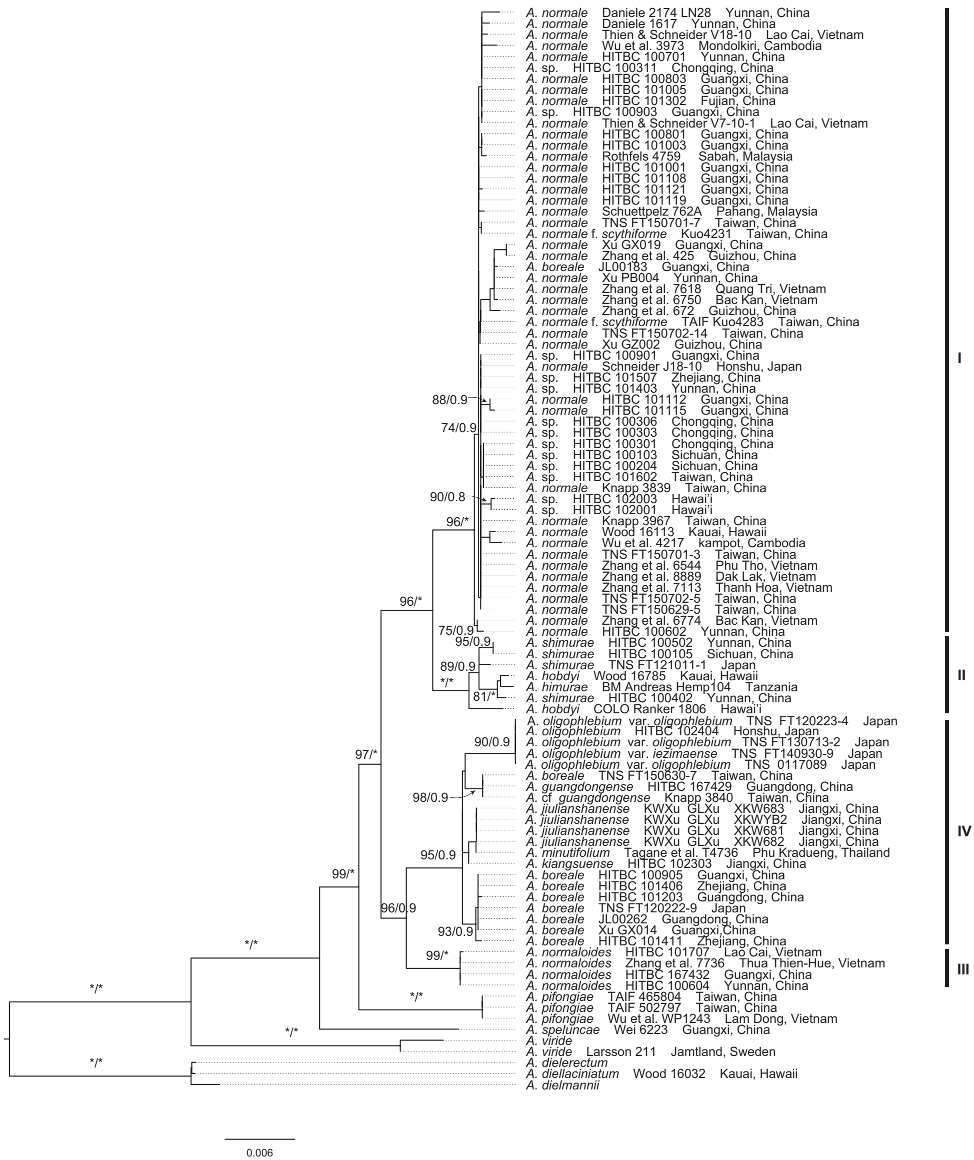


**Figure 3.** The phylogenetic position of *Asplenium jiulianshanense* K.W.Xu & G.L.Xu based on seven plastid markers (*atpB*, *rbcL*, *rps4*, *rps4-trnS*, *trnL*, *trnL-F*, and *trnG*). The numbers associated with branches are maximum likelihood bootstrap (MLBS) values followed by Bayesian inference posterior probabilities (PP). "*" indicates MLBS = 100% or PP = 1. Black vertical bars indicate those major clades identified by Chang et al. (2018).

exospore length 37–43 μm, while the latter has rachises without gemmae near the apex, pinnae 8–20(–22) pairs, pinna margins entire to sinuate, exospore length 31–36 μm.

**Type.** China. Jiangxi province, Ganzhou City, Jiulianshan National Nature Reserve, 256 m, 24°56'2.04"N, 114°49'23.44"E, 8 Jun 2021, *Guo-Liang Xu & Ke-Wang Xu XKW681* (holotype, NF!; isotype, SYS!).

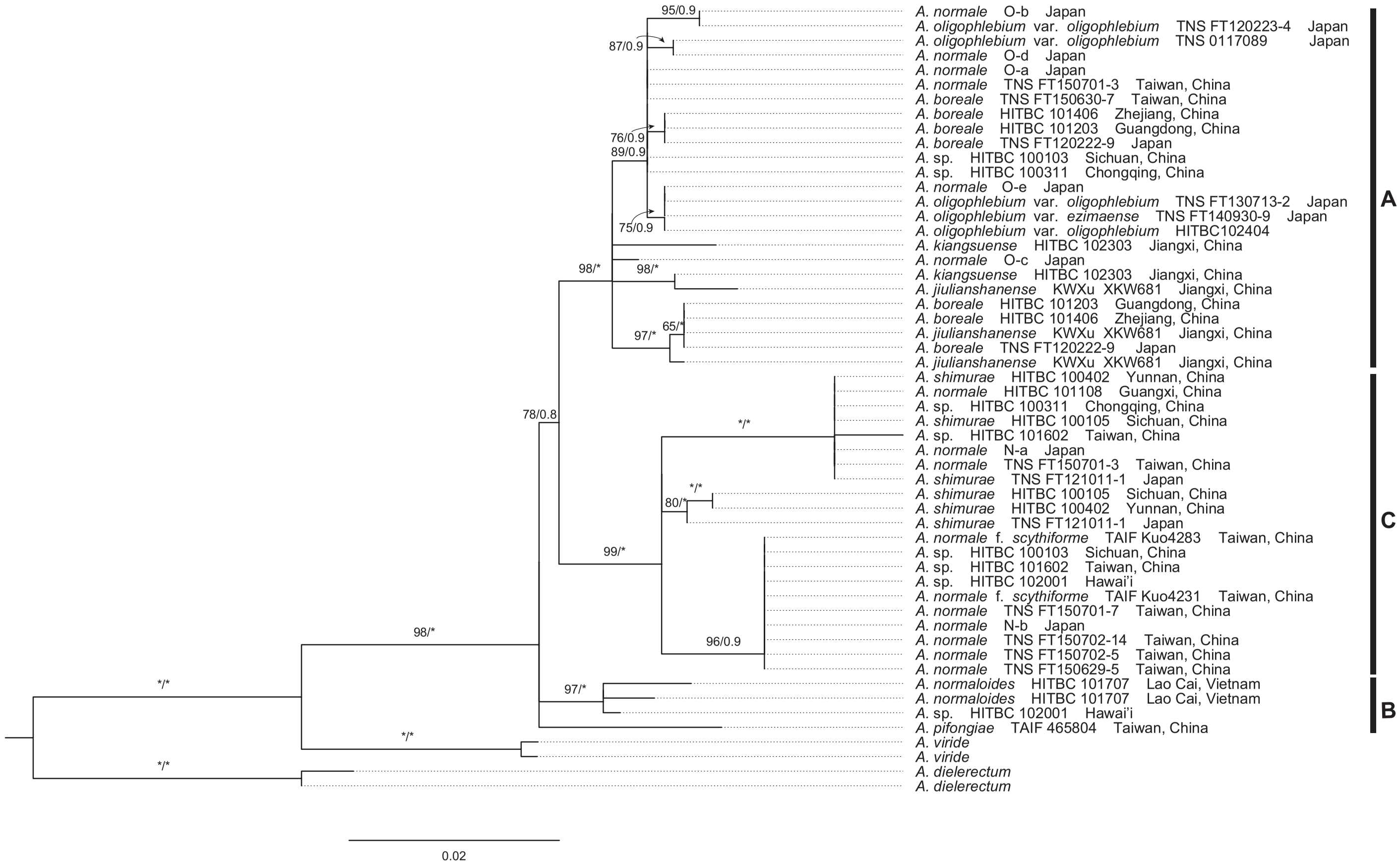


**Figure 4.** The phylogenetic position of *Asplenium jiulianshanense* K.W.Xu & G.L.Xu based on the low-copy nuclear gene *pgiC*. The numbers associated with branches are maximum likelihood bootstrap (MLBS) values followed by Bayesian inference posterior probabilities (PP). "*" indicates MLBS = 100% or PP = 1. Black vertical bars indicate those major clades identified by Chang et al. (2018).

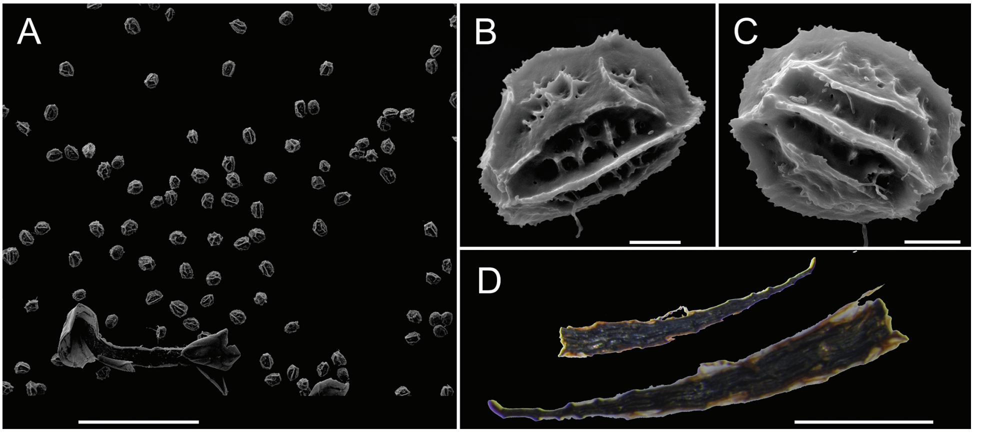


**Figure 5.** *Asplenium jiulianshanense* K.W.Xu & G.L.Xu **A–C** spore morphology of the new species **D** rhizome scale. Scale bars: 300 μm (**A**); 10 μm (**B, C**); 1 mm (**D**).

**Description.** Plants 8–15 cm tall. Rhizome erect, short, apex densely scaly; scales narrowly triangular to linear-subulate, purplish-black, 2–3 × 0.4–0.6 mm. Fronds caespitose; stipe castaneous-brown to purplish-black, shiny, terete, 1–3 cm, glabrous; lamina linear, 8–12 × ca. 1.2 cm, apex acute, 1-pinnate; pinnae (15–)20–35 pairs, lower ones subopposite, hardly reduced, middle pinnae spreading horizontally or slightly reflexed, elliptic to trapeziform-oblong, 3–6 × 3–5 mm, base asymmetrical, acroscopic side truncate and close to rachis, basiscopic side narrowly cuneate, shortly stalked to subsessile, margin entire to sparsely crenate, apex obtuse. Venation anadromously pinnate or with first basiscopic vein lacking, costa with 2 or 3 acroscopic veins, obscure, veins simple or 1-forked. Fronds papery, grayish-green when dry; rachis castaneous-brown to purplish-black, shiny, glabrous, semiterete, and adaxially flat or with 2 slightly raised lateral ridges, often gemmiferous near the apex. Sori (1–)3–4(–6) per pinna, linear-elliptic, ca. 1 mm in length, median on subtending vein; indusia grayish-green, elliptic, membranous, entire, and opening toward costa. Spores with lophate perispore, average exospore length 37–43 μm.

**Etymology.** Based on the Chinese pinyin, Jiulianshan, the name of the National Nature Reserve in southern Jiangxi, China, referring to the type locality of the species.

**Vernacular name.** 九连山铁角蕨 (jiǔ-lián-shān tiě-jiǎo-jué).

**Geographical distribution and habit.** *Asplenium jiulianshanense* is known only from a single locality in Mount Jiulianshan, Jiangxi, China, where there have been multiple collections. It was observed to grow on cliff rocks under shrubs at an elevation of ca. 200 m in subtropical evergreen broad-leaved forest.

**Conservation.** We provisionally assess *A. jiulianshanense* as Endangered based on criterion D of IUCN (2012). Only one population of the new species was found at type locality with no more than 250 mature individuals.

**Cytology.** The chromosome number of *A. jiulianshanense* is 2n = 144 (Fig. 6). The chromosome number of *A. jiulianshanense* indicates that the new species is a tetraploid species.

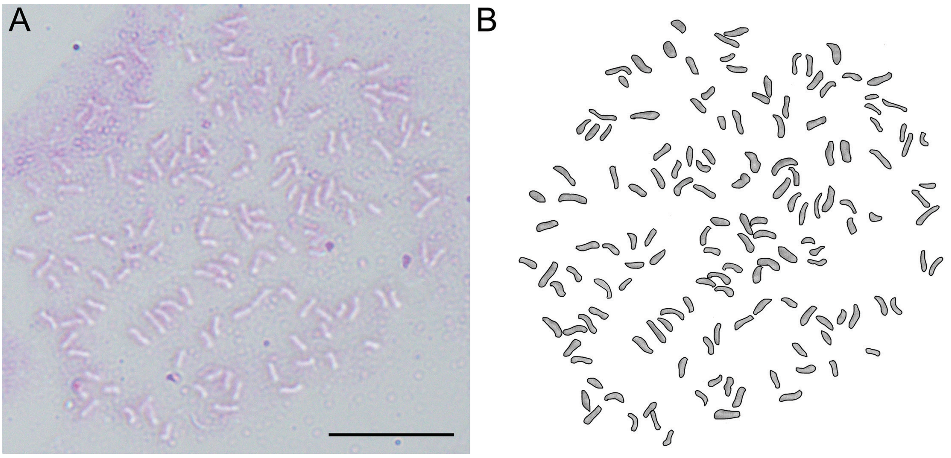


**Figure 6.** Chromosomes of *Asplenium jiulianshanense* K.W.Xu & G.L.Xu in mitotic root-tip cells, 2n = 144. Scale bars: 20 μm.

**Additional specimens examined.** China. Jiangxi province, Ganzhou City, Jiulianshan National Nature Reserve, 256 m, 24°56'2.04"N, 114°49'23.44"E, 10 Jul 2021, *Guo-Liang Xu & Ke-Wang Xu XKW685* (NF!); the same collection information, *Guo-Liang Xu & Ke-Wang Xu XKW686* (NF!).

## A key to *Asplenium jiulianshanense* and its closely related taxa revised from Chang et al. (2018)

1 Pinna dissected ........ **2**
– Pinna subentire ........ **3**
2 Pinna falcate; bud not elongated to whip-shape ... ***A. normale* f. *scythiforme***
– Pinna linear; bud elongated to whip-shape........ ***A. oligophlebium***
3 Fronds with no buds on the rachis ........ **4**
– Fronds with buds on the rachis ........ **8**
4 Rachis adaxially without a deep furrow ........ **5**
– Rachis adaxially with a deep furrow ........ **6**
5 Laminae 0.7 cm in width; rachises wingless; sori usually arranged in a row........ ***A. minutifolium***
– Laminae ca.1 cm in width; rachises with slightly raised lateral wings; sori arranged oppositely........ ***A. kiangsuense***
6 Sori less than 5 and mostly only on, and parallel to, the basiscopic side of pinnae........ ***A. pifongiae***
– Sori normally more than 5 and on both basiscopic side and acrosopic sides of pinnae........ **7**
7 Mean spore size 27–32 μm ........ ***A. guangdongense***
– Mean spore size 34–37 μm ........ ***A. boreale***

8 Frond buds at both the distal end and middle part of the rachis.................**9**
– Frond buds only at the distal end of rachis...............................................**11**
9 Mean spore size 27–32 μm ............................................***A. pseudonormale***
– Mean spore size 34–37 μm .....................................................................**10**
10 Pinna apices obtuse; acroscopic margin of pinnae deeply undulate; endemic to Hawaii .........................................................................................***A. hobdyi***
– Pinna apices acute; acroscopic margin of pinnae slightly undulate; endemic to Japan .......................................................................................***A. shimurae***
11 Plants less than 15 cm tall, sori 2–4 per pinna ...............***A. jiulianshanense***
– Plants more than 15 cm tall, sori more than 4 per pinna..........................**12**
12 Spores with highly perforate perispore; sori 10–14 per pinna; diploids only... ...........................................................................................***A. normaloides***
– Spores without perforate perispore or only slightly perforate; sori usually less than 10 per pinna; diploids or tetraploids ...............................................**13**
13 Pinnae acroscopically auriculate to hastate, margin deeply serrate; tetraploids only ....................................................................................***A. serratipinnae***
– Pinnae acroscopically truncate, margin subentire to crenate; diploids and tetraploids.........................................................................................***A. normale***

## Discussion

### Taxonomy of the *Asplenium normale* complex

The *A. normale* complex is widely distributed in south and southeast Asia, tropical east Africa, and tropical Pacific islands (Chang et al. 2013; Lin and Viane 2013). However, the species delimitation and taxonomic treatment within the complex have been controversial until an integrative taxonomic approach was employed (Wu 1999; Chang et al. 2013, 2018; Lin and Viane 2013). The treatment of one species *A. normale* with some varieties was generally accepted by former studies (Kurata 1963; Ito 1972; Wu 1999). Recent integrative taxonomic studies using cytological, morphological, and DNA sequence data revealed that recurrent reticulation events occurred among members of this species complex (Chang et al. 2013, 2018). The status of an increasing number of taxa within the species complex has been confirmed using integrative taxonomy in recent studies (Chang et al. 2013, 2018, 2020; Fujiwara et al. 2017, 2020).

Chang et al. (2018) recognized seven species (*A. boreale*, *A. guangdongense*, *A. kiangsuense*, *A. normaloides*, *A. normale*, *A. pifongiae*, *A. pseudonormale*) of the *A. normale* complex in China. Morphologically, the new species *A. jiulianshanense* collected from the Jiulianshan National Nature Reserve is most similar to *A. kiangsuense* in having plants less than 15 cm tall, rachises adaxially without a deep furrow, pinnae elliptic to trapeziform-oblong, and 3–4 sori per pinna in the middle part of frond (Fig. 1). However, the new species can be easily distinguished from *A. kiangsuense* by fronds with only one gemma at the distal end of rachis, 8–20(–22) pinnae pairs, pinna margins entire to sinuate, exospore length 37−43 μm (Fig. 1). We also checked the synonyms (e.g. *A. gulingense* Ching & S. H. Wu, *A. hangzhouense* Ching & C. F. Zhang, *A. parviusculum* Ching) related to *A. kiangsuense*. All of them lack gemmae at the distal end of rachis and those pinnae in the lower part of the frond are spreading and divaricate, while *A. jiulianshanense* usually has only one gemma at the distal end of rachis and pinnae in the lower part of the frond are spreading horizontally or reflexed. Within taxa bearing gemmae on the rachis, the gemmae of the new species only occur at the distal end of rachis, which is also different from *A. pseudonormale*. The new species can also be distinguished from *A. normaloides* and *A. normale* by having plants less than 15 cm tall (vs. more than 20 cm tall in *A. normaloides* and more than 15 cm tall in *A. normale*) and 3–4 sori per pinna in the middle part of the frond (vs. 10–14 sori per pinna in *A. normaloides* and usually more than 4 sori per pinna in *A. normale*). In addition, Kanemitsu et al. (2017) described a new species *A. minutifolium* of the *A. normale* complex from Thailand, which is also similar to *A. jiulianshanense* in morphology. However, *A. jiulianshanense* is distinct from *A. minutifolium* by usually having one gemma at the distal end of each rachis (vs. with no buds on the rachis in *A. minutifolium*), pinna margins entire to sparsely crenate (vs. pinna margins entire or slightly undulate in *A. minutifolium*), and sori arranged oppositely (vs. usually arranged in a row in *A. minutifolium*).

## Reticulate evolution in the *A. normale* complex and origin of *A. jiulianshanense*

The reticulate relationships of the *A. normale* complex have been well investigated using evidence from molecular, cytological, and morphological data (Chang et al. 2013, 2018, 2020; Fujiwara et al. 2017). Both diploids and tetraploids were confirmed to exist in the complex and multiple tetraploid species were revealed to originate via autopolyploidy and allopolyploidy (Chang et al. 2013; Fujiwara et al. 2017). For example, the allotetraploid species *A. serratipinnae* T.Fujiw. & Watano originated from their diploid parents of *A. normale* and *A. oligophlebium* (Fujiwara et al. 2017, 2020), and autotetraploid species *A. kiangsuense* and *A. boreale* Nakaike were revealed by the evidence that their two *pgiC* copies nested within the same group (Chang et al. 2013).

For the case of the new species *A. jiulianshanense*, both the spore size and the chromosome number indicate that it was a tetraploid species. The count of 64 spores per sporangium suggests that the new species has sexual reproduction. Phylogenetically, though only one gene region *rbcL* with 525 bp was available for *A. minutifolium* and all the 525 sites were identical to those of *A. jiulianshanense* and *A. kiangsuense*, *A. jiulianshanense* and *A. minutifolium* together were well resolved as a distinct clade sister to *A. kiangsuense* based on the phylogeny reconstructed using seven maternally inherited plastid genes (Fig. 3). As for the phylogeny reconstructed using the low-copy nuclear *pgiC* gene, one allele was resolved as sister to the autotetraploid species *A. kiangsuense* and the other two alleles were nested together with the autotetraploid *A. boreale* (Fig. 4). The plastid and nuclear phylogenies together suggest that the present new species is derived from hybridization between autotetraploids *A. kiangsuense* and *A. boreale*. In any case, the tetraploid taxa in the *A. normale* complex still need more study. More collections of additional species, including molecular data and chromosome counts, are still needed to analyze their phylogenetic position and better understand their pathways of reticulate evolution.

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## Supplementary material 1

**Table S1**

Authors: Chen-Xue Lin, Guo-Liang Xu, Zhi-Fang Jin, Wen-Bo Liao, Ke-Wang Xu

Data type: voucher information (excel file)

Explanation note: List of voucher specimens and Genbank accession numbers used in phylogenetic analyses.



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RESEARCH ARTICLE

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# Systematic reinstatement of the Sumatra endemic species *Mangifera sumatrana* Miq. (Anacardiaceae)

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## Abstract

*Mangifera sumatrana* Miq. is an endemic species from Sumatra. The taxonomic status of *M. sumatrana* remains unclear and is currently treated as a synonym of *M. laurina*. The present study employed morphological and palynological characters and molecular analyses to address the delimitation between the two species. Pollen observations were carried out with a Scanning Electron Microscope (SEM). Phylogenetic relationships were investigated using the ITS and the *trn*l-F intergenic spacer markers. *M. sumatrana* differs from *M. laurina* by having pyramidal panicles with a low density of pale yellow flowers pale, sepals 3–3.5 × 1.7–2 mm, fruit roundish to flattened with pale yellow pulp, a rough fibre texture, and pollen with a prolate spheroidal shape. The MP phylogenetic tree showed a divergent boundary between the two species suggesting that *M. sumatrana* could be an independent species, not a variety of *M. laurina*. The present study supports the view that these two taxa can be treated as different species.

## Keywords

Accepted name, barcoding DNA, morphology, palynology, phylogeny

## Introduction

Mango (*Mangifera* spp.) has become a major fruit crop of the tropics and subtropics, particularly in Asia. The mango has always been one of the most important fruit crops and it has been considered the 'king of fruits'. The genus *Mangifera* is one of the 73 genera belonging to the Anacardiaceae family in the order Sapindales. The latest classification of *Mangifera* by Kostermans and Bompard (1993) describes 69 species.

Morphologically, closely-related *Mangifera* are quite difficult to distinguish, leading to species complexity and misidentification. This is due to the continuity of the characters and the high morphological plasticity of *Mangifera*, as well as the diversity of species boundaries (Fitmawati and Hartana 2010). Continuity of characters or plasticity due to interspecific hybridisation is common in *Mangifera* and can occur due to a chromosomal match between *Mangifera* species, i.e. species are allotetraploids with 40 chromosomes, and these have polembrionic seeds (Litz 2004).

According to Kostermans and Bompard (1993), based on morphological characteristics, there is a species boundary between *M. laurina* Bl., *M. indica* L. and *M. lalijiwa* Kosterm., so that these three *Mangifera* species are separated, but for *M. sumatrana* Miq., which is identical to *M. laurina* Bl. and, until now, the taxonomic status of *M. sumatrana* is synonymous (POWO 2019). Before then, this species was treated as a synonym of *M. longipes* Griff. by Mukherjee (1953) and Hou (1978).

According to Konchummen (1996), *M. laurina* is a variation of *M. indica* and is a synonym of *M. indica.* Phenetic analysis, based on morphological characters, also showed that *M. sumatrana* Miq. has a close relationship with *M. indica* L. and *M. laurina* Bl (Fitmawati et al. 2013). However, based on molecular analysis using the ITS sequence by Fitmawati et al. (2016), the results identified that *M. sumatrana* Miq. did not form a clade with either *M. indica* L. or *M. laurina* Bl. *M. sumatrana* is rarely found in nature, so it is important to clarify its taxonomic status.

Differences of opinion regarding the taxonomic status of *M. sumatrana* and its relatives are caused by differences in the sources of taxonomic evidence used as the basis for compiling different classifications and the rationale for classifying these plants is also different. Therefore, a more comprehensive source of evidence is needed to strengthen the taxonomic status of *M. sumatrana* and its relatives.

Conflicts have also developed amongst taxonomists regarding the taxonomic status of the species *M. sumatrana* due to the great rarity of the species. Therefore, we propose that this species needs to be evaluated using morphological methods, palynological characteristics and molecular phylogeny to confirm the identity of *M. sumatrana*. We hope this study can provide an outstanding example for re-evaluating synonyms for *M. sumatrana.*

## Materials and methods

Fresh leaf samples of *M. sumatrana* were collected from Sumatra, Indonesia. We have been doing exploration since 2013–2017. The voucher specimens of *M. sumatrana* (sheets: HR20130073, HR20130094, HR20160096, HR20170124) were generated and deposited at the Herbarium Riauense, Indonesia.

### Morphological and palynological analysis

The morphological characters observed in this study were qualitative and quantitative characters comprising stems, leaves, fruits and seeds. Morphological comparisons were made through herbarium studies and field observations. Herbarium studies were conducted in Herbarium Riauense, ANDA, BO and Kew (https://powo.science.kew.org/). A total of 2000 *Mangifera* spp. and 30 *M. sumatrana* collections number loaned from the following herbaria were examined for morphological data. Morphological characters are referred to as descriptors of mango (International Plant Genetic Resources Institute 2006) and Kosterman and Bompard 1993). We evaluated the conservation status of species using IUCN Red List categories (IUCN 2012). Pollen observations were carried out with a Scanning Electron Microscope (SEM) and consisted of preparation, mounting, coating, photographing of pollen and data analysis. Pollen grains were prepared in glycerine jelly and measured using an eyepiece (ocular) with a scale and then the measurement results were converted into micrometre units.

### Molecular methods and phylogenetic relationship analyses

Samples used in this study represent each section of *Mangifera* species obtained from Genbank. Fresh leaves of *M. sumatrana* used in this study were collected from Sumatra. Two genera from Anacardiaceae were used as an outgroup (Table 1). The DNA was amplified in a specific target area using the internal transcribed spacer (*ITS*) and the *trn*L-F intergenic spacer (IGS) marker. DNA extraction using the CTAB method of Doyle and Doyle (1987) with modification, was undertaken by using ethanol 96% for about 24 h at 4 °C. Barcoding sequence amplification was done through the PCR technique. The genomic DNA was amplified using universal primers ITS5F (5'-GGAAGTAAAAGTCGTAACAAGG-3') and ITS4R (5'-TCCTCCGCTTATTGATATGC-3') (White et al. 1990) (for the entire ITS regions, nrDNA) and primer E (5'-GGTTCAAGTCCCTCTATCCC-3') and primer F (5'-ATTTGAACTGGTGACACGAG-3') (Small et al. 2004) (for the entire *trn*L-F intergenic spacer region, cpDNA). PCR products were sent to First Base Laboratories, Malaysia. PCR Clean-Up was then used to purify the amplified products by Gel Extraction, depending on visualisation results for Single Pass DNA Sequencing.

DNA sequences were aligned with ClustalW Multiple Alignment used Molecular Evolutionary Genetics Analysis (MEGA) software (Tamura et al. 2013; Kumar et al. 2016). Phylogenetic relationships analysis was performed using the Maximum Parsimony (MP) with the PAUP programme (Swofford 2002).

**Table 1.** Sources of Mangifera sequences and their locality.

| Species | Genbank Acc. No. | Locality | Species | Genbank Acc. No. | Locality |
|---|---|---|---|---|---|
| **ITS sequences** | | | ***trnL-F* sequences** | | |
| *M. sumatrana* Miq. | MF990366 | Indonesia | *M. sumatrana* Miq. | MF997590 | Indonesia |
| *M. indica* L. | KX347960 | Indonesia | *M. indica* L. | KY392616 | Indonesia |
| *M. zeylanica* (Bl) Hook. f. | KX347962 | Indonesia | *M. zeylanica* (Bl) Hook. f. | MF997591 | Indonesia |
| *M. laurina* Bl. | MF678498 | Indonesia | *M. laurina* Bl. | KY392609 | Indonesia |
| *M. lalijiwa* Kosterm. | MF678504 | Indonesia | *M. lalijiwa* Kosterm. | MF997587 | Indonesia |
| *M. torquenda* Kosterm. | MF990365 | Indonesia | *M. quadrifida* Jack. | KY392614 | Indonesia |
| *M. quadrifida* Jack. | MF678511 | Indonesia | *M. foetida* Lour. | MF997585 | Indonesia |
| *M. casturi* Kosterm. | MF678493 | Indonesia | *M. odorata* Griff. | MF945595 | Indonesia |
| *M. foetida* Lour. | MF678506 | Indonesia | *M. kemanga* Bl. | MF919594 | Indonesia |
| *M. odorata* Griff. | KX347957 | Indonesia | *M. andamanica* King | AB598013 | India |
| *M. kemanga* Bl. | MF990368 | Indonesia | *M. camptosperma* | AB598010 | India |
| *M. oblongifolia* Hook. f. | AB071682 | Thailand | *M. flava* Evrard. | MF945595 | India |
| *M. gedebe* Miq. | AB071681 | Thailand | *M. griffithi* Hook. f. | AB598012 | Vietnam |
| *M. macrocarpa* Bl. | AB071688 | Thailand | *M. reba* Pierre | KY067415 | Vietnam |
| *M. sylvatica* Roxb. | AB071689 | Thailand | | | |
| *M. cochinchinensis* Engler. | AB071675 | Thailand | | | |
| *M. griffithii* Hook. f. | AB071685 | Thailand | | | |
| *M. flava* Evrard. | AB071679 | Thailand | | | |
| *M. pentandra* Hooker f. | AB071684 | Thailand | | | |
| *M. pajang* Kosterm. | MF444896 | India | | | |

# Results and discussion

## Morphology

### *Mangifera sumatrana* Miq. first published in Fl. Ned. Ind. 1(2): 630 (1859)

Fig. 1

**Type.** Indonesia. Sumatra, Riau, Pekanbaru, tropical lowland, alt. 32 m, 3 October 2016, *Fitmawati 152* (holotype HR20130073!).

**Diagnosis.** *Mangifera sumatrana* has been considered as a synonym of *Mangifera laurina* Bl. The distinctive characteristics of the *M. sumatrana* are panicles pyramidal and not dense, large and flat fruit, prominent fruit beak type, a quantity of fibre in pulp and high stone. *M. laurina* panicles are conical and dense, with small and thick fruit, round in shape and fruit break type is perceptible (Figs 1, 2).

**Description.** Tree up to 40 m tall and 100–140 cm in diam., growth habit spreading, bark brownish-white with cream sap, the shoot brownish-yellow and crown semi-circular. ***Leaves*** dark green, scattered, semi-drooping on branch, chartaceous, oblong-ovate, apex acuminate, base acute, both surfaces smooth, 14.9–15.4 × 4.51–5 cm, thickness 0.12–0.2 cm, mid-rib 13.7–14.2 cm in length, above and below mid-rib prominent, nerves 21–23 pairs, areola reticulation dense, slightly prominent, two branches. Petiole 2.8–3 cm in length, 0.19–0.22 cm in diameter. ***Panicles*** terminal, semi-erect, yellowish-cream, pyramidal, 9.5–12 cm long, 14.30–15.55 g, non-glomerulate, low flower density. ***Flowers*** pale yellow with light yellow tinge, 5-merous, after anthesis, pale yellow with orangish-yellow tinge, 0.1–0.2 g, 6–6.5 × 5.5–6.2 cm. Bract yellowish-green, 5, 2.6–3.1 × 1.4–1.6 mm, broadly triangular acuminate, even and hairy, both dorsal and ventral smooth. Sepals light green, 5, 3–3.5 × 1.7–2 mm, broad ovate, acute and hairy and smooth. Petals pale yellow, 5, 5–5.4 × 2–2.3 mm, curved-reflexed outwards, elliptic, apex blunt, not hairy, ridges 5. Disc swollen, broader than ovary. Stamen fertile 1, 2.5–2.8 mm long, staminodes 4–5, filaments adnate to the base, 0.7–0.78 × 0.4–0.5 mm. Ovary rather round, lateral-frontal. Stylus slightly to the side and curved, 2–2.5 mm long. ***Fruits*** pale yellow, roundish flattened, thickness 0.2–0.3 cm, apex round, 160.41–182 g, 10.8–11.6 × 4.51–5.4 cm, 5.44–6 cm, skin surface texture smooth, non-waxy, density of lenticels on fruit skin sparse, beak pointed, sinus shallow, slope of fruit central shoulder rising and then rounded, fruit stalk insertion oblique, neck prominence absent. Pulp yellow, texture soft, adherence intermediate, quantity of fibre low, 6.13–6.4 cm long, juicy and sweet. 15.5° Brix. Stones oblong, 23.51–25 g, 8.7–9 × 4.22–4.5 cm,

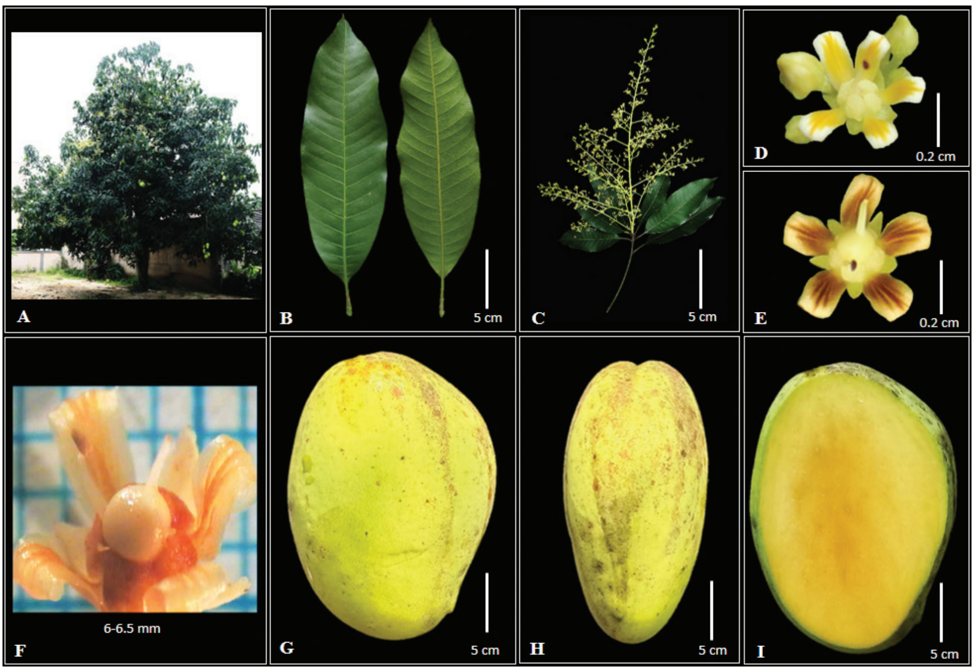


**Figure 1.** *Mangifera sumatrana* **A** habit **B** adaxial and abaxial surface of leaf **C** pyramidal panicles **D** flowers **E** flowers after anthesis; **F** ovary with swollen disc **G** roundish fruit **H** flattened fruit **I** pulp.

1.14–1.3 cm thickness, fibre texture rough, adherence of fibre to stone weak, veins on stone depressed and pattern of stone venation forked. Polyembryony, 2.22–3 g. ***Leaf anatomy*** Anomocytic stomata type. Simple epidermis. Simple palisade mesophyll. Upper mid-rib of *M. sumatrana* has convex and lower mid-rib has concave shape.

**Distribution and habitat.** *M. sumatrana* is an endemic species only found in lowland areas in Sumatra (less than 100 m a.s.l.), collected in southern Sumatra and central Sumatra, but is more commonly found in Riau Province, Sumatra, Indonesia.

**Chemotaxonomy.** In addition, several compounds from the alkaloid, alkane, amino acids, benzene, benzoic acid and fatty acyl groups are only found in *M. sumatrana* Miq. Conversely, several compounds from the phenolic group (gallic acid), amino acids, benzene and benzoic acid are only found in *M. laurina* Bl (Fitmawati et al. 2021). Therefore, it can be reported that *M. sumatrana* Miq. is not a synonym of *M. laurina* Bl and contradicts the morphological classification of Kostermans and Bompard (1993).

**Notes.** Geographically, the distribution of *M. sumatrana* and *M. laurina* is also different. *M. sumatrana* is found in lowland areas of Sumatra (less than 100 m a.s.l.), while *M. laurina* is a cosmopolitan species and is not only found in Sumatra, but also in the Maleisiana area, especially in the highlands (altitude up to 2000 m a.s.l.) (Fitmawati et al. 2013).

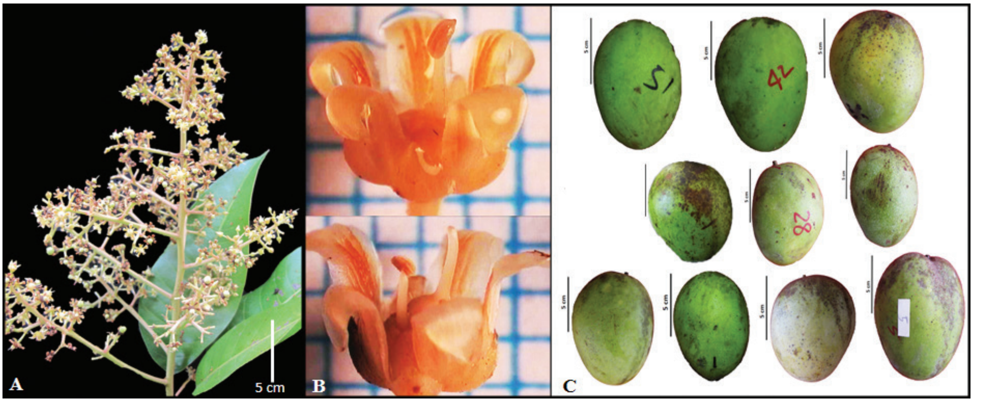


**Figure 2.** *Mangifera laurina* **A** conical panicles **B** flowers **C** roundish thick fruit.

## Palynology

Mukherjee (1953) investigated the pollen morphology of mango and 12 other *Mangifera* species. Their pollen grains were tricolpate of almost the same size. Mondal (1982), cited in Kostermans and Bompard (1993), attempted to correlate pollen morphology with taxonomic relationships of 17 *Mangifera* species, based upon different characteristics of the exine and sporoderm. They demonstrated that all of the species of section II (subgenus *Limus*) possess a coarse exine, whereas there was no clear correlation with pollen type in species within section I (subgenus *Mangifera*).

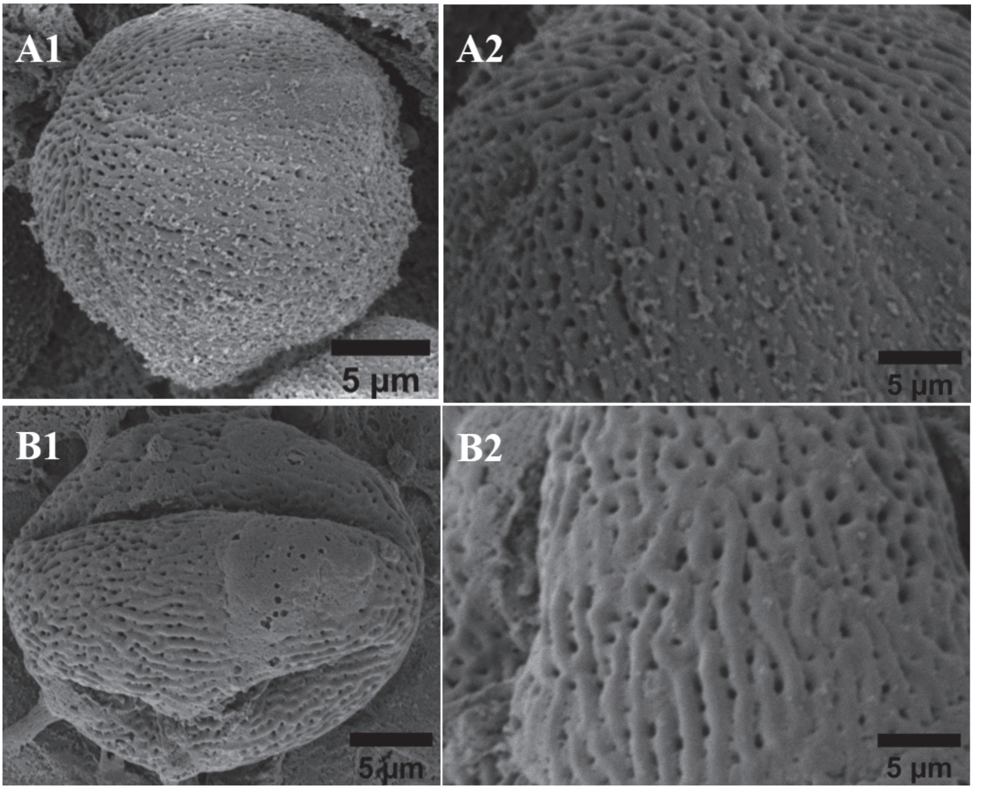


**Figure 3.** Pollen polarity and pollen aperture of the four types *Mangifera*, by electron microscope (A1–B1). Surface ornamentation of *Mangifera* pollen (A2–B2) **A** *M. sumatrana* and **B** *M. laurina*.

*Mangifera* are closely related morphologically and are quite difficult to distinguish, causing differences of opinion amongst experts regarding the taxonomic position of several *Mangifera* species. Therefore, more comprehensive and stable additional data are needed to strengthen the taxonomic status of *Mangifera*, namely using micromorphological pollen characters.

Based on the results of the study, there were five similarities in the characteristics of pollen morphology, namely pollen monad unit, angular polar view, circular/oval equatorial view, isopolar pollen polarity and tricolpate pollen aperture type, while the differences were pollen size, pollen shape and pollen ornamentation, polar diameter, equatorial length and exine thickness.

The relationship, based on a study of pollen micromorphology, shows that the pollen characteristics of *M. sumatrana* are very different from *M. indica*, while the difference between *M. sumatrana*, *M. laurina*, and *M. odorata* lies in the type of pollen ornamentation. *M. laurina* has the closest relationship with *M. odorata*. The results of this study can be a source of supporting evidence in clarifying the taxonomic status of *M. sumatrana* and showing that it differs from its relatives.

*M. sumatrana* has a striate-microreticulate ornamentation type, while *M. laurina* has a striate-reticulate ornamentation type, so that this pollen ornamentation feature can be a source of new taxonomic evidence for refuting the theory of Kostermans and Bompard (1993) which states that *M. sumatrana* is a synonym of *M. laurina*, based on morphological characteristics. This statement is also supported by research conducted by Fitmawati et al. (2018) which states that *M. laurina* and *M. sumatrana* are different and *M. laurina* is not a synonym for *M. sumatrana*, based on an analysis using ITS. This finding can be a source of supporting evidence in clarifying the taxonomic status of *M. sumatrana* and showing that it differs from its relatives (Table 2).

**Table 2.** Morphological and palynological differences between *Mangifera sumatrana* and *M. laurina*.

| Taxonomic traits | *Mangifera sumatrana* | *Mangifera laurina* |
|---|---|---|
| Panicle shape | Pyramidal | Conical |
| Panicle density | Low (14.30–15.55 g) | Medium (15.56–16.81 g) |
| Flowers' colour | Pale yellow | Yellow-orange |
| Bractea | Yellowish-green (2.6–3.1 × 1.4–1.6 mm) | Green (2–2.5 mm × 1.1–1.3 mm) |
| Sepal size | 3–3.5 × 1.7–2 mm | 1.3–1.8 mm × 0.7–1 mm |
| Fruit shape | Roundish flattened | Roundish thicked |
| Fruit stalk insertion | Oblique | Vertical |
| Fruit neck prominence | Absent | Slightly prominent |
| Pulp colour | Pale yellow | Yellow-orange |
| Fibre texture in the pulp | Rough | Soft |
| Pollen ornamentation type | Striate-microreticulate | Striate-reticulate |

## Phylogenetic relationship analysis

ITS sequences were obtained for all 24 species of *Mangifera* and two genera from Anacardiaceae were used as an outgroup. Alignment samples yielded 672 nucleotide sites distributed in the ITS region. The aligned ITS contained 452 (67.2%) conserved sites, 123 (18.3%) variable informative sites and 97 (14.5%) parsimony-informative site characters that were assumed to be informative for phylogenetic analysis using the parsimony method. The research resulted in a length of 369 steps and had a consistency index (CI) and retention index (RI) of 0.726 and 0.690, respectively (Table 3).

**Table 3.** Properties of the two candidate DNA barcoding loci in *M. sumatrana* with its relative species.

| Parameter | ITS regions | trnL-F IGS | ITS+ trnL-F IGS |
|---|---|---|---|
| Sequences length | 672 | 411 | 1582 |
| Conserved sites (%) | 67.20 | 90.75 | 89.60 |
| Variable informative sites (%) | 18.30 | 5.35 | 5.69 |
| Parsimony-informative sites (%) | 14.50 | 3.50 | 4.62 |
| Tree length | 534 | 60 | 221 |
| Consistency index (CI) | 0.72 | 0.67 | 0.91 |
| Retention index (RI) | 0.69 | 0.50 | 0.80 |

*trn*L-F IGS sequences were obtained for all 14 species of *Mangifera* and two genera from Anacardiaceae were used as an outgroup. Alignment samples yielded 411 nucleotide sites distributed in the *trn*L-F IGS. The aligned ITS contained 373 (90.75%) conserved sites, 22 (5.35%) variable informative sites and 16 (3.5%) parsimony-informative characters that were assumed to be informative for phylogenetic analysis using the parsimony method. The analysis resulted in a length of 369 steps and had a consistency index (CI) and retention index (RI) of 0.67 and 0.50, respectively.

The aligned matrix for the combined analysis comprised 1582 characters, of which 89.6% were conserved region and 4.62% parsimony informative. We found one of the most parsimonious trees with a length of 221 steps, CI of 0.91 and RI of 0.80 (Table 3). Additional analysis of genus *M. sumatrana* to its closely related species based on ITS region of nrDNA and trnL-F IGS of chloroplast DNA using MP methods showed that the cladogram was monophyletic. The strict consensus tree is reconstructed by the parsimony method shown in Fig. 4.

Maximum parsimony analysis of the branch leading to *M. sumatrana* with other *Mangifera* species provided a clear resolution. The *M. sumatrana* Miq. is a unique species found in Sumatra and was treated as a synonym of *M. laurina* Bl., based on morphological characters in the latest classification by Kostermans and Bompard (1993) and palynological characters. Based on molecular analysis, using ITS, *trn*L-F IGS sequence and a combination of both, the results can support different species based on morphological and palynological characters (Fig. 4).

The result of BLAST indicated that *Mangifera sumatrana* Miq. ITS sequences (Genbank acc. no. MF990366.1) and *trn*L-F IGS (Genbank acc. no. MF990366.1) have a high similarity to *M. indica* (Table 4). Corresponding to the tree MP, using ITS and *trn*L-F IGS sequence and data from BLAST parameters, *M. sumatrana* Miq. is not a synonym of *M. laurina* Bl (Fig. 4B).

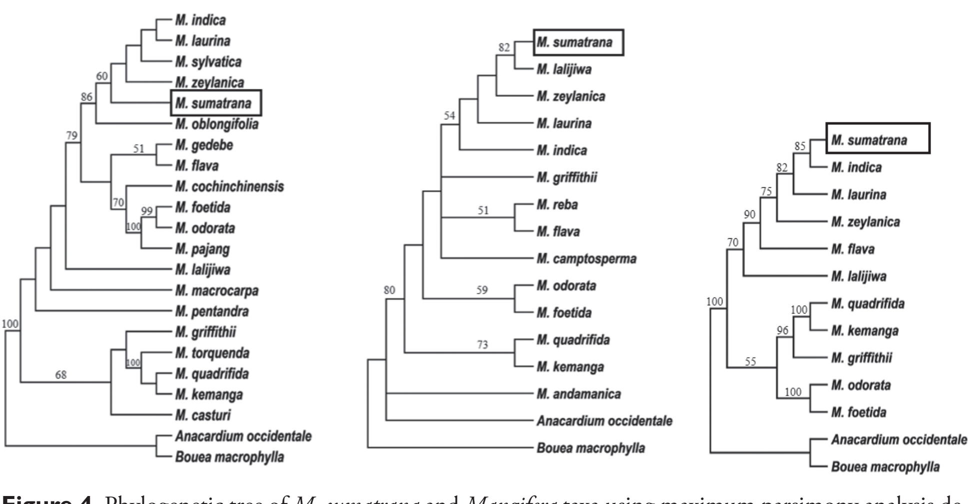


**Figure 4.** Phylogenetic tree of *M. sumatrana* and *Mangifera* taxa using maximum parsimony analysis derived from: **A** ITS sequences **B** *trn*L-F IGS **C** combination ITS+trnL-F IGS sequences. Numbers below branches showed bootstrap values.

**Table 4.** BLAST analysis of ITS and *trn*l-F IGS sequences of *Mangifera sumatrana* Miq.

| Description | Max score | Total score | Query cover (%) | Ident | Accession |
|---|---|---|---|---|---|
| *Mangifera indica* ITS1 (partial), 5.8S rRNA gene, and ITS2 partial), cultivated variety Dasheri. | 841 | 841 | 100 | 98.14 | AJ890466.1 |
| *Mangifera indica* cultivar MKR 8 internal transcribed spacer 1, partial sequence; 5.8S ribosomal RNA gene, complete sequence; and internal transcribed spacer 2, partial sequence. | 833 | 833 | 99 | 97.93 | OL960632.1 |
| *Mangifera indica* cultivar Tuong BP small subunit ribosomal RNA gene, partial sequence; internal transcribed spacer 1 and 5.8S ribosomal RNA gene, complete sequence; and internal transcribed spacer. | 830 | 830 | 100 | 97.72 | MN011941.1 |
| *Mangifera indica* cultivar Gadung internal transcribed spacer 1, partial sequence; 5.8S ribosomal RNA gene and internal transcribed spacer 2, complete sequence; and large subunit ribosomal RNA gene, partial sequence. | 830 | 830 | 98 | 98.11 | MH037250.1 |
| *Mangifera laurina* internal transcribed spacer 1, partial sequence; 5.8S ribosomal RNA gene, complete sequence; and internal transcribed spacer 2, partial sequence. | 830 | 830 | 100 | 97.72 | MF678508.1 |
| *Mangifera indica trn*L-*trn*F intergenic spacer, partial sequence; chloroplast. | 725 | 725 | 97 | 99.25 | MF997590.1 |
| *Mangifera indica* cultivar Arunika *trn*A-Leu (*trn*L) gene, partial sequence; *trn*L-*trn*F intergenic spacer, complete sequence; and *trn*A-Phe (*trn*F) gene, partial sequence; chloroplast. | 723 | 723 | 96 | 99.50 | JX185679.1 |
| *Mangifera lalijiwa trn*L-*trn*F intergenic spacer, partial sequence; chloroplast. | 684 | 684 | 91 | 99.47 | MF997587.1 |
| *Mangifera zeylanica trn*L-*trn*F intergenic spacer, partial sequence; chloroplast. | 721 | 721 | 96 | 99.50 | MF997591.1 |
| *Mangifera foetida trn*L-*trn*F intergenic spacer, partial sequence; chloroplast. | 723 | 723 | 96 | 99.50 | MF997585.1 |

Identification, using DNA barcodes, shows that *M. sumatrana* is related to *M. indica*, *M. zeylanica*, *M. laurina* and *M. lalijiwa*. Based on floral morphological characteristics, these five species of *Mangifera* are grouped with two distinguishing characteristics: panicles glomerulate (*M. indica* and *M. zeylanica*), while *M. laurina*, *M. sumatrana* and *M. lalijiwa* have non-glomerular panicles. However, *M. laurina* was very different from the distinctive features of conical panicles. Meanwhile, the distinguishing feature of *M. lalijiwa* and *M. sumatrana* species is that the crown shape distinguishes between *M. lalijiwa* and *M. sumatrana* species, which are spherical (*M. lalijiwa*) and semi-circular (*M. sumatrana*) crowns. *M. sumatrana* is different. Based on fruit morphological characteristics, *M. sumatrana* has a fruit shape that is very different from other species, namely the fruit is roundish and flattened, a distinguishing feature which is stable and genetic. The differences in *M. sumatrana* shows clearly that *M. sumatrana* is a different species, not a synonym of *M. laurina*. Hence, we propose that *M. sumatrana* is a distinct species amongst the *M. laurina* complex species.

*M. sumatrana* is a narrowly distributed species. It is only found in central Sumatra, with a population of fewer than 100 individuals. Following the Categories and Criteria of the IUCN Red List (IUCN 2012), we categorise *M. sumatrana* as critically endangered according to criteria B and D.

### Taxonomic key of *M. sumatrana* and its related species

| | | |
|---|---|---|
| 1 | Panicles glomerulate, horizontal axis | **2** |
| – | Panicles not glomerulate, semi-erect axis | **3** |
| 2 | Leaves lanceolate to oblong, fruits green, ovate-oblong | ***M. indica*** |
| – | Leaves spathulate to oblanceolate, fruits yellow orange, cordate | ***M. zeylanica*** |
| 3 | Crown shape semi-circular, leaves semi-drooping on branch, panicles terminal, greenish yellow to yellowish-cream, large up 40 cm long | **4** |
| – | Crown shape spherical, leaves semi-erect on branch panicles pseudo-terminal, light green, large up 20 cm long | ***M. lalijiwa*** |
| 4 | Panicles conical, medium densely, flowers yellow-orange small sepal 1.3–1.8 mm × 0.7–1 mm, fruit roundish thickened, pulp yellow-orange, fibre texture soft | ***M. laurina*** |
| – | Panicles pyramidal, low densely, flowers pale yellow, large sepal 3–3.5 × 1.7–2 mm, fruit roundish flattened, pulp pale yellow, fibre texture rough | ***M. sumatrana*** |

## Conclusion

*M. sumatrana* has a fruit shape that is very different from other species. Namely, the fruit is roundish and flattened, a distinguishing feature which is stable. *M. sumatrana* also has a prolate spheroidal pollen. Based on phylogenetic analysis, *M. sumatrana* is not in the same clade as *M. laurina*. The present study showed that ITS and *trn*L-F IGS DNA barcode markers in combination can be used as taxon-specific markers for *Mangifera*. The findings of this study support the view that *M. sumatrana* can be treated as a distinct species from *M. laurina.*

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RESEARCH ARTICLE

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# *Thylacopteris minuta* (Polypodiaceae), a new fern species from Myanmar

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## Abstract
The genus *Thylacopteris* is a small, phylogenetically isolated genus belonging to the fern family Polypodiaceae. This study describes a new species, *Thylacopteris minuta*, based on collections obtained during field surveys of Shan State, Myanmar. This new species is distinct from other species of *Thylacopteris* in its small size and presence of sclerenchyma strands in the rhizome. This species is also distinct from the only other species of *Thylacopteris* with molecular data available, *T. papillosa*, in a plastid *rbcL* phylogeny of Polypodiaceae. This new discovery of *Thylacopteris* from Myanmar suggests that this genus is still overlooked in Southeast Asia.

## Keywords
Myanmar, new species, Polypodiaceae, *Thylacopteris*

## Introduction

With about 1,652 species, Polypodiaceae is the second largest family of pteridophytes (ferns and lycophytes) (PPGI 2016). Species of this family share the presence of some characteristics such as yellowish or greenish spores, round or flat, yellowish-brown, exindusiate sori, and creeping rhizomes usually covered by scales (Zhang et al. 2013). Despite the progress in our understanding of the generic classification of these ferns as summarized in PPGI (2016), some issues are still unresolved. Based on recent molecular studies, Testo et al. (2019) segregated the genus *Bosmania* Testo, *Dendroconche* Copel.

and *Zealandia* Testo from the paraphyletic genus *Microsorum*. Link, and Zhao et al. (2020) expanded the definition of the genus *Lepisorus* (J.Sm.) Ching. In addition, new species are still being discovered in Polypodiaceae in recent studies (Khine et al. 2016; Zhao et al. 2017) around Southeast Asia. To improve the pteridophyte flora of Southeast Asia, collections and molecular studies of Polypodiaceae are still needed in this area. In this study, we address the relationships of *Thylacopteris* specimens obtained in Shan State, Myanmar. The genus *Thylacopteris* includes currently only two species (Rödl-Linder 1994) of which one, *Thylacopteris diaphana* (Brause) Copel., is endemic to New Guinea. The other species, *T. papillosa* (Blume) Kunze ex J.Sm, is known to occur throughout Malesia but has not been found in the north of the Isthmus of Kra (Rödl-Linder 1994).

The genus *Thylacopteris* Kunze ex J.Sm. was established by Smith (1875) with *T. papillosa* as the type species. This species was originally described as *Polypodium pillosum* Blume based on an accession collected in Java (Blume 1828). As distinct characteristics of *Thylacopteris* from *Polypodium* sensu stricto, Blume (1828) mentioned the deeply sunken sori and the articulation of the lateral segments to the rachis. Subsequently, Copeland (1947) added a second species by introducing the combination *T. diaphana* (Brause) Copel. based on *P. diaphanum* Brause, which was based on an accession collected in New Guinea (Brause 1912). Some studies pointed out the close relationships of the genus *Thylacopteris* with either *Goniophlebium* or *Polypodium* (Christensen and Holttum 1934; Ching 1978; Tryon and Tryon 1982). Subsequently, *Thylacopteris* was treated as a group of *Polypodium* (Holttum 1966; Tryon and Lugardon 1991), or of uncertain systematic position in Polypodiaceae (Hennipman et al. 1990). Finally, utilizing DNA-based phylogenetics, *Thylacopteris* was found to be sister to a clade including *Goniophlebium*, *Lepisorus*, and *Microsorum* (Schneider et al. 2004). Considering the reported results of phylogenetic studies focusing on Polypodiacae, *Thylacotperis* was included in a broadly defined Microsoroideae in PPG I (2016). Reflecting its isolated phylogenetic position, Chen et al. (2019, 2021) introduced a tribe Thylacoptereae only including *Thylacopteris*.

In the recent years, some studies have reported new species (Khine et al. 2016) or new records of ferns (Nwe et al. 2016; Khine et al. 2017; Hori et al. 2019; Khine and Schneider 2020) from Myanmar. The discovery of new species and new records reflect the lack of comprehensive fern floristic studies of Myanmar (Khine et al. 2017; Khine and Schneider 2020), which limit the ability to report and manage the conservation of Myanmar's unique biodiversity (Khine and Schneider 2020). Here, we describe a new species of the genus *Thylacopteris* from Myanmar and the first record of this genus in the country based on morphological characteristics and molecular phylogenetic analysis of Polypodiaceae.

## Materials and methods

We collected three specimens in Shan State, Myanmar during the inventories conducted under the leadership of the Makino Botanical Garden team on 13th September 2015, 16th September 2015, and 30th September 2019 together with the team from the

Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. To identify the new species *Thylacopteris minuta* sp. nov., the following characteristics were studied carefully and compared to the description and specimens of previously described species: the size and shape of plants, morphology of leaves including the shape of segments, stipe, anatomy of rhizome, scales, and the morphology of reproductive organs including sori, sporangia, and spores. Voucher specimens were deposited at the herbarium of the Kochi Prefectural Makino Botanical Garden (MBK), Xishuangbanna Tropical Botanical Garden (HITBC), Queen Sirikit Botanic Garden (QBG) and the Forest Research Institute, Myanmar (RAF). Herbarium codes follow Thiers (2021).

The plastid *rbcL* gene was employed for phylogenetic analysis. Total DNA was extracted from silica-dried leaves using cetyltrimethylammonium bromide (CTAB) solution according to the method of Doyle and Doyle (1990). PCR amplification was performed using the primers af3 and cr3 (Hori et al. 2018) and PrimeSTAR Max DNA Polymerase (Takara, Kyoto, Japan). PCR involved an initial denaturation step at 95 °C for 10 min, followed by 35 cycles of denaturation, annealing, and elongation steps at 98 °C for 10 s, 55 °C for 5 s, and 72 °C for 8 s, respectively (Model 9700 Thermal Cycler, Applied Biosystems, Foster City, CA, USA). The PCR products were purified using Illustra ExoStar 1-Step (GE Healthcare, Wisconsin, USA) and used as templates for direct sequencing. Reaction mixtures for sequencing were prepared using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA). The reaction mixtures were analyzed using an ABI 3130 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA).

To estimate the phylogenetic position of the accession of interest, plastid *rbcL* sequences of Polypodiaceae were obtained from Genbank (https://www.ncbi.nlm.nih.gov/genbank/), covering all genera accepted in PPG I (2016) as far as data availability enabled. To reflect recent progress in our understanding of the natural classification of Polypodiaceae, the treatment of some taxa deviated from PPGI by adapting new concepts (Testo et al. 2019; Zhao et al. 2020; Chen et al. 2021). In the Genbank database, some accessions contained indels, which should not be present in *rbcL* since it is a protein-coding gene; we removed such low-quality accessions. The final data set included 94 accessions of Polypodiaceae, three samples of *Thylacopteris minuta* from Myanmar, and a set of outgroup taxa including *Davallia*, *Oleandra*, *Nephrolepis* and *Tectaria* (Table 1). The *rbcL* sequences were aligned using MUSCLE (Edgar 2004) and analyzed with Bayesian inference (BI) using MrBayes 3.2.6 (Ronquist et al. 2012) and maximum likelihood (ML) using MEGA X software (Kumar et al. 2018). Based on BIC values, GTR + G + I model was selected as the best-fit model of sequence evolution for BI analysis by jModelTest 2.1.10 (Darriba et al. 2012), and Tamura 3-parameter + G + I model was selected for the ML analysis by MEGA X software. Four chains of Markov chain Monte Carlo were run simultaneously and sampled every 100 generations for 1 million generations in total. Tracer 1.7.1 (Rambaut et al. 2018) was used to examine the posterior distribution of all parameters and their associated statistics, including estimated sample sizes. The first 2,500 sample trees from each run were discarded as burn-in. In ML analysis, initial trees for the heuristic search were obtained automatically by applying the Neighbor-Join and BioNJ algorithms to a ma-

**Table 1.** Accessions of rbcL sequences in this study.

| Accessions of rbcL sequences | Species |
|---|---|
| AF468205 | *Adenophorus montanus* |
| AY529147 | *Aglaomorpha acuminata* |
| AF470349 | *Aglaomorpha coronans* |
| AY529150 | *Aglaomorpha heraclea* |
| MW138159 | *Alansmia smithii* |
| MT215977 | *Archigrammitis marquesensis* |
| JQ685380 | *Arthromeris lehmannii* |
| MG948938 | *Ascogrammitis anfractuosa* |
| EU482962 | *Bosmania membranacea* |
| MT215995 | *Calymmodon cucullatus* |
| MF318061 | *Campyloneurum brevifolium* |
| MF317971 | *Campyloneurum lorentzii* |
| MF318013 | *Campyloneurum rigidum* |
| MW138183 | *Ceradenia kalbreyeri* |
| KM218797 | *Chrysogrammitis musgraveana* |
| EF178615 | *Cochlidium serrulatum* |
| MT657584 | *Ctenopterella blechnoides* |
| KM218775 | *Dasygrammitis brevivenosa* |
| MZ957125 | *Davallia pulchra* |
| KM114198 | *Davallia solida var. fejeensis* |
| MN018180 | *Dendroconche annabellae* |
| MN018176 | *Dendroconche sayeri* |
| DQ227292 | *Dictymia brownii* |
| DQ164441 | *Dictymia mckeei* |
| MW138254 | *Enterosora trifurcata* |
| KM218794 | *Galactodenia parrisiae* |
| MN017598 | *Goniophlebium amoenum* |
| AB043100 | *Goniophlebium formosanum* |
| DQ078627 | *Goniophlebium microrhizoma* |
| AB043098 | *Goniophlebium niponicum* |
| MT657640 | *Goniophlebium percussum* |
| AB043099 | *Goniophlebium persicifolium* |
| MT657642 | *Goniophlebium subauriculatum* |
| MT216033 | *Grammitis cincta* |
| AB232409 | *Gymnogrammitis dareiformis* |
| AF470322 | *Lecanopteris carnosa* |
| AF470329 | *Lecanopteris crustacea* |
| AF470325 | *Lecanopteris luzonensis* |
| GU387043 | *Lellingeria dissimulans* |
| MT169815 | *Lepisorus carnosus* |
| MN623364 | *Lepisorus hederaceus* |
| MT169813 | *Lepisorus longifolius* |
| MT169824 | *Lepisorus normalis* |
| AY362564 | *Lepisorus nudus* |
| EU482971 | *Lepisorus superficialis* |
| GQ256304 | *Lepisorus thunbergianus* |
| GQ256310 | *Lepisorus uchiyamae* |
| MH768462 | *Leptochilus decurrens* |
| MH768470 | *Leptochilus digitatus* |
| MH768471 | *Leptochilus saxicola* |
| GU376488 | *Leucotrichum mitchellae* |
| KF992501 | *Loxogramme lanceolata* |

| Accessions of rbcL sequences | Species |
|---|---|
| DQ227294 | *Loxogramme salicifolia* |
| GU476898 | *Melpomene anazalea* |
| MW138194 | *Microgramma lycopodioides* |
| AY362579 | *Microgramma squamulosa* |
| MF317960 | *Microgramma vacciniifolia* |
| AY362344 | *Micropolypodium hyalinum* |
| LC496693 | *Microsorum cuspidatum* |
| KY099830 | *Microsorum membranifolium* |
| DQ179633 | *Microsorum scolopendria* |
| MW620392 | *Moranopteris taenifolia* |
| MT216066 | *Nephrolepis cordifolia* |
| MT216068 | *Nephrolepis hirsutula* |
| EF463254 | *Niphidium crassifolium* |
| MF317999 | *Niphidium longifolium* |
| JQ904094 | *Notogrammitis billardierei* |
| EF463242 | *Oleandra articulata* |
| AB232405 | *Oleandra pistillaris* |
| MT657589 | *Oreogrammitis forbesiana* |
| EF463255 | *Pecluma eurybasis* |
| AY362588 | *Pecluma ptilodon* |
| KT780748 | *Pecluma sicca* |
| MW138202 | *Phlebodium pseudoaureum* |
| MN623367 | *Platycerium bifurcatum* |
| AY362591 | *Pleopeltis fructuosa* |
| EF463258 | *Pleopeltis sanctae-rosae* |
| KF909057 | *Pleurosoriopsis makinoi* |
| KF909059 | *Polypodium scouleri* |
| KF186527 | *Polypodium virginianum* |
| AB044899 | *Polypodium vulgare* |
| MT657600 | *Prosaptia alata* |
| EF463259 | *Pyrrosia polydactyla* |
| AY362558 | *Pyrrosia rupestris* |
| EF463260 | *Pyrrosia serpens* |
| KM218771 | *Radiogrammitis holttumii* |
| AY096199 | *Selliguea feei* |
| AF470347 | *Selliguea hastata* |
| AY529171 | *Selliguea laciniata* |
| MW138195 | *Stenogrammitis limula* |
| DQ168808 | *Synammia intermedia* |
| KF667652 | *Tectaria griffithii* |
| EF463274 | *Tectaria trifoliata* |
| KM218802 | *Terpsichore aspleniifolia* |
| KM218758 | *Themelium decrescens* |
| LC685475 | *Thylacopteris minuta* sp.nov., Baba et al. 103191 |
| LC685476 | *Thylacopteris minuta* sp.nov., Baba et al. 103361 |
| LC685054 | *Thylacopteris minuta* sp.nov., Hori et al. 108601 |
| AY459175 | *Thylacopteris papillosa* |
| MH665089 | *Thylacopteris papillosa* |
| KM218780 | *Tomophyllum macrum* |
| MG452028 | *Zealandia powellii* |
| DQ401117 | *Zealadia pustulatum* |
| DQ179635 | *Zealandia vieillardii* |
| KM218793 | *Zygophlebia devoluta* |

trix of pairwise distances estimated using the Tamura 3-parameter model, and then selecting the topology with superior log likelihood value. A discrete Gamma distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 0.9922)). The rate variation model allowed for some sites to be evolutionarily invariable ([+I], 57.20% sites). The tree was drawn to scale, with branch lengths measured in the number of substitutions per site. The bootstrap method with 1,000 replications was employed in ML analysis.

## Results and discussions

The aligned matrix included 1209 bp of *rbcL*, of which 329 bp (27%) were parsimony-informative. The ML (the highest log likelihood = −11294.22) tree showed that the three accessions of *Thylacopteris minuta* sp.nov (Baba et al. 103191, 103361, Hori et al. 108601) comprised a clade with two accessions of *T. papillosa* (Fig. 1). The *rbcL* sequence of Myanmar accessions of *Thylacopteris* had 25 substitutions relative to *T. papillosa*. The phylogenetic placement of *T. diaphana* is unresolved because DNA sequences were not available in this study. However, at least, morphological characteristics of the new species *T. minuta* can be differentiated from those of *T. diaphana* and *T. papillosa* as described below.

### Taxonomic treatment

***Thylacopteris minuta*** **K.Hori & Khine, sp. nov.**
urn:lsid:ipni.org:names:77299336-1

**Diagnosis.** *Thylacopteris minuta* is similar to *T. papillosa* with 20–40 sclerenchyma strands per rhizome in cross-section. However, *T. minuta* is distinct from *T. papillosa* with sori shallowly sunken vs. *T. papillosa* sori deeply sunken. In addition, the lamina of *T. minuta* has a maximal length of 15 cm vs. a maximal length of 59 cm in *T. papillosa*. *Thylacopteris minuta* is distinct from the New Guinea endemic *T. diaphana*, which lacks sclerenchyma strands in the rhizome, has superficial sori, and lamina with a maximal length of 45 cm.

**Type.** Myanmar: Shan State; Ah Lel Chaung reserve forest, Ywangan Township. 20°59'44.8"N, 96°34'26.81"E, ca.1325 m, 30 Sep. 2019, K. Hori, P.K. Khine [“Kine”], T. Fujiwara, M. Nagashima, P.P. Shwe & A.K. Moe 108601 (holotype: MBK 0328421 (herbarium barcode), Figs 2–5 isotype: HITBC, RAF).

**Epilithic.** ***Rhizome*** long-creeping, weakly branched, 1.0–2.0 mm in diam. (without scales), light brown, densely clothed with scales, phyllopodia sometimes prominent, these 1.0–2.0 mm high, 5.0–10.0 mm apart; 20–40 black sclerenchyma strands in rhizome, longitudinal, scattered in the ground tissue. ***Rhizome scales*** evenly inserted, dull brown, fragile, adpressed or apically spreading, quite densely set, deciduous, deltoid or ovate, 1.0–1.5 mm long, 0.5–1.0 mm wide, gradually narrowed from base to apex, sometimes with wavy margins, apex acute or rounded. ***Cell walls of***

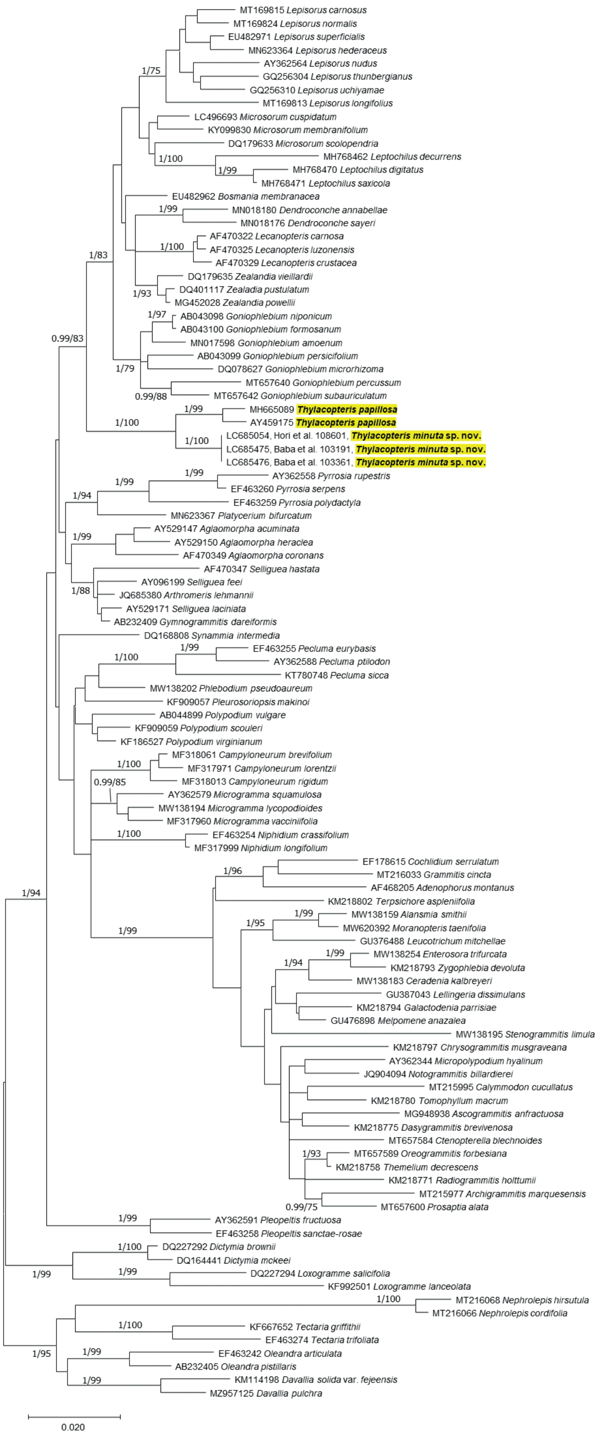


**Figure 1.** Phylogenetic hypothesis selected by applying maximum likelihood (the highest log-likelihood = −11294.22) to *rbcL* sequences. Posterior probabilities (> 0.90) and bootstrap percentages (> 70%) of Bayesian inference/maximum likelihood analyses are depicted at each node.

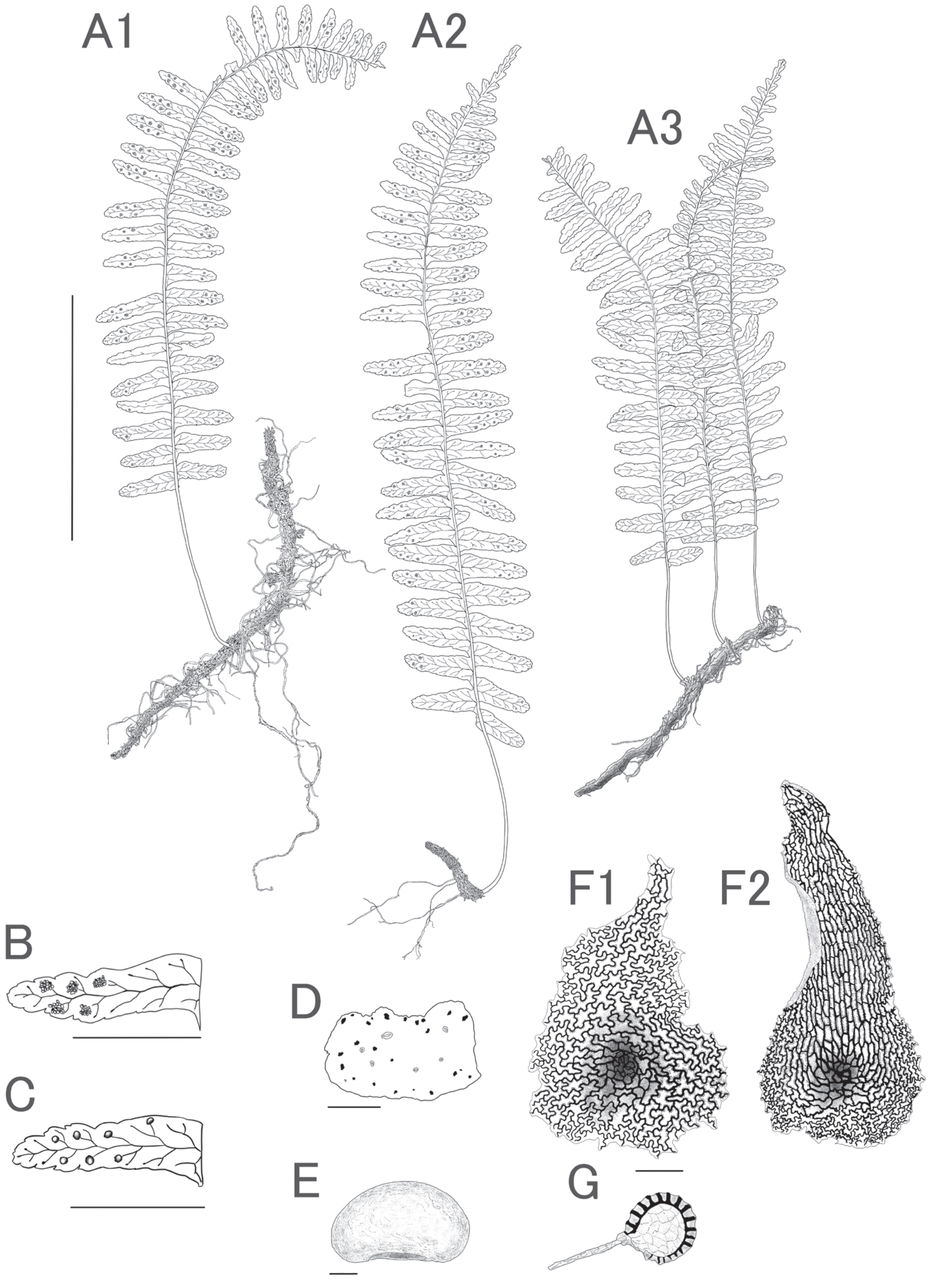


**Figure 2.** *Thylacopteris minuta* K. Hori & P.K.Khine (holotype, *Hori et al. 108601 = MBK0328421*, illustration by K.Hori) **A** habit **B** abaxial view of a middle segment **C** adaxial view of a middle segment **D** cross-section of rhizome **E** spore **F** rhizome scales **G** sporangium. Scale bars: 5 cm (**A1–A3**); 1 cm (**B–C**); 0.5 mm (**D**); 10 µm (**E**); 20 µm (**F**); 200 µm (**G**).

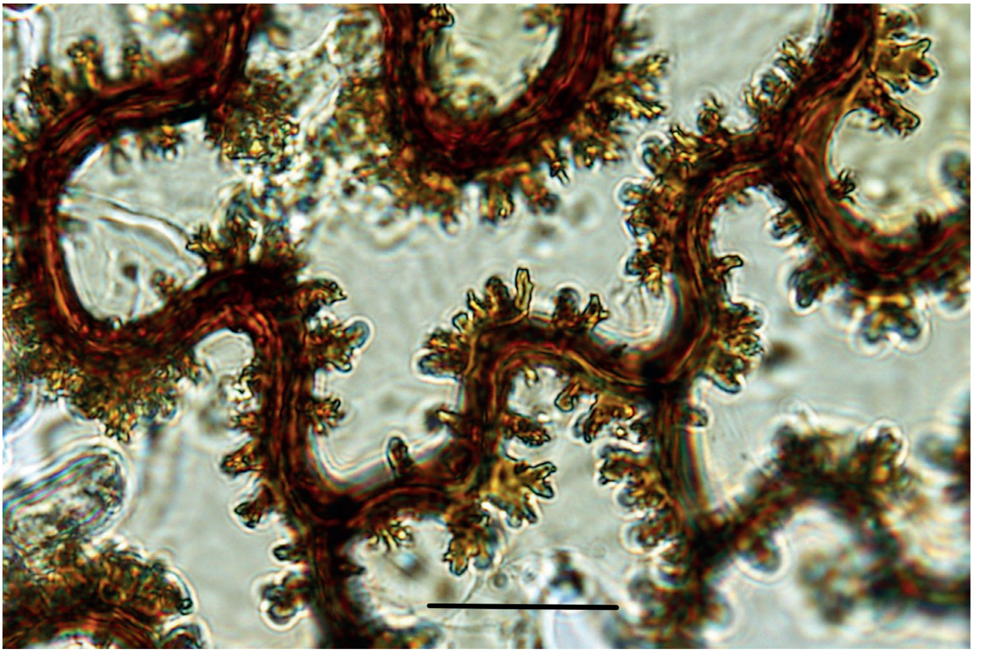

**Figure 3.** Warty, thickened cell walls of rhizome scales (*MBK 0328421*; photo taken using DP20 microscope camera, OLYMPUS, Japan). Scale bar: 2.5 µm.

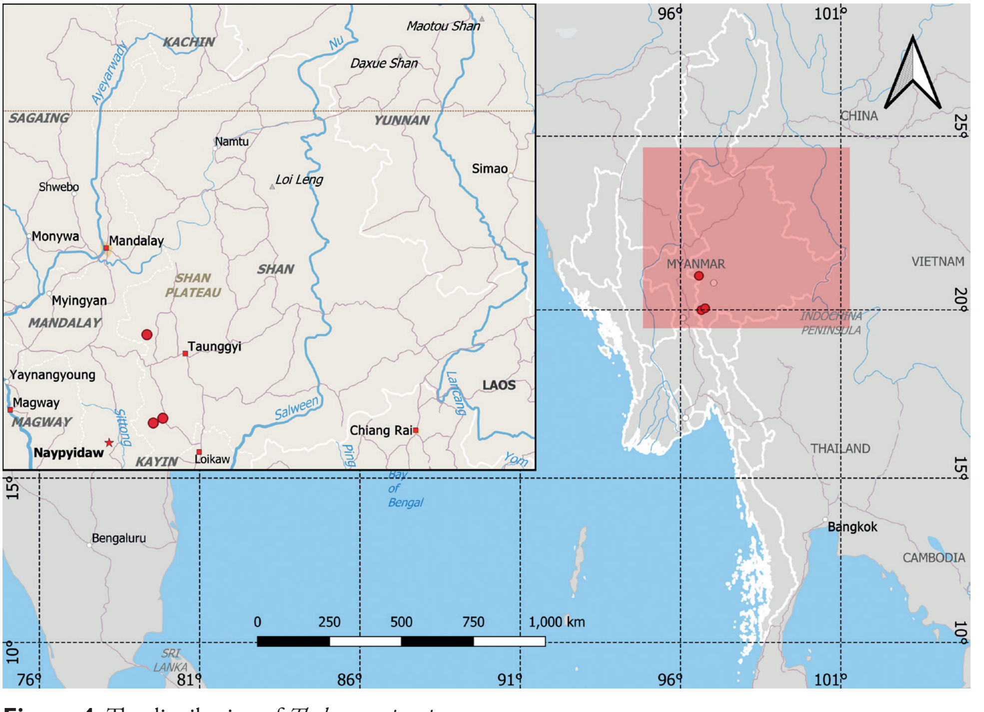


**Figure 4.** The distribution of *Thylacopteris minuta* sp.nov.

**Figure 5.** *Thylacopteris minuta* in its natural habitat (*MBK 0328421*). Scale bar: 5 cm. (Photo by P.K. Khine).

***rhizome scales*** dark brown, jigsaw-puzzle-shaped and wavy at basal and central part of scales, thickened, densely warty, in a single layer or double layers in basal scales. ***Fronds*** monomorphic, articulate to rhizome, petiolate. ***Stipes*** glabrous, 3.0–5.0 cm long, 0.7–1.0 mm diam, yellowish green. ***Blades*** membranous, lanceolate, 7.0–15.0 cm long, 2.0–4.0 cm wide, equally wide all along or rather wider above the basal part, pinnatisect, yellowish green. ***Segments*** glabrous, 20–30 pairs, lanceolate, ascending at an angle of 90°, 0.8–2.3 cm long, 0.3–0.5 cm wide, apically obtuse, entire at basal margin, crenate at apical margin, lower segments sometimes reduced, apical segments continuously reduced, terminal segments adnate or caudate. ***Veins*** free, once-forked, excurrent with terminal hydathodes. *Sori* exindusiate, uniserial on each side of costa, placed medially between costa and margin, shallowly sunken, 0.5–1.0 mm in diam., depth of papillae 0.2–0.5 mm, paraphyses absent. ***Sporangium*** globe-shaped, long stalked, 200–250 µm in diam., annulus vertical, indurated cells 10–13. ***Spores*** bilateral, oblong, light yellow, 40–60 µm long, 25–35 µm wide in lateral view, laesura 20–25 µm long, exospore smooth, perispore thin, surface shallowly wrinkled, globules absent.

**Distribution.** Myanmar.

**Habitat.** Epilithic, growing on shady surfaces of limestones (1–3 m high) in semi-evergreen or evergreen forest; altitude 940–1450 m.

**Etymology.** The name refers to the relatively small size of this species compared to other species of *Thylacopteris*.

**Additional specimens examined.** Myanmar: Shan State; Phaya Taung, Lein Le village, Paunglang Reserve Forest, Pinlaung Township; 19°59'41.0"N, 96°39'3.0"E, ca.947 m alt., 13 Sep. 2015, Y. Baba, K. Kertsawang, C. Kilgour, C. Puglisi, M. Rodda, P. Srisanga, T. Shin & P.P. Hnin 103191 (MBK0306471, duplicates on RAF, QBG). ibid., road between Nyaung Phyu village and Pinglaung village, Paunglang Reserve Forest, Pinlaung Township; 20°02'56.1"N, 96°46'00.1"E, ca.1448 m alt., 16 Sep. 2015, ibid., 103361 (MBK0313746, duplicates in RAF, QBG).

**Notes.** The genus *Thylacopteris* is sometimes confused with *Goniophlebium* and *Polypodium* (Rödl-Linder 1994; Fraser-Jenkins 2020). Warty cell walls of rhizome scales (Fig. 3) can be used to conclusively identify the genus *Thylacopteris* (Rödl-Linder 1994).

### Key to species of the genus *Thylacopteris*

| | | |
|---|---|---|
| 1 | Blades 7–15 cm long | ***T. minuta*** |
| – | Blades 30–60 cm long | **2** |
| 2 | Sori deeply sunken; sclerenchyma present in cross-section of rhizome | ***T. papillosa*** |
| – | Sori not sunken sclerenchyma; absent in cross-section of rhizome | ***T. diaphana*** |

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# *Primula xinningensis* (Primulaceae), a new species from karst caves in Hunan, China

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### Abstract

*Primula xinningensis* Wei Zhang bis & J.W.Shao, a new species from Hunan Province, China, is described. Its leaf morphology is similar to the *P. merrilliana* complex and flower morphology similar to *P. cicutariifolia*, but it can be distinguished from the former by the black pollen sac, corolla lobes apex obviously emarginate and can be differed from the latter by cotyledon triangular obovate, plants densely covered with glandular hairs and special habitat (karst caves). The whole plastid genome of this new species is 151, 601–151, 630 bp in length. Based on the whole plastid genome sequences, phylogenetic trees revealed that the new species did not genetically relate to the above two mentioned morphologically similar species, but it was closely related to *P. hubeiensis*. Currently, only three populations were discovered within a small distribution area, thus, it is preliminarily considered as Vulnerable (VU) according to criteria of the IUCN Red List.

### Keywords

Homostyly, *P. cicutariifolia*, *P. hubeiensis*, *P. merrilliana* complex, section *Ranunculoides*

## Introduction

*Primula* L. is the largest genus in Primulaceae and comprises about 500 species worldwide. The genus is mainly distributed in temperate and alpine regions of the Northern Hemisphere, with only a few species in the Southern Hemisphere, i.e. Africa, tropical Asia and South America (Richards 2002). There are approximately 300 native *Primula* species in China and the modern distribution centres of this genus are located along both sides of the Himalayas to Yunnan and western Sichuan (Hu and Kelso 1996).

The sect. *Ranunculoides* C.M.Hu is a unique group in *Primula*, characterised by pinnately compound leaves and calyx not inflated at the base (Hu 1990; Hu and Kelso 1996). This section now includes *P. ranunculoides* F.H.Chen, *P. cicutariifolia* Pax, *P. jiugongshanensis* J.W.Shao, *P. hubeiensis* X.W.Li and *P. merrilliana* complex (Shao et al. 2012; He et al. 2017; Li et al. 2018; He et al. 2021). They are all endemic to central or eastern China and often grow at the waterside or the edge of broadleaf deciduous forests between 50 and 1600 m (Shao et al. 2012; He et al. 2017; Zhang et al. 2021).

In March 2016, during our field expeditions in Shimen Village, Xinning County, Hunan Province, China, we encountered a suspicious species of sect. *Ranunculoides*. The plants were restricted to growing on the walls and ground near the entrance to karst caves and are quite different from other known related species. After careful morphological observations, together with evidence from molecular phylogenetic analyses, based on the chloroplast genome, this suspicious species was confirmed as a new species. Here, the investigation results are reported, the new species is named as *Primula xinningensis* Wei Zhang bis & J.W.Shao and is described.

## Materials and methods

### Sampling and morphological analyses

The studied specimens were collected in Shimen Village (26°30'27.22"N, 110°40'56.82"E, altitude: 468 m), Xinning County, Hunan Province, China. Voucher specimens were deposited at the Herbarium of Anhui Normal University (ANUB). The morphological description of the new species was based on examination of fresh material and herbarium specimens. A total of 10 diagnostic characteristics of the new species were identified and compared to related species in the *Primula* sect. *Ranunculoides* (Shao et al. 2012; He et al. 2017; Li et al. 2018; He et al. 2021).

### Genome sequencing, assembly and annotation

Genomic DNA was extracted from dried leaves using a modified CTAB protocol (Doyle and Doyle 1987). The quality and concentration of DNA products were assessed via agarose gel electrophoresis and spectrophotometry and the qualified DNA sample was sent to BGI-Shenzhen (Shenzhen, China) for library construction and next-generation sequencing. Finally, we obtained ca. 2 Gb of high-quality clean data, the complete chloroplast genome was assembled using GetOrganelle described in Jin et al. (2019) and the annotation was conducted with Plastid Genome Annotator (Qu et al. 2019), coupled with manual correction using Geneious v. 9.1.4 (Kearse et al. 2012). The plastome of *P. hubeiensis* (Genbank accession number: MT268976) was used as the reference genomes for annotation. The cp genome maps were drawn using OGDRAW (Greiner et al. 2019). All sequences generated in this study were submitted to the NCBI database, the accession numbers are ON208991 (*P. xinningensis*), ON208990 (*P. xinningensis*) and ON221323 (*P. hubeiensis*), respectively.

### Phylogenetic analyses

In order to determine the phylogenetic relationship of the new species, we downloaded 28 accessions cp genome sequences of *primula* from the NCBI (Fig. 2). All sequences were aligned with MAFFT v.7 (Katoh and Standley 2013) using the default settings and adjusted manually where necessary using MEGA 7.0.14 (Kumar et al. 2016). Phylogenetic analyses were conducted using Maximum Likelihood (ML) and Bayesian Inference (BI) methods with *Androsace paxiana* and *Lysimachia congestiflora* as outgroups (Xu et al. 2020). The ML analysis was conducted using RAxML-HPC BlackBox v.8.1.24 at the CIPRES Science Gateway website (Miller et al. 2010; Stamatakis 2014) with 1000 bootstrap replicates, the (GTR) + G + I model being used in ML analyses. For the BI analysis, the best substitution model was determined according to Bayesian Information Criterion (BIC) with ModelFinder (Kalyaanamoorthy et al. 2017). The BI analysis was performed using MrBayes v.3.2 (Ronquist et al. 2012). The Markov Chain Monte Carlo (MCMC) algorithm was run for 10 million generations and the trees were sampled every 1000 generations. Convergence was determined by examining the average standard deviation of the split frequencies (< 0.01). The first 25% of the trees were discarded as burn-in and the remaining trees were used to generate the consensus tree.

## Results

### Characteristics of the complete plastid genome

The length of complete plastid genome of *P. xinningensis* comprised 151,601–151,630 bp (Fig. 1). It possessed typical quadripartite structure: IRa, IRb, LSC and SSC; the characteristics and statistics of the plastid genome are summarised in Table 1.

**Table 1.** Basic characteristics of cp genomes of *Primula xinningensis* sp. nov.

| Characteristic | *Primula xinningensis* |
|---|---|
| Total length (bp) | 151,601–151,630 |
| GC% | 36.8%–36.8% |
| LSC length (bp) | 83,421–83,466 |
| SSC length (bp) | 17,583–17,599 |
| IR length (bp) | 25,292 |
| Total genes | 113 |
| Protein-coding genes | 80 |
| rRNA genes | 4 |
| tRNA genes | 29 |

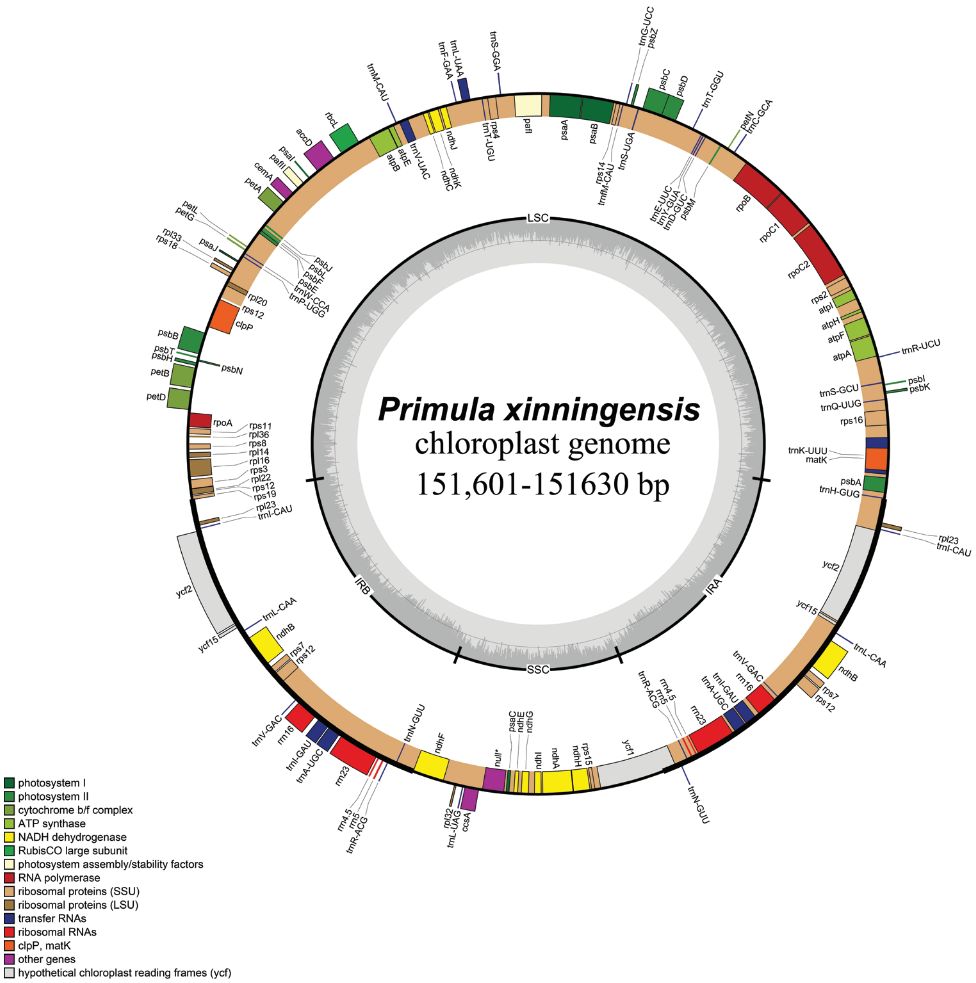


**Figure 1.** Plastid genome map of *P. xinningensis* sp. nov.

## Molecular phylogenetic relationship

Phylogenetic relationships of the new species and related species were constructed, based on the whole plastid genome using ML and BI analyses. The results showed that *P. xinningensis* affiliate to sect. *Ranunculoides*. In sect. *Ranunculoides*, *Primula merrilliana* complex, *P. cicutariifolia* and *P. jiugongshanensis* clustered in one clade and the other three species (*P. xinningensis*, *P. hubeiensis* and *P. ranunculoides*) clustered in another clade (Fig. 2). *Primula xinningensis* is a sister species of *P. hubeiensis*, and their individuals were respectively grouped into a monophyly with high support (posterior probability (PP) = 1, bootstrap support (BS) = 100%) (Fig. 2).

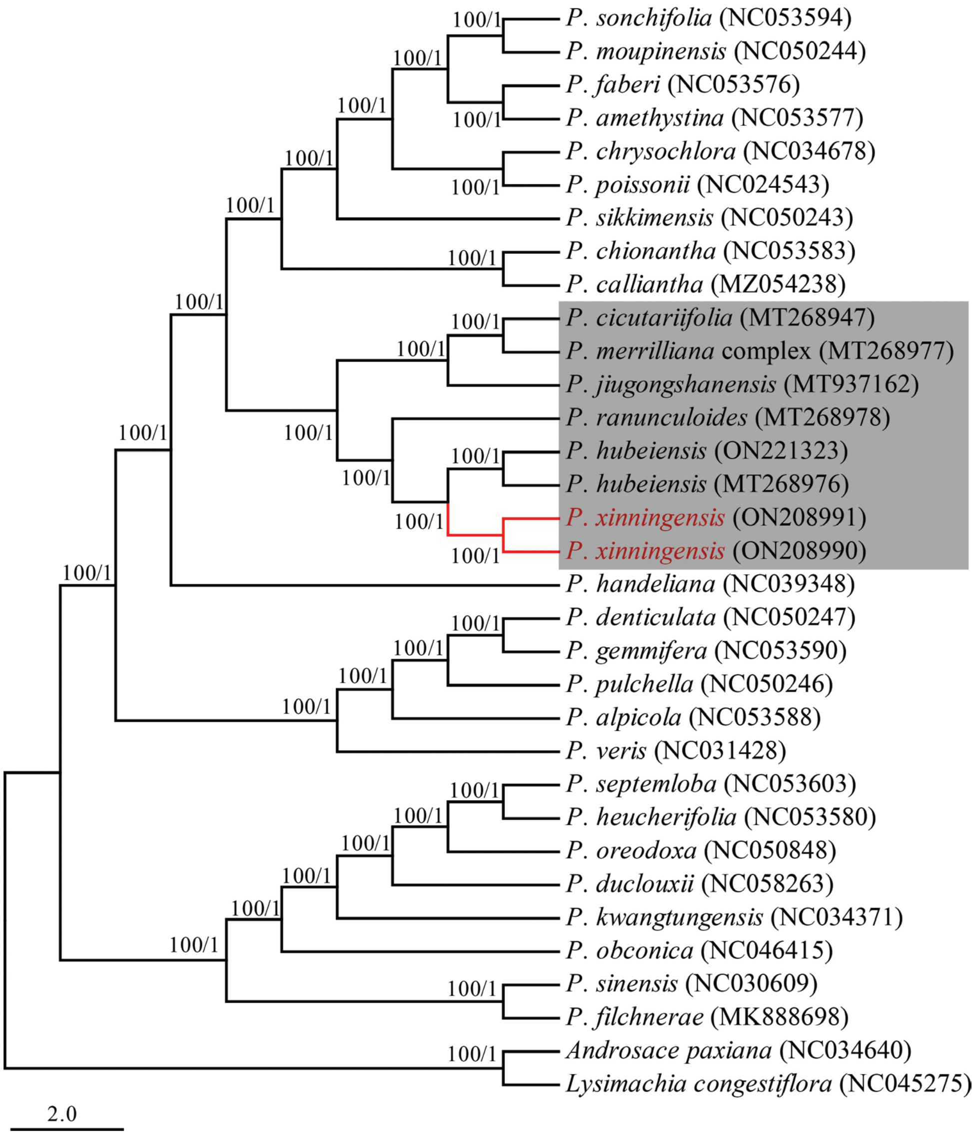


**Figure 2.** Phylogenetic relationships of *P. xinningensis* sp. nov. and related species inferred from ML and BI analyses, based on the whole plastid genome. Numbers on the branches indicate the bootstrap support of the ML and the posterior probability of BI analyses. NCBI accession numbers were shown in the parentheses.

## Morphological comparison

In morphology, this new species is very similar to *P. merrilliana* complex in leaf pinnae shape and degree of division and similar to *P. cicutariifolia* in floral characters, but can be easily distinguished from the former by the black pollen sac, corolla lobes apex obviously

**Table 2.** Morphological and ecological features comparison between *P. xinningensis* sp. nov. and its related species.

| Features | *P. xinningensis* | *P. hubeiensis* | *P. cicutariifolia* | *P. merrilliana* complex |
|---|---|---|---|---|
| Floral morph | Homostylous | Distylous | Homostylous | Distylous or homostylous |
| Umbel layers | 1 | 1–2 | 1 | 1–3 |
| Corolla diameter | 8–12 mm | 13–18 mm | 6–10 mm | 9–19 mm |
| Corolla lobes | Apex conspicuously emarginate | Apex conspicuously emarginate | Apex conspicuously emarginate | Apex rounded |
| Scape length | 0.8–2 cm | 3.5–9.6 cm | 1–3 cm | 1.3–9 cm |
| Pollens | Pantoporate | Pantoporate | Pantoporate | Pantoporate or stephanocolpate |
| Pollen sac | Black | Yellow | Yellow | Yellow |
| Cotyledon | Triangular obovate | Ovate | Ovate | Ovate |
| Older Leaves | Pinnatisect, with 11–19 pinnae, the terminal pinna similar to others, 3-lobed or parted | Pinnatisect, with 13–19 pinnae, the terminal pinna similar to others, 3-lobed or parted, margin coarsely dentate | Pinnatisect, with 7–17 pinnae, the terminal pinna similar to others, 3-lobed | Pinnatisect, with 11–21 pinnae, the terminal pinna similar to others, 3-lobed or parted |
| Glandular hairs | Leaves and scape densely covered with glandular hairs (0.07–0.42 mm) | Leaves and scape densely covered with glandular hairs (0.76–0.88 mm) | without | without |
| Distribution | Hunan | Hubei | Anhui, Zhejiang | Anhui, Zhejiang |
| Habitat | Karst caves | Shady damp rock crevices | Stream sides or under broadleaf deciduous forests of northern slopes | Stream sides or under broadleaf deciduous forests of northern slopes |

emarginate and can be differed from the latter by cotyledon triangular obovate, pinna margin usually pinnatipartite and plants densely covered with glandular hairs (Table 2, Figs 3, 4). Although, in the phylogenetic relationship, *P. xinningensis* is closely related to *P. hubeiensis*, there were obvious morphological differences between them in pinna division pattern (segments margin entire vs. segments margin serrate), the length of glandular hair (0.07–0.42 mm vs. 0.76–0.88 mm) and flowers size and type (homostylous and corolla diameter 8–12 mm vs. distyly and corolla diameter 13–18 mm) (Table 2, Figs 3, 4). Detailed morphological comparisons between the new species and other related species in sect. *Ranunculoides* are summarised in the following key:

## Key to the species of sect. *Ranunculoides*

| | | |
|---|---|---|
| 1 | Corolla lobe apices rounded | ***P. merrilliana* complex** |
| – | Corolla lobe apices obviously emarginated | **2** |
| 2 | Compound leaves with 3–9 pinnae; scape apices differentiating to bulblets late in flowering | ***P. ranunculoides*** |
| – | Compound leaves with 7–21 pinnae; scape apices lacking bulblets | **3** |
| 3 | Plants densely covered with glandular hairs | **4** |
| – | Plants glabrous | **5** |

4 Cotyledon triangular obovate, pinna segments margin entire, flower homostylous, corolla diameter 8–12 mm ........................................ ***P. xinningensis***
– Cotyledon ovate, pinna segments margin serrate, flower distylous, corolla diameter 13–18 mm .................................................................... ***P. hubeiensis***
5 Flower homostylous, umbels solitary, limb ca. 6–10 mm across .................... ........................................................................................... ***P. cicutariifolia***
– Flower distylous, umbels usually 2, limb ca.11–19 mm across ...................... ........................................................................................ ***P. jiugongshanensis***

## Taxonomic treatment

***Primula xinningensis*** **Wei Zhang bis & J.W.Shao, sp. nov.**
urn:lsid:ipni.org:names: 7299424-1
Figs 3–5

**Type.** China. Hunan, Xinning County, Shimen Village, 26°30'27.22"N, 110°40'56.82"E, alt. 458 m, 28 Mar 2016, *Wei.Zhang & Jian.Wen.Shao* ZW20160328 (holotype: ANUB!; isotypes: ANUB!, PE!) (Fig. 5).

**Diagnosis.** Cotyledon triangular obovate, leaves and scape densely covered with short glandular hairs, flowers long homostyled, corolla lobe apices conspicuously emarginate, pollen sac black.

**Description.** Herb biennial, dwarf, densely covered with short glandular hairs. Leaves 9–25 in an open rosette; petiole 1.0–2.0 cm long; leaf blade pinnatisect, 4.0–8.0 cm long, 1.0–2.0 cm wide; pinnae 5–9 pairs, elliptic, margin usually pinnatifid, segments 3–5, apex mucronulate. Scapes 1–8 in each plant, 0.8–2.0 (–2.5) cm tall, carrying one umbel, usually 3 flowers per umbel; bracts linear lanceolate, 2–3 mm long. Pedicel slender, 0.3–0.8 cm. Flowers long homostylous. Calyx narrowly campanulate, 1.0–3.0 mm long, split to the middle; lobes lanceolate, apex acuminate, not outward curvature. Corolla pale red, flowers' limb 8.0–12.0 mm across, lobes obovate, ca. 2.5 mm wide, apex conspicuously emarginate, corolla tube 5.8–7.0 mm, both stamens and stigma at the mouth of the corolla tube, pollen sac black. Capsule subglobose, 1.0–3.0 mm in diam., dehiscing by valves.

**Phenology.** Flowering from March to April, fruiting from April to May.

**Chinese name.** Xīn níng yǔ yè bào chūn (新宁羽叶报春).

**Etymology.** The specific epithet '*xinningensis*' refers to the locality, Xinning County, Hunan, China.

**Distribution and ecology.** *P. xinningensis* is known only from Shimen Village, Xinning County, Hunan, China. Growing on the walls or ground of karst caves, at an altitude of 385–487 m. The main accompanied species were *Primulina latinervis* (W.T.Wang) Mich. Möller & A. Weber. (Gesneriaceae), *Cyrtomium fortunei* J.Sm. (Dryopteridaceae) and *Pteris multifida* Poir. (Pteridaceae).

**Conservation status.** Vulnerable (VU D1 and D2). This species is endemic to China, Hunan Province, Xinning County, Shimen Village. We only found three populations,

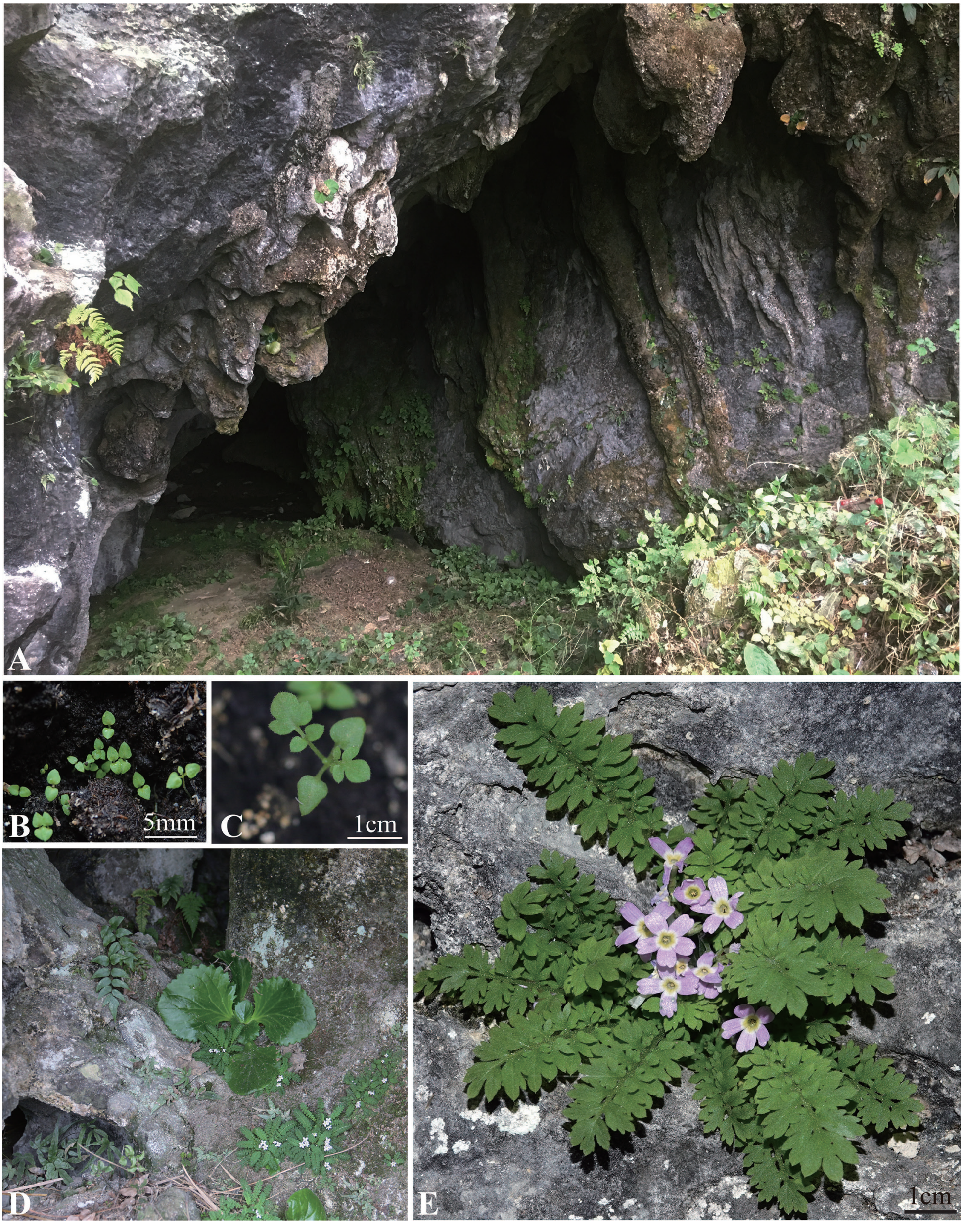


**Figure 3.** Living images of *P. xinningensis* sp. nov. **A, D** habitat **B, C** plant in seedling **E** plant in flowering.

all of them near the entrance to the karst caves and each with about 100–250 individuals. The surrounding area is cultivated field with strong human activities. The Extent of Occurrence (EOO) is less than 10 km$^2$ and the known Area of Occupancy (AOO) is less than 0.5 km$^2$. Therefore, the conservation status of this new species is evaluated as 'Vulnerable' (VU) as it meets criterion D1 and D2, according to the IUCN Red List Categories and Criteria (IUCN 2019). In addition, *P. shimemensis* is a homostylous

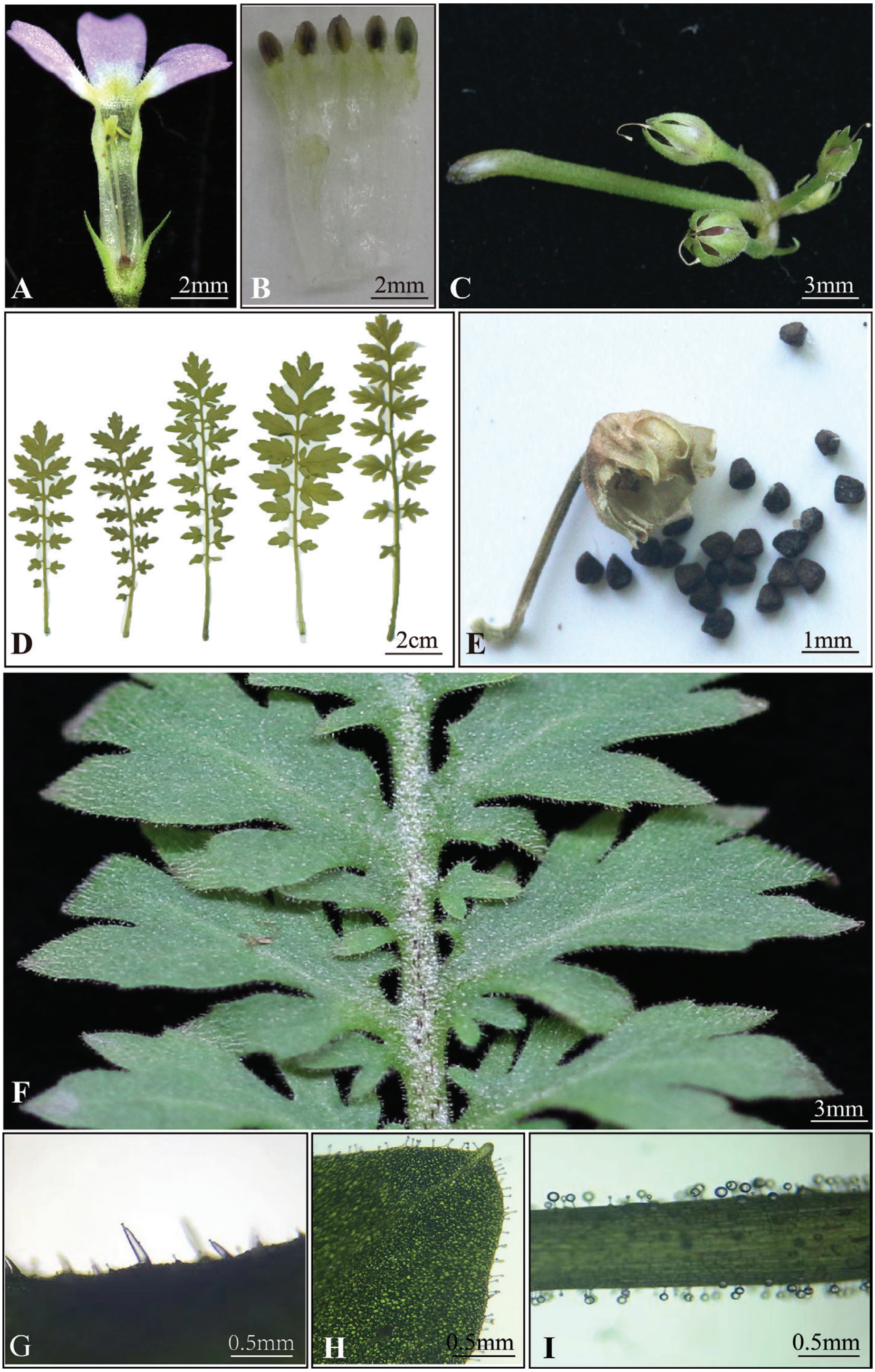


**Figure 4.** Morphological characters of *P. xinningensis* sp. nov. **A, B** longitudinally dissected of floral tube **C** infructescence **D, F** leaves morphology **E** opened capsule and seeds **G** leaf surface glandular hairs **H** leaf margin glandular hairs **I** rachis glandular hairs.

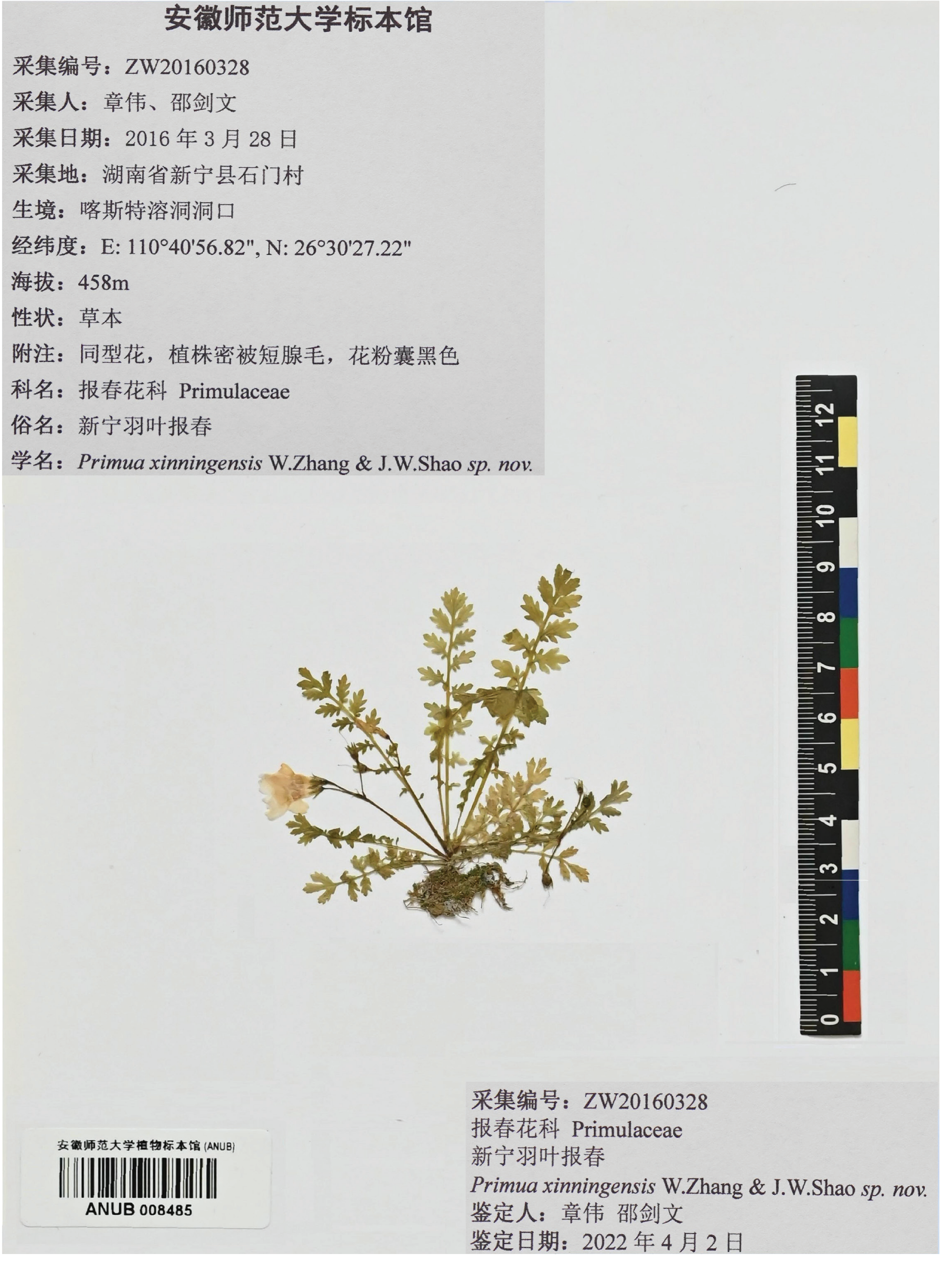


**Figure 5.** Holotype of *P. xinningensis* Wei Zhang bis & J.W.Shao, sp. nov.

species. Although *Primula* containing ca. 500 species, there are only ca. 45 species having monomorphic populations (Mast et al. 2006). Therefore, the recognition of this new species increases the homostylous species diversity in *Primula* and can provide valuable material for studying the evolution and maintenance mechanism of distylous flowers.

**Additional specimen examined.** China. Hunan: Xinning County, Wanfeng Forest Farm, alt. 450 m, 22 Apr 1995, *Lin Bo Luo* 00205565 (PE); Xinning County, Wanfeng Forest Farm, alt. 450 m, 22 Apr 1995, *Lin Bo Luo* 00353811 (IBK); Xinning County, Shuimiao Town, Jiangmu Village, alt. 347 m, 19 Feb 2014, *Xun Lin Yu & Hui Zhou* 028303 (CSFI); Xinning County, Shuimiao Town, Jiangmu Village, alt. 347 m, 19 Feb 2014, *Xun Lin Yu & Hui Zhou* 028304 (CSFI).

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# *Polypleurum chinense* (Podostemaceae), a new species from Fujian, China, based on morphological and genomic evidence

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## Abstract
We describe *Polypleurum chinense*, a new species of Podostemaceae from Yunxiao County, Fujian Province, China, based on morphological and molecular data and the genus *Polypleurum* is recorded here for the first time from China. *Polypleurum chinense* has a gross morphology similar to *P. longistylosum*, but it can be distinguished from the latter by its narrower roots, more numerous and longer leaves, shorter stigmas and more numerous ovules per locule. To distinguish the new *Polypleurum* species and study its phylogenetic position, its complete plastome was sequenced and characterised. The plastome is 132,110 bp in length, including a pair of inverted repeat regions (IRs) of 20,389 bp divided by the large single-copy (LSC) and small single-copy (SSC) regions of 79,022 bp and 12,310 bp, respectively. The plastome size of *P. chinense* is relatively smaller compared to most angiosperms due to the absence of the *ycf*1 and *ycf*2 genes in the IR regions. The phylogenetic analyses also strongly support the separation of the new species from other taxa.

## Keywords
Fujian Province, molecular identification, morphology, Podostemaceae, *Polypleurum chinense*

## Introduction

Podostemaceae, widely known as "river-weeds", are a vast family of unique haptophtic angiosperms that grow in a variety of wetlands in the tropics and subtropics around the world (Philbrick and Novelo 1995; Cook 1996; Koi et al. 2015). During the wet season, the vegetative phase of Podostemaceae is immersed in rapid and turbulent currents and is tightly adherent to the surface of rocks. As the water level drops over the following dry season, the plants sprout, flower, produce fruit and eventually wither (Tăng and Kato 2020). During the rainy season, the seeds are spread by wind, birds and running water, the seed coat becomes sticky and sticks to the rock surface, the seeds germinate and the seedlings develop submerged (Koi et al. 2015). Their habitats are unique and are hard to recreate if the water of the stream is contaminated.

Phylogenetically, Podostemaceae are placed in the eudicot order Malpighiales and are sister to Hypericaceae (Wurdack and Davis 2009). Podostemaceae contain 200–280 species in 60 genera, widespread mostly in tropical regions, with a few species in temperate regions. Podostemaceae are divided into three subfamilies, i.e. Podostemoideae, Weddellinoideae and Tristichoideae (Kita and Kato 2001; Koi et al. 2015). Podostemoideae evolved structures and properties obviously unknown in *Hypericum* (Hypericaceae), including loss of apical meristem, reduction or loss of primary shoot and loss of primary root and notably dorsiventral or crustose root and spathella, while Tristichoideae is morphologically similar to Hypericaceae and other terrestrial angiosperms (Koi et al. 2015).

Podostemoideae, the largest subfamily, is divided into various clades, including *Ceratolacis*, *Cipoia*, *Diamantina* & *Podostemum*, American genera (*Apinagia*, *Castelnavia*, *Jenmaniella*, *Marathrum*, *Monostylis*, *Mourera*, *Noveloa*, *Rhyncholacis*, *Wettsteiniola*), *Aulea* (*Saxicolella pro parte*), African genera (*Dicraeanthus*, *Djinga*, *Inversodicraea*, *Ledermanniella*, *Leiothylax*, *Letestuella*, *Macropodiella, Monandriella*, *Saxicolellas.s.*, *Stonesia*, *Winklerella*), Madagascan genera (*Endocaulos*, *Thelethylax*) and Asian/Australian genera (*Cladopus*, *Farmeria*, *Griffithella*, *Hanseniella*, *Hydrobryum*, *Hydrodiscus*, *Paracladopus*, *Polypleurum*, *Thawatchaia*, *Terniopsis*,*Willisia*, *Zeylanidium*) (Qiu and Philbrick 2003; Koi et al. 2012).

Podostemoideae are the largest subfamily in the family and are widely distributed in Asia, especially in Thailand (42 species with 4 varieties in 10 genera) (Kato 2006; Kato and Koi 2009), India (28 species in 11 genera) (Khanduri et al. 2015), Laos (17 species in 6 genera) (Koi and Kato 2012), Vietnam (7 species in 5 genera) (Kato 2011). In China, nine species in three genera (*Terniopsis*, *Cladopus* and *Hydrobryum*) were reported from Fujian, Guangdong, Hainan, Yunnan, Guizhou, Hong Kong (Kato and Kita 2003; Qiu and Philbrick 2003; Lin et al. 2016; Kato et al. 2017; Zhang et al. 2022).

*Polypleurum* (Taylor ex Tul.) Warm. is a genus previously known from Sri Lanka, India, Thailand and Laos with 17 species (Kato 2006). It is distinguished from *Cladopus* and *Paracladopus* by its more or less flattened, ellipsoid, rough capsule with longitudinal ribs and from *Hanseniella*, *Hydrobryum* and *Thawatchaia* by its ribbon-like root.

*Polypleurum* species differ in number of capsule ribs and stamens. Species in Sri Lanka and India, including *P. wallichii* (R. Br. ex Griffz) Warm., the type of the genus, have two stamens and eight capsule ribs, while species in Thailand and Laos have a single stamen and eight to fifteen ribs (Kato 2006).

In January 2021, during a field investigation in Yunxiao County, within the Wushan Mountains in Zhangzhou City, Fujian, China, we unexpectedly discovered a little-known Podostemaceae species during anthesis in a stream. The species has a completely distinct morphology from the other three known genera identified in China. In March and August of 2021, we collected its fruits and vegetative parts for molecular study. Based on morphological analysis and molecular phylogeny, we established that our recently obtained specimen is a new species of *Polypleurum*, a hitherto not recorded genus of Podostemaceae in China.

## Material and methods

### Morphological description

The morphological description of the new species was based on the study of specimens collected in a variety of spots in 2021. Live material adhering to rock surfaces from a river in Wushan Mountains, Yunxiao County, Fujian, China, was collected for DNA extraction. A stereoscopic zoom microscope (Carl Zeiss, Axio zoom. v.16, Germany), equipped with an attached digital camera (Axiocam) and a digital caliper were used to record details of roots, leaves, bracts, spathella, tepals, stamen, pistil and seeds. Field observations provided habitats and phenology for the new species.

### DNA extraction, amplification and sequencing

In this study, total DNA was extracted from freeze-dried material using DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA). The phylogenetic position of the new species was determined by nrITS and plastid *matK* sequences. The nrITS and plastid *matK* regions were amplified via polymerase chain reaction (PCR) using MiniAmp Thermal Cycler (Applied Biosystems, Foster City, CA, USA) and 1.1xT3 Super PCR Mix (Tsingke Biotechnology, Beijing, China) under the following conditions: 5 min at 94 °C; 30 cycles of 45 s at 94 °C, 45 s at 55 °C, 60 s at 72 °C; and 10 min at 72 °C (Zhou and Jin 2018) and 3 min at 94 °C; 30 cycles of 30 s at 94 °C, 30 s at 55 °C, 90 s at 72 °C; and 7 min at 72 °C (Koi et al. 2012), respectively. The PCR products were treated with Mag-MK 96 Well PCR Products Purification Kit (Sangon Biotech, Shanghai) to remove the extra primers. Sequencing was conducted using the BigDye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems) and the ABI 3130xl Genetic Analyser (Applied Biosystems). The primers used for the DNA amplification and the cycle sequencing are listed in Suppl. material 1: Table S1.

## Genome sequencing, assembly, annotation and analysis

Purified total DNA of *Polypleurum chinense* was fragmented, genome skimming was performed using next-generation sequencing technologies on the Illumina Novaseq 6000 platform with 150 bp paired-end reads and 350 bp insert size by Wuhan Onemore-tech Co. Ltd. (Wuhan, China) and 15.88 GB of reads was obtained.

The paired-end reads were filtered and assembled into complete plastome using GetOrganelle v.1.7.5.0 with appropriate parameters, with K-merset "21,45,65,85,105", the word size being 0.6 (Jin et al. 2020a). Following previous studies, our workflow includes five key steps as well (Camacho et al. 2009; Bankevich et al. 2012; Langmead and Salzberg 2012; Jin et al. 2020a). Graphs of the final assembly were visualised by Bandage to assess their completeness (Wick et al. 2015). Gene annotation was performed using CPGAVAS2 and PGA. The different annotations of protein coding sequences were confirmed using BLASTx. The tRNAs were checked with tRNAscan-SE v.2.0.3. Final chloroplast genome maps were created using OGDRAW.

## Phylogenetic analysis

In an attempt to reconstruct the evolutionary history of *Polypleurum chinense*, phylogenies were constructed using Maximum Likelihood (ML) and Bayesian Inference (BI) analyses of the nrITS and *matK* sequences. To construct a phylogenetic tree, based on *matK* sequence, 114 samples (Suppl. material 1: Table S2) of *Terniopsis*, *Cladopus*, *Paracladopus*, *Hanseniella*, *Hydrobryum*, *Hydrodiscus*, *Thawatchaia*, *Hydrobryopsis*, *Zeylanidium*, *Griffithella*, *Polypleurum*, *Willisia* and *Cratoxylum* were included in our analysis. *Cratoxylum cochinchinense* was selected as the outgroup. Each individual sequence was aligned using MAFFT 7.310 (Katoh and Standley 2013) with default settings. A concatenated supermatrix of the two sequences was generated using PhyloSuite v.1.1.15 (Zhang et al. 2019) for the phylogenetic analysis. All missing data were treated as gaps. Gblocks 0.91b (Castresana 2000) was applied to eliminate poorly-aligned regions of the concatenated supermatrix with gaps set as no different from the other positions. The best nucleotide substitution model according to Bayesian Information Criterion (BIC) was TVM+F+R3, which was selected by Model Finder (Kalyaanamoorthy et al. 2017) implemented in IQTREE v.1.6.8. Maximum Likelihood phylogenies were inferred using IQ-TREE (Nguyen et al. 2015) under the model automatically selected by IQ-TREE ('Auto' option in IQ-TREE) for 1000 ultrafast (Minh et al. 2013) bootstraps. Bayesian Inference phylogenies were inferred using MrBayes 3.2.6 (Ronquist et al. 2012) under GTR+F+G4 model (2 parallel runs, 2,000,000 generations), in which the initial 25% of sampled data were discarded as burn-in. Phylograms were visualised in iTOL v.5.

To construct a phylogenetic tree based on nrITS, 42 species of *Cladopus*, *Hanseniella*, *Hydrobryum*, *Hydrobryopsis*, *Zeylanidium*, *Griffithella*, *Polypleurum*, *Willisia* and *Cratoxylum* were included in the analysis (Suppl. material 1:Table S3). *Cratoxylum cochinchinense* was employed as the outgroup. The study was carried out as described above and, according to the Bayesian Information Criterion (BIC), the optimal nucleotide substitution model was GTR+F+I+G4.

# Results

## Taxonomic treatment

***Polypleurum chinense*** **B.Hua Chen & Miao Zhang, sp. nov.**
urn:lsid:ipni.org:names:77299427-1
Figs 1–4

**Diagnosis.** The new species can be easily distinguished from most other species, except *Polypleurum longistylosum*, by tufts of leaves on both sides of the root between the root branches, a more or less flattened, ellipsoid, rough capsule with a greater number of longitudinal ribs (> 12), a spathella nearly completely enclosing the ovary and stamen at anthesis, a solitary stamen and a very short capsule stalk (< 2 mm). The narrower roots (0.6–0.8 mm vs.1.0–1.5 mm) with leaves 8–12 per tuft (vs. 4–8), up to 23.1 mm (vs. 5 mm) long, fewer (4 vs. 6) bracts, short spiny or glandular hairs on the spathella (vs. papillate) in the new species differentiate it from *P. longistylosum* (Table 1).

**Type.** China. Fujian Province: Yunxiao County, Wushan Mountains, elevation 430 m, 117°14'E, 23°53'N, 4 January 2021, *Bing-Hua Chen CBH 04407* (Holotype FNU barcode FNU0041131; isotype FNU barcode FNU0041132).

Root creeping, adhering to rock surfaces, ribbon-like, branched, 0.6–0.8 (–1.0) mm wide, with tufts of leaves on both flanks, not associated with root branching, 2–4 mm apart; leaves 6–12 per tuft, in two ranks, to 17.6 (12.4–23.1) mm long, 0.2–0.4 mm wide, needle-like (Fig. 1). Flowering shoots on both flanks of root, very short; bracts 2–6, needle-like, to 5–6 mm long, caduceus. Flower just prior to anthesis, with only two remaining bracts, pale purplish-red. The anthesis begins when the water level is further reduced, the bracts disappeared, but the base remained. Flower1, bud covered by ellipsoid

**Table 1.** Morphological differences between *Polypleurum chinense*, *P. longistylosum* and *P. schmidtianum*.

| Characteristics | *P. chinense* | *P. longistylosum* | *P. schmidtianum* |
|---|---|---|---|
| Root width/mm | 0.6–0.8(–1.0) | 1–1.5 | 2–4 |
| Tufts of leaves position | On both flanks, alternate, subopposite or opposite | On both flanks | Near both sides |
| The number of leaves | 6–12, usually 8–12 | 4–8 | 2–4 |
| Leaves length/mm | 12.4–23.1 | 5 | 1.5–3(–6) |
| The number and morphology of bracts | 4, needle-like | 6, needle-like | 3–4(–6), sheathed |
| Bracts length(mm) | 5–6 | 4 | 2–3 |
| Spathella length/mm | 3 | - | 1.5–2 |
| Spathella coat | Short spiny or glandular hairs | Papillate | Not papillate |
| Peduncle length/mm | 0.7 | 1 | 6–7 |
| Tepals length/mm | 0.3 | 0.2 | 0.5–0.7 |
| Stamen length (mm) | 2.9 | 1.7 | 1.2 |
| Ovary locular | 1 | 1 | 2 |
| Ovary length (mm) | 1.8 | 1 | 1.2–1.5 |
| Stigmas quantity | 2, unequal | - | 2 or 3 |
| Stigmas length (mm) | 0.6–1.2 | 1–1.2 | 0.2–0.4 |
| Ovules locule | 25–35 | 10–15 | 25–35 |
| Capsule stalk length (mm) | 1.1–1.6 | - | 6–12 |
| Capsule ribs | 12–14, conspicuous | 10–12, inconspicuous | 8 |

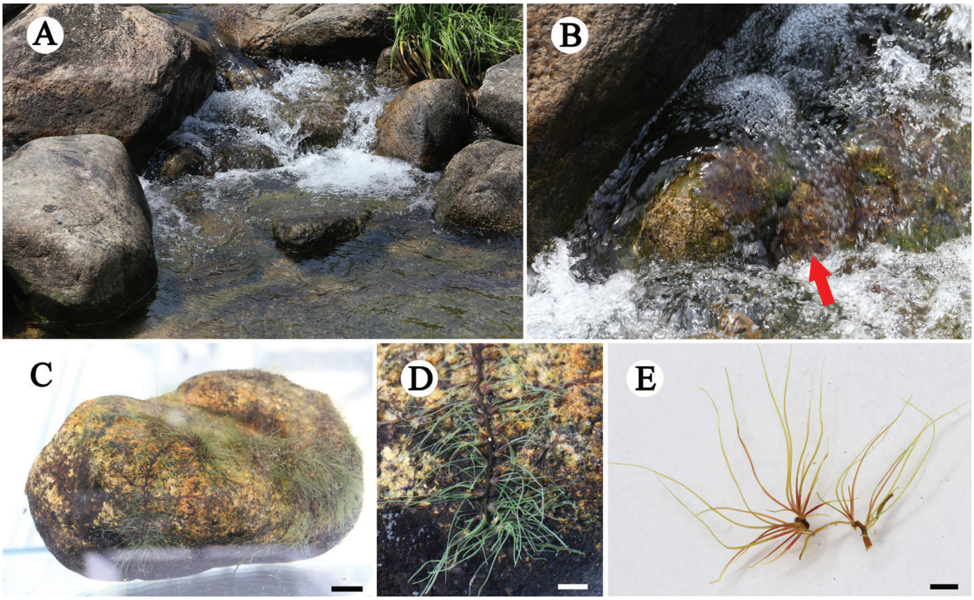


**Figure 1.** *Polypleurum chinense* **A** habitat **B** habit, showing plants (red arrow) on rock surface in rapids **C** plants adherent to rock surface (photo in aquarium) **D** roots with tufts of leaves on both flanks **E** tufts of 1eaves. Scale bars: 5 mm (**C**); 2 mm (**D**); 1 mm (**E**).

spathella, spathella stalk ca. 3 mm in length, coated with short spiny hairs or glandular hairs, with a papilla-like tip, the papilla ruptured near apex at anthesis, but persisting spathella base keeps the ovary and lower bottom of stigma enclosed. Pedicel ca. 0.7 mm long; tepals 2, one on each side of stamen, linear, ca. 0.3 mm long; stamen 1, up to 2.9 mm long, protruding from spathella; ovary dark green, ellipsoid, ca. 1.8 mm long, 0.9 mm wide, 1-locular, free central placenta; stigmas 2, forked near base, thin, needle-like, ca. 0.9 mm long, as long as, or slightly shorter than ovary, branched at the top, upper part exerted from spathella; ovules on marginal surface of septum, 25–35 per septum (Fig. 2). Post-pollination, the spathella and ovary developed into a pale ellipsoid, ca. 2 mm long, arranged on both sides of the root, the ovary stalk lengthened and developed into pedicels (ca. 0.7 mm). Mature capsule 12–14-ribbed, conspicuous under microscope, fissured longitudinally; seed yellowish-brown, with shallow groove, ca. 300 μm long (Fig. 3).

**Distribution and habitat.** *Polypleurum chinense* is only known from Fujian, China (Fig. 5), where it grows on rocks in unpolluted streams. In addition, *Cladopus austrosinensis* M. Kato & Y. Kita from the same family was found on the rock surfaces in the lower reaches of the stream. Many other plants grow in the surrounding habitat, whose tree layer includes *Pinus massoniana* Lamb. (Pinaceae), *Ficus fistulosa* Reinw. ex Bl. (Moraceae), *Casearia glomerata* Roxb. (Salicaceae), *Carallia brachiata* (Lour.) Merr. (Rhizophoraceae) and planted *Eucalyptus grandis* × *urophylla* (Myrtaceae) and others; the shrub layer includes *Ficus pyriformis* Hook. & Arn. (Moraceae), *Illicium dunnianum* Tutch. (Schisandraceae); the vegetation layer includes woody vine plants

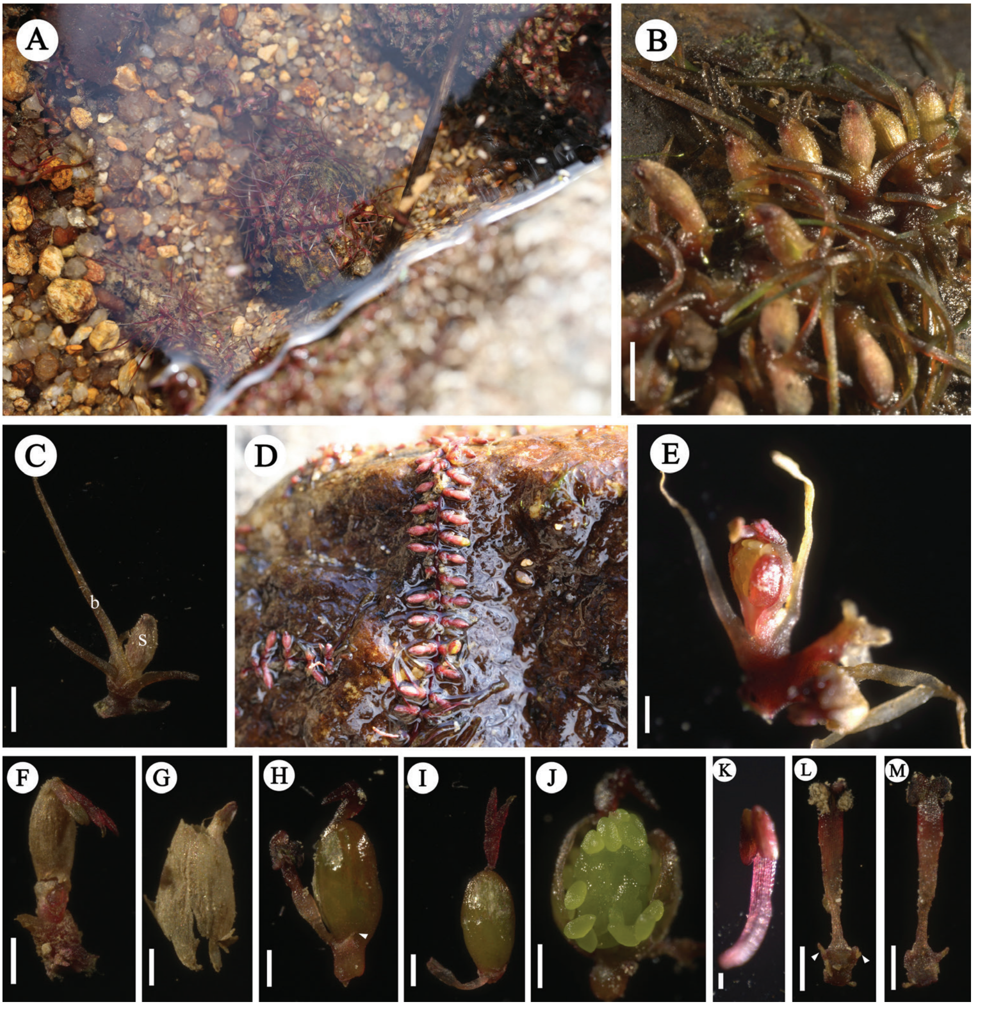


**Figure 2.** *Polypleurum chinense* **A** plants in bud adhering to rock surface **B** ribbon-like root with young floriferous shoots on flanks **C** flower bud covered by spathella(s) above bracts (b) **D** shoots along the flanks of the ribbon-like root between the root branches **E, F** flower at anthesis on peduncle with ruptured spathella **G** spathella **H** flower with spathella removed, stamen, and ovary, arrow shows a tepal on side of stamen **I** gynoecium without bracts **J** ovules on ovary septum **K, L, M** stamen, arrows show two tepals on sides of stamen. Scale bar: 1 mm (**C, F, J**); 2 mm (**B, E, M**); 500 µm (**G, H, I, K, L**).

*Melodinus suaveolens* (Hance) Champ. ex Benth. (Apocynaceae), *Dendrotrophe varians* (Blume) Miquel (Santalaceae), *Toddalia asiatica* (L.) Lam. (Rutaceae), *Mappianthus iodoides* Hand.-Mazz. (Icacinaceae), *Byttneria grandifolia* Candolle (Malvaceae), *Uvaria boniana* Finet & Gagnep. (Annonaceae) and more; the herbaceous layer includes *Arundina graminifolia* (D. Don) Hochr. (Orchidaceae); on the cliff, there are *Cryptochilus roseus* (Lindley) S. C. Chen & J. J. Wood, *Pholidota chinensis* Lindl., *Dendrolirium lasiopetalum* (Willdenow) S. C. Chen & J. J. Wood and other Orchidaceae.

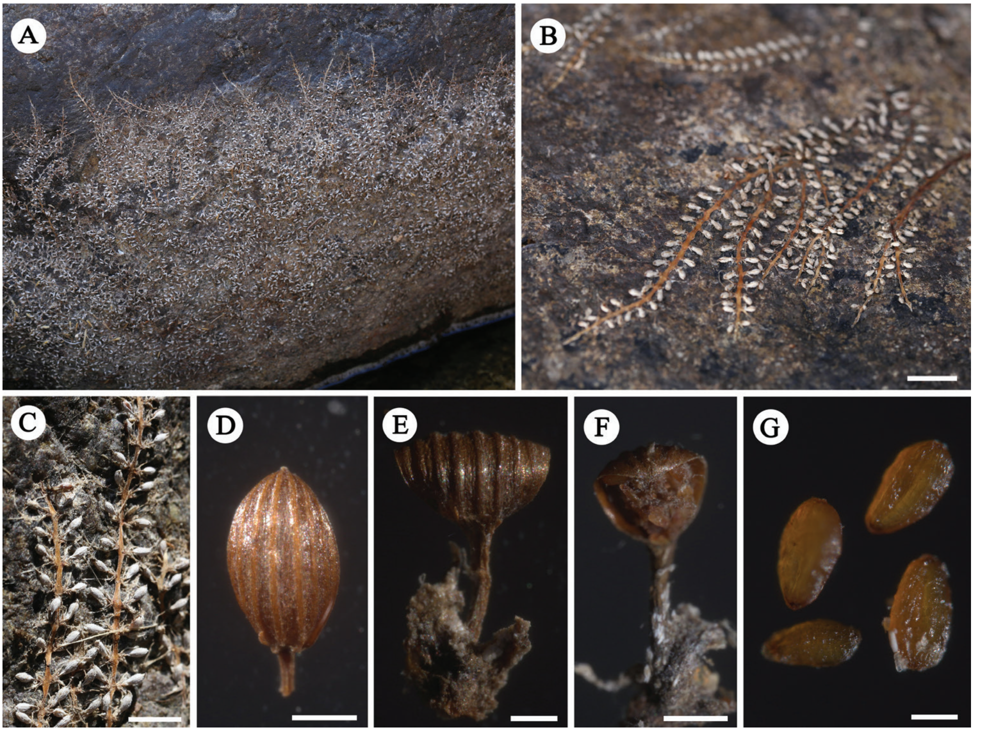

**Figure 3.** *Polypleurum chinense* **A** habitat in the dry season when the river level is reduced **B** habitat showing mature fruits **C** elliptic pale bodies along the flank of the root **D** stalked fruit, showing ribs **E** dehisced capsule, showing seven ribs on the half of capsule, conspicuous **F** dehisced capsule, showing persistent valve and seeds **G** seeds. Scale bars: 20 mm (**B**); 5 mm (**C**); 500 μm (**D**); 400 μm (**E**); 1 mm (**F**); 200 μm (**G**).

**Phenology.** *Polypleurum chinense* was observed flowering and fruiting in its habitat from December to February when the water level is reduced to partly expose the rocks.

**Etymology.** The Zhong Guo Cha Pu Chao (中国叉瀑草). The specific epithet "*chinense*" refers to China, as the distribution of this genus was first identified there and it was proven to be a new species of *Polypleurum*.

**Conservation status.** According to our investigation, *Polypleurum chinense* was found in patches attached to rock surfaces in rapid-flowing streams in the Wushan Mountains range in Zhangzhou City, Fujian Province, China. It is difficult to count the exact number of individuals in the population. Its habitat is vulnerable to anthropogenic destruction and projects like reservoir construction. To determine the exact distribution of this species, further fieldwork is required around the Wushan Mountains in Zhangzhou City and nearby mountainous areas. Therefore, we suggest the species be classified as category DD (Data Deficient), according to the International Union for Conservation of Nature (IUCN 2022). According to the Updated List of National Key Protected Wild Plants (Decree No. 15) by the country's State Forestry

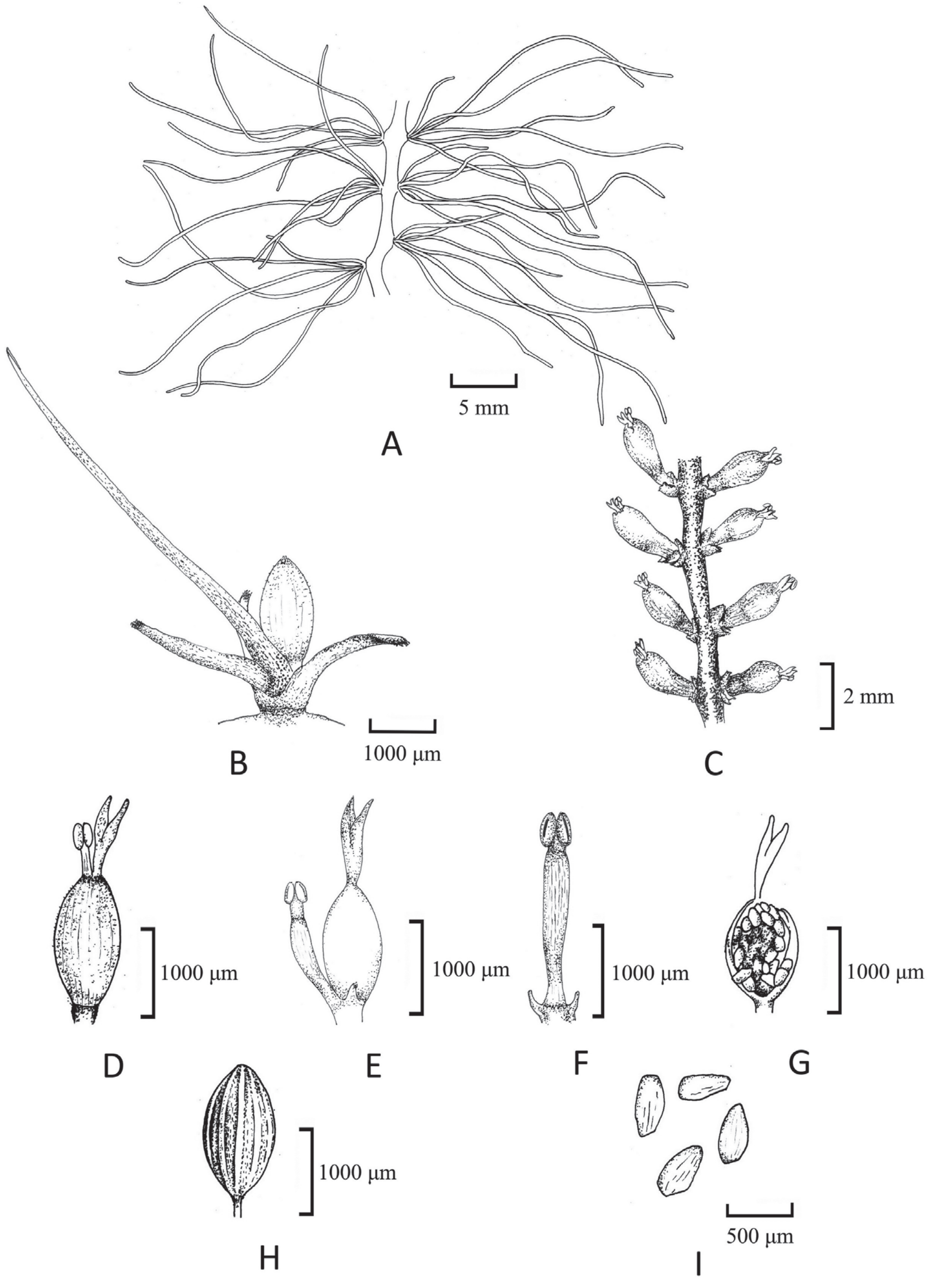


**Figure 4.** Illustration of *Polypleurum chinense* **A** ribbon-like root with tufts of leaves **B** flower bud covered by spathella above bracts **C** floriferous shoots along the flanks of the root between the root branches **D** flower at anthesis on peduncle with ruptured spathella **E** flower with spathella removed, stamen and ovary, a tepal on side of stamen **F** stamen **G** ovules on ovary septum **H** stalked fruit, showing ribs **I** seeds.

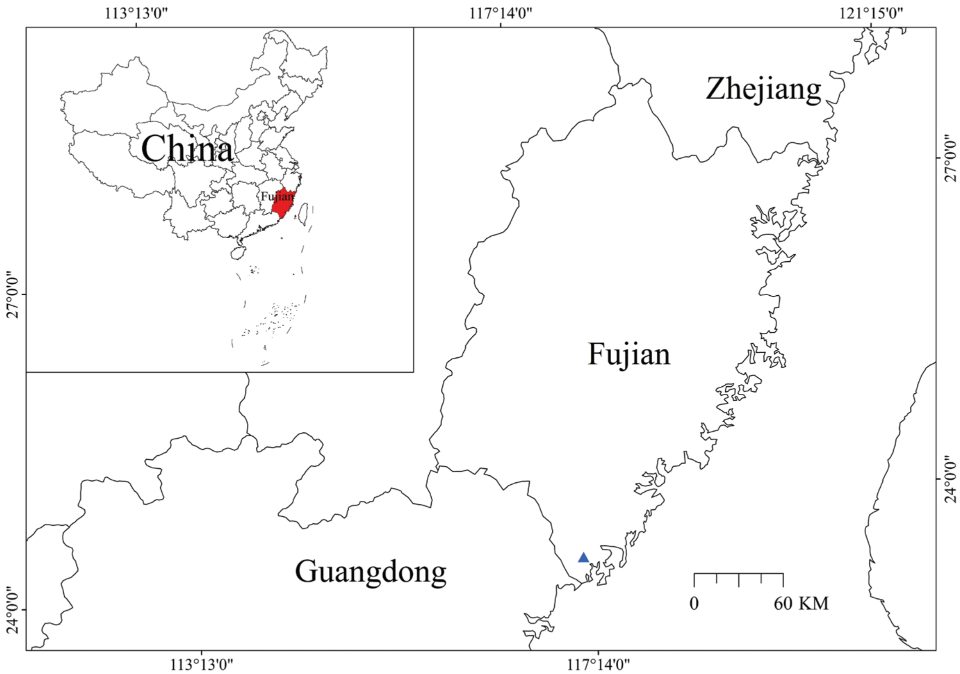


**Figure 5.** Geographical distribution map of *Polypleurum chinense* (▲). (Map constructed using ArcGis 9.2 software).

and Grassland Administration and the Ministry of Agriculture and Rural Affairs, all of the known genera of Podostemaceae found in China are classified in the national secondary protection list. The new recorded genus should also be included on the national secondary protection list during the upcoming revision process.

## Morphology

The new species is morphologically similar to most *Polypleurum* species in that it has ribbon-like roots, tufts of linear leaves on roots, a single flower, a bud covered by spathella and an ellipsoid and rough capsule with longitudinal ribs. However, the new species differs from *P. longtistylosum* and *P. schmidtianum* in the length of leaves, the number of leaves per tuft and capsule ribs, as well as the spathella coat appearance (Table 1).

## Characteristics of the *Polypleurum chinense* plastome

The complete plastome of *Polypleurum chinense* was sequenced and characterised in this study. It is 132,110 bp in length and exhibits a typical quadripartite structure, consisting of a large single copy (LCS) region of 79,022 bp and a small single copy

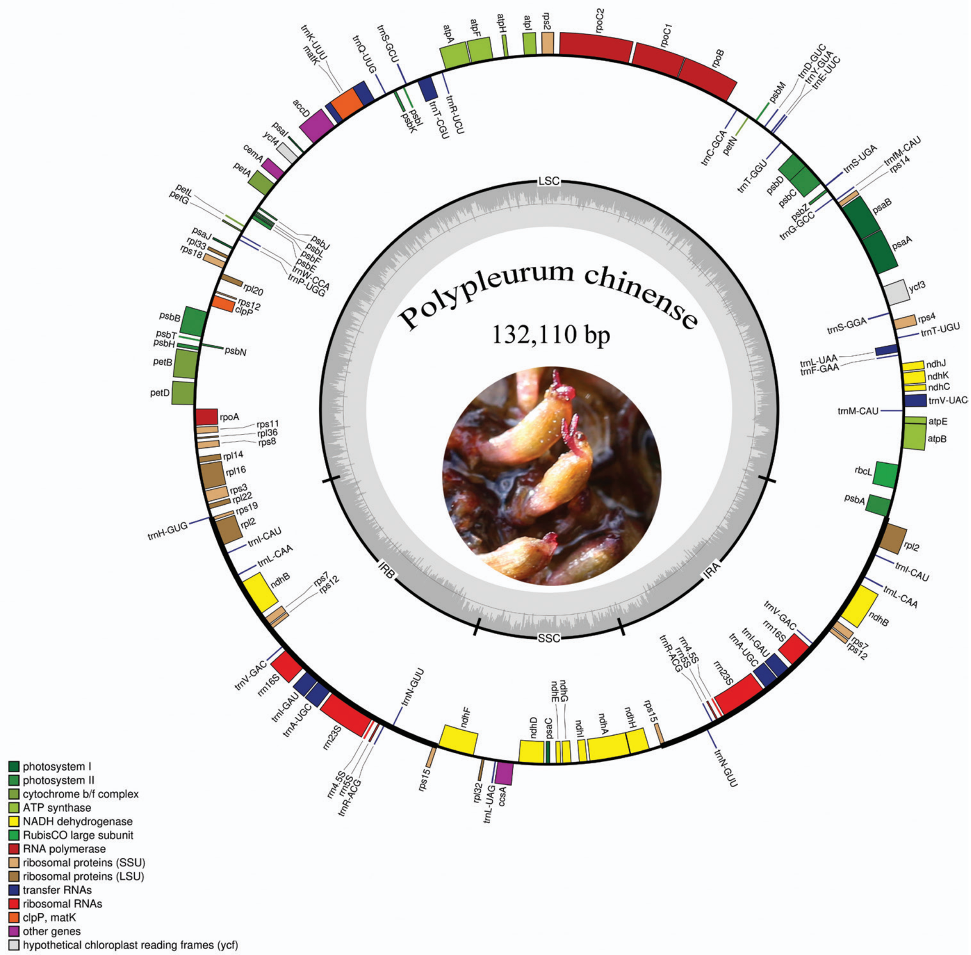


**Figure 6.** Circular gene map of the plastid genome of *Polypleurum chinense*. Genes inside the circle are transcribed clockwise, while those drawn outside are transcribed counterclockwise. Genes are colour-coded according to their functional groups. The circle inside the GC content graph marks the 50% threshold.

(SSC) region of 12,310 bp, which were separated by a pair of 20,389 bp inverted repeat regions (IRs). The gene map of *P. chinense* plastome is presented in Fig. 6. The gene composition in the plastome of *P. chinense* could be divided into four categories: genes related to photosynthesis, genes related to self-replication, protein-coding genes with unknown functions and other genes. A total of 108 unique genes were identified in the plastome and it contains 72 protein-coding genes, 30 tRNAs, and 4 rRNAs. A total of 16 genes were duplicated in the IR regions, including *ndhB*, *rpl2*, *rps7*, *rps12*, *rps15*, *rrn4.5S*, *rrn5S*, *rrn16S*, *rrn23S*, *trnA-UGC*, *trnI-GAU*, *trnI-CAU*, *trnL-CAA*, *trnN-GUU*, *trnR-ACG* and *trnV-GAC* (Table 2). There were four genes lost, including *rpl23*, *infA* and uncommon losses of *ycf1* and *ycf2*. The annotated plastome was documented in GenBank (accession number OL944404).

**Table 2.** Gene contents in the plastid genome of *Polypleurum chinense*.

| Category, Group of Genes | Gene Names |
|---|---|
| **Photosynthesis:** | |
| Subunits of ATP synthase | atpA, atpB, atpE, atpF*, atpH, atpI |
| Subunits of NADH dehydrogenase | ndhA*, ndhB*(x2), ndhC, ndhD, ndhE, ndhF, ndhG, ndhH, ndhI, ndhJ, ndhK |
| Cytochrome b/f complex | petA, petB*, petD*, petG, petL, petN |
| Subunits of photosystem I | psaA, psaB, psaC, psaI, psaJ |
| Subunits of photosystem II | psbA, psbB, psbC, psbD, psbE, psbF, psbH, psbI, psbK, psbJ, psbL, psbM, psbN, psbT, psbZ |
| Large subunit of rubisco | rbcL |
| **Other genes:** | |
| Subunit of Acetyl-CoA-carboxylase | accD |
| c-type cytochrome synthesis gene | ccsA |
| Envelope membrane protein | cemA |
| Protease | clpP |
| Maturase | matK |
| **Self-replication:** | |
| Large subunit of ribosome | rpl2*(x2), rpl14, rpl16*, rpl20, rpl22, rpl32, rpl33, rpl36 |
| DNA-dependent RNA polymerase | rpoA, rpoB, rpoC1*, rpoC2 |
| Small subunit of ribosome | rps2, rps3, rps4, rps7(x2), rps8, rps11, rps12*[a](x2), rps14, rps15(x2), rps18, rps19 |
| rRNA Genes | rrn4.5S(x2), rrn5S(x2), rrn16S(x2), rrn23S*(x2) |
| tRNA Genes | trnA-UGC*(x2), trnC-GCA, trnD-GUC, trnE-UUC, trnF-GAA, trnfM-CAU, trnG-GCC, trnH-GUG, trnI-GAU*(x2), trnI-CAU(x2), trnK-UUU*, trnL-CAA(x2), trnL-UAA*, trnL-UAG, trnM-CAU, trnN-GUU(x2), trnP-UGG, trnQ-UUG, trnR-ACG(x2), trnR-UCU, trnS-UGA*, trnS-GCU, trnS-GGA, trnT-CGU, trnT-GGU, trnT-UGU, trnV-GAC(x2), trnV-UAC*, trnW-CCA, trnY-GUA |
| **Unknown function:** | |
| Conserved open reading frames | ycf3*, ycf4 |

Note: *genes containing introns; (x2) genes present as two copies in the IR regions; [a] indicates trans-spliced gene.

## Phylogenetic analysis

Phylogenies were reconstructed by the Maximum Likelihood (ML) and Bayesian Inference (BI) analyses using the *matK* and nrITS sequences. The phylogenetic study, based on *matK* sequences suggested the two subfamilies, Tristichoideae and Podostemoideae are sister groups. *Polypleurum* is a monophyletic group within Podostemoideae, which is divided into two subclades. *Polypleurum* is closer to *Griffithella*. *Polypleurum chinense* is sister to *P. longistylosum* with strong support (PP = 1, BS = 100) and nested in a clade formed by nine other species of *Polypleurum*. *Polypleurum chinense* 1 is extracted from the complete chloroplast genome and *P. chinense* 2 is a cloned *matK* sequence (Fig. 7). The phylogenetic analysis, based on the nrITS sequences, suggested that *P. chinense* is sister to a clade formed by *Hydrobryopsis sessilis*, *P. stylosum*, *P. schmiditianum*, *P. wallichii*, *P. munnarense*, *Zeylanidium lichenoides* and *Z. olivaceum* with strong support (PP = 0.99, BS = 86%) (Fig. 8).

# Discussion

## Morphology

Amongst the 17 known species of *Polypleurum*, only two species, i.e. *P. longistylosum and P. schmidtianum*, have a single stamen and the shoots or tufts of leaves borne on both

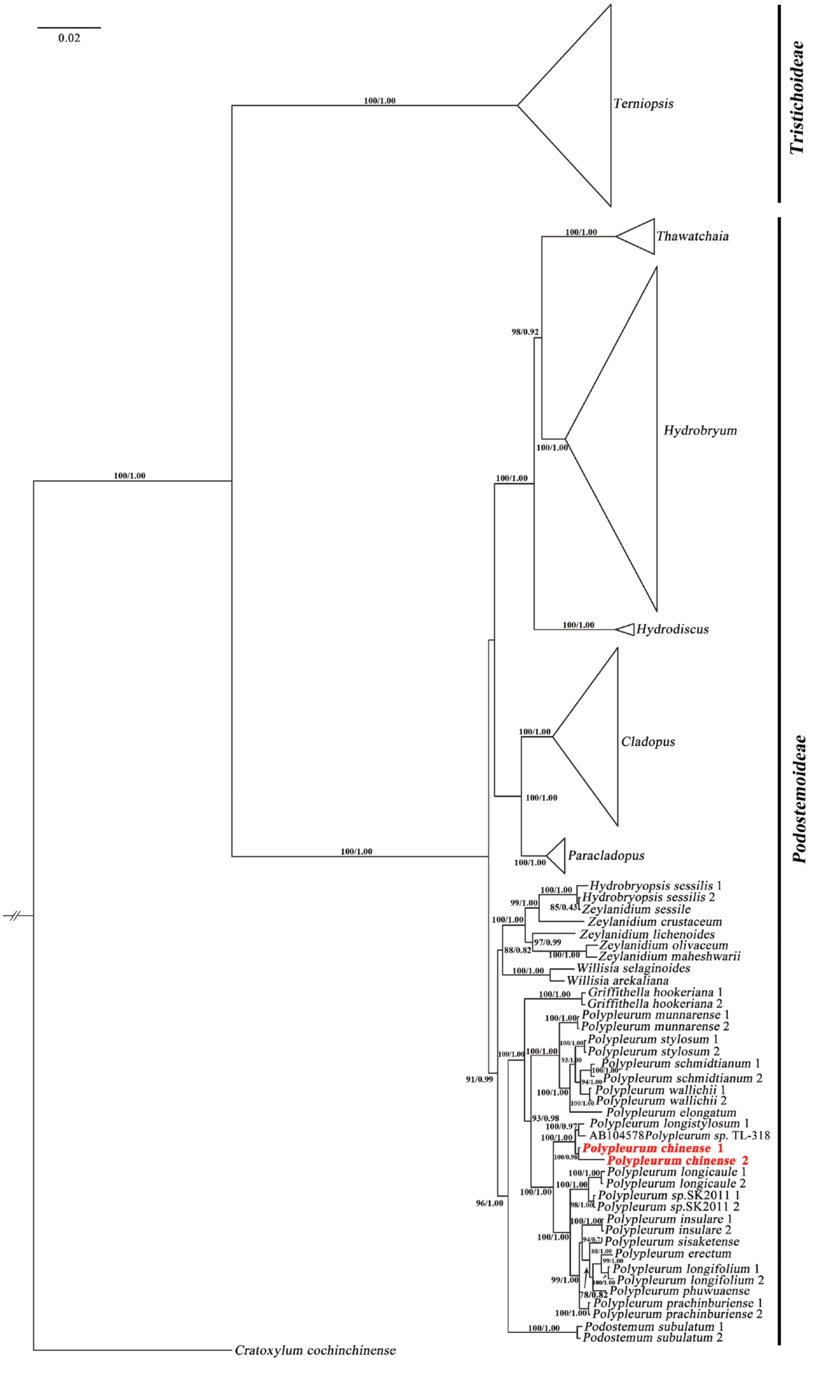


**Figure 7.** Phylogenetic tree of Asian Podostemaceae, based on Bayesian Inference of *matK* sequences. Numbers above and below branches indicate RAxML (left) bootstrap probabilities (BP) and Bayesian (right) posterior probabilities (PP), respectively. Triangles indicate clades containing multiple species (samples) of one genus examined and the vertical lengths of triangles reflect the number of species (samples) examined.

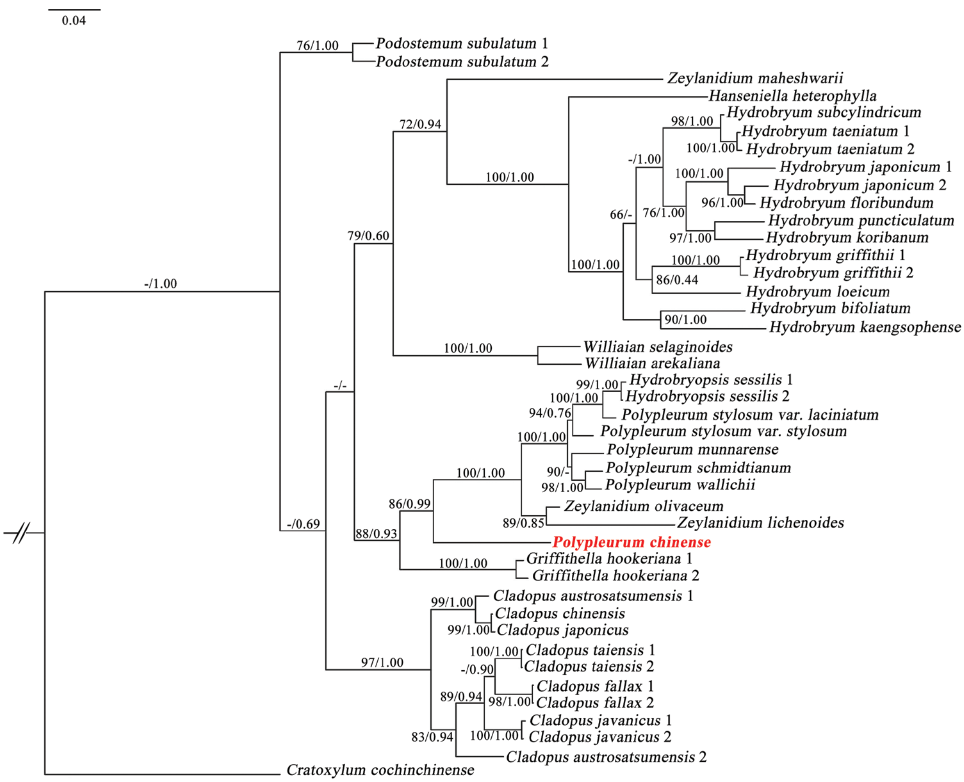


**Figure 8.** Phylogenetic tree of Asian Podostemaceae, based on Bayesian Inference of nrITS sequences. Numbers above and below branches indicate RAxML (left) bootstrap probabilities (BP) and Bayesian (right) posterior probabilities (PP), respectively.

sides of the root between the root branches. Although *P. chinense* has an overall morphology similar to *P. longistylosum*, there are some obvious differences, such as narrower roots (0.6–0.8 mm vs.1.0–1.5 mm), leaves appearing in tufts of 8–12 (vs. 4–8) and being as long as 23.1 mm (vs. 5 mm) long; fewer bracts (4 vs. 6); spathella with short spiny or glandular hairs (vs. papillate) on its coat; capsule with 12–14 conspicuous ribs (vs. 10–12 inconspicuous ribs) (Kato 2006). The morphological differences between *P. chinense* and *P. schmidtianum* are more prominent. In *P. schmiditianum*, the roots are wider (ca. 2–4 mm), the peduncle is much longer (ca. 6–7 mm); the ovary is protruding from the spathella at anthesis, 2-locular; the stigmas are much shorter than the ovary; and the capsule is 8-ribbed (Kato 2006) (Table 1). In addition, the previous study reported that the capsule stalk length of *Polypleurum* species was 4–20 mm (Kato 2006), but the capsule stalk of the new species is less than 2 mm long, which is the shortest of all the known species.

## Comparative analysis of the plastomes

A comparison of the plastome of *Polypleurum chinense* is made with six other species of Podostemaceae with available data (Table 3). The plastome lengths of the seven species

**Table 3.** Statistics on the basic features of the plastid genomes of *Polypleurum chinense* and related taxa.

| Species | Voucher | Accession no. | Length (bp) | LSC (bp) | SSC (bp) | IR(bp) | GC content (%) | No. of PCGs | No. of tRNA | No. of rRNA |
|---|---|---|---|---|---|---|---|---|---|---|
| *Polypleurum chinense* | CBH 04407 | OL944404 | 132,110 | 79,022 (~ 59.8%) | 12,310 (~ 9.3%) | 20,389 × 2(~ 30.9%) | 34.85 | 74 | 30 | 4 |
| *Apinagia riedelii* | C.P. Bove 2513 (R) | MN165812 | 134,912 | 85,377 (~ 61.0%) | 12,437 (~ 8.9%) | 21,049 × 2 (~ 30.1%) | 34.90 | 74 | 30 | 4 |
| *Marathrum utile* | AMB 497 (ANDES) | MN165814 | 131,951 | 79,778 (~ 60.5%) | 12,283 (~ 9.3%) | 19,945 × 2 (~ 30.2%) | 35.10 | 73 | 29 | 4 |
| *Marathrum capillaceum* | C.P. Bove 2493 (R) | MN165813 | 134,374 | 79,990 (~ 59.5%) | 12,302 (~ 9.2%) | 21,041 × 2 (~ 31.3%) | 35.00 | 75 | 30 | 4 |
| *Marathrum foeniculaceum* | W. D. Stevens - 32072 | MK995178 | 131,600 | 79,506 (~ 60.4%) | 12,262(~ 9.3%) | 19,916×2 (~ 30.3%) | 35.10 | 76 | 30 | 4 |
| *Tristicha trifaria* | A. Mesterhazy MLI 128(Z) | MN165816 | 130,285 | 78,925 (~ 60.6%) | 12,662 (~ 9.7%) | 19,349 × 2 (~ 29.7%) | 36.40 | 74 | 30 | 4 |
| *Terniopsis yongtaiensis* | CBH 04587 | OM717943 | 129,074 | 79,000 (~ 61.2%) | 13,066 (~ 10.1%) | 18,504 × 2 (~ 28.7%) | 36.20 | 72 | 30 | 4 |

varied from 129,074 bp (*Terniopsis yongtaiensis*) to 134,912 bp (*Apinagia riedelii*), with *T. yongtaiensis* being the shortest. For the LCS and SSC regions, the extent of length variation between these species is not evident. The number of PCGs in these species is similar to that of most angiosperms, according to a comparative analysis of gene content (Jin et al. 2020b). The numbers of tRNA and rRNA genes, as well as the GC content, are substantially conserved in all of these plastomes, as shown by our findings. The structure of the IR greatly influences the structural integrity of the entire genome. In all compared species, the *ycf1* and *ycf2* genes, which are two giant open reading frames found in most higher plants, are lost, resulting in a significant reduction of IR regions, hence reducing the size of their plastomes. The loss of *ycf1* and *ycf2* genes were also found in the plastome of Poaceae (Guisinger et al. 2010), Geraniaceae (Weng et al. 2014) and Ericaceae (Braukmann et al. 2017). The functions of *ycf1* and *ycf*2 genes are still controversial and they have not been classified as genes involved in the genetic and photosynthetic systems (Drescher et al. 2000). The size of the IR regions varied amongst compared species, largely due to the evolutionary transfer of complete genes from the SSC regions into the IR or vice versa (Chumley et al. 2006; Wicke et al. 2011).

In *Polypleurum chinense*, *Tristicha trifaria* and *Terniopsis yongtaiensis*, the *rps15 gene* is found at the SSC/IR border, but it is shifted to IRs in *Apinagia riedelli*, *Marathrum utile*, *M. capillaceum* and *M. foeniculaceum* due to the expansion at the IR/SSC boundary. Jin et al. (2020b) found that the relocation of *rps15* gene in *M. foeniculaceum* did not accumulate significant mutations, either because it occurred recently or because the substitution rate was too low to detect. In *P. chinense*, the *trnG-UCC* gene mutates to *trnT-CGU* and, in *M. capillaceum*, it is lost. In addition, it is found that all the species compared have a gene inversion from *trnK-UUU to rbcL*in the LSC region and the size of the inversions for each species is similar (ranging from 51 kb for *P. chinense* to 52 kb for *A. riedelli*). It represents an essential mechanism for plastome rearrangements (Mower and Vickrey 2018). The *rpl23* gene is lacking in plastomes of the other five compared species, except *T. yongtaiensis* (Zhang et al. 2022). However, it is present in plastomes of non-Podostemaceae species, such as *Bonnetia paniculata* and *Cratoxylum cochinchinense* (Bedoya et al. 2019; Jin et al. 2020b). We do not know the extent of gene loss amongst other Podostemaceae species in China and future sequencing projects will inevitably offer insights into rates and mechanisms of gene loss in plastid genomes.

## Phylogenetic analysis

The present study confirmed *Polypleurum chinense* is a new species, based on the phylogenetic analysis of *matK* and nrITS sequences, which indicated that *P. chinense* is related to *P. longistylosum*. The phylogenetic study demonstrated that *matK* sequence performed better for the phylogenetic analysis of *P. chinense*, which was consistent with the previous studies (Koi et al. 2012; Kato et al. 2017). The ability of discrimination between species based on nrITS was comparatively poor (Khanduri et al. 2015). Despite the fact that nrITS performed quite well (79%) in angiosperms, lower discrimination success was reported for Ranunculales (6.7%) and Laurales (14.3%) (China Plant BOL 2011). The inconsistencies in species ascriptions between nrITS may result from hybridisation and introgression or incomplete lineage sorting (Alvarea and Wendel 2003; Rieseberg et al. 2006; Feliner and Rosselló 2007). As a result, utilising plastid DNA markers alone may not be sufficient to discriminate between closely-related species. Furthermore, using a single individual for each species, based on plastid DNA markers, might be deceptive (China Plant BOL 2011).

## The establishment of the new species

The identification of the new *Polypleurum* brings the total number of genera of Podostemaceae to four in China. The discovery of *Polypleurum* in China not only enriches the angiosperm flora of China, but also provides strong evidence for a close connection between the subtropical flora of Fujian and the tropical flora of Southeast Asia.

## Key to the genera of Podostemaceae of China

| | |
|---|---|
| 1 | Flowers axillary; spathella absent; tepals 3; stamens 2 or 3............***Terniopsis*** |
| – | Flowers terminal; spathella present; tepals 2; stamens 1 or 2 .......................**2** |
| 2 | Leaves of fertile stems digitate, 3–9-segmented, scattered, imbricate; capsule smooth ..........................................................................***Cladopus*** |
| – | Leaves of fertile stems scale-like or needle-like, distichous; capsule ribbed...**3** |
| 3 | Stamens 2, forked; leaves of fertile stems scale-like; capsules appressed to roots; bracts boat-shaped, entire; roots foliose, with tufts of linear leaves scattered over dorsal surface.........................................................***Hydrobryum*** |
| – | Stamen 1, simple; leaves of fertile stems needle-like, capsules erect; bracts ribbon-like; roots, ribbon-like, with tufts of leaves along both sides of root... ...................................................................................***Polypleurum*** |

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## Supplementary material 1

**Appendix**

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Data type: Primers, Voucher information (docx. file)

Explanation note: **Table S1.** Primers used in this study. **Table S2.** Voucher information for the taxa used in the present study (*matK*). **Table S3.** Voucher information for the taxa used in the present study (ITS).



Link: https://doi.org/10.3897/phytokeys.199.85679.suppl1

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# Pollen morphology of the genera *Hidalgoa* and *Dahlia* (Coreopsideae, Asteraceae): implications for taxonomy

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## Abstract

*Hidalgoa* and *Dahlia* are two closely related genera in Asteraceae, tribe Coreopsideae whose limits need to be clarified. Pollen morphology has been useful for delimitation at the genus level in this family. To better define these genera, the morphology of pollen grains was observed and measured using light and scanning electron microscopy. The pollen grains of 25 species of *Dahlia* and *Hidalgoa* were acetolyzed and analyzed. Pollen is tricorporate in most of the species studied, although in a few species in *Dahlia*, grains were found to be hexacolporate. The most outstanding differentiating characters among species of *Dahlia* and *Hidalgoa* are colpus length (greater in *Hidalgoa*) and shape of spines (conical in *Hidalgoa*). In addition, lalongate ora are larger in *Hidalgoa* than in *Dahlia*. A PCA analysis of thirteen pollen characters, identified species of *Hidalgoa* in a discrete group and *Dahlia cuspidata* as an outlier. These distinctive attributes in pollen morphology support the idea that pollen morphology is useful for delimitation at the generic level in the *Dahlia* clade. Further evidence from other sources, genetic or anatomical, might contribute to demarcating *Dahlia* and *Hidalgoa*, and provide insight into the family's evolutionary history.

## Keywords

Asteraceae, *Dahlia*, hexacolporate, *Hidalgoa*, pollen morphology, tricolporate

## Introduction

*Hidalgoa* La Llave and *Dahlia* Cav. are two closely related genera in tribe Coreopsideae of the Asteraceae (Sørensen 1969; Turner 2010; Sánchez-Chávez et al. 2019). *Hidalgoa* comprises four accepted species (Panero 2007; Turner 2010), with *H. ternata* La Llave having the most widespread distribution, from Mexico to northern South America. The rest have restricted distributions. *H. pentamera* Sherff and *H. uspanapa* B.L. Turner are endemic to southeastern Mexico, and *H. werklei* Hook.f. is distributed in Costa Rica and in the Andean region of Colombia. Habitats for the species in *Hidalgoa* are cloud forests, mainly in microhabitats associated with rivers and very humid places. Remarkably, plants of *Hidalgoa* are vines, climbing onto vegetation by twisting petioles. The heads of *Hidalgoa* have five to twelve pistillate, fertile ray florets, and functionally staminate disc florets (Fig. 1A, B). Cypselae are compressed, with two apical lateral cusps (Panero 2007; Crawford et al. 2009; Turner 2010; Pruski and Robinson 2015).

*Dahlia* includes 40 species, of which 37 are endemic to Mexico (Villaseñor and Redonda-Martínez 2018; Carrasco-Ortiz et al. 2019; Reyes-Santiago et al. 2019), distributed mostly in pine and oak forests (Carrasco-Ortiz et al. 2019). Based on their chromosome numbers and morphological descriptors such as life form, size, shape, and segmentation of the compound leaves, four sections were recognized in *Dahlia* (Sørensen 1969): sect. *Epiphytum* with a single epiphytic species (*D. macdougallii* Sherff), sect. *Pseudodendron* with three suffrutescent species, sect. *Entemophyllon* with eight suffrutescent species with solid petioles, and sect. *Dahlia* with 28 herbaceous species with hollow petioles (Suppl. material 1: Table S1). With the exception of the epiphytic species, the rest possess tubers, and a few are rupicolous. Some of the species in sect. *Entemophyllon* that live for more than one season, have stems that become quite woody and give the full-grown plants a shrubby aspect. In *Dahlia* the ray florets can be neutral, pistillate fertile or sterile, while the disk florets are hermaphroditic, and vary in number from 15 to 170 (Fig. 1C, D) (Sørensen 1969; Pruski and Robinson 2015). Cypselae are compressed, linear to spatulate, sometimes shallowly tuberculate, with pappus absent or consisting of 2(5) small teeth, weak filiform, sometimes elongated to 1 mm caducous bristles (Sørensen 1969; Panero 2007; Pruski and Robinson 2015).

*Hidalgoa* was thought to be closely related to the genera *Fitchia* Hook. f, *Moonia* Arn., *Oparanthus* Sherff, and *Petrobium* R. Br., for sharing the character of functional male disc florets (Ryding and Bremer 1992). The similar floral morphology of *Hidalgoa* and *Dahlia* was suggested to be the result of a close relationship (Sørensen 1969; Turner 2010). Furthermore, a previous phylogenetic molecular study that included species of *Dahlia* and *Hidalgoa* found that the latter was embedded in a large clade with *Dahlia*; species of the two genera formed a well-supported monophyletic group (Sánchez-Chávez et al. 2019). However, taxonomic decisions will not be made until additional anatomical and palynological characters, as well as further molecular data, can be analyzed.

In spite of the uniform pollen morphology in the genera of Asteraceae, some pollen characters have been shown to be useful for supporting recognition and delimitation in numerous genera (El-Ghazaly and Anderberg 1995). Some examples

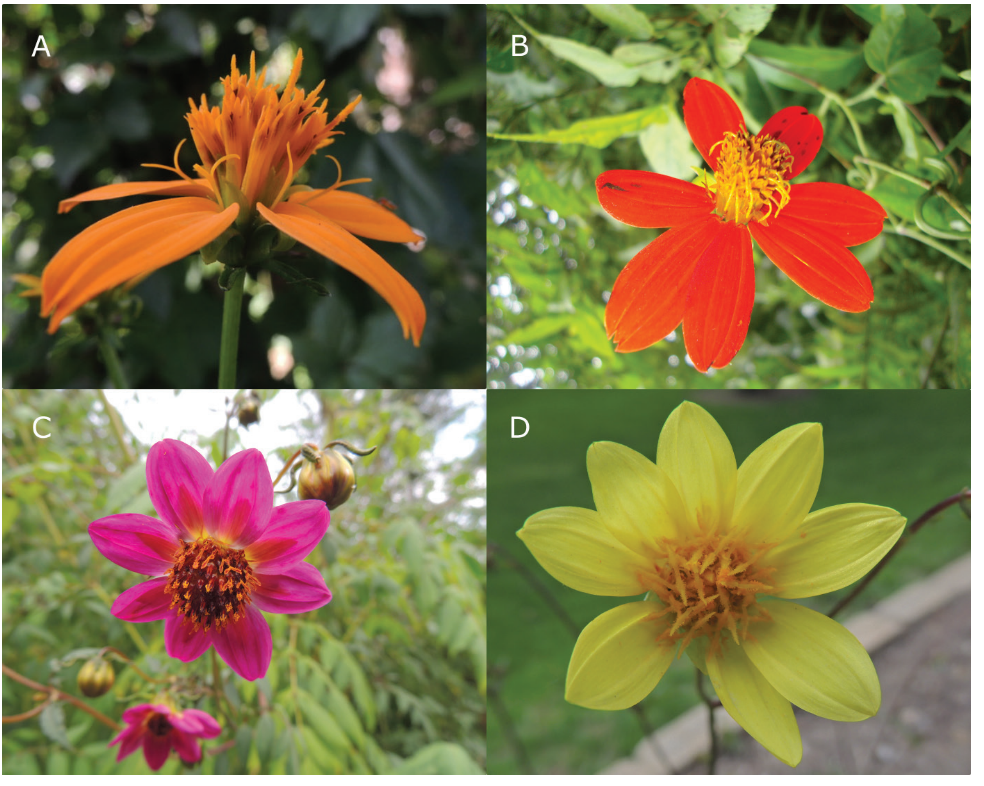


**Figure 1.** Morphological variation in *Dahlia* and *Hidalgoa* species **A** *Hidalgoa pentamera* **B** *Hidalgoa uspanapa* **C** *Dahlia moorei* **D** *Dahlia mixtecana*. Photos by E. Sánchez-Chávez (**A, C, D**) and Andrés Ortiz (**B**).

of differentiating characters in the taxa of this family are the polar diameter and dimensions of the colpus and endoaperture in *Viguiera* Kunth (Magenta et al. 2010) and in *Xanthium* L., the length and number of spines and the number of columellae (Coutinho et al. 2020). Sexine thickness, the type of aperture, and spine dimensions are the differentiating traits for species of *Stilpnopappus* and *Strophopappus* (Carrijo et al. 2013), as is pollen surface ornamentation in the complex *Phaeostigma* of the genus *Ajania* (Huang et al. 2017). Pollen type and pollen grain shape are taxonomically useful for distinguishing species and genera of the subtribe Lepidaploinae (Marques et al. 2021).

The pollen in tribe Coreopsideae is helianthoid (exine with columellae containing internal foramina and clearly caveate), predominantly spheroidal, tricolporate, echinate, with internal foramina, full cavea present, and endexine much thicker than the foot layer (Blackmore et al. 2009).

Pollen morphology has not been analyzed in detail for the species of *Hidalgoa* or *Dahlia*. Previous palynological research by Wodehouse (1929) on four *Dahlia* species identified the presence of six apertures (hexacolporate) in pollen grains. This attribute constitutes a notable exception within the family. Further studies examined and described the meiotic stages of the pollen mother cell in *Dahlia* to determine the development of these apertures (Wodehouse 1930).

The aims of this study are to compile and compare pollen morphology of the species of *Hidalgoa* and *Dahlia* to identify informative characters and understand the relationships and limits of these taxa.

## Materials and methods

Twenty-five samples of pollen grains were obtained from herbarium specimens deposited in the IBUG (Instituto de Botánica de la Universidad de Guadalajara) and XAL (Instituto de Ecología, A. C.) herbaria. Vouchers of specimens are included in Table 1.

Pollen grains were acetolyzed according to the methodology of Erdtman (1960), and for difficult material in which compounds formed thin coats on the grains that interfered during the scanning process, the suggestions of Fonnegra (1989) were implemented. The grains were immersed in glacial acetic acid for 24 hours before acetolysis and then transferred to the acetolysis mixture for 1 to 6 hours and the temperature of

**Table 1.** Studied species of *Hidalgoa* and *Dahlia* for analyzing pollen grains, indicating their voucher and the herbarium in which they were deposited. Herbarium acronyms are according to Index Herbariorum.

| Species | Locality | Collector | Herbarium |
|---|---|---|---|
| *Dahlia atropurpurea* P.D. Sørensen | Guerrero | A. Castro C. 2251 | IBUG |
| *Dahlia australis* (Sherff) P.D. Sørensen | Puebla | A. Rodriguez C. 6491 | IBUG |
| *Dahlia barkerae* Knowles & Westc. | Jalisco | A. Castro C. 2304 | IBUG |
| *Dahlia brevis* P.D. Sørensen | México | A. Rodriguez C. 5869 | IBUG |
| *Dahlia campanulata* Saar, P.D. Sørensen & Hjert. | Oaxaca | A. Rodriguez C. 6495 | IBUG |
| *Dahlia coccinea* Cav. | Jalisco | A. Rodriguez C. 7490 | IBUG |
| *Dahlia cordifolia* (Sessé & Moc.) McVaugh | Guerrero | A. Rodriguez C. 5224 | IBUG |
| *Dahlia cuspidata* Saar, P.D. Sørensen & Hjert. | Guanajuato | E. Ventura 9581 | IBUG |
| *Dahlia dissecta* S. Watson | | A. Rodriguez C. 6412 | IBUG |
| *Dahlia imperialis* Roezl ex Ortgies | Chiapas | A. Rodriguez C. 6983 | IBUG |
| *Dahlia linearis* Sherff | Guanajuato | E. Ventura 6143 | IBUG |
| *Dahlia merckii* Lehm. | | L. Gutierrez s/n | IBUG |
| *Dahlia mollis* P.D. Sørensen | Hidalgo | A. Rodriguez C. 6414 | IBUG |
| *Dahlia neglecta* Saar | Hidalgo | A. Rodriguez C. 6466 | IBUG |
| *Dahlia parvibracteata* Saar & P.D. Sørensen | Guerrero | A. Rodriguez C. 6092 | IBUG |
| *Dahlia pugana* Aarón Rodr. & Art. Castro | Jalisco | A. Rodriguez C. 7731 | IBUG |
| *Dahlia rudis* P.D. Sørensen | | A. Ma. Hernández 12 | XAL |
| *Dahlia rupicola* P.D. Sørensen | Durango | A. Rodriguez C. 6133 | IBUG |
| *Dahlia scapigera* Knowles & Westc. | Queretaro | E. Gonzalez P. 560 | IBUG |
| *Dahlia sorensenii* H.V. Hansen & Hjert. | | J. Suárez J. 584 | IBUG |
| *Dahlia spectabilis* Saar & P.D. Sørensen | San Luis Potosí | A. Rodriguez C. 6352 | IBUG |
| *Dahlia tenuicaulis* P.D. Sørensen | Jalisco | M. Chazaro B. 5736 | IBUG |
| *Dahlia wixarika* Art. Castro, Carr.-Ortiz & Aarón Rodr. | Jalisco | A. Castro C. 2983 | IBUG |
| *Hidalgoa pentamera* Sherff | Veracruz | E. Sánchez-Chávez 28 | XAL |
| *Hidalgoa ternata* La Llave | Veracruz | T. B. Croat 25505 | XAL |

the water bath was raised to 96 °C. For light microscopy (LM), the pollen grains were mounted in glycerol jelly, sealed, and then examined with a Carl Zeiss Fomi III Optical Microscope, equipped with a Cannon Power Shot G9 digital camera. Permanent slides were deposited in the Palynological Laboratory of the Instituto de Ecología, A. C. The following pollen measurements were obtained from 25 grains per sample: polar axis, equatorial diameter, exine thickness, colpus length, colpus width, ora width, ora length, spinae length, spine width at base and number of apertures.

To observe the pollen with a scanning electron microscope (SEM), acetolyzed pollen grains were washed in ethanol and later in water. Grains were sputter-coated with gold and observed using a Carl Zeiss EVO-50 scanning electron microscope. The terminology of Halbritter et al. (2018) was used, and for pollen structure the terminology of Erdtman (1969) was followed. Number of spines/100 $\mu m^2$, colpus end, base of spine and pollen surface ornamentation were described for five grains per sample. Final morphological data are presented in Table 2.

A matrix based on thirteen pollen characters was constructed. To estimate the quantitative variation within *Dahlia* and *Hidalgoa*, each character was measured and the average for each species was estimated. Qualitative characters were coded with

**Table 2.** Pollen attributes analyzed on the studied species of *Hidalgoa* and *Dahlia*. The values given in exine, colpus, ora, spine are averages. Cl colpus length, Cw colpus width, Ow Os width, Ol Os length, Swab Spine Width at base.

| Specie | Polar axis (P)(µm) | | | Equatorial diameter (E)(µm) | | | P/E | Pollen shape | Number of apertures |
|---|---|---|---|---|---|---|---|---|---|
| | Min | Max | Mean | Min | Max | Mean | | | |
| *Dahlia atropurpurea* | 28.18 | 32.70 | 30.43 | 28.85 | 32.46 | 30.92 | 0.98 | Oblate-spheroidal | Tricolporate |
| *Dahlia australis* | 25.38 | 29.98 | 28.43 | 23.88 | 30.49 | 28.32 | 1.00 | Spheroidal | Tricolporate |
| *Dahlia barkerae* | 30.62 | 36.15 | 33.78 | 30.86 | 34.82 | 33.34 | 1.01 | Prolate-spheroidal | Tricolporate |
| *Dahlia brevis* | 26.41 | 32.33 | 29.04 | 25.53 | 32.58 | 29.41 | 0.99 | Oblate-spheroidal | Tricolporate |
| *Dahlia campanulata* | 30.61 | 34.72 | 32.84 | 30.50 | 34.48 | 32.96 | 1.00 | Spheroidal | Tricolporate |
| *Dahlia coccinea* | 29.42 | 39.47 | 34.74 | 31.66 | 39.83 | 34.79 | 1.00 | Spheroidal | Tricolporate |
| *Dahlia cordifolia* | 27.80 | 32.03 | 29.64 | 28.00 | 33.46 | 30.61 | 0.97 | Oblate-spheroidal | Tricolporate |
| *Dahlia cuspidata* | 31.21 | 35.48 | 33.16 | 31.63 | 37.05 | 34.44 | 0.96 | Oblate-spheroidal | Hexacolporate/ Tricolporate |
| *Dahlia dissecta* | 28.34 | 32.50 | 30.55 | 27.72 | 32.21 | 30.31 | 1.01 | Prolate-spheroidal | Hexacolporate/ Tricolporate |
| *Dahlia imperialis* | 25.95 | 30.64 | 28.04 | 25.78 | 31.50 | 28.94 | 0.97 | Oblate-spheroidal | Hexacolporate/ Tricolporate |
| *Dahlia linearis* | 29.83 | 33.79 | 31.82 | 29.85 | 34.99 | 32.68 | 0.97 | Oblate-spheroidal | Tricolporate |
| *Dahlia merckii* | 26.19 | 31.65 | 28.54 | 28.64 | 34.78 | 31.61 | 0.90 | Oblate-spheroidal | Hexacolporate/ Tricolporate |
| *Dahlia mollis* | 26.59 | 30.26 | 28.38 | 28.14 | 32.36 | 29.93 | 0.95 | Oblate-spheroidal | Tricolporate |
| *Dahlia neglecta* | 32.72 | 37.48 | 35.06 | 30.75 | 37.77 | 35.77 | 0.98 | Oblate-spheroidal | Tricolporate |
| *Dahlia parvibracteata* | 29.58 | 32.88 | 31.29 | 28.73 | 32.67 | 31.57 | 0.99 | Oblate-spheroidal | Hexacolporate/ Tricolporate |
| *Dahlia pugana* | 29.11 | 33.23 | 31.09 | 29.56 | 33.94 | 31.78 | 0.98 | Oblate-spheroidal | Tricolporate |
| *Dahlia rudis* | 30.08 | 35.73 | 33.29 | 33.40 | 36.78 | 34.94 | 0.95 | Oblate-spheroidal | Hexacolporate/ Tricolporate |
| *Dahlia rupicola* | 28.20 | 35.37 | 31.16 | 26.92 | 32.40 | 30.08 | 1.04 | Prolate-spheroidal | Tricolporate |
| *Dahlia scapigera* | 26.68 | 32.66 | 30.56 | 27.01 | 31.57 | 29.38 | 1.04 | Prolate-spheroidal | Tricolporate |
| *Dahlia sorensenii* | 28.87 | 34.80 | 31.90 | 30.73 | 36.42 | 33.90 | 0.94 | Oblate-spheroidal | Hexacolporate/ Tricolporate |
| *Dahlia spectabilis* | 27.71 | 34.07 | 30.33 | 25.20 | 32.12 | 30.11 | 1.01 | Prolate-spheroidal | Tricolporate |
| *Dahlia tenuicaulis* | 28.54 | 32.84 | 31.03 | 31.58 | 35.37 | 33.01 | 0.94 | Oblate-spheroidal | Tricolporate |
| *Dahlia wixarika* | 27.85 | 33.23 | 30.12 | 27.24 | 32.07 | 30.15 | 1.00 | Spheroidal | Tricolporate |
| *Hidalgoa pentamera* | 25.73 | 30.35 | 27.97 | 25.10 | 30.27 | 26.94 | 1.04 | Prolate-spheroidal | Tricolporate |
| *Hidalgoa ternata* | 28.01 | 34.07 | 30.36 | 26.45 | 32.08 | 29.63 | 1.02 | Prolate-spheroidal | Tricolporate |

**Table 2.** Continued.

| Specie | Exine (μm) | Colpus (μm) | | | Os (μm) | | Spine | | Number of spines/100 μm$^2$ | Base of spine |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Cl | Cw | Copus ends | Ol | Ow | Length (μm) | Swab (μm) | | |
| *Dahlia atropurpurea* | 2.88 | 3.79 | 3.12 | acute | 2.28 | 2.55 | 7.80 | 5.99 | 7–8 | distended |
| *Dahlia australis* | 2.63 | 3.01 | 3.08 | acute | 2.56 | 2.05 | 6.01 | 4.51 | 6–8 | distended |
| *Dahlia barkerae* | 3.58 | 6.38 | 5.63 | acute | 2.20 | 3.09 | 7.55 | 7.21 | 4–5 | distended |
| *Dahlia brevis* | 1.81 | 4.83 | 4.74 | obtuse | 2.06 | 2.93 | 7.37 | 5.79 | 7–10 | distended |
| *Dahlia campanulata* | 2.24 | 4.34 | 1.54 | obtuse | 1.44 | 1.92 | 7.35 | 6.99 | 5–7 | smooth |
| *Dahlia coccinea* | 3.05 | 5.42 | 4.53 | obtuse | 3.18 | 2.71 | 9.81 | 8.17 | 4–5 | distended |
| *Dahlia cordifolia* | 2.96 | 5.75 | 4.26 | obtuse | 2.32 | 2.74 | 7.87 | 6.64 | 6–7 | smooth |
| *Dahlia cuspidata* | 1.64 | 8.61 | 6.22 | obtuse | 4.75 | 5.24 | 9.07 | 6.94 | 4–6 | distended |
| *Dahlia dissecta* | 2.88 | 3.80 | 2.95 | obtuse | 2.18 | 2.35 | 7.33 | 6.57 | 5–7 | smooth |
| *Dahlia imperialis* | 1.98 | 3.85 | 2.93 | obtuse | 2.17 | 2.93 | 7.46 | 5.95 | 6–8 | smooth |
| *Dahlia linearis* | 2.19 | 3.98 | 4.44 | obtuse | 2.42 | 3.70 | 5.29 | 5.59 | 8–10 | smooth |
| *Dahlia merckii* | 3.05 | 4.59 | 3.16 | obtuse | 1.45 | 2.75 | 6.97 | 6.25 | 7–8 | distended |
| *Dahlia mollis* | 1.88 | 4.14 | 2.42 | obtuse | 2.20 | 2.42 | 7.79 | 6.27 | 5–7 | distended |
| *Dahlia neglecta* | 4.20 | 4.81 | 3.34 | obtuse | 2.35 | 3.03 | 6.82 | 6.80 | 4–5 | distended |
| *Dahlia parvibracteata* | 3.11 | 4.82 | 2.97 | obtuse | 2.05 | 2.97 | 8.97 | 6.86 | 6–7 | distended |
| *Dahlia pugana* | 3.42 | 4.41 | 4.08 | obtuse | 2.68 | 2.23 | 6.22 | 6.35 | 6–7 | distended |
| *Dahlia rudis* | 3.06 | 4.19 | 2.50 | acute | 2.41 | 2.50 | 8.19 | 7.74 | 6–7 | narrower |
| *Dahlia rupicola* | 1.71 | 3.36 | 2.76 | obtuse | 2.41 | 2.76 | 8.36 | 5.99 | 6–7 | distended |
| *Dahlia scapigera* | 2.15 | 6.58 | 2.65 | acute | 2.68 | 2.65 | 7.90 | 6.09 | 4–5 | narrower |
| *Dahlia sorensenii* | 1.68 | 5.17 | 2.40 | obtuse | 1.73 | 2.40 | 9.07 | 6.12 | 4–5 | narrower |
| *Dahlia spectabilis* | 2.46 | 4.72 | 2.05 | obtuse | 1.54 | 2.05 | 8.57 | 6.00 | 6–8 | distended |
| *Dahlia tenuicaulis* | 2.82 | 4.19 | 4.94 | obtuse | 2.56 | 2.79 | 9.22 | 6.43 | 7 | distended |
| *Dahlia wixarika* | 2.42 | 3.36 | 2.63 | obtuse | 2.95 | 2.63 | 7.44 | 6.01 | 7–9 | narrower |
| *Hidalgoa pentamera* | 1.78 | 14.97 | 3.29 | acute | 2.06 | 9.98 | 5.47 | 6.09 | 4–5 | narrower |
| *Hidalgoa ternata* | 1.71 | 14.55 | 3.34 | acute | 2.89 | 8.21 | 5.80 | 4.63 | 4 | narrower |

the following states: number of apertures (tricolporate:0/ hexacolporate:1), colpus end (obtuse:0/ acute:1), base of spine (narrower:0/ distended:1) lalongate ora (absent:0/ present:1; present/absent:2) (Suppl. material 1: Table S2). A principal component analysis (PCA) was run in R (R Core Team. 2019) to evaluate the contribution of each pollen variable to the affiliation of species (Table 3). Graphical representation displayed distribution of thirteen pollen characters.

## Results

Pollen grains from a total of 25 species belonging to *Dahlia* (23 species) and *Hidalgoa* (2 species) were analyzed. Table 2 summarizes measurements and character states and Figs 2, 3 and 4 show the diversity in their pollen morphology.

The majority of species analyzed in *Dahlia* are tricoloporate. However, two out of ten pollen grains are hexacolporate in *D. cuspidata*, *D. dissecta*, *D. imperialis*, *D. merckii*, *D. parvibracteata*, *D. rudis* and *D. sorensenii*, with three apertures on one hemisphere and three on the other hemisphere (Fig. 2U). The shape is spheroidal-oblate, spheroidal or spheroidal-prolate (P/E = 0.90–1.04) and radially symmetric. Pollen size

**Table 3.** Palynological characters used in the multivariate analysis of *Hidalgoa* and *Dahlia* species. The contribution of every character for Axis 1 and Axis 2 is indicated (see Fig. 4).

| | | Character | Axis 1 | Axis 2 |
|---|---|---|---|---|
| 1 | Pa | Polar axis (μm) | 1.63 | 23.53 |
| 2 | Et | Exine thickness (μm) | 6.59 | 2.30 |
| 3 | Cl | Colpus length (μm) | 25.18 | 1.19 |
| 4 | Cw | Colpus width (μm) | 8.88 | 10.75 |
| 5 | Ow | Os width (μm) | 22.82 | 1.34 |
| 6 | Ol | Os length(μm) | 3.75 | 11.48 |
| 7 | Sl | Spinae length (μm) | 7.98 | 10.97 |
| 8 | Swab | Spine width at base (μm) | 5.48 | 20.32 |
| 9 | Na | Number of apertures | 1.06 | 2.37 |
| 10 | Ns | Number of spines/100 μm$^2$ | 4.49 | 11.70 |
| 11 | Ce | Colpus ends | 8.81 | 0.25 |
| 12 | Sb | Base of spine | 3.14 | 1.55 |
| 13 | Osl | Os lalongate | 0.20 | 2.23 |

is P = 25.3 (31) 39.4 μm, E = 23.8 (31.6) 39.8 μm (Fig. 6A), and corresponds to a medium grain (Erdtman 1969). The ora are rarely lalongate, and situated distally from the equator, length 1.04 (2.51) 5.41 μm, and width 1.27 (3.60) 8.61 μm (Figs 2B, 2F, 6B), rarely acute. Colpus usually short, almost equal to ora length, more or less oval to oblong, length 2.24 (4.81) 9.2 μm, and width 1.27 (2.85) 5.89 μm (Figs 3E, 3H, 3K, 3N, 4I, 4M, 6C), apices obtuse to acute. Exine thickness thin, excluding spines, ranging from 1.1 (2.59) to 5.6 μm (Fig. 2). Ornamentation echinate; spines 4 (6–7) 10/100 μm$^2$, spine length from 4.2 (7.75) to 12.26 μm, and width at base from 3.06 (6.40) to 10.35 μm, shape of spines more deltate than conical (Fig. 6D), with a distended or narrower base and with acuminate apex (Figs 3, 4). Tectum with the base of the spine always microperforate.

Pollen grains in the species of *Hidalgoa* analyzed are tricolporate and spheroidal-prolate (P/E = 1.02–1.04), radially symmetric. Pollen size is P = 25.7 (29.1) 34 μm, E = 25.1 (28.5) 32 μm (Fig. 6A), and corresponds to a medium grain (Erdtman 1969). The lalongate ora length 1.71 (2.47) to 4.87 μm, and width 6.32 (9.39) to 13.02 μm (Figs 2W, 6B), usually wider than longer and with acute apices. The colpus is elliptical, length 11.28 (14.76) to 16.83 μm, and width 2.69 (3.31) to 4.21 μm (Fig. 6C), apex always acute (Figs 3A, 3B, 4N). Exine is thinner, 1.12 (1.74) 2.95 μm excluding the spines. Ornamentation is echinate; spines 4–5/100 μm$^2$, spine length ranging from 4 (5.6) to 6.77 μm and width at base 3.6 (5.3) to 7.3 μm, shape of spines conical (Figs 3C, 4O, 6D), with apex acute. Tectum with base of spine always microperforate. Palynological characters of the two studied species of *Hidalgoa* are similar, only a slight variation in pollen grain size was detected.

Results of the PCA indicate that the first two components explain 46.04% of the observed variation (see Table 3 to for the contribution of each variable to Dim 1 and Dim 2). A bidimensional projection of the axes of the two first components is displayed in Fig. 5. The first principal component explains 25.19% of the variation and is associated with colpus length (Cl) and os width (Ow). The second principal component explains

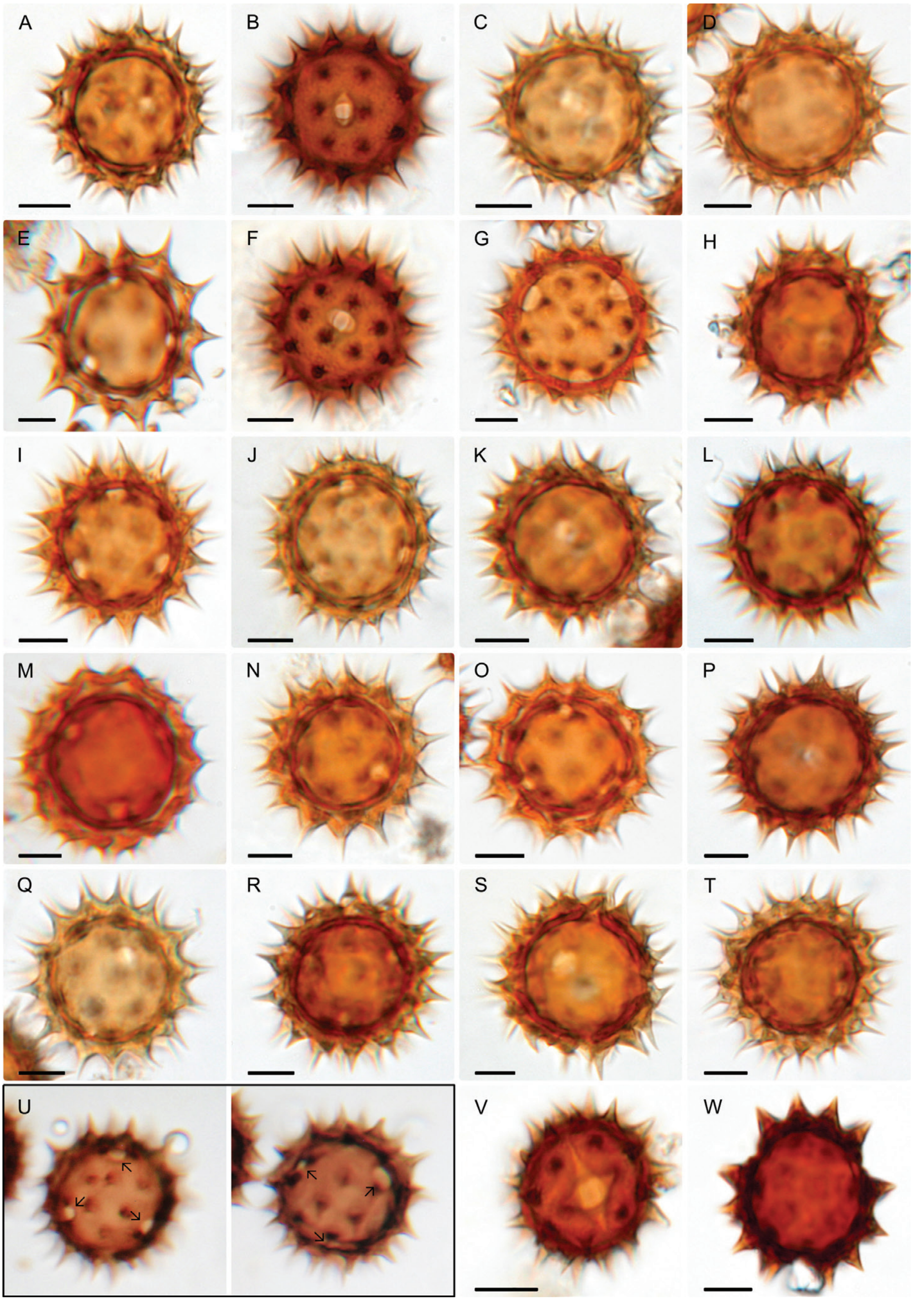


**Figure 2.** Pollen grains of *Dahlia* and *Hidalgoa* observed with light microscopy (LM) **A** *D. australis* **B** *D. barkerae* **C** *D. brevis* **D** *campanulata* **E** *D. coccinea* **F** *D. cordifolia* **G** *D. cuspidata* **H** *D. dissecta* **I** *D. imperialis* **J** *D. linearis* **K** *D. merckii* **L** *D. mollis* **M** *D. neglecta* **N** *D. parvibracteata* **O** *D. pugana* **P** *D. rudis* **Q** *D. rupicola* **R** *D. scapigera* **S** *D. sorensenii* **T** *D. spectabilis* **U** *D. rudis*, pollen grain hexacolporate with three apertures on one hemisphere and three on the other hemisphere **V** *H. ternata* **W** *H. pentamera*. Scale bars: 10 µm.

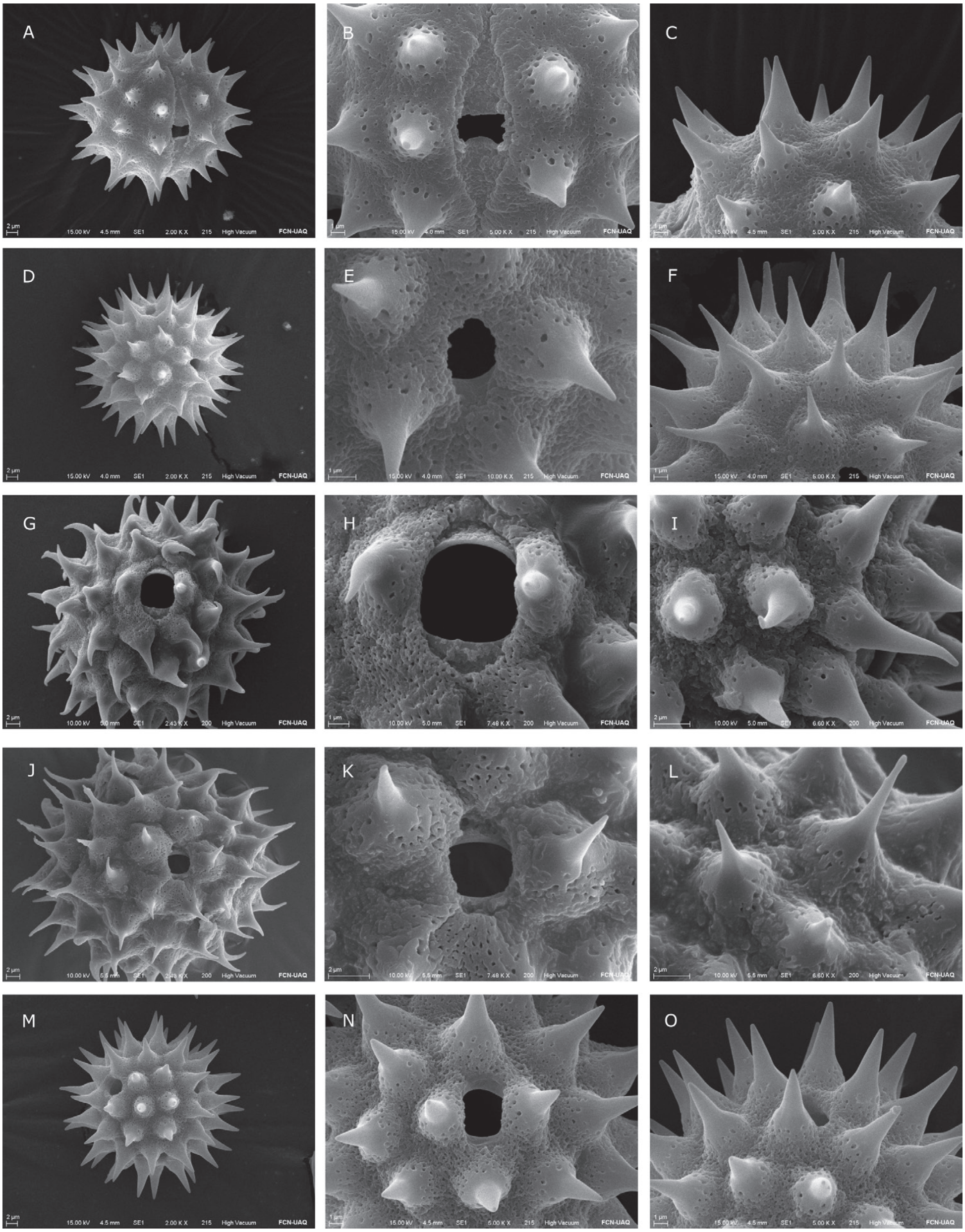


**Figure 3.** Scanning Electron Microscope (SEM) images of *Dahlia* and *Hidalgoa* pollen grains **A–C** *Hidalgoa ternata* **A** equatorial view **B** detail of colpus **C** detail of spine **D–F** *Dahlia australis* **D** polar view **E** detail of colpus **F** detail of spine **G–I** *Dahlia cuspidata* **G** equatorial view **H** detail of colpus **I** detail of spine **J–L** *Dahlia neglecta* **J** equatorial view **K** detail of colpus **L** detail of spine **M–O** *Dahlia coccinea* **M** equatorial view **N** detail of colpus **O** detail of spine.

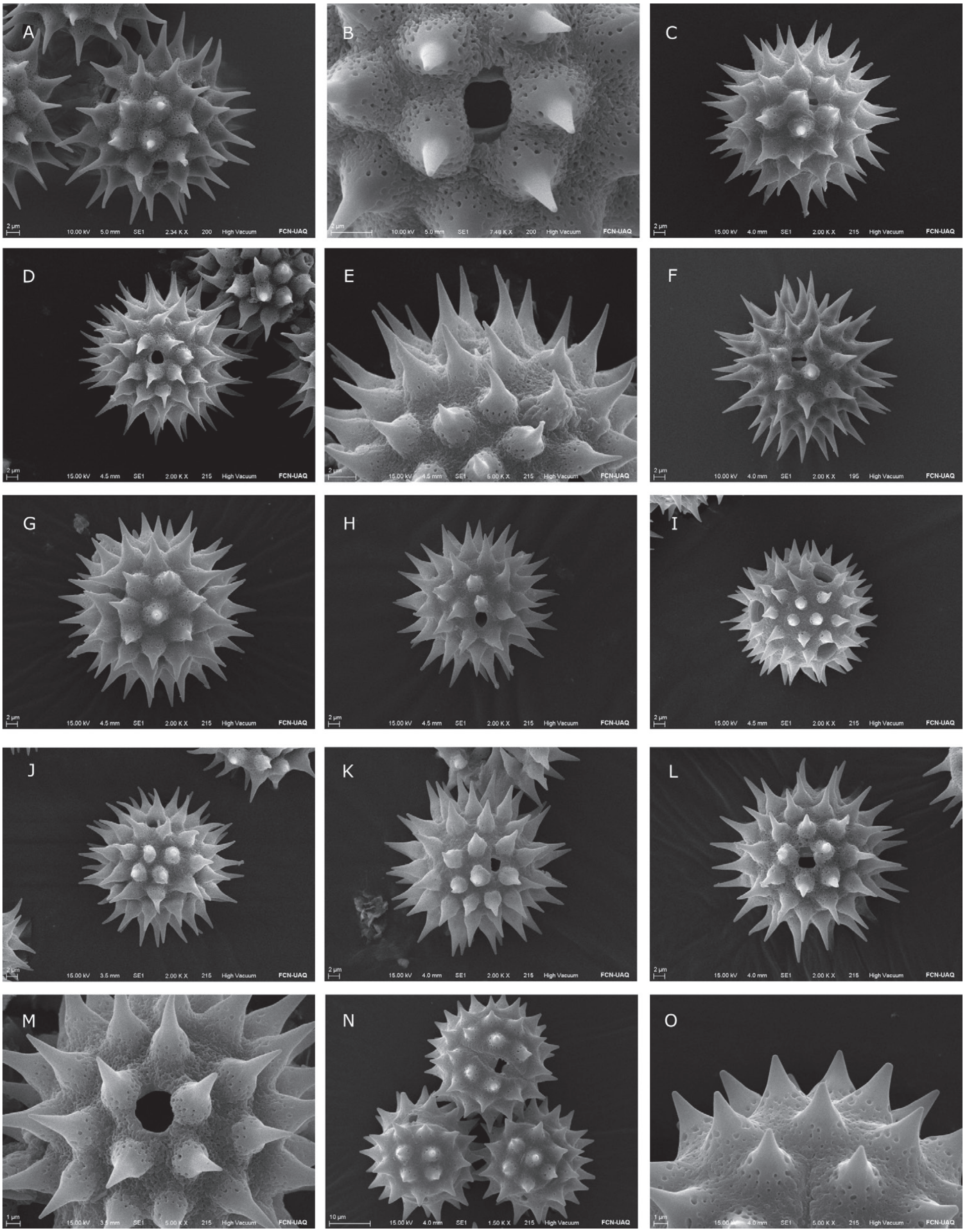


**Figure 4.** Scanning Electron Microscope (SEM) images of *Dahlia* and *Hidalgoa* pollen grains **A, B** *Dahlia atropurpurea* **C** *Dahlia barkerae* **D, E** *Dahlia brevis* **F** *Dahlia dissecta* **H** *Dahlia imperialis* **I** *Dahlia linearis* **J** *Dahlia merckii* **K** *Dahlia scapigera* **L** *Dahlia tenuicaulis* **M** *Dahlia wixarika* **N–O** *Hidalgoa pentamera*.

20.85% and variables that contributed the most are polar axis (Pa), spine width at base (Swab), spine length (Sl), colpus width (Cw), os length (Ol), number of spines/100 $\mu m^2$ (Ns). Length of arrows in Fig. 5 suggests adequate sampling for all characters, except for lalongate os (Osl), number of apertures (Ap) and base of spine (Sb).

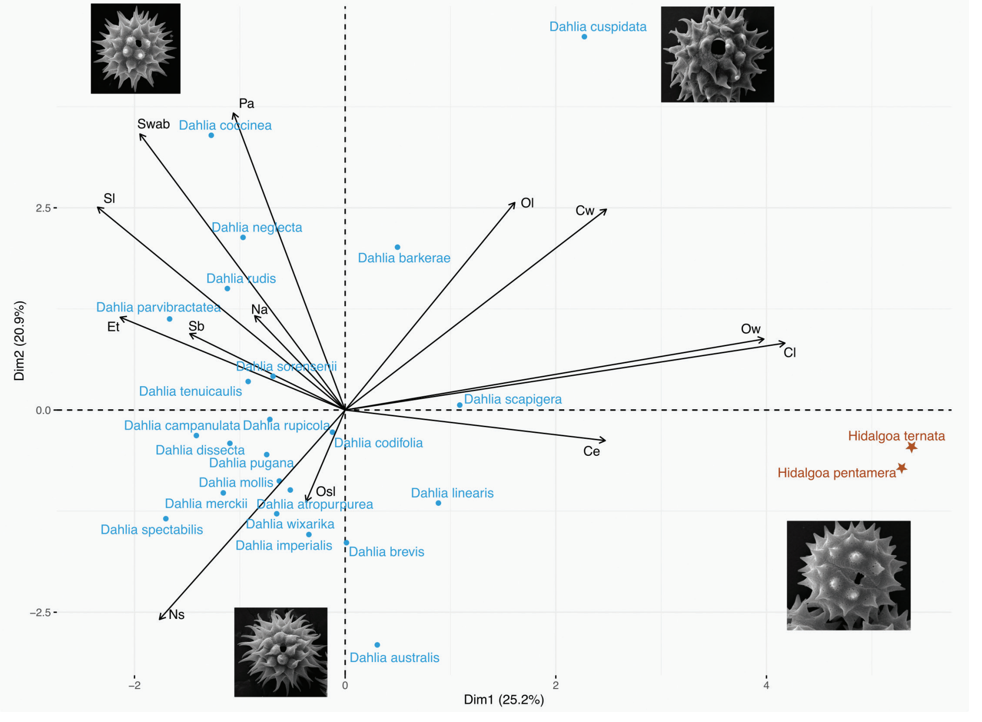


**Figure 5.** Principal Components Analysis graph showing contribution of the thirteen attributes to explain variation in pollen grains of the studied *Dahlia* and *Hidalgoa* species. **Pa** Polar axis, **Et** Exine thickness, **Cl** Colpus length, **Cw** Colpus width, **Ol** Os length, **Ow** Os width, **Sl** Spine length, **Swab** Spine width at base, **Na** Number of apertures, **Ns** Number of spines/100 μm$^2$, **Ce** Colpus ends, **Sb** Base of spine, **Osl** Os lalongate.

## Discussion

The pollen grains of the 25 species of *Dahlia* and *Hidalgoa* we studied share the pollen type common to tribe Coreopsideae: more or less spheroidal, round in both views, tricolporate, ora lalongate, tectum microperforate, echinate, spines irregularly distributed, conical to long-pointed and smooth or distended bases with perforations (Blackmore et al 2009). The pollen of the species studied is quite homogeneous, with little variation in size and shape. Pollen grains size ranges from 25.3 to 39.4 μm in *Dahlia* and 25.7 to 34 μm in *Hidalgoa*, and the ratio of polar axis and equatorial diameter is 0.90–1.04 (*Dahlia*: 0.90–1.04, *Hidalgoa*: 1.02–1.04). The largest grains were observed in *D. neglecta* and the smallest in *D. australis* and *H. pentamera*. Based on the classification proposed by Erdtman (1969), the pollen of both genera corresponds to medium-sized grains (25–50 μm), like those described by Tellería (2017) for tribe Coreopsideae. Pollen grains in *Dahlia* and *Hidalgoa* are radially symmetrical, isopolar, and mostly spheroidal, similar to those described in *Coreopsis* (Tadesse et al. 1995).

Apertures are the most variable attribute between *Dahlia* and *Hidalgoa*, but not within the genera. Pollen in *Hidalgoa* is always tricolporate, while in pollen grains of *Dahlia*, the

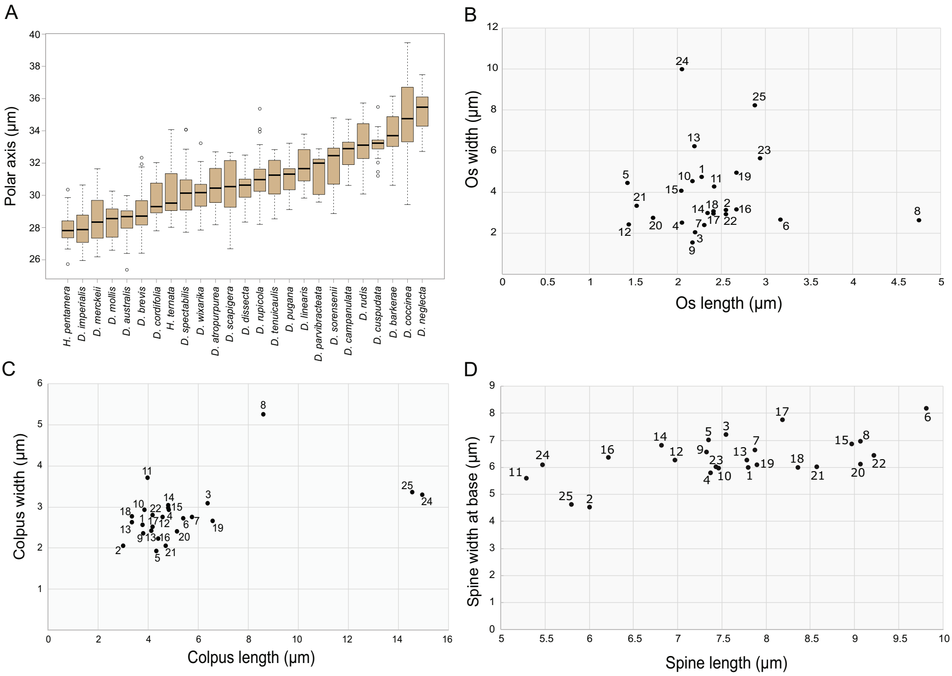


**Figure 6.** Comparison of *Dahlia* and *Hidalgoa* pollen grains **A** box plot of Polar diameter **B** os length/width **C** colpus length/width **D** spine length/width at base. **1** *Dahlia atropurpurea*. **2** *Dahlia australis*. **3** *Dahlia barkerae*. **4** *Dahlia brevis*. **5** *Dahlia campanulata*. **6** *Dahlia coccinea*. **7** *Dahlia cordifolia*. **8** *Dahlia cuspidata*. **9** *Dahlia dissecta*. **10** *Dahlia imperialis*. **11** *Dahlia linearis*. **12** *Dahlia merckii*. **13** *Dahlia mollis*. **14** *Dahlia neglecta*. **15** *Dahlia parvibracteata*. **16** *Dahlia pugana*. **17** *Dahlia rudis*. **18** *Dahlia rupicola*. **19** *Dahlia scapigera*. **20** *Dahlia sorensenii*. **21** *Dahlia spectabilis*. **22** *Dahlia tenuicaulis*. **23** *Dahlia wixarika*. **24** *Hidalgoa pentamera*. **25** *Hidalgoa ternata*.

aperture varies from tricolporate to hexacolporate. Hexacolporate species observed here were: *D. cuspidata*, *D. dissecta*, *D. imperialis*, *D. merckii*, *D. parvibracteata*, *D. rudis* and *D. sorensenii*. Wodehouse (1930) recognized the same pattern in *D. brevis*, *D. coccinea*, *D. pinnata* and *D. imperialis*. However, Wodehouse (1930) described these six apertures as uniform in all pollen grains; the observations were made on species belonging to the San Francisco *Dahlia* Society, plants that are probably of hybrid origin. The specimens collected from the herbariums for this study do not display characters of hybrid origin. Furthermore, hexacolporate grains have been indeed reported in Old World Vernonieae and *Adenanthemum* (Blackmore et al 2009). Other members of Coreopsideae such as *Bidens* also vary in the number of colpi from 3–4 (Tadesse et al. 1995) or polypentoporate (Younis et al. 2020).

The os and colpus displayed more variation in *Dahlia* than in *Hidalgoa*. In *Hidalgoa* the os is lalongate, the widest is up to 13 µm width, and the longest colpus is approximately 17 µm, with apices always acute. These traits of *Hidalgoa* are similar to those observed in *Bidens* (Tadesse et al. 1995). In *Dahlia* the ora are either lalongate or lolongate. The os is slightly wider than larger and apices are obtuse, rarely acute. The widest and largest colpus was observed in *D. cuspidata* (5.89 µm and 9.2 µm respectively) and *D. scapigera* (ca. 7 µm), and the smallest in *D. australis* (2.9 µm). Variation in the apertures like those of *Dahlia* has not been reported in other genera of the tribe Coreopsideae (Blackmore et al. 2009).

Spines are variable between *Dahlia* and *Hidalgoa*. In *Hidalgoa* they are conical and smaller (4.08 to 6.77 µm) while in *Dahlia* they are deltate and larger (4.29 to 12.26 µm), with exception of *D. linearis* (smaller). Spines in *Dahlia* varied more in shape and size. They are commonly triangular or deltate with a broadened base (distended base), as described by Tellería (2017) for tribe Coreopsideae. Sometimes spines emerge abruptly from the exine surface, e.g. *D. campanulata*, *D. imperialis*, *D. parvibracteata*, *D. scapigera*. These spines are similar to those described in *Coreopsis* (Tadesse et al. 1995). The transition between the microperforate basal portion of the spine and the unperforated apical portion is abrupt in almost all species, except in *D. cordifolia*, *D. linearis* and *D. sorensenii*. Exine thickness did not vary among *Hidalgoa* and *Dahlia* species. The thinnest was observed in *D. cuspidata* and *D. sorensenii* (1.6 µm) and the thickest in *D. neglecta* (4.2 µm).

Multivariate analyses did not reveal a clear clustering among species of *Dahlia* according to the sections proposed by Sørensen (1969), based mainly on life form and in the phylogeny of Saar et al. (2003). Nevertheless, *D. cuspidata* and the *Hidalgoa* species are significantly different from the other *Dahlia* species included in this study. *Hidalgoa* species have long colpi and wide ora, and *D. cuspidata* has long ora. *Dahlia cuspidata* possesses unusual morphological characters such as large involucral outer bracts and cuspidate leaf shape. Thus, further research might decide the position of this species.

The most recent phylogeny that included *Dahlia* and *Hidalgoa* (Sánchez-Chávez et al. 2019) identified *Hidalgoa* within the *Dahlia* clade. However, both genera are morphologically complex (Sørensen 1969; Turner 2010), and contrasting characters such as life form, number and arrangement of fertile and sterile flowers have been used to separate these two groups. A further phylogeny, including all species, may help us to better understand pollen evolution in the genus.

## Conclusions

The palynological descriptions for *Hidalgoa* presented here are the first, and despite the similarities in its floral morphology to that of *Dahlia*, its pollen is remarkably different, mostly in colpus length and shape of their spines. *Hidalgoa* has pollen grains with large colpi and small, conical spines. In addition, the length of the lalongate ora differ. Hexacolporate grains with a distended base, were found in a number of *Dahlia* species but have not been identified in *Hidalgoa*. Likewise, morphological characters such as pistillate fertile ray florets, cypselae with two apical lateral cusps and twisting petioles in *Hidalgoa* contrast with the ray florets, which can be fertile, pistillate or sterile, cypselae with pappus absent or present with 2(5) small teeth or of two weak filiform, caducous bristles of *Dahlia*; characters that have been utilized to tell these two genera apart. The results obtained in this palynological study support the idea that pollen morphology is useful for delimitation at the generic level in the *Dahlia* clade. These differentiating attributes in pollen morphology in the species of *Dahlia* and *Hidalgoa* indicate that they should be recognized as separate genera. However, as indicated above, additional anatomical and molecular characters are needed to make the taxonomic decision and help us understand evolution in the genera, and their relationship to other genera in Coreopsideae.

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## Supplementary material 1

**Tables S1, S2**

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Data type: Tables (docx. file)

Explanation note: **Table S1**. *Dahlia* diversity. Sections proposed by Sorensen (1969). **Table S2**. Data matrix showing the values found for the 13 characters (columns) in the 25 species (rows) of *Hidalgoa* and *Dahlia* included in this study. (Characters designated according to Table 3).



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