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Research Article

Checklist of the genus *Ridsdalea* (Rubiaceae, Gardenieae) in Vietnam with description of the new species *R. backanensis*

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Abstract

The paper provides an identification key and an annotated list of all six species of the genus *Ridsdalea* J.T.Pereira & K.M.Wong (Rubiaceae, Gardenieae) recorded in the flora of Vietnam, along with data on their valid names, synonyms, types, and distribution. A new species, *R. backanensis*, discovered in the limestone area of Bac Kan Province (northern Vietnam), is described and illustrated. Detailed data on its characters, ecology, distribution, phenology, preliminary IUCN conservation status, and taxonomical notes are given. The newly discovered species is potentially interesting for cultivation as an ornamental tree that may be effectively used in garden and urban green architecture.

Key words: Ba Be National Park, Bac Kan Province, endemism, flora of Vietnam, new species, plant diversity, plant taxonomy, *Rothmannia*

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Introduction

The genus *Ridsdalea* J.T.Pereira & K.M.Wong (in Wong and Pereira 2016: 42) was segregated from *Rothmannia* Thunb. (Thunberg 1776: 65) mainly because its corolla lobes are contorted to the left, whereas the lobes in *Rothmannia* s.str. are contorted to the right. Both genera are closely related and belong to the tribe Gardenieae, subfamily Ixoroideae of the coffee family (Rubiaceae) (Wong and Pereira 2016). While species of *Rothmannia* are distributed in Africa, representatives of the closely related *Ridsdalea* inhabit wide areas in the tropics of Southeast mainland Asia and Malesia (Wong and Pereira 2016).

The twelve genera of the tribe Gardenieae occurring in Vietnam, namely *Aidia* Lour., *Aidiopsis* Tirveng., *Alleizettella* Pit., *Brachytome* Hook.f., *Dioecrescis* Tirveng., *Duperrea* Pierre ex Pit., *Gardenia* J.Ellis, *Kailarsenia* Tirveng., *Oxyceros* Lour., *Randia* L., *Rubovietnamia* Tirveng., and *Vidalasia* Tirveng. (Pham 2000; Tran 2005), are well segregated from each other morphologically and well-supported by molecular data (Robbrecht and Manen 2006; Bremer 2009; Mouly et al. 2014). Besides left-contorted corolla lobes, typical diagnostic characteristics of the genus *Ridsdalea* are such features as large shrub or tree habit; unarmed shoots with opposite or verticillate leaves (in groups of 3); interpetiolar stipules without distinct venation; terminal or pseudoaxillary, 1–7-flowered, cymose inflorescences; bisexual flowers; 2-celled ovaries with axile placentation; and, large, baccate, many-seeded fruits (Chen and Taylor 2011; Wong and Pereira 2016).

All species of *Ridsdalea* are rather large shrubs or small, medium, or large trees scattered in lowland or submontane woods on soils derived from various parental rocks. Some species prefer exclusively alluvial soils in limestone areas and often inhabit rocky, steep slopes of rocky karstic hills.

Twenty-eight species of *Ridsdalea* distributed in Indochina and Malesia were recognized in a comprehensive monograph of the genus (Wong and Pereira 2016, POWO 2023), and a few species were added by recent studies in Thailand (Kwanjai et al. 2018) and the Philippines (Bustamante and Pelser 2022). In Vietnam, five species were previously reported (Zhang et al. 2007; Bui and Nguyen 2015; Ton et al. 2019), which are listed below together with the newly discovered species.

During botanical fieldwork in November 2022 in limestone areas of Bac Kan Province in northern Vietnam, we collected several specimens sharing the above-mentioned generic characteristics of *Ridsdalea*, but morphologically different from all species hitherto known by a number of unique characteristics. After consulting relevant literature (Thunberg 1776; Pitard 1923; Tirvengadum 1983; Shui et al. 2003; Zhang et al. 2007; Bui and Nguyen. 2015; Wong and Pereira 2016; Kwanjai et al. 2018; Ton et al. 2019; Bustamante and Pelser 2022), as well as examining available herbarium specimens stored at HN, HNPI, HNU, K, LE, P, VNF, and VNM, we identified our plants as a new species on the basis of the morphological features indicated in the identification key and diagnosis, and protologue. With the new data reported here, the number of species of the genus *Ridsdalea* in the flora of Vietnam reaches six. The paper aims at formally recognizing the novelty, with a key to the Vietnamese species and a briefly annotated checklist.

Materials and methods

All collected and studied herbarium specimens of the newly discovered species are presently stored in the herbaria of the Vietnam National University of Forestry (VNF) and the Komarov Botanical Institute of the Russian Academy of Sciences (LE). Color photos of plants were taken in natural habitats. Morphological observations and measurements were made on living plants, dried specimens, and alcohol-preserved materials. Morphological characters were described using the terminology proposed by Harris and Harris (2006), Hickey and King (2000), and Beentje (2016). Institutes where studied specimens are kept are indicated by their internationally accepted herbarium acronyms (Thiers 2024).

Taxonomic treatment

Ridsdalea species in the flora of Vietnam

Ridsdalea J.T.Pereira & K.M.Wong (in Wong and Pereira 2016: 42).

Type. *Ridsdalea grandis* (Korth.) J.T.Pereira (in Wong and Pereira 2016: 46). ≡ *Gardenia grandis* Korth. (Korthals 1851: 191).

Description. Large shrubs to small, medium or large trees with unarmed trunk and branches. Branches opposite and decussate on the trunk, sympodial in development. Leaves opposite or verticillate in groups of 2–3, each trifoliate group based on a distal node with only one leaf normally developed and the proximal node with a pair of normal leaves; leaves petiolate to subsessile, axils of the midrib, secondary veins, and sometimes other vein junctions frequently with domatia on the abaxial leaf surface; margin entire. Stipules interpetiolar, without distinct venation, free or hardly fused at the base, persistent to caducous, inner surface hairy with colleters restricted to 1–several rows. Inflorescence terminal or pseudoaxillary (terminal in origin, later appearing lateral because of displacement to one side during sympodial branch development), distinctly cymose, several-flowered or sometimes reduced to a 1-flowered structure, distinctly pedunculate to subsessile. Flowers bisexual, pedicellate or sometimes subsessile, small or large with corolla tube less than 15 cm long. Calyx 5–8(–10)-lobed, colleters present in small groups on the inner surface, glabrous or glabrescent to hairy on the outside. Corolla commonly 5-, rarely 6–8-merous; hypocrateriform or campanulate; the tube white or white with reddish purple speckles or blotches inside, the outer and inner surface glabrous or hairy; lobes contorted to the left in the flower bud; stamens attached at the upper part of the corolla tube, anthers sessile or subsessile, linear or narrowly lanceolate; style shorter than, as long as, or slightly exceeding the corolla tube, mostly glabrous; stigma clavate to fusiform, 2-lobed, smooth to somewhat ribbed; ovary 2-celled; ovules many; placentation axile. Mature fruits baccate, indehiscent, globose or broadly ellipsoid, 2–5 cm across, 2-locular, outer surface smooth. Seeds many, immersed in a dark brown pulp-like placental tissue (Chen and Taylor 2011; Wong and Pereira 2016).

32 species in Myanmar, SW China, Thailand, Laos, Cambodia, Vietnam, Malacca Peninsula. Indonesia, Philippines, New Guinea. In Vietnam 6 species (2 endemic, found in Bac Kan and Lam Dong provinces).

Key for the identification of *Ridsdalea* species in the flora of Vietnam

1 Flowers solitary in leaf axils, almost sessile; peduncle 0.5–1 mm long .... ***R. kampucheana***
– Inflorescences terminal or axillary (pseudoaxillary), 1–7-flowered; on distinct peduncle 7–15 mm long **2**
2 Leaf blade tapering gradually to acute or hardly acuminate apex .... ***R. eucodon***
– Leaf blade distinctly acuminate with suddenly narrowing apex **3**
3 Inflorescence usually 4–7 flowered; corolla tube narrowly conoid, dilating gradually in distal direction, near the apex 1–1.3 cm in diameter; throat 3.5–4 cm in diameter .... ***R. vietnamensis***
– Inflorescence usually 1–5 flowered; corolla tube broadly campanulate, dilating suddenly near the base, near the apex 2.5–3.5 cm in diameter; throat 4.5–5.5 cm in diameter **4**
4 Inflorescence usually 3–5 flowered; calyx tube 3–5 mm long, calyx lobes broadly triangular, less than 3 mm long .... ***R. wittii***
– Inflorescence usually 1–3 flowered; calyx tube 1.2–2.5 mm long, calyx lobes linear oblong or subulate, 6.5–16 mm long **5**

5 Inflorescence uniflorous; pedicels 2–2.5 cm long; calyx tube funnel-shaped, 2–2.5 mm long, calyx lobes linear oblong, 14–16 mm long; corolla outside glabrous; anthers linear, ca. 1 mm wide .... ***R. daweishanensis***

– Inflorescence 1–3 flowered; pedicels 3.5–7 mm long; calyx tube cup-shaped, 1.2–2.2 mm long, calyx lobes subulate, 6.5–11 mm long; corolla outside shortly sparsely hairy; anthers oblanceolate, 2–3 mm wide........... ....***R. backanensis***

Ridsdalea backanensis C.H.Nguyen & Aver., sp. nov.

urn:lsid:ipni.org:names:77337445-1
Figs 1, 2

Diagnosis. *Ridsdalea backanensis* differs from *R. daweishanensis* mainly in the smaller leaves, 7–11 cm long (vs. leaves 10–14 cm long in *R. daweishanensis*), the 1–3-flowered inflorescence (vs. inflorescences uniflorous), the much shorter pedicels, 3.5–7 mm long (vs. pedicels 20–25 mm long), the shorter subulate calyx lobes, 6.5–11 mm long (vs. calyx lobes narrowly oblanceolate, 14–16 mm long), the corolla outside sparsely hairy (vs. corolla outside glabrous), and the oblanceolate anthers, 2–3 mm wide (vs. anthers linear, about 1.5 mm wide).

Type. Vietnam, Bac Kan Province: Ba Be District, Ba Be National Park, dry evergreen broad-leaved old secondary forest with domination of *Burretiodendron hsienmu* Chun & F.C.How, *Streblus asper* Lour., and *Arenga pinnata* (Wurmb) Merr., on crystalline highly eroded rocky limestone near the boat station at elev. 250–300 m a.s.l., tree 10–15 m on shady rocky steep slope, not common, 18 November 2022, *Nguyen Huu Cuong*, *Cao Xuan Hai*, *L. Averyanov*, *T. Maisak*, *AL 1682* (Holotype: VNF NHC20221118006!; Isotypes: LE LE01169974! https://en.herbariumle.ru/?t=occ&id=160358, LE LE01169975! https://en.herbariumle.ru/?t=occ&id=160361, LE LE01169983! https://en.herbariumle.ru/?t=occ&id=163681; photos of living material made before preparation of type herbarium specimens: LE LE01123672! https://en.herbariumle.ru/?t=occ&id=155829, LE LE01123671! https://en.herbariumle.ru/?t=occ&id=155828).

Etymology. The species is named after the area of origin (Bac Kan Province, northeastern Vietnam).

Description. Evergreen tree, (4)5–20(22) m tall with obscurely ovoid crown and solitary trunk to 30(35) cm DBH. Bark lenticellate, smooth greenish gray. Young twigs dichotomous, slightly flattened or angular, older ones terete, glabrous. Leaves entirely glabrous, shortly petiolate, opposite, or in whorls of 3; petiole obscurely half circular in cross section, adaxially shallowly grooved, (1.5)2–5(7) mm long, (2.5)3–5(5.5) mm wide; stipules interpetiolar, broadly triangular (1)1.5–2.2(2.5) mm long, (2.5)3–5(5.5) mm wide, broad and slightly fused at the base, shortly acuminate at apex, adaxially densely hairy with short hairs; leaf blade chartaceous to slightly coriaceous, narrowly ovate or narrowly obscurely rhomboid, (7)8–10(11) cm long, (3)3.5–5(5.5) cm wide, tapering from the middle to cuneate base and to shortly acuminate, obtuse apex; both surfaces dark green, glossy, median vein shallowly canaliculate on adaxial side, prominent abaxially, secondary (lateral) veins (4)5–6(7) pairs. Inflorescence cymose, 1–3-flowered, terminal or pseudoaxillary; peduncle (1.5)2–8(9) mm long, glabrous or sparsely hairy with stiff adpressed hairs, with 1–2 very small adpressed triangular alternate bracts, (1)1.2–1.8(2) mm long and wide. Pedicels (3.5)4–6(7) mm long, sparsely hairy with sericeous adpressed hairs, with 1(2) bracteoles; bracteoles alternate, triangular, (1.5)2(2.5) mm long and wide, acute to apiculate, glabrous outside, densely hairy with stiff hairs inside. Calyx green, deciduous; calyx tube and lobes glabrous or sparsely hairy with sericeous adpressed hairs outside, inside densely hairy with stiff, yellowish gray hairs; calyx tube (1.2)1.5–2(2.2) mm long, (4)4.5–6(7) mm in diameter; free calyx lobes recurved, subulate, tapering from base to obtuse apex, (6.5)7–10(11) mm long, (0.7)0.8–1.2(1.4) mm wide, without distinct veins. Corolla campanulate, outside pure white, sparsely hairy with small sericeous adpressed hairs, inside glabrous, finely transversally folded (seen when fresh, Fig. 2Q), white with light yellow tint and many purple speckles and longitudinal streaks, lasting 3–4 days, (5)5.5–6(6.5) cm long, (2.5)2.8–3.2(3.5) cm in diameter at the middle, abruptly contracted at the base into a short, narrow, 2.5(3–3.5(4) mm wide tube over a length of (7)8–10(11) mm; corolla lobes 5, overlapping to left, glabrous or sparsely hairy with small sericeous adpressed hairs outside, glabrous inside, triangular broadly ovate, (1.2)1.4–1.6(1.8) cm long and wide, blunt to obtuse at apex, white outside, purple-mottled inside, recurved. Stamens 5, alternate to corolla lobes, subsessile, inserted on the upper part of the corolla tube; anthers oblanceolate, narrowing and obtuse at the apex, (1.8)1.9–2.1(2.2) cm long, (2)2.2–2.5(3) mm wide, longitudinally dehiscent by linear thecae. Disc prominent, annular, (2.4)2.5–2.8(3) mm in diameter, glossy yellow. Style and stigma erect, (4)4.5(5) cm long; style white, terete, about 2.5–3 cm long, 0.8–1 mm in diameter; stigmatic part pale yellow, narrowly ellipsoid, longitudinally ribbed, 1.5–2 cm long, 2–2.5 mm in diameter; ovary inferior, unilocular, with many ovules in two rows. Fruit berry-like, indehiscent, dark green to dull olive-brownish, glabrous, globular to broadly ellipsoid or ovoid, (4.5)5–7(7.5) cm long, (3.5)4–4.5(5) cm in diameter, with semi-woody wall; seeds (15)20–55(65), white, flattened, obscurely triangular to lenticular, (7)8–12(13) mm long and wide, (2.5)3–4(4.5) mm thick, sunk in a dark brown or black pulpy matrix.

Distribution. The new species is only known from Nam Mau Commune, Ba Be District (in the limits of the territory of Ba Be National Park), Bac Kan Province, northeastern Vietnam. It is likely endemic to a very limited area of karstic rocky limestone associated with Ba Be National Park. This location lies near the northeast border of the generic area in Indochina.

Habitat. Primary and old secondary dry evergreen broad-leaved forest with domination of *Burretiodendron hsienmu* Chun & F.C.How, *Streblus asper* Lour., and *Arenga pinnata* (Wurmb) Merr. on crystalline highly eroded rocky limestone at elevations of 150–300 m a.s.l., commonly on shady rocky steep slopes or in rocky valleys between limestone hills. Occasional.

Phenology. Flowering from November to December, fruiting from December to January next year.

Preliminary IUCN conservation status. Only two subpopulations were discovered on rocky karstic limestone in the middle part of Ba Be National Park, with few mature trees. The species meets the following conditions (Red List IUCN 2023): extent of occurrence (EOO) < 100 km^2 (B1) and area of occupancy (AOO) < 10 km^2 (B2) with one known location (a), and continuing decline of quality of habitat (b). We estimate that in the two subpopulations currently known, fewer than 50 mature individuals occur. These conditions identify the conservation status of the new species as globally Critically Endangered CR B1ab(iii) + B2ab(iii) As a result, *Ridsdalea backanensis* deserves the highest priority for conservation.

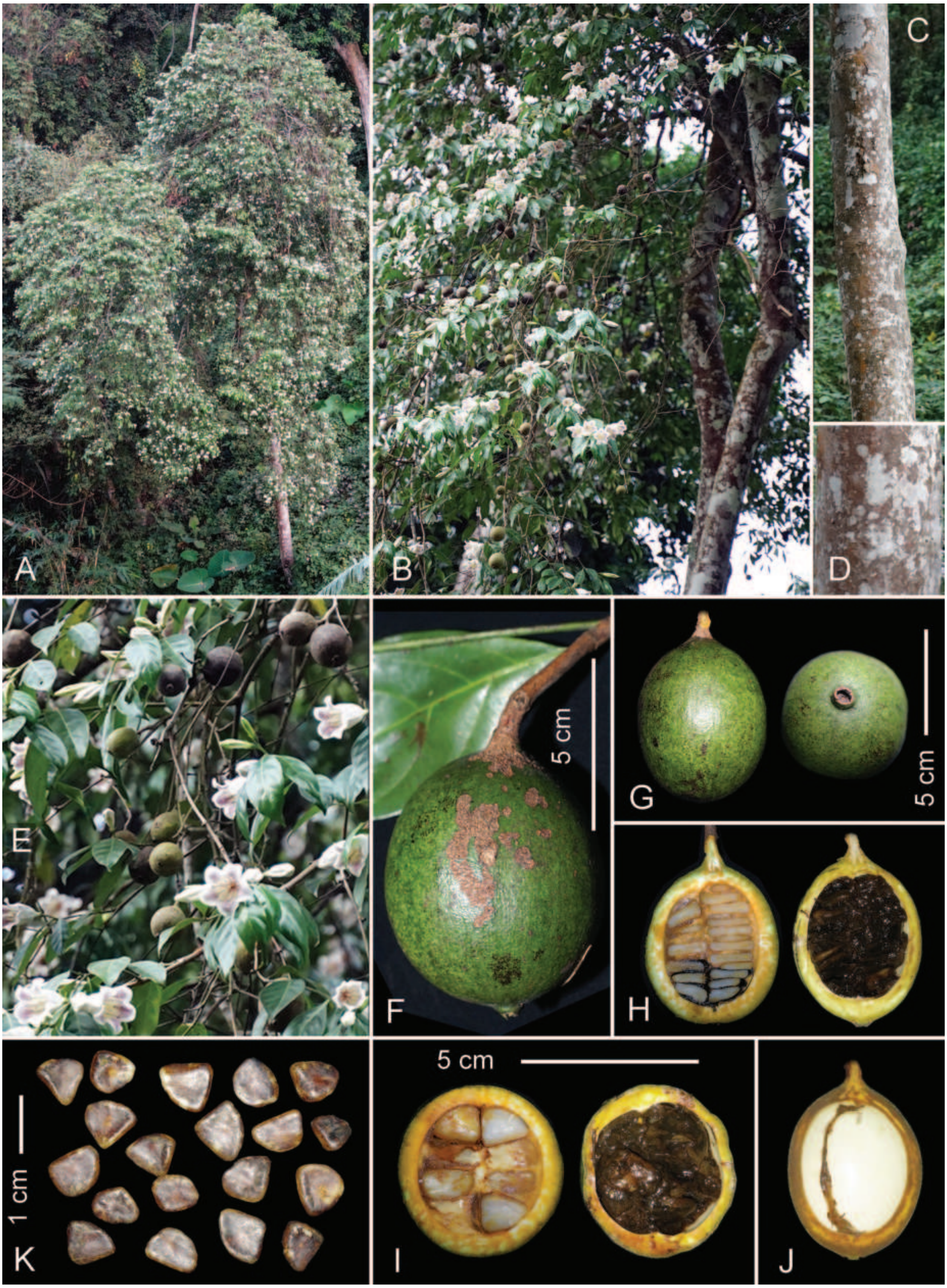

Figure 1. *Ridsdalea backanensis* **A** mature tree in natural habitat **B** part of crown with two main trunks **C** trunk of mature tree **D** bark at DBH **E** flowering and fruiting branches **F, G** ripe fruits **H** ripe fruits, sagittal section **I** ripe fruit, cross section **J** fruit, sagittal section, seeds removed **K** ripe seeds. Photos by C.H. Nguyen (**A–E**) and L. Averyanov (**F–K**) from plant used for preparation of the paratype voucher specimens (*AL 1680*), photo-correction, and design by L. Averyanov and T. Maisak.

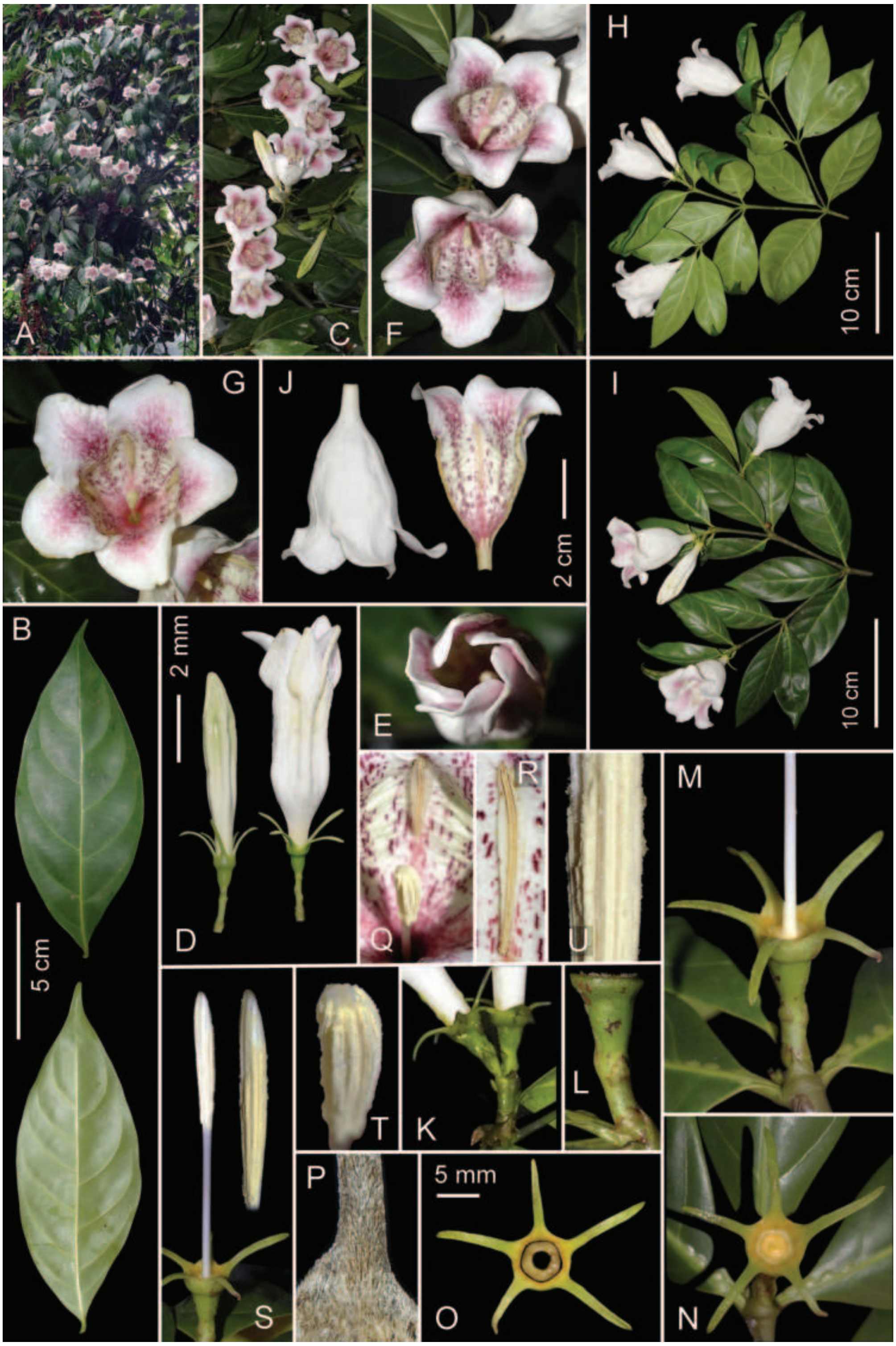

Figure 2. *Ridsdalea backanensis* **A** part of crown of flowering tree in natural habitat **B** leaves, adaxial and abaxial surface **C** flowering branches **D** flower bud and opening flower, side view **E** Opening flower, frontal view **F, G** flowers, frontal view **H** flowering branch showing leaves from abaxial side **I** flowering branch showing leaves from adaxial side **J** corolla, sagittal section outside and inside **K** peduncle, pedicels and calyxes, side view **L** peduncle and pedicel, side view **M** peduncle, pedicel, calyx and base of style, side view, corolla removed **N** calyx, frontal view, corolla removed **O** separated, upper part of calyx tube, calyx lobes, and nectary disc, frontal view **P** indumentum of abaxial surface of calyx on dry specimen **Q** portion of adaxial surface of corolla, sessile stamen and apical part of stigma **R** stamen **S** pedicel, calyx and pistil with magnified stigma, side view **T** apical part of stigma **U** middle part of stigma Photos by L. Averyanov (**A, C, F–K, P**) and C.H. Nguyen (**B, D, E, L–O, Q–U**) from plant used for preparation of the type voucher specimens (*AL 1682*), photo-correction and design by L. Averyanov and T. Maisak.

Notes. The new species is most similar in its morphology to *Ridsdalea daweishanensis* described from SE Yunnan (Maguan & Hekou counties) and also reported for NW Vietnam, Lao Cai Province (Zhang et al. 2007; Chen and Taylor 2011; Bui and Nguyen 2015). The new species differs from *R. daweishanensis* in its height to 22 m tall (vs. height of tree to 15 m), the leaf blades 7–11 cm long and 3–5.5 cm wide (vs. 10–14 cm long, 4–5 cm wide), the 1–3-flowered inflorescences (vs. inflorescences uniflorous), the 3.5–7 mm long pedicels (vs. pedicels 2–2.5 cm long), the free subulate calyx lobes, tapering from base to apex and broadest at the base, 6.5–11 mm long, without distinct veins (vs. calyx lobes narrowly oblanceolate, broadest above the middle, 14–16 mm long, 1-nerved), the 5–6.5 cm long corolla, sparsely hairy with small sericeous adpressed hairs outside and glabrous inside, contracted at the base into a narrow tube, 7–11 mm long, 2.5–4 mm in diameter (vs. corolla 5–5.5 cm long, entirely glabrous, contracted at the base into 6–7 mm long tube, 5 mm in diameter), the corolla lobes glabrous or sparsely hairy with small sericeous adpressed hairs outside and glabrous inside, 1.2–1.8 cm wide (vs. corolla lobes entirely glabrous, 2.2–2.3 cm wide), the oblanceolate, 2–3 mm wide anthers (vs. anthers linear, about 1.5 mm wide), and the globular to broadly ellipsoid or ovoid fruits, containing 15–65 seeds (vs. fruits globular, containing fewer than 20 seeds).

The newly discovered plant species will doubtless be of considerable interest for cultivation as an ornamental, since it is a nice-flowering tree that may be effectively used for gardens and urban green architecture.

Additional material studied (*paratypes*). VIETNAM, Bac Kan Province: Ba Be District, central part of Ba Be National Park, dry evergreen broad-leaved old secondary forest with domination of *Burretiodendron hsienmu*, *Streblus asper* and *Arenga pinnata* on crystalline highly eroded rocky limestone along Ba Be River at elev. c. 250 m a.s.l., tree 10–15 m tall on rocky slope in humid valley between limestone hills, occasional, 17 November 2022, *Nguyen Huu Cuong*, *Cao Xuan Hai*, *L. Averyanov*, *T. Maisak*, *AL 1680* (LE LE01169964 https://en.herbariumle.ru/?t=occ&id=163682, VNF-NHC 20221117004, photos of living material made before preparation of voucher herbarium specimens: LE LE01123669 https://en.herbariumle.ru/?t=occ&id=155826). Vietnam, Bac Kan Province, Ba Be District, Ba Be National Park, dry evergreen broad-leaved secondary forest on steep rocky slopes composed by white crystalline marble-like highly eroded limestone near Dau Dang Waterfall of Nang River around point 22°27'09"N, 105°34'16"E, at elevation of about 150 m a.s.l., tree about 5 m tall on shady steep rocky slope, young flower buds green, locally common, 20 October 2023, *Nguyen Huu Cuong*, *Chu Ngoc Quan*, *L. Averyanov*, *Nguyen Van Ly*, *T. Maisak*, *AL2330* (LE LE01253796 https://en.herbariumle.ru/?t=occ&id=212995, photos of living material made before preparation of voucher herbarium specimens: LE LE01124442 https://en.herbariumle.ru/?t=occ&id=207144, VNF). Vietnam, Bac Kan Province, Ba Be District, Ba Be National Park, dry evergreen broad-leaved secondary forest on steep rocky slopes composed by white crystalline marble-like highly eroded limestone near Dau Dang Waterfall of Nang River around point 22°27'09"N, 105°34'16"E, at elevation of about 150 m a.s.l., tree about 8 m tall on shady steep rocky slope, fruits broadly ellipsoid, dirty green to almost black, locally common, 20 October 2023, *Nguyen Huu Cuong*, *Chu Ngoc Quan*, *L. Averyanov*, *Nguyen Van Ly*, *T. Maisak*, *AL2331* (LE LE01253792 https://en.herbariumle.ru/?t=occ&id=212991, LE LE01253793 https://en.herbariumle.ru/?t=occ&id=212992, photos of living material made before preparation of voucher herbarium specimens: LE LE01124443 https://en.herbariumle.ru/?t=occ&id=207145, VNF). Vietnam, Bac Kan Province, Ba Be District, Ba Be National Park, dry evergreen broad-leaved secondary forest on very steep rocky slopes composed by white crystalline marble-like highly eroded limestone along lake shore on point 22°24'58"N, 105°36'48"E, at elevation of about 250 m a.s.l., tree about 10 m tall on very steep rocky slope, not common, 29 October 2023, *Nguyen Huu Cuong*, *Chu Ngoc Quan*, *L. Averyanov*, *Nguyen Van Ly*, *T. Maisak*, *AL2369* (LE LE01253794 https://en.herbariumle.ru/?t=occ&id=212993, LE LE01253795 https://en.herbariumle.ru/?t=occ&id=212994, photos of living material made before preparation of voucher herbarium specimens: LE LE01124480 https://en.herbariumle.ru/?t=occ&id=207183, VNF).

Ridsdalea daweishanensis **(Y.M.Shui & W.H.Chen) J.T.Pereira (in Wong and Pereira 2016: 45).**

≡ *Rothmannia daweishanensis* Y.M.Shui & W.H.Chen (Shui et al. 2003: 322, Zhang et al. 2007: 92). Type. China. Yunnan: Maguan, Gulinqing, Woody Station nearby Nanxi Community of Hekou, *Shui et al. 14496* (Holotype: KUN; Isotypes: KUN, MO).

Distribution. S China (SE Yunnan), NW Vietnam (Lang Son Province).

Ridsdalea eucodon **(K.Schum.) J.T.Pereira (in Wong and Pereira 2016: 45).**

≡ *Randia eucodon* K.Schum. (in Schmidt 1902: 333). Type. Thailand. Koh Chang, *Schmidt 717* (Holotype: C; Isotype: K).

= *Randia exaltata* Griff. var. *griffithiana* Pierre ex Pit. (Pitard 1923: 246). Lectotype. Vietnam. Bienhoa: Bao Chiang, *Pierre 1625* (Lectotype: P P00199261 designated by Wong and Pereira 2016: 45; Isolectotypes: K, NY, P P00199260).

Distribution. S Thailand, S Vietnam (Dong Nai and Khanh Hoa provinces).

Ridsdalea kampucheana **(Tirveng.) J.T.Pereira (in Wong and Pereira 2016: 46).**

≡ *Rothmannia kampucheana* Tirveng. (Tirvengadum 1983: 466). Type. Cambodia. Nord de Kampot, 5 Feb 1928, *Poilane 14676* (Holotype: P).

Distribution. SW Cambodia, S Vietnam (An Giang and Kien Giang provinces).

Ridsdalea vietnamensis **(Tirveng.) J.T.Pereira (in Wong and Pereira 2016: 43).**

≡ *Rothmannia vietnamensis* Tirveng. (Tirvengadum 1983: 469). Type. Vietnam. Annam, col de Braian, Haut Douai, 14 Feb (rec. Jul) 1935, *Poilane 24313* (Holotype: P).

Distribution. S Vietnam (Lam Dong Province).

Ridsdalea wittii **(Craib) J.T.Pereira (in Wong and Pereira 2016: 53).**

≡ *Randia wittii* Craib (Craib 1911: 392). Type. Thailand. Lower Siam: Korat, in dry deciduous jungle, 60 m, *Witt s.n.* (not located).

Distribution. NE Thailand, Laos, S Vietnam (Khanh Hoa Province).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization, Khoa Van Phung, Cuong Huu Nguyen; Formal analysis, Khoa Van Phung, Leonid V. Averyanov, Tatiana V. Maisak, Ludmila I. Krupkina, Cuong Huu Nguyen; Funding acquisition, Khoa Van Phung; Investigation, Leonid V. Averyanov, Tatiana V. Maisak, Hai Xuan Cao, Cuong Huu Nguyen; Methodology, Khoa Van Phung, Leonid V. Averyanov, Tatiana V. Maisak, Hai Xuan Cao, Cuong Huu Nguyen; Supervision, Khoa Van Phung; Writing - original draft, all authors; Writing - review and editing, Khoa Van Phung, Leonid V. Averyanov, Cuong Huu Nguyen; All authors have read and agreed to the published version of the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Chimonobambusa farcta (Poaceae, Bambusoideae), a new species from western Guangxi, China with taxonomic notes on *C. pubescens* and *C. luzhiensis*

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Abstract

Chimonobambusa farcta, a new species of temperate woody bamboos from western Guangxi, China is described and illustrated. The new species is similar to *C. pubescens* in the solid internodes of culms, but differs in having taller culm to 7 m with longer verrucose internodes to 23.5 cm and intranodes to 4 mm, intranode usually with a ring of 7–9 root thorns below mid-culm, abaxially brown or brown-purple verrucose-setose culm leaf sheaths with indistinct transverse veins, conspicuously developed culm leaf blades to 3.2 cm long, longer foliage leaf sheaths to 5.2 cm, larger and broader foliage leaf blades to 22 × 1.4 cm. It also somewhat resembles *C. convoluta*, but can be easily distinguished by having solid internodes and longer intranode 2–4 mm, very prominent nodes with supranodal ridge obviously more elevated than sheath scar, usually persistent and sometimes brownish striate culm leaf sheaths, longer culm leaf blades to 3.2 cm, and abaxially glabrous foliage leaf sheaths. Based on the morphological characteristics, this new species is assigned to *C.* sect. *Chimonobambusa*. The character description of *C. pubescens* are revised for its culm to 2.1 m tall, 1.1 cm in diameter and glabrous foliage leaf blades. The systematic position of *C. luzhiensis* is discussed, and this species is proposed as a member of *C.* sect. *Chimonobambusa*.

Key words: Amphipodial rhizome, Arundinarieae, taxonomy, temperate woody bamboos

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Introduction

Chimonobambusa Makino (s. l., including *Qiongzhuea* Hsueh & Yi), as a relatively large genus in Bambusoideae, is distributed from the south part of East Asia through the middle and north parts of Southeast Asia to the north part of South Asia subcontinent, with a distribution center around the Yunnan-Guizhou Plateau and Sichuan Basin (Hsueh and Zhang 1988; Wen 1994; Xue and Zhang 1996). So far, 69 Latin binomens were published or transferred under this genus (urn:lsid:ipni.org:names:17734-1), of which about 38 species were recognized by several works (Wen 1994; Ohrnberger 1999; Li and Stapleton 2006; Naithani 2009), with 25 species in the distribution center. Only one species spreads eastward to the south of central Honshu, Japan, and a few species reach southward to northern

Vietnam, Laos, northern Myanmar, and westward to Tibet, China and northern India (Wen 1994; Ohrnberger 1999). According to Huang and Dai (2009), there are five species of *Chimonobambusa* in Guangxi, a provincial administrative region located in the south of Chinese Mainland and near the modern distribution center of this genus. Later, Xia et al. (2016) recorded six species, including a cultivated species in "*Flora of Guangxi Vol.5*". Compared with Yunnan (Li and Xue 2003), Guizhou (Lan 1988) and Sichuan (Yi 1997), although the plants of this genus in Guangxi are not abundant, two species, *C. damingshanensis* Hsueh & W. P. Zhang and *C. convoluta* Q. H. Dai & X. L. Tao, are endemic to the region. In recent years, the investigation and taxonomy of this genus are still continuing, and some taxa were reported as new species or transferred into this genus (Cao et al. 2022; Niu et al. 2022). The economic value of plants in this genus is relatively high. Generally, the bamboo shoots taste delicious and can be used for fresh food or making pickled and dried shoots. Many species have high ornamental value for their more or less square culms, root thorns in the intranodes, and narrow and dense leaves, and are used for gardening, landscaping or ornamentation in urban and rural greening. Some species grow on steep hillsides or under broadleaved forests, which are also good plants for soil and water conservation.

During the introduction process of building Guangde National Bamboo Germplasm Resource Bank, we made some investigations on the scattered bamboo species distributed in the subtropical zone of China. In early November 2022, on the way back to the west of Lingyun County in western Guangxi after a special expedition to *Sinobambusa* Makino ex Nakai, a shrubby bamboo forest on the steep hillside at the roadside drew our attention. At that time, it was in the late stage of shooting, and its characteristics, including scattered culms, intranodes with developed root thorns, persistent culm leaves, underdeveloped culm leaf blades, and narrow foliage leaf blades clearly indicate that it belongs to *Chimonobambusa*. The internodes of both new and old culms of this unknown bamboo are solid, which is similar to that of *Chimonobambusa pubescens* Wen. However, it can be readily distinguished from the latter by having taller culm, longer verrucose internodes, longer intranodes with developed root thorns, abaxially brown or brown-purple verrucose-hispid culm leaf sheath and relatively developed culm leaf blade. It also somewhat resembles *C. convoluta* Q. H. Dai & X. L. Tao, but obviously differs in having culm with solid internodes, very elevated nodes and usually persistent culm leaves. On the basis of further investigations and morphological comparison, it was identified as a new species different from all the known species of the genus *Chimonobambusa*, and is described and illustrated here.

Materials and methods

The specimens of the new species were collected from Lingyun County in western Guangxi on 5 November 2022, and supplementary investigations and collections were separately made on 24 May 2023 and 22 October 2023. The morphological characteristics were observed and recorded from living materials, and some quantitative traits with taxonomic value were measured with a folding ruler rod and a vernier caliper. Specimens of the new species were deposited in AAUF, the herbarium of Guangde Forestry Institute, Anhui Province, China, the herbarium of Research Institute of Subtropical Forestry, Chinese Academy of Forestry and Anji Bamboo Exposition Garden, Zhejiang, China. Herbarium acronyms follow Thiers (2023). The terminology follows Soderstrom and Calderón (1978), Xue and Zhang (1996), Clark and Cortés (2004), Li and Stapleton (2006) and Qin et al. (2021).

Taxonomy

***Chimonobambusa farcta* G.H.Lai & J.J.Yue, sp. nov.**
urn:lsid:ipni.org:names:77314616-1
Figs 1–3

Diagnosis. *Chimonobambusa farcta* with solid internodes of culms is similar to *C. pubescens*, but differs in having taller culm to 7 m (vs. 2.1 m) with longer internodes to 23.5 cm (vs. 14 cm) and intranodes to 4 mm (vs. 2 mm), intranode usually with a ring of 7–9 root thorns below mid-culm, abaxially brown or brown-purple verrucose-setose culm leaf sheaths with indistinct transverse veins, conspicuously developed culm leaf blade to 32 mm (vs. ca. 2 mm)long, longer foliage leaf sheaths to 5.2 cm (vs. 2.8 cm), larger and broader foliage leaf blade to 22 × 1.4 (vs. 12 × 0.9 cm) cm. It also somewhat resembles *C. convoluta*, but can be easily distinguished by having culm with solid internodes and longer intranode 2–4 mm (vs. 1–2 mm), very prominent nodes with supranodal ridge obviously more elevated than sheath scar, usually persistent and sometimes brownish striate culm leaf sheaths, longer culm leaf blade to 32 mm (vs. 20 mm), and abaxially glabrous foliage leaf sheaths (Table 1).

Type. China. Guangxi: Lingyun County, Sicheng Town, Jinbao Village, Dashipo, 24°25'22"N, 106°30'29"E, 1261 m alt., 5 November 2022, *G. H. Lai & J. J. Yue 22111* (holotype: AAUF!; isotypes: herbarium of Guangde Forestry Institute! and herbarium of Research Institute of Subtropical Forestry, Chinese Academy of Forestry!).

Description. Shrubby bamboo. Rhizome amphipodial. Culms 3–7 m tall, 0.5–1.5 cm in diameter, erect, straight or sometimes middle and lower part of culm slightly zigzag and more or less oblique at nodes; internodes 12–23.5 cm long, cylindrical, basically weakly flattened on branch-bearing side, hard, solid (rarely subsolid on upper culm), dark green (rarely purple striate) and not pruinose when young, with white or pale brown curved verrucae (more on bare part) and white short retrorse hairs arranged in longitudinal rows, green or brown when old, scarred and rough after verrucae falling, glabrescent, obviously dirty-powdery; intranode 2–4 mm long, usually with a ring of 7–9 hard root thorns below mid-culm; thorns top-shaped or conical, 2–5 mm long, horizontally spreading or slanted downward; supranodal ridge very prominent, sometimes geniculate-swollen on bud-bearing opposite side, obviously more elevated than sheath scar; sheath scars prominent, densely persistently brown setoses; buds 3 at each node, adnate, narrowly ovate or conical, middle one longer, prophyll ovate or broadly ovate, abaxially glabrous, margin brownish ciliate; branches initially 3 per node, later to more than 10 on upper nodes of culm, spreading. Culm leaves usually persistent, rarely late deciduous, obviously shorter than internodes (1/2–2/3 as long as them) on lower culm, subequal in length to, or longer than internodes on middle and upper culm; sheaths papery, variable in color, initially brownish, yellowish-green, yellowish-brown or purplish-brown, tinged with green and brownish-red toward convex apex, soon straw-colored, with small and dense purple-brown spots, sometimes brownish

Table 1. Morphological comparison of *Chimonobambusa farcta* and its related species.

Character	*Chimonobambusa farcta*	*Chimonobambusa pubescens*	*Chimonobambusa convoluta*
Culm height	3–7 m	0.7–2.1 m	2–3 m
Culm internode	12–23.5 cm long, solid, basically weakly flattened on branch-bearing side, with retrorse white hairs arranged in longitudinal rows and curved verrucae	(5–) 8–14 cm long, solid, flattened on branch-bearing side, initially white pubescent, without verrucae	12–20 cm long, hollow, grooved on branch-bearing side, initially sparsely fulvous verrucose-hispid and becoming verrucose after setae falling
Culm intranode	2–4 mm long, usually with a ring of 7–9 root thorns at nodes below mid-culm	2 mm long, with some short aerial roots at nodes of basal culm	1–2 mm long, usually with a ring of 5–7 root thorns at nodes below mid-culm
Culm node	very prominent, supranodal ridge obviously more elevated than sheath scar	prominent, supranodal ridge more elevated than sheath scar	moderately prominent, supranodal ridge slightly more elevated than or equaling to sheath scar
Culm leaf	usually persistent	usually persistent	deciduous
Culm leaf sheath	with dense small purple-brown spots, sometimes brownish stirate, abaxially sparsely brown or brown-purple setose, with indistinct transverse veins	unspotted, abaxially mainly glabrous, with distinct transverse veins	with small purple-brown spots, abaxially sparsely brown setose, with indistinct transverse veins
Culm leaf fimbriae	absent, sometimes 1or 2 on each shoulder	absent	absent, sometimes 1or 2 on each shoulder
Culm leaf ligule	shorter than 1 mm tall, truncate or slightly arched,	ca. 2 mm tall, convex	shorter than 1 mm tall, slightly arched
Culm leaf blade length	4–32 mm	ca. 2 mm	11–20 mm
Foliage leaf	(2–)3–6(–9) per ultimate branchlet	3 or 4 per ultimate branchlet	2–4 per ultimate branchlet
Foliage leaf sheath	2.8–5.2 cm long, abaxially glabrous	2.5–2.8 cm long, abaxially glabrous	2.5–4.5 cm long, abaxially densely brown tomentose
Foliage leaf fimbriae	5–10 (–12) on each shoulder, 3–8 mm long	a few on each shoulder, 4–8 mm long	5–9 on each shoulder, 8–10 mm long
Foliage leaf blade	linear-lanceolate, 9–22 × 0.7–1.4 cm, secondary veins 3–6(–7)-paired	linear-lanceolate, 9–12 × 0.7–0.9 cm, secondary veins 3–5-paired	lanceolate, 16–22 ×1–1.5 cm, secondary veins 4- or 5-paired
Habitat and distribution	under evergreen broadleaved forests at the elevation of 1200–1500 m, Lingyun, western Guangxi	along the stream or under coniferous forests and thickets at the elevation of 350–800 m, southwestern Hunan	under broadleaved forests at the elevation of 800–1400 m, Tianlin and Napo, western Guangxi

stirate, abaxially sparsely uniformly upward appressed brown or brown-purple verrucose-setose, long brown hispid near base, densely brown bristly at bottom together with sheath scar, marginally densely brown ciliate, obviously longitudinally ribbed, indistinctly transversely veined; auricles absent, fimbriae not developed, sometimes 1or 2 on each shoulder, suberect; ligule shorter than 1 mm, purple-brown, truncate or slightly arched, margin extremely shortly ciliolate or subglabrous; blade narrowly triangular, subulate or narrowly linear-lanceolate, initially green or brownish-green, tinged with yellow toward apex, 4–32 × 1.5–2.5 mm, erect, not articulate with sheath. Foliage leaves (2–)3–6(–9) per ultimate branchlet; sheaths 2.8–5.2 cm long, abaxially glabrous, margins white or yellowish ciliolate sometimes hardly ciliate; auricles inconspicuous, fimbriae developed, 5–10(–12) on each shoulder, 3–8 mm long, grey-white, neatly arranged, straightly extended, easily deciduous or broken; ligule not exserted, shorter than 1 mm, truncate, apex hardly or very shortly ciliolate; petiole 1–2 mm long, glabrous; blade linear-lanceolate, 9–22 × 0.7–1.4 cm, adaxially green and glabrous, abaxially greenish and white pubescent, secondary veins 3–6(–7)-paired, transverse veins distinct, apex long acuminate, base cuneate, one margin minutely serrulate-scabrid. Inflorescence and caryopsis unknown.

Vernacular names. 凌云寒竹(Chinese name), líng yún hán zhú (Chinese Pinyin); 实竹(Local common name), shí zhú (Chinese Pinyin).

Distribution and habitat. *Chimonobambusa farcta* was only found from Lingyun County, between Mt. Qinglong and Mt. Donglan, western Guangxi, China. It grows under the evergreen broadleaved forest of steep hillsides at an altitude of 1200–1500 m (Figs 3, 4).

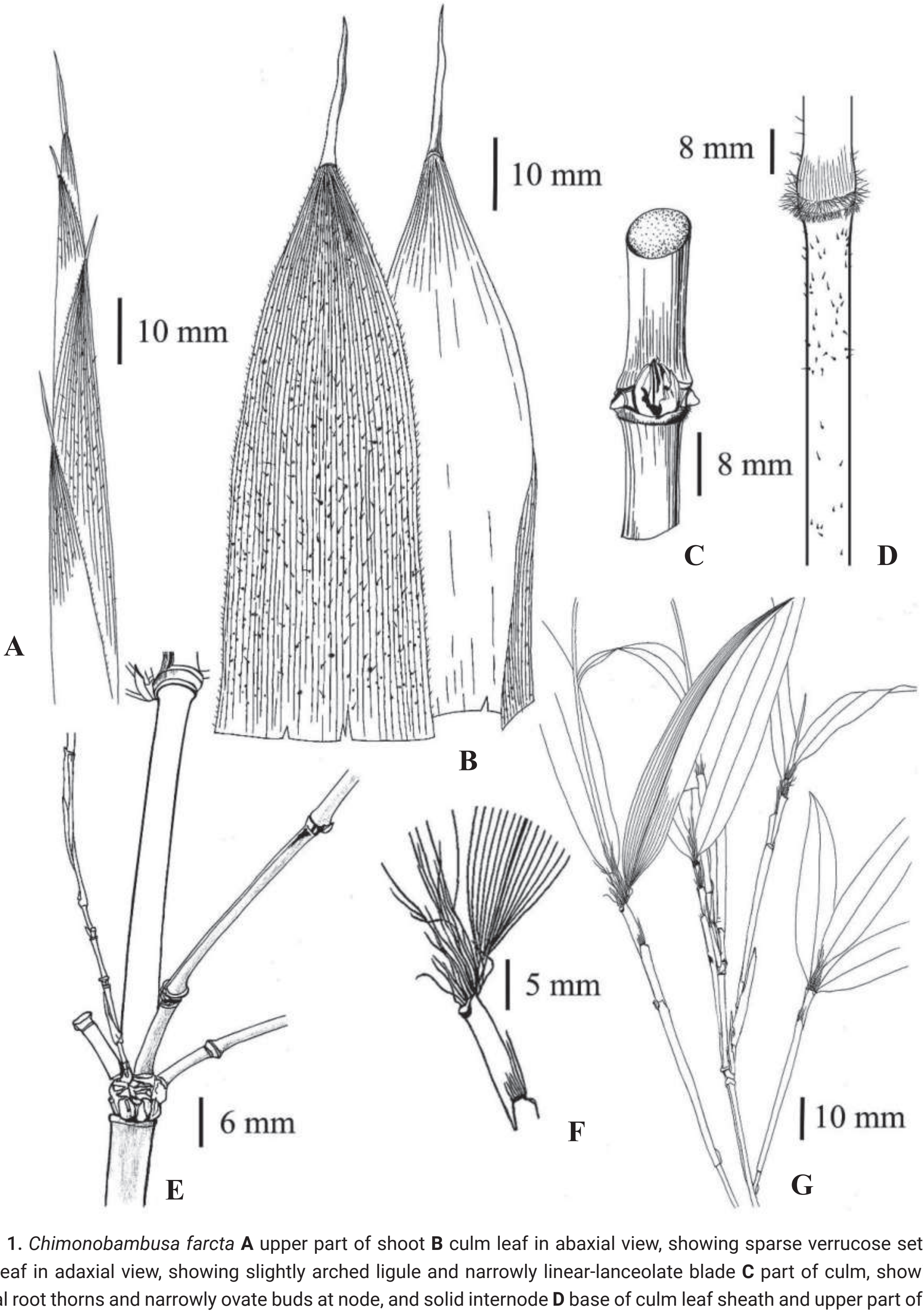

Figure 1. *Chimonobambusa farcta* **A** upper part of shoot **B** culm leaf in abaxial view, showing sparse verrucose setae; culm leaf in adaxial view, showing slightly arched ligule and narrowly linear-lanceolate blade **C** part of culm, showing conical root thorns and narrowly ovate buds at node, and solid internode **D** base of culm leaf sheath and upper part of an internode of young culm, showing indumentum and curved verrucae **E** a node of mid-culm, showing branch complement **F** mouth of foliage leaf sheaths, showing developed fimbriae **G** branchlets and ultimate branchlets, showing foliage leaf complement. Illustrated by Sai-Jun Ma based on *G. H. Lai & J. J. Yue 22111*.

Figure 2. *Chimonobambusa farcta* **A** clump **B** rhizome **C** a node in lower culm, showing bud complement **D** intranodes of lower culms, showing an arrangement of conical or top-shaped, hard root thorns **E, F** cross section of old and young culms, showing solid internode **G** part of culm internode, showing dense curved verrucae **H** upper part of an internode of young culm, showing short, retrorse hairs arranged in longitudinal rows **I, J** node of mid-culm or upper culm, showing branch complement **K** branchlet and foliage leaves in adaxial view, showing sheaths, fimbriae, and blades **L** base of foliage leaves in abaxial view **M** part of foliage leaves in abaxial view, showing pubescent abaxial surface. Photos by Guang-Hui Lai.

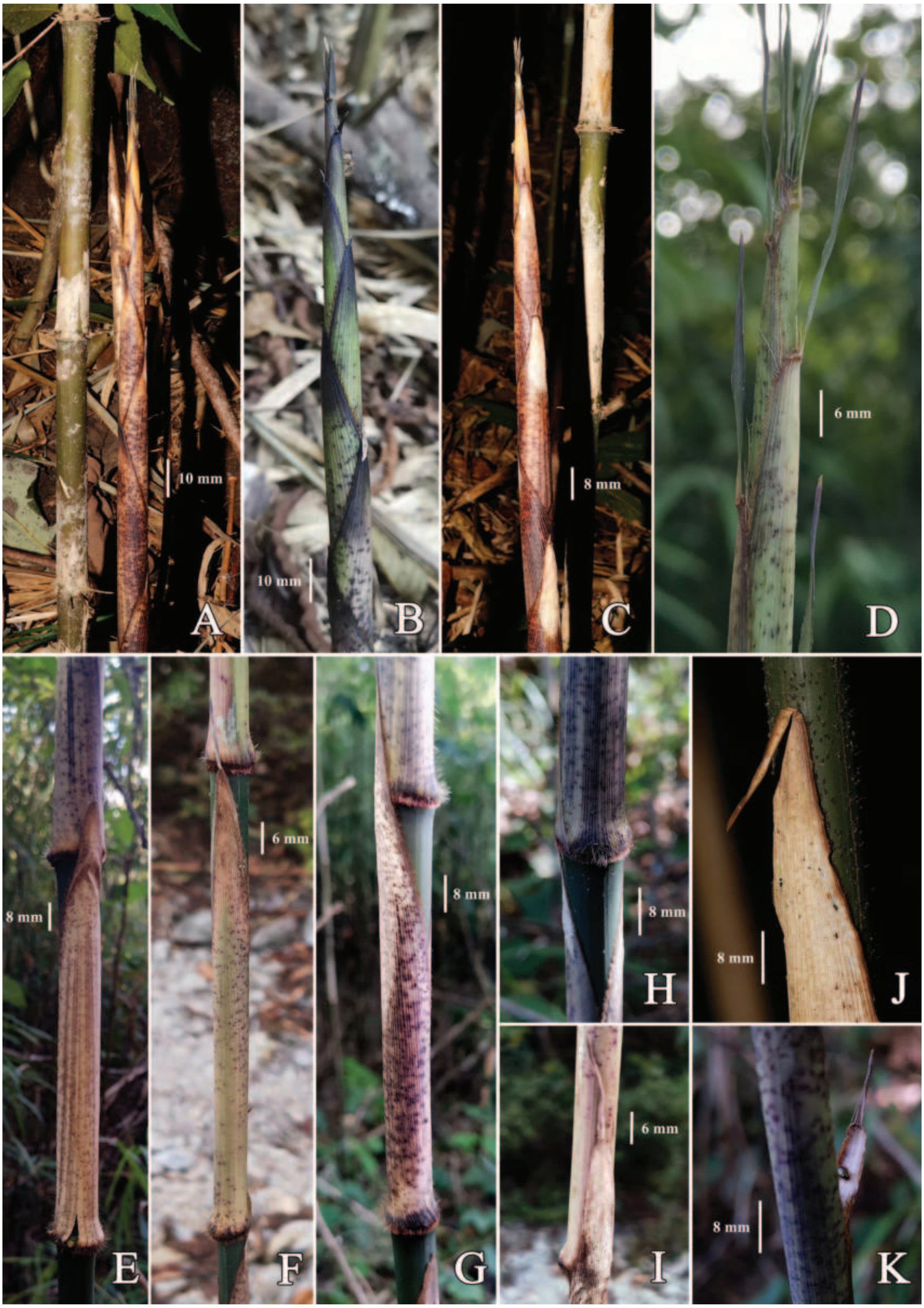

Figure 3. *Chimonobambusa farcta* **A, B, C** shoots, showing variable colors on sheaths **D** upper part of shoot, showing a few fimbriae and nearly erect blade **E, F** culm leaf sheath in abaxial view, with small purple-brown spots and sparse verrucose setae, sometimes with brownish stripes **G** culm leaf sheath in lateral view, showing densely brown ciliate margins **H** base of culm leaf sheath, showing indumentum **I** upper part of culm leaf in abaxial view, showing arched top of sheath **J** upper part of culm leaf in abaxial view, showing truncate short ligule and blade **K** upper part of culm leaf in adaxial view, showing slightly arched short ligule. Photos by Guang-Hui Lai.

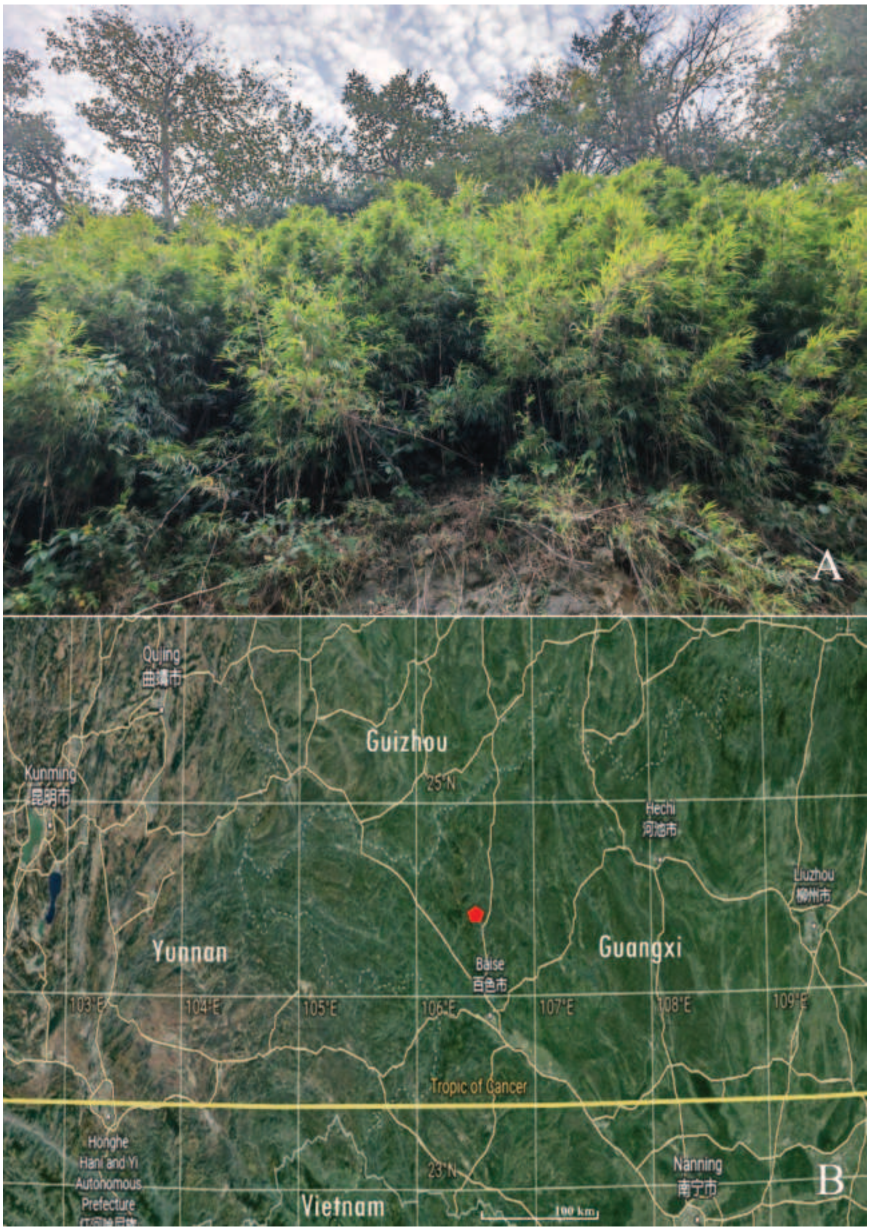

Figure 4. The habitat and geographical distribution of *Chimonobambusa farcta* **A** clump growing in natural habitat **B** the red pentagon showing its distribution area. Photo A by Guang-Hui Lai.

Conservation status. This new species has been commonly found in the northwestern mountainous area of Lingyun County with quite a few populations, where its area of occupancy is less than 50 km^2. Fortunately, its current distribution area happens to be included in the Sishuihe Nature Reserve and is under effective protection. Thus, it is assigned the status of "Least Concern" (LC) according to the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2022).

Phenology. New shoots developed in October.

Etymology. The specific epithet "*farcta*" refers to the culms of the new species with solid internodes.

Additional specimens examined (paratypes). China. Guangxi: Lingyun County, Sicheng Town, Jinbao Village, Dashipo, 24°25'52"N, 106°30'30"E, 1294 m alt., 5 November 2022, *J. X. Ma & D. D. Zhao 22001* (Anji Bamboo Exposition

Garden); same locality, 24 May 2023, *G. H. Lai & J. J. Yue 23030* (herbarium of Guangde Forestry Institute); Lingyun County, Sicheng Town, Jinbao Village, Bajiaoshan, 24°24'51"N, 106°30'17"E, 1316 m alt., 22 October 2023, *G. H. Lai & J. J. Yue 23042* (herbarium of Guangde Forestry Institute).

Discussion

Chimonobambusa Makino (s. l.) was divided into three sections by Wen and Ohrnberger (Ohrnberger 1990), namely *C.* sect. *Chimonobambusa*, *C.* sect. *Oreocalamus* (Keng) T.H.Wen & Ohrnb. and *C.* sect. *Qiongzhuea* (Hsueh & Yi) T.H.Wen & Ohrnb. They actually originated from three prior genera, *Chimonobambusa* Makino, 1914, *Oreocalamus* Keng, 1940 and *Qiongzhuea* Hsueh & Yi, 1980. Subsequently, Wen (1994) followed this treatment in his monographic study on the genus *Chimonobambusa* with 5 species under *C.* sect. *Chimonobambusa*. Xue and Zhang (1996) partially adopted this treatment in "*Flora Reipublicae Popularis Sinicae Tomus 9 (1)*", and Xue and Yi (1996) restored *C.* sect. *Qiongzhuea* to a separate genus *Qiongzhuea* whose shoots are not black under the action of enzymes, but *C.* sect. *Chimonobambusa* and *C.* sect. *Oreocalamus* were reserved in *Chimonobambusa*. Later, Stapleton and Xia (2004) pointed out the illegality of the generic name *Qiongzhuea* Hsueh & Yi, 1980 because its type species had not been effectively published, and regarded that *Qiongzhuea* was legally established in 1983 according to a *descriptio generico-specifico* with the type species *Chimonobambusa szechuanensis* (Rendle) Keng f., but its morphological characteristics were the same as those of the *C.* sect. *Oreocalamus*. Therefore, *Chimonobambusa* sect. *Qiongzhuea* were treated as a synonym of *C.* sect. *Oreocalamus*, and most of the species described under the former were transferred into the latter, only two swollen node species were separated to establish a new group *C.* sect. *Neoqiongzhuea* Stapleton & N. H. Xia. Li and Stapleton (2006) recognized *Chimonobambusa* (s. l.) in "*Flora of China Vol. 22*", but no infrageneric group was defined. Both Yi et al. (2008) and Shi et al (2021) agree with the generic concept of Xue and Zhang (1996), but did not recognize the division of sections. We believe that there are about 9 species similar to the type species of *Chimonobambusa*, i.e. *C. marmorea*, with distinctive features in having persistent culm leaves and thinly papery or rarely papery culm leaf sheaths and constituted a relatively natural group. It is appropriate to place these species into *C.* sect. *Chimonobambusa* because they are obviously different from other bamboo species with deciduous culm leaves, papery or thickly papery culm leaf sheaths in the genus *Chimonobambusa* (s. l.). Some key vegetative characteristics of this new species, such as its slender and shorter culms with persistent culm leaves and very thin culm leaf sheaths, and new shoots developed in October, are rather consistent with those of *C.* sect. *Chimonobambusa*. Thus, this new species should be placed in this section. A key to the species of *C.* sect. *Chimonobambusa* is provided.

Key to the species of *Chimonobambusa* sect. *Chimonobambusa*

1a Culm leaf blades on middle and upper part of culm well-developed, longer than 10 mm...**2a**

2a Culm intranodes without root thorns, initially glabrous................................ ....***Chimonobambusa sichuanensis***

2b Culm basal to middle intranodes with root thorns, initially pubescent....**3a**

3a Culm internodes solid, verrucose; intranode 3–4 mm long; foliage leaf usually 3–6 per ultimate branchlet, foliage leaf blades 0.7–1.4 cm wide... ....***Chimonobambusa farcta***

3b Culm internodes hollow, verrucose-hispid; intranode 1–2 mm long; foliage leaf usually 1 or 2 per ultimate branchlet, foliage leaf blades usually 1.4–2.5 cm wide..***Chimonobambusa leishanensis***

1b Culm leaf blades on middle and upper part of culm slightly developed, shorter than 9 mm..**4a**

4a Culm leaves shorter than internodes; culm leaf sheaths abaxially unmarked **5a**

5a Culm 0.7–2.1 m tall; internodes solid, pubescent; culm leaf blade ca. 2 mm long; foliage leaf blades 9–12 × 0.7–0.9 cm... ***Chimonobambusa pubescens***

5b Culm 2.5–5 m tall; internodes hollow, glabrous; culm leaf blade 2–9 mm long; foliage leaf blades 15–23 × 1.6–2 cm..***Chimonobambusa luzhiensis***

4b Culm leaves longer than internodes; culm leaf sheaths abaxially grey or brown spotted...**6a**

6a Culm internodes initially glabrous; culm leaf sheaths abaxially grey spotted, glabrous or sparsely setose **7a**

7a Culm 1–1.5(–3) m tall, only basal intranodes with aerial roots or root thorns, culms cylindrical .... ***Chimonobambusa marmorea***

7b Culm taller than 3 m, basal to middle intranodes with root thorns, culms slightly 4-angular ....***Chimonobambusa purpurea***

6b Culm internodes initially white pubescent; culm leaf sheaths abaxially brown spotted, densely setose..**8a**

8a Culm internodes 10–13 cm long, hollow; culm leaf blade 3–4 mm long; foliage leaf ligule ca. 6 mm long .... ***Chimonobambusa damingshanensis***

8b Culm internodes 7–8 cm long, subsolid; culm leaf blade shorter than 1 mm; foliage leaf ligule shorter than 1 mm long.......***Chimonobambusa brevinoda***

We also found that a vegetative description of *Chimonobambusa pubescens* Wen is incomplete. In the protologue, Wen (1986) stated that the abaxial surface of foliage leaf blade was covered with silky hair in the diagnosis part, while he mentioned that both surfaces of foliage leaf blades were glabrous in the description part. Obviously, the description is inconsistent. In fact, both surfaces of foliage leaf blades of this species are glabrous (Fig. 5). *Chimonobambusa solida* B. M. Yang & C. Y. Zhang, which is morphologically very similar to *C. pubescens*, was described by Yang (1988) based on the specimens collected from Yiyang Forestry Institute where the propagating materials were introduced from Zhijiang County of Hunan Province. During our investigation on scattered bamboos from this province in 2022, we discovered that the original site of this species is not far away from the type locality of *C. pubescens* with only a straight-line distance of about 100 km. The habitats of the two species are almost the same, and many of the common characteristics are shared by them, such as relatively short and slender culm with solid and initially white pubescent internodes, basal nodes with some short aerial roots, abaxially mainly glabrous culm leaf sheaths and relatively narrow foliage leaf blades. Therefore, we support that Wen (1994) reduced *C. solida* into a synonym of *C. pubescens*. However, it is found that both Wen and Yang incompletely recorded the

Figure 5. *Chimonobambusa pubescens* **A** clump **B** intranode of lower culm, showing an arrangement of short root thorns **C** cross section of old culm, showing solid internode **D** part of foliage leaves in abaxial view, showing glabrous abaxial surface. Photos by Guang-Hui Lai.

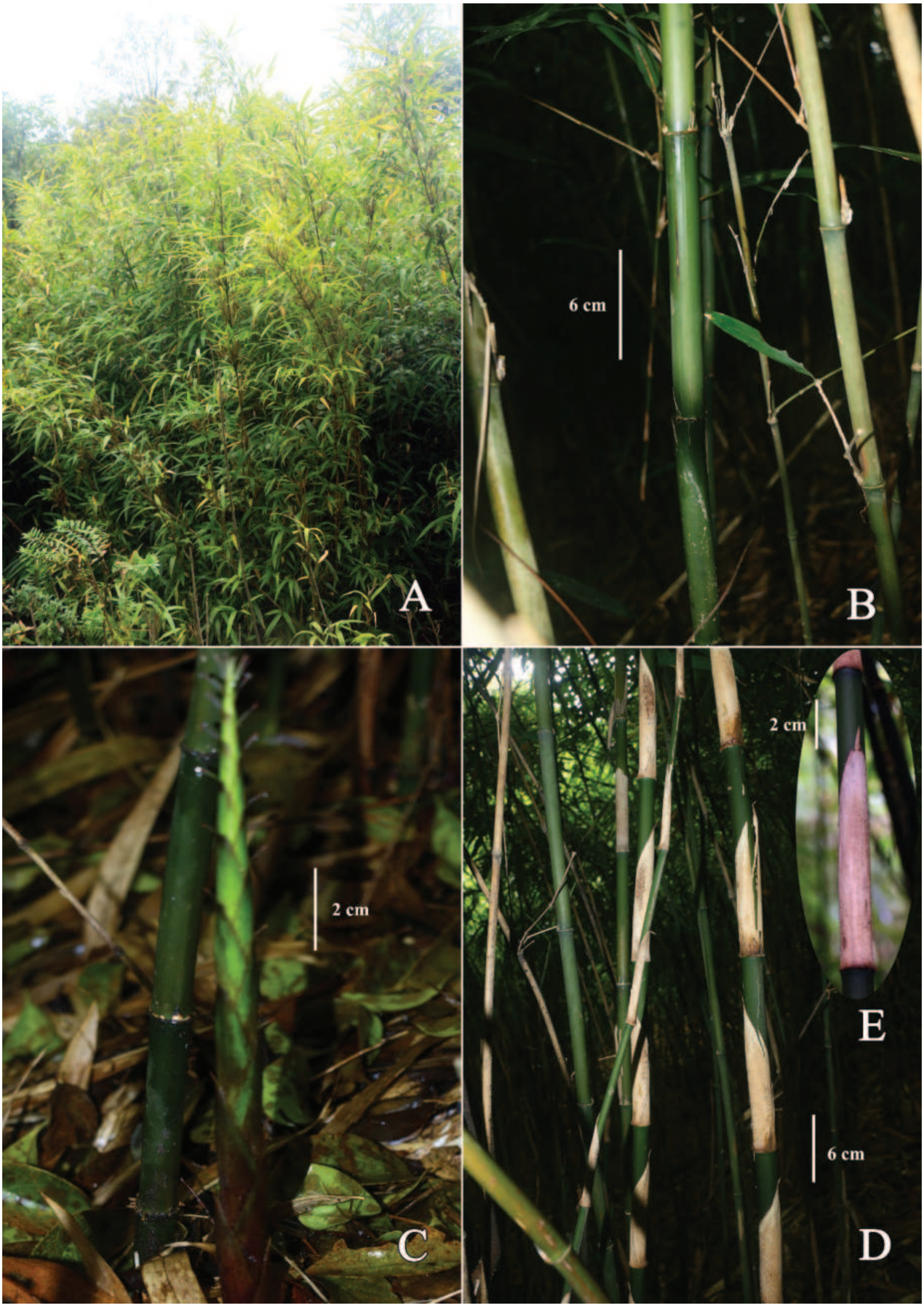

Figure 6. *Chimonobambusa luzhiensis* **A** clump **B** a part of culms, showing cylindrical internodes **C** shoot and base of culm, showing nodes with protuberances or short aerial roots **D, E** persistent culm leaves. Photos by Guang-Hui Lai.

height and thickness of their culms. In a superior habitat, this species can grow to 2.1 m tall and 1.1 cm in diameter, which can also be supported by Zhang (2009). *Chimonobambusa luzhiensis* was placed in *Qiongzhuea* when it was first published (Hsueh and Yi 1983), but it is characterized by culm usually with cylindrical internodes, basal nodes with protuberances or short aerial roots, persistent culm leaves with smaller culm leaf blades 2–9 mm long (Fig. 6), new shoots developed in October, which shows that it is just right to fall into *C.* sect. *Chimonobambusa*, so we support the treatment of Lan (1988), Ohrnberger (1990) and Wen (1994) to transfer it into *Chimonobambusa*.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: GHL. Investigation and collection: GHL, JJY. Taking photos: GHL. Writing – original draft: GHL. Writing – review and editing: GHL, JJY.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Taxonomic revision of *Camellia* (Theaceae) in Thailand

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Abstract

Natural plants of *Camellia* (Theaceae) in Thailand are taxonomically revised with a key, a distribution map, descriptions, specimens examined, and figures of living plants and/or dry specimens. Nine taxa comprising seven species and two varieties are recognized, including *C. caudata*, *C. connata*, *C. furfuracea*, *C. kissi*, *C. kissi* var. *confusa*, *C. laotica*, *C. sinensis* var. *assamica*, *C. suddeeana*, and *C. taliensis*. *Camellia caudata* and *C. laotica* are new records to Thailand, and *C. connata* and *C. suddeeana* are endemic to the country. Formerly recorded *C. pleurocarpa* and *C. tenii* are excluded from Thai flora because of misidentification, and *C. oleifera* and *C. sinensis* are merely cultivated in the country. Morphological descriptions of *C. connata* and *C. laotica* are improved based on additional collections examined.

Key words: Assam tea, Indochina, new records, oil camellias

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Introduction

Camellia L. (Theaceae) contains economically important plants, including tea, oil camellia and camellias. They are evergreen shrubs or trees distributed in East, South and Southeast Asia (Zhao et al. 2023). Plants of *Camellia* generally bear a smooth bark, simple and alternate leaves without stipules, coriaceous leaf blades, axillary and bisexual flowers, dorsifixed anthers, a superior ovary, a loculicidal capsule with a columella and wingless seeds. Sealy (1958) recorded 82 species and 24 doubtful names in his monograph of *Camellia*. Chang (1998) counted about 280 species in the genus but Ming (2000) revised the number of species into 119. Since 2000, more than 100 species have been described in *Camellia* (e.g., Orel and Curry 2015, 2019; Liu et al. 2020; Ye et al. 2022; Zhao 2023). However, previous monographers of *Camellia*, such as Sealy (1958), Chang (1981, 1998) and Ming (2000), generally focused on the species distributed in China but hardly examined the collections at local herbaria in Indochina (Zhao 2022a). For example, the specimens of *Camellia* at Thai herbaria have not been thoroughly inspected since Keng's (1972) work.

Craib (1925) recognized three species of *Camellia* for Thailand, including *C. confusa* (Craib) Cohen-Stuart, *C. connata* (Craib) Craib and *C. theifera* Griff., in his "Florae Siamensis Enumeratio". Keng (1972) subsequently recorded six taxa of the genus, viz. *C. connata*, *C. oleifera* C. Abel var. *confusa* (Craib) Sealy, *C. pleurocarpa* (Gagnep.) Sealy, *C. sinensis* (L.) Kuntze var. *assamica* (Royle ex

Hook.) Steenis (Assam tea), *C. taliensis* (W.W. Sm.) Melch. and *C. tenii* Sealy, in “Flora of Thailand”. Later, Ming (2000) and Zhao (2021) added *C. kissi* Wall. and *C. furfuracea* (Merr.) Cohen-Stuart to the Thai flora, respectively. Zhao (2023) described a new species, *C. suddeeana* D.Wei Zhao from Thailand. However, Thailand is a botanically under-collected country (Parnell et al. 2003). Here I present a taxonomic revision for *Camellia* in Thailand based on taxonomic literature (Craib 1925; Sealy 1958; Keng 1972; Smitinand 1975; Chang 1981; Gardner et al. 2000; Ming 2000; Maxwell and Elliott 2001; Zhao et al. 2023), herbarium specimens, and fieldwork performed by myself. Two new records are reported along with an up-to-date taxonomic revision of *Camellia* for the country.

Material and methods

Morphological characters were described based on living plants, herbarium specimens or their images from BK, BKF, BM, C, CMUB, E, GXMI, HITBC, IBK, IBSC, K, KKU, KUN, L, MO, NSW, P, PE, PNH, QBG, SING, SYS, and TCD (acronyms following Thiers 2024, continuously updated). Geographic distribution data were retrieved from the specimen records and mapped using ArcMap 10.7 (ArcGIS, ESRI) and optimized in Adobe Illustrator CS3. All photos of dry specimens and living plants in the figures were taken and adapted by the author.

Results

A key to all nine taxa of *Camellia* occurring in Thailand is present below. Taxa in Thailand are subsequently listed alphabetically.

Key to taxa of *Camellia* in Thailand

1 New branchlet and petiole glabrous **2**
– New branchlet and petiole hairy **3**
2 Pedicel 1–3 mm long, sepals abaxially pubescent .... ***C. furfuracea***
– Pedicel 4–8 mm long, sepals abaxially glabrous .... ***C. taliensis***
3 Sepals caducous after flowering **4**
– Sepals persistent after flowering **5**
4 Flowers 1–4.5 cm in diam., styles 1.5–7 mm long, pericarp 0.5–1.5 mm thick .... ***C. kissi***
– Flowers 4.5–10 cm in diam., styles 8–12 mm long, pericarp 2–8 mm thick .... ***C. kissi* var. *confusa***
5 Style 1, apically (2–)3–5 lobed **6**
– Styles 3, distinct **8**
6 Sepals 3–4, ovary glabrous .... ***C. laotica***
– Sepals 5, ovary hairy **7**
7 Bracteoles caducous, sepals abaxially glabrous .... ***C. sinensis* var. *assamica***
– Bracteoles persistent, sepals abaxially pubescent .... ***C. caudata***
8 Filaments yellowish orange, completely united into a tube, ovary pubescent .... ***C. connata***
– Filaments white, basally connate ca. 1/3, ovary glabrous .... ***C. suddeeana***

1. *Camellia caudata* Wall., Pl. Asiat. Rar. 3: 36. 1832.

= *Camellia assimilis* Champ. ex Benth., Hooker's J. Bot. Kew Gard. Misc. 3: 309. 1851. Lectotype (designated by Chang & Bartholomew [1984: 205]): China. Hong Kong, *J.G. Champion 65* (K 000380537!).
= *Camellia gracilis* Hemsl., Ann. Bot. (Oxford) 9(33): 146. 1895. Holotype: China. Taiwan: Bankinsing mountains, *A. Henry 1612* (K 000380535!).
= *Camellia triantha* Hung T. Chang, Taxon. Gen. Camellia 144. 1981. Holotype: China. Guangxi: Yongning, 20 October 1963, *F.S. Huang 17625* (SYS 00094835!).
= *Camellia tubiformis* Hung T. Chang & S.X. Ren, Acta Sci. Nat. Univ. Sunyatseni 31(1): 75. 1992. Holotype: China. Guangdong: Fengkai, Heishiding, 580 m, 1 January 1991, *R.X. Jiang s.n.* (SYS 00094839!).

Type material. ***Lectotype*** (designated by Zhao et al. [2017a: 172]): India. [Meghalaya: Khasia Hills], the district of Sylhet, November 1827, *H. Bruce s.n.* in *N. Wallich 978* (right-hand specimen of K 001110475!).

Description. Trees or shrubs up to 15 m tall. ***New branchlets*** and ***terminal buds*** pubescent. ***Petioles*** 1–5 mm long, pubescent; ***leaf blades*** elliptic, oblong or lanceolate, 3.5–11.5 × 1.5–3 cm, thinly coriaceous or papery, abaxially pale green, sparsely appressed pubescent or villous, adaxially yellowish or dark green, shiny, hirsute along midrib, midrib abaxially elevated and adaxially slightly impressed, secondary veins 8–12 on each side of midrib, abaxially slightly elevated and adaxially obscure, base attenuate to obtuse, margin serrulate, apex caudate. ***Flowers*** solitary or up to 3 in a cluster, 2–4 cm in diam. ***Pedicel*** 2.5–7 mm long. ***Bracteoles*** 3–6, alternate, persistent, deltate to semi-orbicular, 1–2.5 × 1–3 mm, abaxially sparsely pubescent to pubescent, adaxially glabrous, margin ciliolate. ***Sepals*** 5, persistent, suborbicular, 2–3 × 2–4 mm, abaxially pubescent, adaxially glabrous. ***Petals*** 5–7 in 1–2 whorls, white, elliptic to obovate, 11–20 × 8–14 mm, abaxially pubescent, adaxially glabrous, apex rounded to emarginate, inner 4–5 petals basally adnate to filament whorl for 2–4 mm. ***Stamens*** numerous, 10–15 mm long; filaments white, outer filaments basally connate for 6–10 mm, distinct part villous. ***Ovary*** globose to ovoid, densely pubescent. ***Style*** 1, 8–18 mm long, basally densely pubescent and gradually becoming sparsely pubescent apically, apically 3-lobed for 1–3 mm. ***Capsule*** globose to ovoid, 11–15 mm in diam., 1-loculed with 1 seed; pericarp 0.4–1 mm thick. ***Seeds*** fuscous, globose, 1–1.5 cm in diam., glabrous Fig. 1.

Phenology. Flowering October–December, fruiting March–December.

Distribution and habitat. *Camellia caudata* occurs in semi-evergreen, evergreen and deciduous montane forests at the elevations of 500–2000 m in China, India, Laos, Myanmar, Nepal, Thailand (Fig. 2), and Vietnam.

Additional specimens examined. Chiang Rai: Wiang Pa Pao, Doi Luang, Doi Mok Mountain, close to source of Man Mae Nga Stream, 19°15'36"N, 99°20'24"E, 950 m, 23 July 1998, *Morci 1365.0* (CMUB).

Nan: Doi Tiu, 1100 m, 8 March 1921, *Kerr 5041* (BK 203924, BM, K, L.2399739); Tha Wang Pha, Pa Kha, Doi Wao, 1400–1700 m, 10 September 1995, *Larsen et al. 46319* (BKF SN147973) & *46292* (IBSC 0256482).

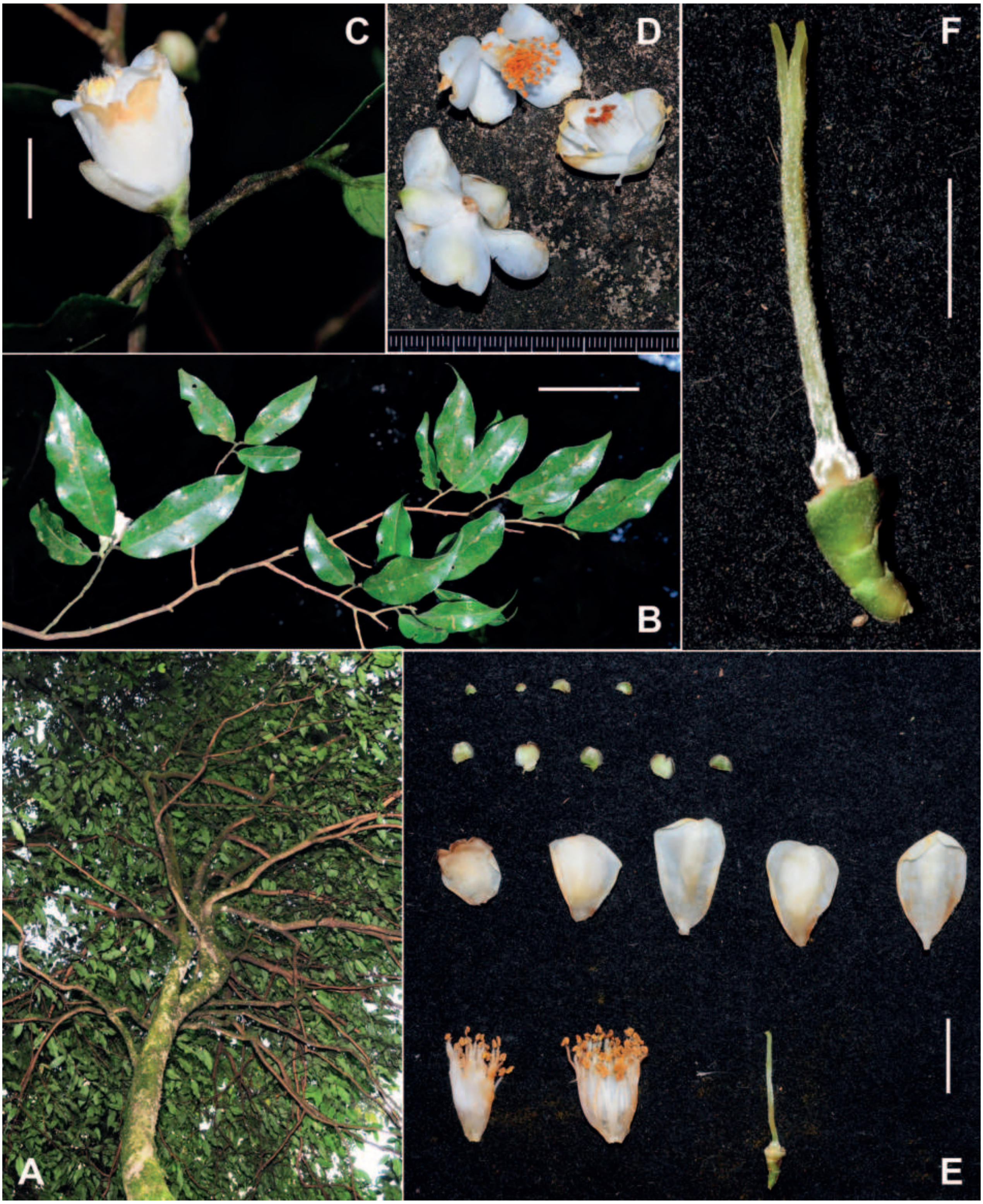

Figure 1. *Camellia caudata* **A** canopy of a tree **B** branch **C** flower **D** petals and androecia **E** a dissected flower **F** gynoecium and pedicel. Scale bars: 5 cm (**B**); 1 cm (**C, E**); 5 mm (**F**). The minimum graduation of the ruler in **D** indicates 1 mm.

Uttaradit: Phu Soi Dao, 1531 m, 17 November 2009, *Norsaengsri & Intamusik 6104* (QBG 42621), 1570 m, 18 November 2009, *Norsaengsri & Intamusik 6202* (QBG 42737).

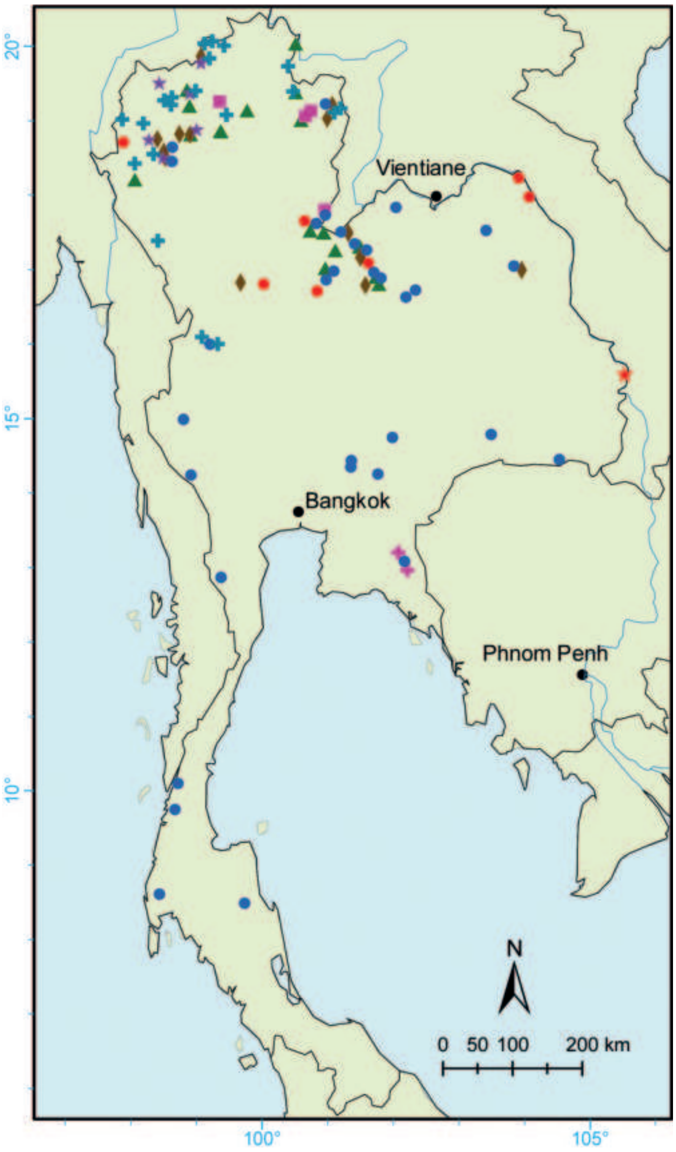

Figure 2. Distribution of *Camellia* taxa in Thailand: *C. caudata* (Pink square), *C. connata* (Purple star), *C. furfuracea* (Pink plus), *C. kissi* (Blue dot), *C. kissi* var. *confusa* (Brown diamond), *C. laotica* (Red star), *C. sinensis* var. *assamica* (Green triangle), *C. suddeeana* (Red dot) and *C. taliensis* (Blue plus).

Notes. Wallich (1829) provided a *nomen nudum* of *C. caudata*, the name was subsequently validated in Wallich (1832). In the protologue of *C. triantha*, Chang (1981: 146) stated that the filaments, styles and ovaries of the species were glabrous and indicated the holotype at SYS. The holotype consists of a single leaf and two dissected flower buds upon which Chang's (1981: 146, 1998: 159) descriptions were generally based. However, two isotypes of *C. triantha* (GXMI 050183, GXMI 050184) with mature flowers clearly show that the filaments, styles and ovaries of the species are not glabrous but densely pubescent. Therefore, I agree with Ming's (2000: 201) view and treat *C. triantha* as a heterotypic synonym of *C. caudata*.

Camellia caudata is a new record to Thailand. It generally occurs in the montane forests at elevations of 900–1700 m of Northern Thailand. The species is one of several camellias that are widely distributed in Indochina, along with

Assam tea, *C. furfuracea* and *C. kissi*. Kerr A.F.G. collected specimens of *C. caudata* in 1921 (*Kerr 5041* at BK, BM, K and L). The specimens were, however, misidentified as *C. connata* by Keng H. in 1970 as shown on the sheet conserved at BM. *Camellia caudata* can be distinguished from *C. connata* by its basally connate styles whereas the latter bears distinct styles.

2. *Camellia connata* (Craib) Craib, Fl. Siam. 1(1): 131. 1925.

≡ *Thea connata* Craib, Bull. Misc. Inform. Kew (1): 6. 1914. Lectotype (first-step designated by Sealy [1958: 146]; second-step designated by Zhao et al. [2017a: 174]): THAILAND. Chiang Mai: Doi Suthep, 1520 m, 25 June 1911, *A.F.G. Kerr 1878* (K 000704325!).

Description. Shrubs or trees up to 8 m tall. ***New branchlets*** puberulous; ***terminal buds*** pubescent. ***Petioles*** 2.5–7 mm long, sparsely puberulous; ***leaf blades*** elliptic to oblong, 5.5–12 × 3–5 cm, thinly coriaceous, abaxially yellowish green and brown punctate, glabrous or sparsely puberulous along midrib, adaxially yellowish or dark green, shiny, hirsute along midrib, midrib abaxially elevated and adaxially slightly raised, secondary veins 9–12 on each side of midrib, slightly raised on both surfaces, base attenuate to rounded, margin serrulate, apex acute to attenuate. ***Flowers*** solitary or paired, ca. 2 cm in diam., subsessile. ***Bracteoles*** 3–6, alternate, persistent, gradually transitioning to sepals, deltate to semi-orbicular, 1.5–3 × 1–2.5 mm, abaxially glabrous or sparsely puberulous, adaxially glabrous. ***Sepals*** 4–5, persistent, sub-orbicular or ovate, 3.5–5 × 4–6 mm, abaxially glabrous or sparsely puberulous, adaxially glabrous, margin ciliolate and usually lacerate. ***Petals*** 6–7 in 2 whorls, elliptic or ovate, glabrous, outer 2 petals 5–7 × 7–9 mm, greenish white, inner 4–5 petals basally adnate to filament whorl for ca. 3 mm. ***Stamens*** 14–20; filaments yellowish orange, glabrous, outer 9–14 filaments completely united into a 7–12 mm long tube, ca. 5 mm in diam., apex irregularly dentate, each tooth bearing an anther, remaining filaments 6–9 mm long, borne on the inside of filament tube. ***Ovary*** globose to ovoid, pubescent. ***Styles*** 3, distinct, ca. 1.5 mm long, glabrous or sparsely puberulous at base. ***Capsule*** ovoid or globose, 10–25 mm in diam., 1–3-loculed with 1–3 seeds; pericarp 0.5–1 mm thick. ***Seeds*** black to brown, globose or hemispherical, 1–1.5 cm in diam., glabrous Fig. 3.

Phenology. Flowering April–August, fruiting July–November.

Distribution and habitat. *Camellia connata* is endemic to northern Thailand (Fig. 2), in the evergreen, mixed evergreen and deciduous forests at the elevations of 550–2000 m.

Additional specimens examined. Chiang Mai: 610 m, 16 July 1923, *Winit 1134* (BKF SN060818, K); Chiang Dao, Doi Chiang Dao, east side of Sop Huay Pah Dahng-Huay Nah Lao Station, 575 m, 18 August 1995, *Bella & Nanny 5* (CMUB 06549); Chom Thong, Doi Inthanon, Mae Uam Station, ca. 1700 m, 2 April 2008, *Watthana 2735* (QBG 37391); Fang, Doi Ang Khang, ca. 1500 m, 14 July 1922, *Kerr 6294* (BK 203711, BM, K), 1400–1800 m, 8 June 1976, *Charoensorn s.n.* (BK 203714); Mae Chaem, ca. 800 m, 22 October 1922, *Kerr 6428* (BK 203710, K), Doi Inthanon, between 34 km and 35 km, on the road to Mae Aum Watershed Management Station, 1590–1640 m, 12 November 2015, *Zhao et al.*

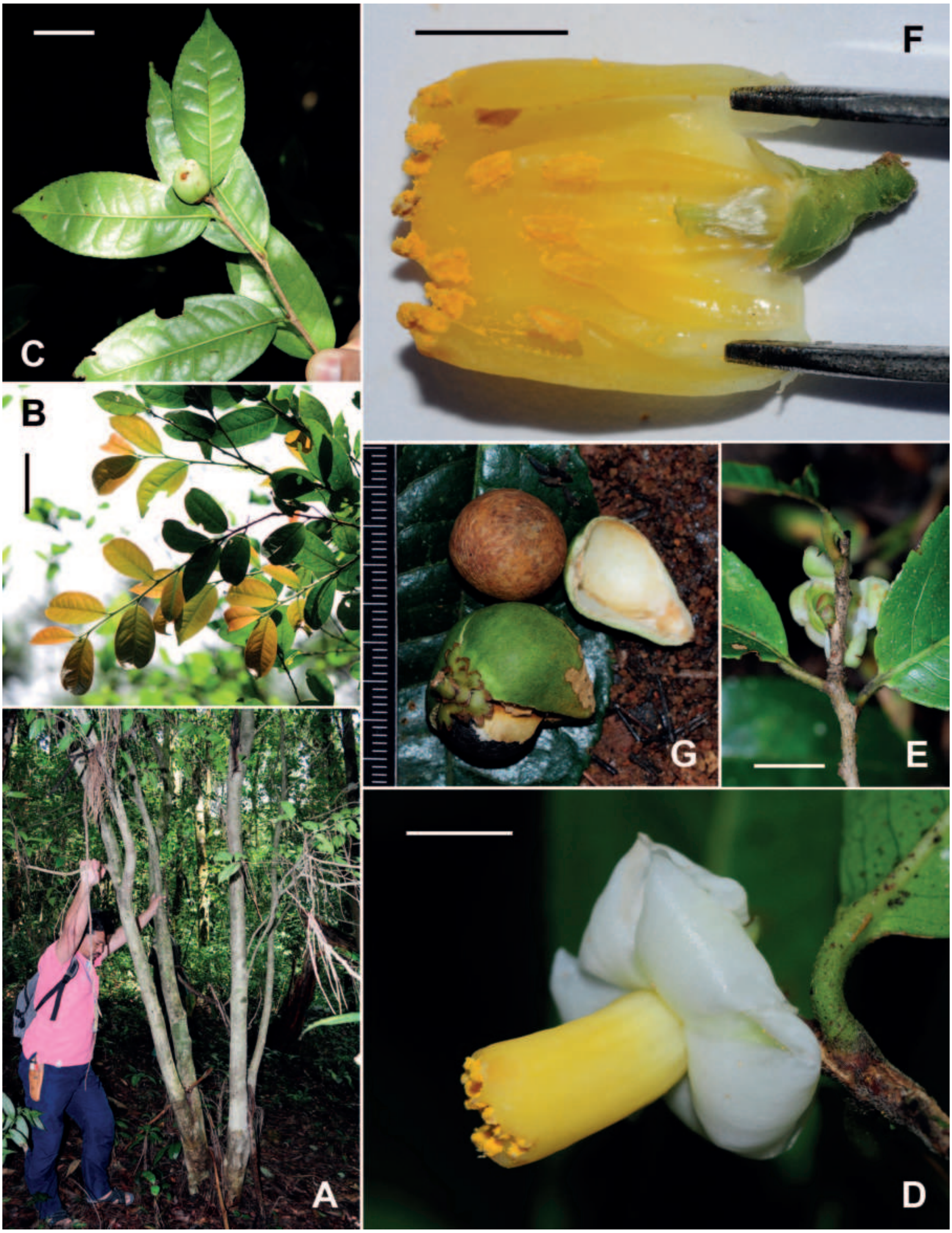

Figure 3. *Camellia connata* **A** habit **B** branchlets **C** a branch with an immature fruit **D, E** flowers **F** a dissected flower without corolla **G** a fruit and seeds. Scale bars: 5 cm (**B**); 2 cm (**C**); 5 mm (**D, F**); 1 cm (**E**). The minimum graduation of the ruler in **G** indicates 1 mm.

84 (BKF, TCD), *85–88* (TCD), *89* (BKF, TCD), *90* (BKF, KUN, TCD), *91*(KUN, TCD), *92* (BKF, KUN, TCD), *93 (1), (2)* (TCD) & *94* (BKF, KUN, TCD); Mueang Chiang Mai, Doi Suthep-Pui, 18°49'42"N, 98°53'26"E, 1636 m, 13 November 2015, *Zhao* *et al. 97 (1) & (2)* (TCD). **Mae Hong Son:** Pai, Doi Chang, 2000 m, 31 May 1977, *Santisuk 1131* (BKF SN178498).

Notes. Cohen-Stuart (1916, 1919) established *Camellia* sect. *Calpandria* (Blume) Cohen-Stuart based on *C. lanceolata* (Blume) Seem. and thought that *T. connata* might be a heterotypic synonym of *C. lanceolata*. Sealy (1958) suggested that the two species were distinct from each other and placed *C. connata* in sect. *Calpandria* because both plants bore a filament tube. Subsequent monographers of *Camellia*, including Chang (1981), Chang and Bartholomew (1984) and Ming (2000), agreed with the treatment of Sealy (1958). However, phylogenetic analysis (Zhao et al. 2023) suggested that *C. connata* was nested in the clade of Heterogenea and did not have a close relationship with *C. lanceolata*, which implies that the filament tube is not a synapomorphy in *Camellia*. The descriptions of *C. connata* provided in Sealy (1958) and Ming (2000) were based on several specimens collected by Kerr and Winit about a century ago. A detailed account of *C. connata* is supplied here with recent collections and photos of living plants (Fig. 3).

3. *Camellia furfuracea* (Merr.) Cohen-Stuart, Bull. Jard. Bot. Buitenzorg 1(4): 240. 1919.

≡ *Thea furfuracea* Merr., Philipp. J. Sci., C 13: 149. 1918. Holotype: CHINA. Guangdong: Huizhou, Boluo, Luofu Mountain, 9–27 August 1917, *E.D. Merrill 10681* (PNH 87432, image!).

= *Thea bolovenensis* Gagnep., Notul. Syst. (Paris) 10: 124. 1942. Lectotype (designated by Ming [2000: 225]): LAOS. Champasak: Plateau des Boloven, entre Nong Bok Kao et Phong Tham, 900 m, 6 October 1928, *E. Poilane 15856* (K 000704324!).

= *Camellia suaveolens* C.X. Ye, X.J. Wang & X.G. Shi, Acta Sci. Nat. Univ. Sunyatseni 43(3): 129. 2004. Holotype: CHINA. Guangdong: Yingde, cultivated, introduced from Lechang, 27 October 2002, *C.X. Ye 5919* (SYS 00142796!).

= *Camellia maiana* Orel, Novon 20(2): 198. 2010. Holotype: VIETNAM. Lam Dong: Dalat Plateau, 19 November 2002, *G. Orel et al. 21149* (NSW 901884, image!).

= *Camellia curryana* Orel & Luu, Nordic J. Bot. 32(1): 42. 2014. Holotype: VIETNAM. Lam Dong: Dalat Plateau, 27 February 2002, *G. Orel et al. 21147* (NSW 901031, image!).

= *Camellia duyana* Orel, Curry & Luu, Novon 23(3): 308. 2014. Holotype: VIETNAM. Lam Dong: Dalat Plateau, ca. 1400 m, 27 November 2010, *G. Orel & N.V. Duy 0719* (NSW 901883, image!).

= *Camellia albata* Orel & Curry, Pursuit Hidden Camellias Vietnam China 239. 2015. Holotype: VIETNAM. Quang Ninh, 2 December 1999, *G. Orel et al. 991202c* (NSW 901898 [sheet 1 of 2, image!] and NSW 849513 [sheet 2 of 2, image!]).

= *Camellia reflexa* Orel & Curry, Pursuit Hidden Camellias Vietnam China 209. 2015. Holotype: VIETNAM. Vinh Phuc: Tam Dao National Park, 2 April 2001, *G. Orel et al. 1240* (NSW 901749, image!).

= *Camellia viscosa* Orel & Curry, Pursuit Hidden Camellias Vietnam China 214. 2015. Holotype: VIETNAM. Lam Dong: Dalat Plateau, 19 November 2002, *G. Orel et al. 21148G* (NSW 901821, image!).

Figure 4. Dry specimens of *Camellia furfuracea*, *Smitinand 12023* at BKF **A** specimen sheet **B, C** flower fragments **D** a part of pericarp along a branchlet bearing a pedicel and gynoecium remains **E** a broken seed. The minimum graduation of the rulers represents 1 mm.

Description. Shrubs or trees up to 15 m tall. ***New branchlets*** glabrous; ***terminal buds*** glabrous or puberulous. ***Petioles*** 3–12 mm long, glabrous; ***leaf blades*** elliptic or oblong, 7.5–17 × 3–7 cm, coriaceous, abaxially yellowish or pale green, brown punctate or glabrous, adaxially dark green, glabrous and shiny, midrib abaxially elevated and adaxially channelled, secondary veins 7–11 on each side of midrib, abaxially raised and adaxially slightly impressed, base attenuate, cuneate or obtuse, margin sparsely serrulate, apex attenuate, acute or obtuse. ***Flowers*** solitary or paired, 4–6 cm in diam. ***Pedicels*** 1–3 mm long. ***Bracteoles*** and ***sepals*** 6–9, caducous, crescent or ovate, 2–13 × 3.5–20 mm, abaxially puberulous or pubescent, adaxially glabrous, margin membranous. ***Petals*** 6–9 in 1–2 whorls, white, elliptic or obovate, 17–25 × 9–15 mm, abaxially puberulous or glabrous, adaxially glabrous, basally connate for 1–2 mm. ***Stamens*** numerous, 10–15 mm long; filaments glabrous, basally adnate to petals for ca. 2 mm. ***Ovary*** ovoid or globose, pubescent. ***Styles*** 3–4, distinct, 6–10 mm long, pubescent and gradually becoming glabrous apically. ***Capsule*** oblate or globose, 3–5 cm in diam., 2–3 cm in height; usually 3-loculed with 1–3 seed per locule; pericarp 1–10 mm thick, furfuraceous. ***Seed***s brown or fuscous, hemispherical or polyhedral, 1.5–2 cm in diam., glabrous Fig. 4.

Phenology. Flowering October–February, fruiting December–April.

Distribution and habitat. *Camellia furfuracea* is distributed in the evergreen forest, on slopes or along streams at elevations of 450–1800 m in China, Laos, Thailand (Fig. 2), and Vietnam.

Additional specimens examined. Chanthaburi: Pong Nam Ron, Khao Soi Dao, ca. 1600 m, 23 January 1956, *Smitinand 3242* (BKF SN060898), 1100 m, 5 April 1974, *Smitinand 11994* (BKF SN060894), 1650 m, 9 February 1975, *Smitinand 12023* (BKF SN060895, BKF SN060896, P 04500286; Fig. 4); Soi Dao, Khao Soi Dao, 1300–1400 m, 12 December 1924, *Kerr 9638* (BK 203925, BM, C, K, P 04500307).

Notes. *Camellia furfuracea* is absent in Keng (1972). A specimen of *C. furfuracea* collected in 1956, *Smitinand 3242* at BKF, was misidentified as *C. oleifera* var. *confusa* by Keng in 1970. Zhao (2021) recognized six heterotypic synonyms of *C. furfuracea* and referenced specimens from Thailand (listed above), which made the species a new record to the country. *Camellia furfuracea* widely occurs in subtropical and tropical China and Indochina. It can be distinguished from *C. kissi* Wall. var. *confusa* (Craib) T.L. Ming by its glabrous new branchlets, usually abaxially punctate leaves and apically divided ovary with distinct styles (Fig. 4), whereas the latter bears puberulous new branchlets, abaxially glabrous leaves and basally connate styles.

4. ***Camellia kissi*** **Wall., Asiat. Reschs. 13: 429. 1820.**

= *Camellia keina* Buch.-Ham. ex D. Don, Prodr. Fl. Nepal. 224. 1825. Holotype: Nepal. Narain hetty, 9 September 1802, *F. Buchanan-Hamilton s.n.* (BM 000521691!).

= *Camellia symplocifolia* Griff., Itin. Pl. Khasyah Mts. 40, No. 652. 1848. Lectotype (designated by Zhao [2022b: 16]): India. Khasya Hills, *W. Griffith s.n.* (TCD 0018254!).

= *Thea bachmaensis* Gagnep., Notul. Syst. (Paris) 10: 124. 1942. Lectotype (first-step designated by Sealy [1958: 199]; second-step designated by Zhao et al. [2017a: 173]): Vietnam. [Thua Thien Hue]: Núi Bach Ma Station d'altitude de Huê, 1400–1500 m, 12 December 1940, *E. Poilane 31118* (P 01903389! Image: https://science.mnhn.fr/institution/mnhn/collection/p/item/p01903389).

= *Thea brachystemon* Gagnep., Notul. Syst. (Paris) 10: 125. 1942. Lectotype (designated by Zhao et al. [2017a: 173]): Laos. [Attapeu]: entre Nong Met et B. Thuôt, plateau des Boloven, 8 October 1928, *E. Poilane 15908* (P 01903386! Image: https://science.mnhn.fr/institution/mnhn/collection/p/item/p01903386).

= *Theopsis euonymifolia* Hu, Acta Phytotax. Sin. 10(2): 140. 1965. Holotype: China. Yunnan: Pu'er, Jingdong, 1050 m, 13 December 1939, *M.G. Li 1506* (KUN 1206027!).

= *Camellia thailandica* Hung T. Chang & S.X. Ren, Acta Sci. Nat. Univ. Sunyatseni 30(1): 67. 1991. Holotype: Thailand. Khao Yai National Park, Khao Khieo, 14°21'N, 101°22'E, 1200–1300 m, 29 October 1970, *C. Charoenphol et al. 4205* (MO; isotypes BKF!, C!, K!).

= *Camellia ligustrina* Orel, Curry & Luu, Novon 23(3): 310. 2014. Holotype: Vietnam. Lam Dong: Mount Lang Biang, 1850 m, 16 December 2011, *G. Orel & A.S. Curry 0734* (NSW 900397, image!).

= *Camellia cuongiana* Orel & Curry, Pursuit Hidden Camellias Vietnam China 180. 2015. Holotype: Vietnam. Lam Dong: Bidoup-Nui Ba National Park, 5 November 2012, *G. Orel et al. 0721* (NSW 901040, image!).

Type material. *Holotype*: NEPAL. 1818, *Gardner s.n.* (BM 000948697!).

4a. *Camellia kissi* var. *kissi*

Description. Shrubs or trees up to 9 m tall. ***New branchlets*** puberulous; ***terminal buds*** puberulous or glabrous. ***Petioles*** 2–7 mm long, puberulous; ***leaf blades*** elliptic, oblong or obovate, 3–13.5 × 1.5–5 cm, coriaceous, abaxially yellowish green and sparsely puberulous or glabrous, adaxially dark green, hirsute along midrib, midrib abaxially elevated and adaxially slightly impressed or flat, secondary veins 6–11 on each side of midrib, base attenuate, cuneate or rounded, margin serrate, apex attenuate, acuminate or caudate. ***Flowers*** 2–4.5 cm in diam., subsessile. ***Bracteoles*** and ***sepals*** 5–12, caducous, crescent to broadly ovate, 1.5–7 × 2.5–9 mm, abaxially glabrous, puberulous or pubescent, adaxially glabrous, margin ciliolate. ***Petals*** 5–6, white, elliptic or obovate, 8–25 × 4–17 mm, abaxially glabrous, puberulous or pubescent at apex, adaxially glabrous. ***Stamens*** numerous, 4–9 mm long; filaments yellow, glabrous, basally connate for 1–2 mm. ***Ovary*** globose, pubescent. ***Styles*** 3, basally connate, 2–7 mm long, basally pubescent and gradually becoming glabrous apically. ***Capsule*** globose or ovoid, 1–3 cm in diam., 1.5–3.5 cm in height, 1–3-loculed with 1–3 seeds; pericarp 0.5–1.5 mm thick. ***Seeds*** brown or black, hemispherical, polyhedral or globose, 1–2 cm in diam., glabrous Fig. 5.

Phenology. Flowering October–February, fruiting March–August.

Distribution and habitat. *Camellia kissi* occurs in evergreen and mixed deciduous forests, usually by streams, at elevations of 50–2150 m in Bhutan, Cambodia, China, India, Laos, Myanmar, Nepal, Thailand (Fig. 2), and Vietnam.

Additional specimens examined. Chiang Mai: Chom Thong, Doi Inthanon, 3 December 1964, *Bunchuai 1420* (BKF SN060820), from 23 km point on the main road to Bang Nong Lum, ca. 1100 m, 16 February 1998, *Konta et al. 4312* (BKF); Mae Chaem, Doi Inthanon, 1700 m, 24 December 1996, *Hara A178* (BKF SN173304).

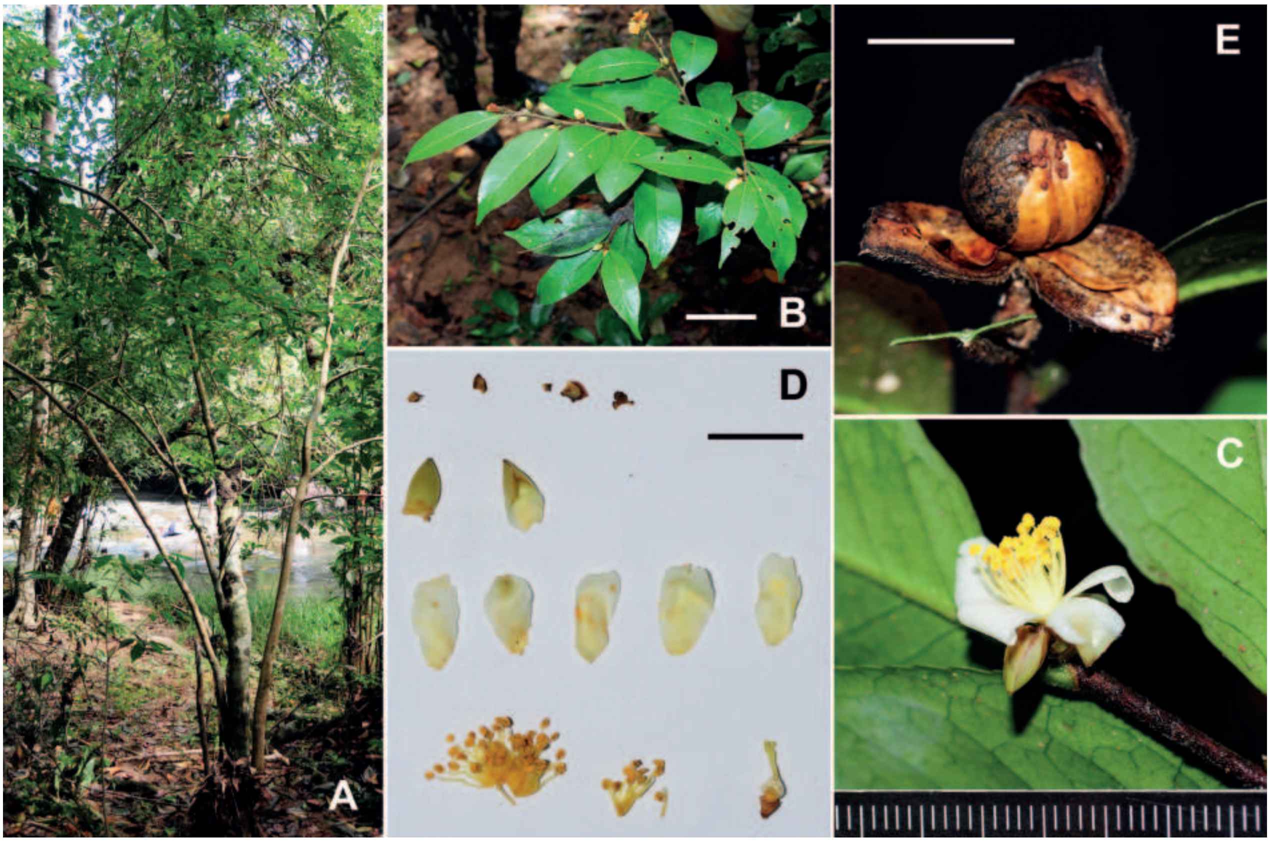

Figure 5. *Camellia kissi* **A** habitat **B, C** branches with flowers **D** a dissected flower **E** a mature fruit with a single seed. Scale bars: 5 cm (**B**); 1 cm (**D, E**). The minimum graduation of the ruler in **C** represents 1 mm.

Chanthaburi: Soi Dao, Khao Soi Dao, ca. 1400 m, 13 December 1924, *Kerr 9651* (BK 203727, BM, C).

Kamphaeng Phet: Pang Sila Thong, Mae Wong, 900–1140 m, 14 June 1995, *Niyomdham et al. 4379* (BKF).

Kanchanaburi: Sai Yok, Chongkhaosoong, ca. 900 m, 12 August 1995, *Wongprasert s.n.* (BKF SN112557); Tong-pha-phum, E-tong, 28 January 2001, *Veesommai 1.38* (BKF SN145916).

Khon Kean: Phu Wiang, Tap Phaya Suea, 1 December 2003, *Mattapha 472* (KKU), 16°37'58"N, 102°12'59"E, 430 m, 22 December 2015, *Zhao et al. 137* (BKF, KKU, KUN, TCD).

Loei: Dan Sai, Phu Lom Lo, 1500–1600 m, 8 April 1922, *Kerr 5782* (BK 203732, BM, C); Phu Kradueng, ca. 1200 m, 12 March 1924, *Kerr 8695* (BK 203922, BM), 16°53'–54'N, 101°47'–49'E, 31 October 1984, *Mitsuta et al. T-40368* (BKF SN107567) & *T-42270* (BKF SN060860), Pha Nok En, 1 September 1988, *Fukuoka T-63791* (BKF SN103457), summit plateau, trail from Than Sawan to Tham Sor Nue waterfall, 1100–1200 m, 12 September 1990, *Chantaranothai et al. 90/143* (K); Phu Ruea, 1300 m, 4 May 1997, *Pooma 1550* (BKF), Phu Luang, 16 June 2004, Bunwong 296 (KKU), Khoknokkraba, ca. 950 m, 17 November 2000, *Wongprasert 11-13* (BKF SN133293); Wang Saphung, Phu Luang, 15 April 1968, *Chermsirivathana 899* (BK 203742).

Nakhon Nayok: Mueang Nakhon Nayok, Khao Yai, 14°26'10"N, 101°22'28"E, 730 m, 8 May 2003, *Charoenchai & Phomphuang 399* (BK 263128, CMUB

26064); Pak Phli, Khao Yai, 14°21'N, 101°22'E, 1200–1300 m, 29 October 1970, *Charoenphol et al. 4205* (BKF SN060889).

Nakhon Ratchasima: Pak Chong, Khao Yai, ca. 600 m, 11 August 1974, *Maxwell 74-786* (BK 203724), Orchid waterfall, 600–750 m, 18 November 1982, *Koyama et al. T-30008* (BKF SN060882), Haew Suwat waterfall, 700–730 m, 19 November 1982, *Koyama et al. T-30110* (BKF SN060881), 14°26'10"N, 101°22'29"E, 730 m, 7 October 2002, *Charoenchai & Phomphuang 343* (BK 263207, CMUB 26356).

Nakon Si Thammarat: Lan Saka, Khao Luang, 950–1000 m, 25 May 1968, *Beusekom & Phengkhlai 1002* (BKF SN060906, C).

Nan: Pua, Doi Phukha, 1700 m, 26 June 2008, *Pooma & Tamura 7113* (BKF SN188552).

Phang-Nga: Khao Pawta Luang Keow, 900–1000 m, *Geesink et al. 7690* (BKF SN060902).

Phetchaburi: Kaeng Krachan, Panoen Thung Ranger Substation, 12°52'12"N, 99°22'12"E, 123 m, 26 January 2005, *Williams et al. 1112* (K), summit of Khao Phanoen Thung, 12°52'5"N, 99°22'20"E, 1240 m, 8 May 2005, *Middleton et al. 3271* (BKF SN168267, E 00226065).

Phitsanulok: Chat Trakan, Phu Soi Dao, 1600 m, 14 August 2000, *Suksanthan 2684* (QBG 19436); Nakhon Thai, on the way to the headquarters of Phu Hin Rong Kla National Park, 16°57'5"N, 101°1'24"E, 1600 m, 9 November 2015, *Zhao et al. 71* (BKF, TCD).

Prachin Buri: ca. 1000 m, 4 July 1924, *Kerr 10824* (BK 203739); Khao Yai, at the Heo Suwat Falls, 750 m, 8 July 1966, *Larsen et al. 99* (C).

Ranong: 50 m, 17 November 1973, *Santisuk 597* (C); Muang Len, 160 m, 11 January 1966, *Hansen & Smitinand 11909* (BKF SN060905, C); Suk Samran, Khlong Na kha, ca. 9°45'N, 98°40'E, 50 m, 22 June 1974, *Geesink et al. 7381* (K) & *7404* (C, K).

Sakon Nakhon: Phu Phan, 19 November 1962, *Suwanakoset 1916* (BKF, K), ca. 30 km SW of Sakonnakhon city, ca. 380 m, 13 November 1984, *Murata et al. T-48771* (BKF SN060859), Huay Yai waterfall, 22 June 2003, *Chantaranothai et al. s.n.* (KKU); Sawang Daen Din, Ban Thon, 1 December 1962, *Adisai 194* (BK 203726).

Si Sa Ket: Kantharalak, Phanom Dongrak, 200 m, 25 November 2005, *Suddee et al. 2632* (BKF SN181662, QBG 29057), Sao Thongchai Phulaor Falls, Phanom Dongrak WS, trail to waterfalls, 200 m, 22 December 2005, *Pooma et al. 6068* (BKF SN183620, K).

Surin: Mueang Surin, Arloor-Doonban Community Forest, 124 m, 3 February 2008, *Petrmitr 840* (CMUB 29794).

Udon Thani: Na Yung, Phu Luang, 1050–1300 m, 8 January 1966, *Hennipman 3556* (BKF SN060870, C, K).

Uttaradit: Nam Pad, Phu Soi Dao, 1613 m, 17 November 2009, *Norsaengsri & Intamusik 6145* (QBG 42661).

Notes. Wallich's (1820: 429) original epithet of the species, *kissi*, cannot be replaced by "*kissii*" as shown in "Flora of China" (Ming and Bartholomew 2007), because it derived from the vernacular name (see Article 60 Ex. 21 of the Shenzhen Code, Turland et al. 2018; Zhao 2022c). *Camellia kissi* is the most widely distributed species of the genus in Thailand (Fig. 2). Edible oil can be extracted from its seeds (Baral and Acharya 1997), which may supply unique value in the breeding of oil camellias.

4b. *Camellia kissi* var. *confusa* (Craib) T.L. Ming, Fl. Yunnan. 8: 300. 1997.

≡ *Thea confusa* Craib, Bull. Misc. Inform. Kew (1): 5 1914. Lectotype (first-step designated by Craib [1925: 131]; second-step designated by Zhao et al. [2017a: 174]): THAILAND. Chiang Mai: Doi Suthep, 1200–1500 m, 31 October 1909, *A.F.G. Kerr 889* (K 000704304!).

Description. Trees or shrubs up to 12 m tall. ***New branchlets*** puberulous; ***terminal buds*** puberulous or glabrous. ***Petioles*** 5–15 mm long, puberulous; ***leaf blades*** elliptic, obovate, oblong or ligulate, 5.5–13 × 2–4.5 cm, coriaceous, abaxially yellowish green and glabrous, adaxially dark green, hirsute along midrib, midrib abaxially elevated and adaxially slightly impressed or flat, secondary veins 7–11 on each side of midrib, flat or obscure on both surfaces, base attenuate, cuneate or rounded, margin sparsely serrate, apex attenuate, acute, acuminate or caudate. ***Flowers*** solitary, 4.5–10 cm in diam., subsessile. ***Bracteoles*** and ***sepals*** 6–8, caducous, crescent to broadly ovate, 1.5–20 × 3–10 mm, abaxially glabrous, puberulous or pubescent, adaxially glabrous, margin ciliolate. ***Petals*** 6–8 in 1–2 whorls, white, elliptic or obovate, 2.5–5.5 × 1.5–4 cm, abaxially glabrous, puberulous or pubescent at apex, adaxially glabrous, apex bilobed. ***Stamens*** numerous, 1–1.5 cm long; filaments yellow, glabrous, basally connate for 2–3 mm. ***Ovary*** globose, pubescent. ***Styles*** 3(–4), basally connate or distinct, 8–12 mm long, basally pubescent and gradually becoming glabrous apically. ***Capsule*** globose or oblate, 2.5–6 cm in diam., 2–5 cm in height, 1–3-loculed with 1–3 seeds; pericarp 2–8 mm thick. ***Seeds*** brown or fuscous, hemispherical, polyhedral or globose, 1.5–2.5 cm in diam., glabrous Fig. 6.

Phenology. Flowering October–January, fruiting December–September.

Distribution and habitat. *Camellia kissi* var. *confusa* is distributed in the evergreen forest at elevations of 350–1700 m in China, Laos, Myanmar, Thailand (Fig. 2) and Vietnam.

Additional specimens examined. Chiang Mai: Chom Thong, Ban Pha Mon, 900 m, 31 May 1979, *Vidal & Vidal 6247C* (K); Doi Inthanon, 18°40'N, 98°25'E, 1400 m, 3 January 1975, *Geesink et al. 8045* (BKF SN060804, C), 1680 m, 19 December 1983, *Fukuoka & Ito T-35316* (BKF SN060813), 1700 m, 18 November 1998, *Hara et al. C002* (BKF SN173305) & *C044* (BKF SN173303), road to Khun Wang, 1310 m, 24 October 2000, *Chayamarit et al. 2204* (BKF SN173163); Fang, Doi Ang Khang, 1490 m, 8 December 1934, *Garrett 905* (BKF SN060834, E 00681092, K); Mae Cham, Mae Sanga, 1300 m, 6 May 2000, *Sangnin & Sillapasuwan 3346* (BKF SN138882), between 34 and 35 km, on the road to Mae Aum Watershed Management Station, 18°30'30"N, 98°30'19"E, 1636 m, 12 November 2015, *Zhao et al. 83* (BKF, KUN, TCD); Mueang Chiang Mai, Doi Suthep, ca. 1600 m, 22 December 1920, *Kerr 4680* (BK 203745), 1300 m, 20 February 1959, *Sørensen et al. 6967* (BKF SN060827, C, K), ca. 900 m, 17 November 1922, *Kerr 6676* (BK 203730, BM, K) & *6676A* (BK 203741, BM, E 00681089, K), 1050 m, 7 November 1987, *Maxwell 87-1379* (BKF SN060825); east side of Doi Pui at the Chang Kian Agricultural Station, 1350 m, 24 November 1988, *Maxwell 87-1351* (BKF SN060851); Samoeng, Samoeng Tai, Ban Pa Kar, 1424 m, 24 June 2008, *Jatupol 08-233* (QBG 35892).

Loei: Phu Kradueng, top area of Phu Kradueng, 1200–1300 m, 19 December 1982, *Koyama et al. T-31384* (BKF SN060872); Phu Ruea, 13 December 1966,

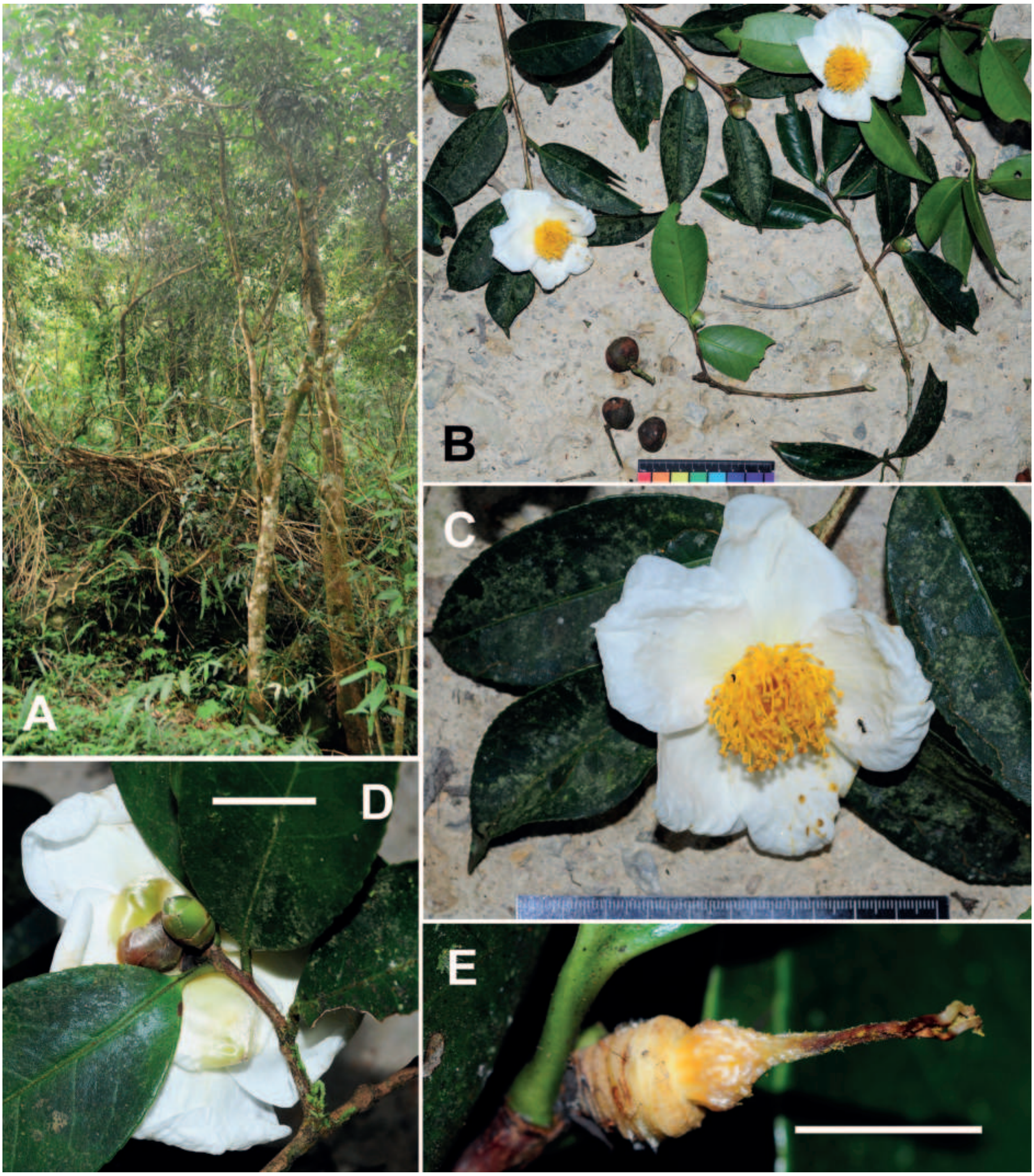

Figure 6. *Camellia kissi* var. *confusa* **A** habitat **B** branchlets with flowers, flower buds and caducous fruits **C, D** branchlet with flower **E** a pedicel and gynoecium. Scale bars: 2 cm (**D**); 1 cm (**E**). The minimum graduation of the rulers in **B, C** represents 1 mm.

Umpai 311 (BK 203736); Phu Luang, 17°17'2"N, 101°31'8"E, 1440 m, 3 November 2015, *Zhao et al. 26, 27, 32* (BKF, KUN, TCD) & *33* (TCD); Wang Saphung, Phu Luang, 900–1000 m, 15 November 1968, *Chermsirivathana 1057* (BK 203722); 1410 m, 13 May 1998, *Chayamarit et al. 1357* (BKF).

Nan: Pua, Doi Phu Kha, 1100 m, 17 August 1995, *Pooma 1104* (BKF SN167083), 19°13'N, 101°5'E, 1500 m, 8 October 1998, *Srisanga 293* (QBG 12268) & *294* (QBG 12269).

Sakon Nakhon: Phu Phan, ca. 17°N, 104°E, 380–450 m, 12 November 1984, *Murata et al. T-51155* (BKF SN115022); Huai Lub Num Lud, 9 March 1996, *Puudjaa 195* (BKF SN091534).

Sukhothai: Khiri Mat, Kao Luang, ca. 1000 m, 2 May 1922, *Kerr 5917* (BK 203747).

Notes. The variety usually bears a larger flower and a thicker pericarp than *C. kissi* var. *kissi* (Figs 5, 6; also see the key above). It is sometimes difficult to distinguish them because the size of flowers and fruits can vary gradually in the forests. However, the taxonomic treatment of two varieties suggested by Ming (2000) is provisionally followed here before more data, especially those of population genetics, are available.

5. *Camellia laotica* (Gagnep.) T.L. Ming, Acta Bot. Yunnan. 21(2): 153. 1999.

≡ *Thea laotica* Gagnep., Notul. Syst. (Paris) 10: 128. 1942. Lectotype (first-step designated by Sealy [1958: 222]; second-step designated by Zhao et al. [2017a: 176]): LAOS. Savannakhet: entre Lang a xinhxa ne et L. xoan, 10 April 1927, *E. Poilane 13693* (P 04511456! Image: https://science.mnhn.fr/institution/mnhn/collection/p/item/p04511456).

Description. Shrubs up to 5 m tall. ***New branchlets*** puberulous; ***terminal buds*** pubescent. ***Petioles*** 2–5 mm long, puberulous; ***leaf blades*** elliptic to oblong, 4–9 × 1–4.3 cm, thinly coriaceous, abaxially sparsely appressed pubescent, especially along midrib, adaxially glabrous, midrib and secondary veins abaxially elevated and adaxially channelled, secondary veins 6–8 on each side of midrib, base attenuate, margin sparsely serrulate, apex attenuate to shortly caudate. ***Flowers*** solitary or up to 3 in a cluster. ***Pedicels*** 7–14 mm long, glabrous or puberulous at base. ***Bracteoles*** 2, opposite or alternate, caducous. ***Sepals*** 3–4, persistent, sub-orbicular or broadly ovate, 3–8 × 6–9 mm, abaxially glabrous, adaxially sericeous, margin ciliolate. ***Petals*** 5, white, broadly ovate to obovate, 8–12 × 5–7 mm, glabrous on both surfaces, margin ciliolate. ***Stamens*** numerous, 5–7 mm long; filaments glabrous. ***Ovary*** ovoid, glabrous. ***Style*** 1, 5–7 mm long, glabrous, apically 3–5-lobed for 1–2 mm. ***Capsule*** globose, 12–20 mm in diam.; pericarp 2–3 mm thick. ***Seeds*** glabrous when immature Fig. 7.

Phenology. Flowering October, fruiting April–August.

Distribution and habitat. *Camellia laotica* is distributed in the evergreen or mixed deciduous forests at elevations of 400–750 m in Laos and Thailand (Fig. 2).

Additional specimens examined. Ubon Ratchathani: Khong Chiam, Ban Na Klang Pho, Dong Na Tham forest, ca. 400 m, 24 October 1998, *Wongprasert s.n.* (BKF SN121590, BKF SN121591; Fig. 7).

Notes. Gagnepain (1942) described the species based on three gatherings, including *Poilane 13268*, *13693* and *13743*. Sealy (1958) suggested that *Poilane 13268* and *13693* represented *C. laotica* whereas *Poilane 13743* was a distinct species, which was subsequently given a name, *C. sealyana* T.L. Ming by Ming (1999). Sealy (1958) and Ming (2000) supplied a short description of *C. laotica*, without the characters of flowers, based on two gatherings (*Poilane 13268 & 13693*) in Laos. I add an account of flowers and provide a detailed description above.

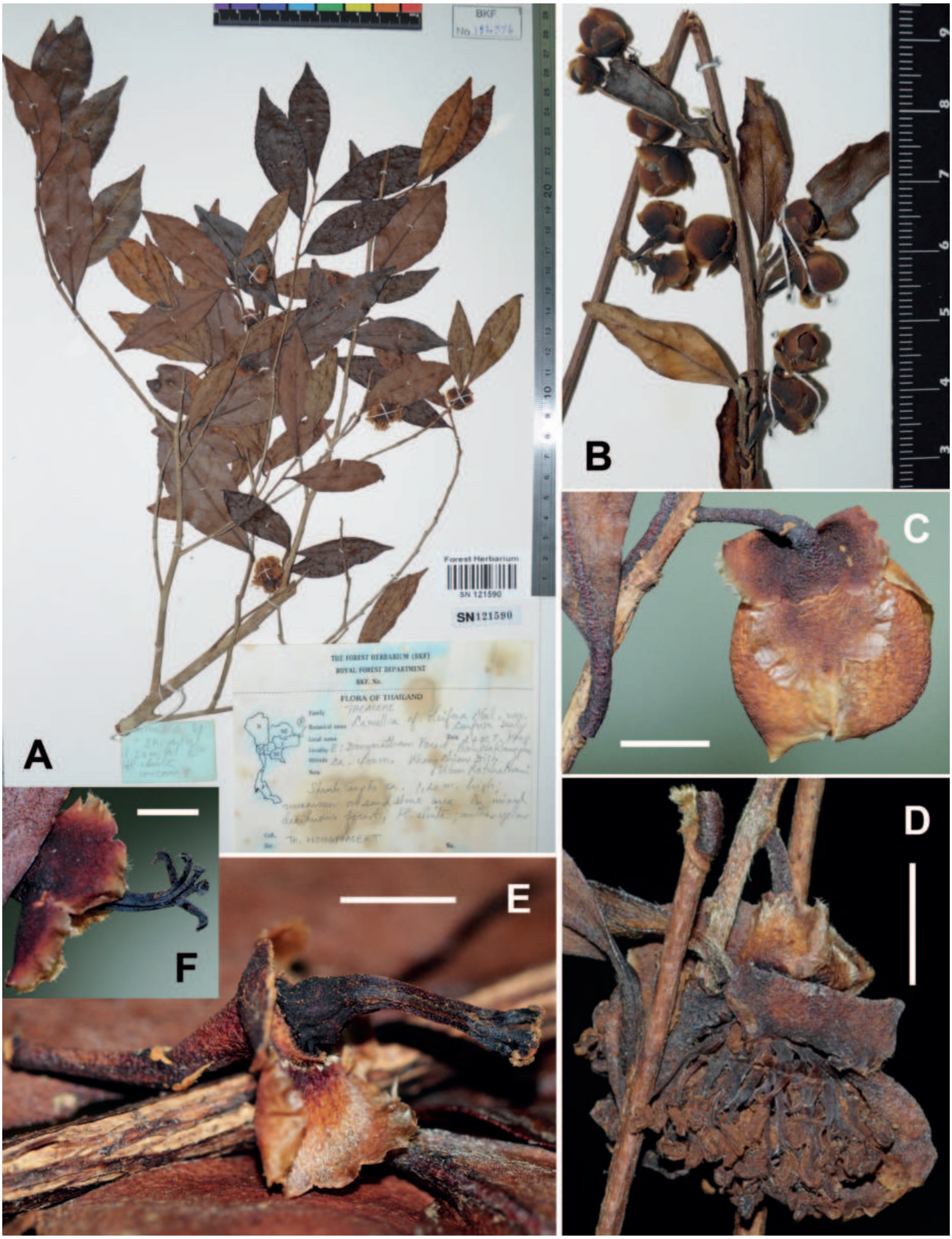

Figure 7. Dry specimens of *Camellia laotica*, *Wongprasert s.n.* at BKF **A** specimen sheet **B** branchlet with flower buds **C** a flower bud **D** a flower **E, F** flower fragments showing sepals and gynoecia. Scale bars: 5 mm (**C, D**); 3 mm (**E, F**). The minimum graduation of the rulers in **A, B** represents 1 mm.

Camellia laotica is a new record to Thailand. It is represented by a single collection, *Wongprasert s.n.* at BKF (Fig. 7). The specimen was collected in Eastern Thailand, along Thai-Laos border (Fig. 2). The leaves of *C. laotica* in Thailand seem to be narrower than those of the syntypes (*Poilane 13268 & 13693*) from Laos, and they do not bear cork-warts on the abaxial surface by which *C. sealyana* (cork-warts present) can be distinguished (Fig. 7).

6. *Camellia sinensis* (L.) Kuntze var. *assamica* (Royle ex Hook.) Steenis, Fl. Scholen. Indon. 280. 1949.

≡ *Thea assamica* Royle ex Hook., Kew Gardens 28. 1847. Neotype (designated by Mabberley [2021: 1354]): India. Assam, January–February 1836, *W. Griffith s.n.* (K 000939670!).

= *Thea cochinchinensis* Lour., Fl. Cochinch. 1: 338. 1790. Neotype (designated by Zhao et al. [2017b: 1453]): Vietnam. Yen Bai: Bao Ha, 21 February 1936, *E. Poilane 25282* (P 04511587! Image: https://science.mnhn.fr/institution/mnhn/collection/p/item/p04511587).

= *Camellia theifera* Griff., Trans. Agric. Soc. India. 5: t. C. 1838. Lectotype (designated by Zhao et al. [2017b: 1453]): India. Upper Assam, *W. Griffith s.n.* (TCD 0017977!).

= *Thea yersinii* A. Chev. ex Gagnep., Fl. Indo-Chine [P.H. Lecomte et al.], Suppl. 1: 310. 1943 ("*Thea yersini*"). Lectotype (designated by Zhao et al. [2017b: 1453]): Vietnam. Khanh Hoa: Massif du Hòn bà, province de Nhatrang, 1000–1500 m, 12 September 1918, *A. Chevalier 38684* (P 02142599! Image: https://science.mnhn.fr/institution/mnhn/collection/p/item/p02142599).

= *Camellia multisepala* Hung T. Chang & Y.J. Tan, Acta Sci. Nat. Univ. Sunyatseni 23(1): 11. 1984. Holotype: China. Yunnan: Mengla, Xiangming, cultivated, 1050 m, 3 December 1982, *Y.J. Tan & S.C. Ma A31002* (SYS 00095167!).

= *Camellia polyneura* Hung T. Chang & Y.J. Tan, Acta Sci. Nat. Univ. Sunyatseni 23(1): 10. 1984. Holotype: China. Yunnan: Luchun, Qimaba, in tea garden, 1400 m, 18 November 1982, *Y.J. Tan & S.C. Ma A26001* (SYS 00090671!).

= *Camellia sinensis* var. *kucha* Hung T. Chang & Ping S. Wang, Acta Sci. Nat. Univ. Sunyatseni 23(1): 10. 1984. Holotype: China. Yunnan: Jinping, Tongchang, 1371 m, 11 November 1982, *B.H. Chen & Y.J. Yang A22003* (SYS 00095188!).

= *Camellia tenuistipa* Orel, Curry & Luu, Pursuit Hidden Camellias Vietnam China: 263. 2015. Holotype: Vietnam. Gia Lai: Kon Ka Kinh National Park, 22 Jan 2011, *H.T. Luu & Q.D. Nguyen KKK 221* (NSW 901734, image!).

Description. Trees or shrubs up to 20 m tall. ***New branchlets*** puberulous or pubescent, ***terminal buds*** pubescent or puberulous. ***Petioles*** 2–9 mm long, puberulous; ***leaf blades*** elliptic, oblong or obovate, 8–29 × 3.5–10 cm, coriaceous, abaxially yellowish green, puberulous, especially along midrib, adaxially dark green, shiny, midrib abaxially elevated and adaxially slightly raised or flat, secondary veins 7–15 on each side of midrib, abaxially slightly elevated and adaxially slightly impressed or flat, base cuneate or attenuate, margin serrulate, apex attenuate or acuminate. ***Flowers*** solitary or up to 4 in a cluster, 2–3.5 cm in diam. ***Pedicels*** 4–14 mm long, slender or gradually swollen towards the top, ***bracteoles*** 2–3, alternate, caducous. ***Sepals*** 5, persistent, sub-orbicular or broadly ovate, 3–4.5 × 3–5 mm, abaxially glabrous, adaxially sericeous, margin ciliolate. ***Petals*** 5–7 in 1–2 whorls, white or outer 1–3 petals with a tinge of green at apex, obovate, elliptic or rounded, 1–2.5 × 1–2 cm, glabrous on both surfaces. ***Stamens*** numerous in 3–5 whorls, 7–16 mm long, filaments pale yellow, glabrous, outer filaments basally adnate to petals for 1–3 mm. ***Ovary*** oblate or globose, pubescent. ***Style*** 1, 6–15 mm long, glabrous or gradually becoming glabrous upwards, apically (2–)3(–4)-lobed for 1–3 mm. ***Capsule*** oblate, bi-coccal or globose, 1.5–4.5 cm in diam., 1–2 cm in height, 1–3-loculed with 1–3 seeds; pericarp 0.5–1.5 mm thick. ***Seeds*** brown or fuscous, globose, hemispherical or polyhedral, 1.2–2 cm in diam., glabrous Fig. 8.

Phenology. Flowering September–January, fruiting February–December.

Distribution and habitat. *Camellia sinensis* var. *assamica* occurs in the evergreen and semi-deciduous forests at the elevations of 200–2700 m in China, India, Laos, Myanmar, Thailand (Fig. 2) and Vietnam.

Additional specimens examined. Chiang Mai: Chiang Dao, 25 November 1963, *Bunchuai 1359* (BKF SN060849, C, K); Khun Awn, 900 m, 30 January 1921, *Kerr 4726* (BK 203758, BM, K); Mae On, Huai Kaeo, trail along Mae Kampong Waterfall, 1100 m, 7 September 2011, *Pooma et al. 7791* (BKF SN196689); Mae On, Jae Son, 18°51'20"N, 99°22'1"E, 1500 m, 28 May 2011, *Pooma & Pattharahirantricin 7729* (BKF SN196803); Mae Taeng, Mae Taman, 1300 m, 27 September 1994, *Nanakorn et al. 1808* (QBG 1808); Mueang Chiang Mai, Doi Suthep, 1050 m, 7 November 1987, *Maxwell 87-1378* (BKF SN060836), 15 July 1988, *Maxwell 88-875* (BKF SN209981), 1 June 1993, *Maxwell 93-522* (BKF SN169943, BKF SN192202, CMUB 02747), 18 September 1995, *Kopachon s169b1* (BM, CMUB 07853).

Chiang Rai: Wiang Kaen, 600 m, 26 December 2009, *Pongamornkul 2806* (QBG 51200).

Loei: Dan Sai, Pu Lom Lo, 1500 m, 8 April 1922, *Kerr 5780* (BK 203759, BM, K); Phu Kradueng, 16°53'–54'N, 101°47'–49'E, 1150–1250 m, November 1984, *Murata et al. T-42519* (BKF SN060857) & *T-42796* (BKF SN060856), 1160–1180 m, 2 September 1988, *Fukuoka T-63807* (BKF SN103447); Phurea, Phuluang, 17°18'N, 101°30'E, 1070–1100 m, 4 November 2015, *Zhao et al. 37–41* (BKF, TCD); Na Haeo, Phu Suan Sai, 10 February 2004, *Pornpongrungrueng 441* (KKU), 1300 m,16 May 2006, *Maknoi 850* (QBG 27664), 14 May 2008, *Maknoi & Srisanga 2185* (BKF SN190334, QBG 38413), 2 September 2008, *Maknoi 2738* (BKF SN191010, QBG 40367), 3 September 2008, *Maknoi 2806* (BKF SN188351, QBG 40435), 17°30'N, 100°56'E, 1300–1330 m, 6 November 2015, *Zhao et al. 49, 50, 52 & 54* (BKF, TCD), *Zhao et al. 51 & 53* (TCD).

Mae Hong Son: Mae Sariang, Wat Chan, Ban Den, 988 m, 29 April 2014, *Norsaengsri 10930* (QBG 77549).

Nakhon Sawan: Khao Pado, 4 June 1922, *Kerr s.n.* (BK 203756).

Nan: Tha Wang Pha, 19°04'N, 100°40'E, 1100 m, 23 July 1992, *Larsen et al. 43513* (BKF); Song Khwae, Tham Sokoen, 19°23'3"N, 100°31'5"E, 1210 m, 30 November 2011, *Laongsri et al. 1957* (QBG 56767).

Phayao: Mueang Phayao, Doi Luang, 625 m, 19 November 1997, *Petrmitr 148* (CMUB 13047).

Phitsanulok: Chat Trakan, Phu Miang-Phu Thong, 800 m, 18 February 2010, *Romklao Botanical Garden 0005/2553* (QBG 59399); Nakhon Thai, Phu Hin Rong Kla, 16°59'38"N, 101°0'9"E, 1300 m, *Zhao et al. 72* (BKF, TCD); Phu Rom

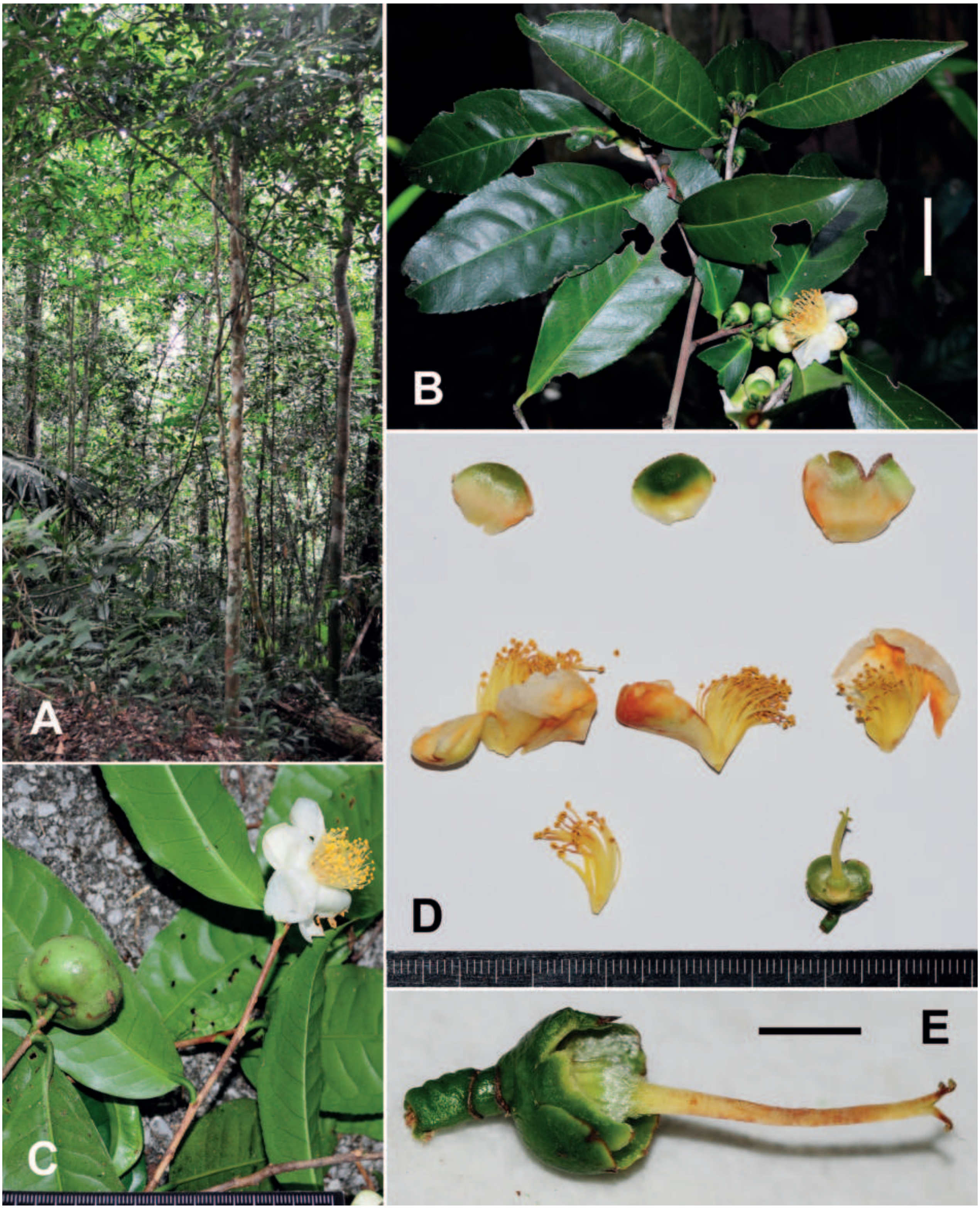

Figure 8. *Camellia sinensis* var. *assamica* **A** habitat **B** branchlets with flowers and flower buds, adaxial surface of leaves **C** branchlets with flower and fruit, abaxial surface of leaves **D** a dissected flower **E** a flower without petals, androecium and a half sepal. Scale bars: 3 cm (**B**); 5 mm (**E**). The minimum graduation of the rulers in **C, D** represents 1 mm.

Rot, one of the peaks of Phu Miang, 1200–1600 m, 3 October 1967, *Shimizu et al. T-11514* (BKF SN060844, K) & *T-11515* (BKF SN060845), 1200–1650 m, 4 October 1967, *Shimizu et al. T-11653* (BKF SN060843, K).

Notes. The nomenclature of *C. sinensis* var. *assamica* has been clarified in recent studies (Zhao et al. 2017b; Mabberley 2021; a review in Chinese see Zhao 2022a). *Thea assamica* was not validly published in Masters (1844) but later validated in Hooker (1847). Steenis (1949), rather than Kitamura (1950), firstly proposed the name at new rank, *C. sinensis* var. *assamica*. Zhao et al. (2017b) provided a detailed description of Assam tea, which is supplied above with adjustments to meet the requirements of a taxonomic revision here (Maxted 1992).

As an important resource of commercial tea, Assam tea is widely cultivated in the tropical areas of the world. Local Thai people collected natural seeds or seedlings and planted them around houses to use the new branchlets or leaves as a vegetable or fermented beverage (Khanongnuch et al. 2017; Zhao 2022a).

7. *Camellia suddeeana* D.Wei Zhao, Phytotaxa 594: 232. 2023.

Type material. ***Holotype*:** Thailand. Nakhon Phanom: Ban Phaeng, Phu Lang Ka NP, trail to hill top, 17°58'58"N, 104°7'38"E, 373 m, 23 October 2015, *S. Suddee et al. 4981* (BKF SN235114!).

Description. Shrubs or trees up to 10 m tall. ***New branchlets*** pubescent to villous, ***terminal buds*** puberulous. ***Petioles*** 2–10 mm long, pubescent or puberulous; ***leaf blades*** elliptic or oblong, 3.5–14 × 1.3–5.5 cm, coriaceous, abaxially dull green, sparsely appressed puberulous especially along midrib, or glabrous, adaxially dark green, glabrous or hirsute along midrib, midrib and secondary veins abaxially elevated and adaxially impressed, secondary veins 5–8 pairs, base attenuate, margin serrulate, apex acute, attenuate to caudate. ***Flowers*** axillary, solitary or paired, 1.5–3.5 cm in diam. ***Pedicels*** ca. 2 mm long. ***Bracteoles*** 3–6, persistent, deltate to semi-orbicular, 1–3 × 1.5–4 mm, abaxially glabrous or puberulous at apex, adaxially glabrous to slightly sericeous, margin ciliolate. ***Sepals*** 5–7, persistent, suborbicular, 2–5 × 4–5 mm, abaxially glabrous, adaxially sericeous. ***Petals*** 6–8 in 1–2 whorls, white, elliptic to obovate, 7–18 × 4–9 mm, abaxially glabrous, adaxially glabrous or sericeous at apex, apex obtuse to rounded, inner 4–5 petals basally adnate to filament whorl for ca. 2 mm. ***Stamens*** numerous, 6–10 mm long; filaments white, glabrous, outer filaments basally connate for 2–3 mm. ***Ovary*** globose to ovoid, glabrous. ***Styles*** 3(–4), distinct, 3–9 mm long, glabrous. ***Capsule*** globose or bi-coccal, 2.5–4.5 cm in diam., 1–2-loculed with 1–2 seeds; pericarp 0.5–2 mm thick, smooth or furfuraceous. ***Seeds*** light brown to fuscous, globose, 1.5–2.5 cm in diam., glabrous Fig. 9.

Phenology. Flowering October–November, fruiting April–July.

Distribution and habitat. *Camellia suddeeana* is native to Thailand (Fig. 2) and occurs in the evergreen or deciduous forests at the elevations of 250–1200 m.

Additional specimens examined. Loei: Ban Na Luang, 300 m, 20 November 1968, *Chermsirivathana 1185* (BK 203761, BKF SN060858). Phu Luang, ca. 1200 m, 23 November 1957, *Dee 1025* (BKF SN060875).

Mae Hong Son: Khun Youm, 8 April 1977, *Nimanong & Phusomsaeng 1816* (BKF).

Nong Khai: Bueng Khla, Phu Wua Wildlife Sanctuary, trail from Pha Nang Khoi to Tham Noi, 18°14'14"N, 103°57'38"E, 350 m, 30 July 2008, *Pooma et al.*

Figure 9. Dry specimens of *Camellia suddeeana*, *Pooma et al. 7333* at BKF **A** specimen sheet **B** flower fragments **C** fruits and seed **D** calyx and gynoecium remains. The minimum graduation of the rulers in **A–C** represents 1 mm.

7333 (BKF SN191784; Fig. 9); Phu Wua, 20 April 1996, *Niyomdham 4925* (BKF SN209980, BKF SN102858).

Phetchabun: Wang Thong, Thung Salaeng Luang National Park, 700 m, *Koyama et al. T-31930* (BKF SN060873).

Pitsanulok: Nahaew to Romklao Rd, 700 m, *Pooma 1237* (BKF SN090320).

Uttaradit: Nampad, Thud Phra Kiet National Park, ca. 650 m, 9 December 1994, *Santisuk et al. s.n.* (BKF SN109856).

Notes. A specimen of *C. suddeeana*, *Chermsirivathana 1185* at BKF, were misidentified as *C. tenii* by Keng in 1970. *Camellia tenii* bears a smaller leaf (2.5–4.2 × 1.2–2.3 cm), villous ovary and pubescent seeds, whereas *C. suddeeana* has a larger leaf (3.5–14 × 1.3–5.5 cm), glabrous ovary and seeds (Fig. 9; Zhao 2023). The former is native to Yunnan, China and absent in Thailand but was included in Keng's (1972) "Flora of Thailand". As an essential element of a taxonomic revision (Maxted 1992), Zhao's (2023) description of *C. suddeeana* is provided above with revisions.

8. ***Camellia taliensis*** **(W.W. Sm.) Melch. in Engler, Nat. Pflanzenfam. 2(21): 131. 1925.**

≡ *Thea taliensis* W.W. Sm., Notes Roy. Bot. Gard. Edinburgh 10: 73. 1917. Lectotype (first-step designated by Ming [2000: 119]; second-step designated by Zhao et al. [2017a: 177]): China. Yunnan: Ghi Shan east of Tali Lake, 25°48'N, 2740 m, August 1914, *G. Forrest 13477* (E 00284542! Image: https://data.rbge.org.uk/herb/E00284542).

= *Polyspora yunnanensis* Hu, Bull. Fan Mem. Inst. Biol. Bot. 8: 135. 1938. Lectotype (designated by Zhao et al. [2019: 299]): China. Yunnan: Lu-hsi Hsien, 1750 m, 6 February 1934, *H.T. Tsai 56805* (PE 00024542! Image: https://www.cvh.ac.cn/spms/detail.php?id=0756fff6).

= *Camellia irrawadiensis* Barua, Camellian 7(4): 18. 1956. Holotype: Myanmar. Raised from seed collected by L.O. Wilson, 1917, presumably in the region 26°–27°N, 98°–99°E (valley of Irrawadi in North Burma), January 1956, *Ex. Herb. I.T.A. 3253* (consisting of 2 sheets: K 000704313! & K 000704314!).

= *Camellia pentastyla* Hung T. Chang, Acta Sci. Nat. Univ. Sunyatseni 20(1): 92. 1981. Lectotype (designated by Zhao et al. [2018: 93]): China. Yunnan: Fengqing, cultivated, 2050 m, 12 February 1963, *L.F. Xia & Z.H. Yang 28* (KUN 1206061!).

= *Camellia quinquebracteata* Hung T. Chang & C.X. Ye, Acta Sci. Nat. Univ. Sunyatseni 26(1): 20. 1987. Holotype: China. Yunnan: Lianghe, Dachang, 4 January 1983, *P. Zeng & Q.J. Xie 17055* (SYS, isotype: KUN 1206063!).

Description. Trees or shrubs up to 15 m tall. ***New branchlets*** glabrous, ***terminal buds*** glabrous or sparsely puberulous. ***Petioles*** 4–8 mm long, glabrous; ***leaf blades*** elliptic to oblong, 7.5–15.5 × 3–6.5 cm, coriaceous, abaxially yellowish green and adaxially dark or yellowish green, shiny and glabrous on both surfaces, midrib abaxially elevated and adaxially slightly raised, secondary veins 8–14 on each side of midrib, slightly elevated on both surfaces, base attenuate to obtuse, margin sparsely serrulate to nearly entire, apex attenuate or acute. ***Flowers*** solitary or up to 3 in a cluster, 3–5 cm in diam. ***Pedicels*** 8–15 mm long.

Bracteoles 2–4, alternate, 2-ranked, caducous. ***Sepals*** 5, persistent, sub-orbicular or broadly ovate, 4–6.5 × 5.5–9 mm, abaxially glabrous, adaxially sericeous, margin ciliolate. ***Petals*** 7–11 in 2–3 whorls, white, elliptic to obovate, 16–30 × 10–21 mm, glabrous on both surfaces or inside sericeous at apex, inner petals basally adnate to filaments for 2–4 mm. ***Stamens*** numerous, 1–2.5 cm long; filaments pale yellow, glabrous. ***Ovary*** oblate, pubescent. Style 1, 11–20 mm long, basally sparsely pubescent and gradually becoming glabrous apically, apically (3–)5-lobed for 2–5 mm. ***Capsule*** oblate, 2.5–5 cm in diam., 2–3 cm in height,1–5-loculed with 1–5 seeds; pericarp 1.5–4 mm thick. ***Seeds*** brown, hemispherical or polyhedral, 1.5–2 cm in diam., glabrous Fig. 10.

Phenology. Flowering October–February, fruiting April–November.

Distribution and habitat. *Camellia taliensis* occurs in the montane evergreen forest at the elevations of 1100–2750 m in China, Myanmar and Thailand (Fig. 2).

Additional specimens examined. Chiang Mai: Chiang Dao, Doi Chiang Dao, Den Ya Khat, 1500 m, 4 August 2007, *Watthana 2420* (QBG 30728); Chom Thong, Doi Inthanon, 1900 m, 1 May 1921, *Kerr 5298* (BK 203709, BM, K), 18°40'N, 98°25'E, 1700 m, 11 December 1969, *Beusekom & Phengklai 2462* (BKF SN061415, P 06838120), 1900–2025 m, 14 January 1994, *Fukuoka T-62168* (BKF SN102755); Fang, 1250 m, 24 February 1958, *Smitinand 4331* (BKF SN060803) & *4331A* ((BKF SN060831; Fig. 10A, B); Doi Ang Khang, 1700 m, 27 May 1998, *Wongprasert s.n.* (BKF SN121562); Doi Pha Hom Pok, 1400 m, 12 February 1958, *Sørensen 1607* (BKF SN060805, C, K), 1920 m, 1 February 2007, *Srisanga et al. 2919* (CMUB 29155, HITBC 143571, QBG 31244); Mae Ai, Bumuhn (Lahu) Village area, 1150 m, 21 October 1994, *Maxwell 94-1102* (BKF SN060837, CMUB 05366); Mae on, Ban Mae Kam Pong, 1300 m, 26 October 2007, *Pongamornkul 2121* (QBG 34196); Mae Taeng, 1600–1950 m, 5 December 1977, *Santisuk 1480* (C, K); Doi Chang, 1700–1900 m, 23 October 1979, *Shimizu et al. T-20524* (BKF SN060811, QBG 50044); Doi Kiew Lom, Huai Nam Dang, 1700 m, 18 January 2002, *Chayamarit et al. 3107* (BKF SN162068); Nanthaburi, Mae Tuen, 12 March 1991, *Smitinand s.n.* (BKF SN119850).

Kampaeng Phet: Klong Lam, Mae Wong, 1320 m, 30 October 2002, *Bult 609* (CMUB 20961).

Mae Hong Son: Khun Yuam, 20 November 1998, *Chusie KY308* (QBG 47303); Mae La Noi, Ban Dong, 1300 m, 15 December 2002, *Pongamornkul 1871* (QBG 35067), 2 May 2011, *Pongamornkul 2899* (QBG 64350); Mueang Mae Hong Son, along the trail to the peak of Doi Pui, 1100–1750 m, 16 December 2007, *Tanaka et al. HN8479* (QBG 35641); Doi Khun Huai Pong, 18°58'N, 98°10'E, 1850 m, 3 March 1968, *Hansen & Smitinand 12770* (BKF SN060846, C, E 00681068, K, P 04511721); Pai, en route to Doi Chang, 1800 m, 31 May 1972, *Santisuk 149* (BKF SN060809); Doi Mae Ya, 1800 m, 3 November 1999, *Suksathan 2030* (QBG 16229).

Nan: Pua, Doi Phu Kha, 19°17'N, 101°7'E, 1680 m, 10 April 1999, *Srisanga & Watthana 685* (QBG 14019), 19°10'N, 101°7'E, 1700 m, 26 May 2000, *Srisanga 1429* (QBG 17650), 1600 m, 22 August 2001, *Srisanga & Maknoi 2027* (QBG 21153).

Phayao: Muang, Doi Luang, 19°5'N, 99°27'E, 1500 m, 22 April 1998, *Sidisunthorn & Gardner 2568.0* (CMUB 13844); Phu Sang, Doi Pha Mon Noi, 19°44'8"N, 100°24'21"E, 1482 m, 30 April 2013, *Laongsri et al. 2849* (QBG 66589); Pong, Phu Lanka, 1500 m, 4 September 2006, *Watthana & Pumicong 2141* (QBG 28151).

Tak: Umpang, Umpang, near top of Khao Kheeo, 2150 m, 25 April 2001, *Bult 419* (CMUB 18159).

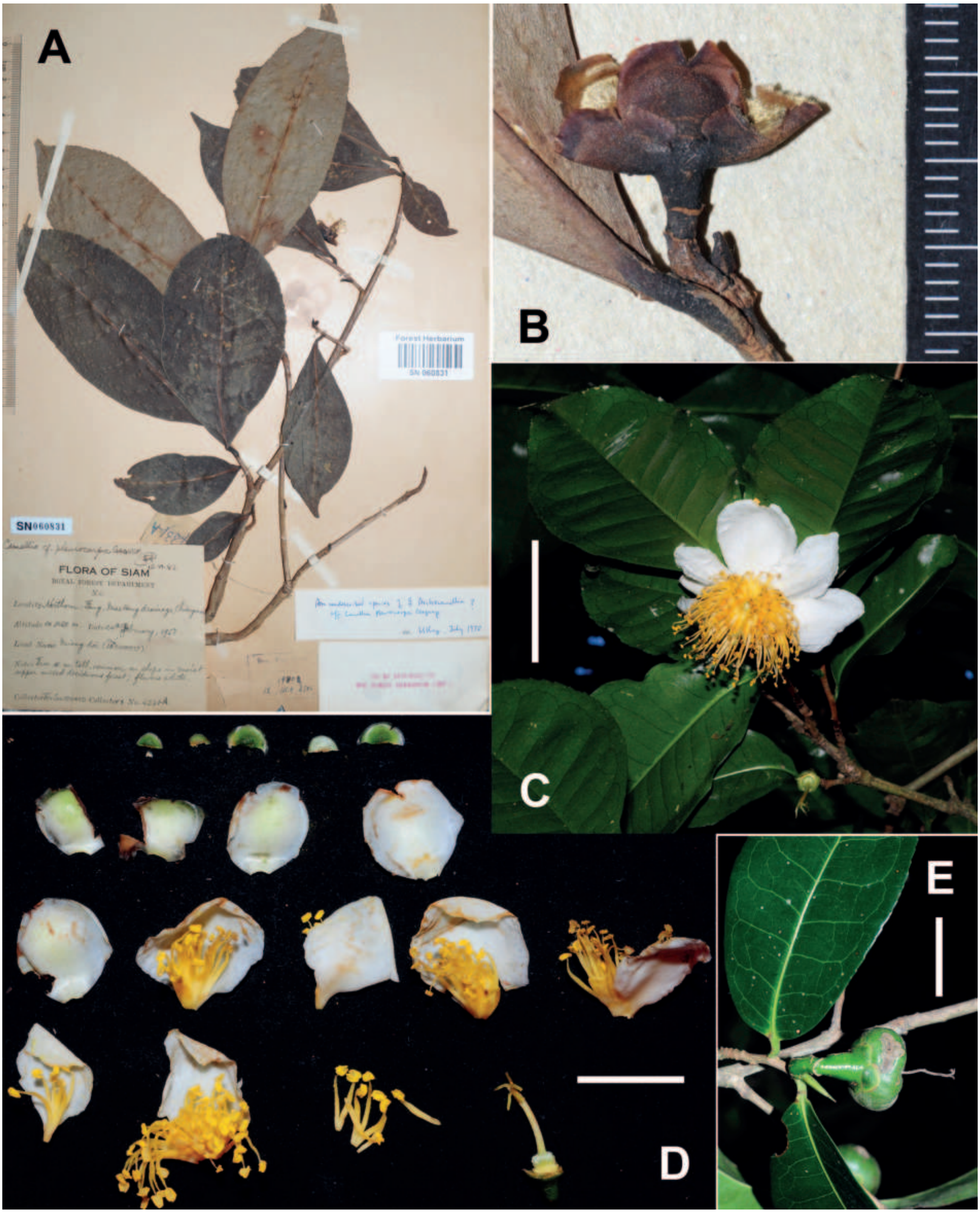

Figure 10. *Camellia taliensis* **A, B** dry specimens of *Smitinand 4331A* at BKF **C** branchlet with flower **D** a dissected flower **E** branchlet with immature fruit. Scale bars: 3 cm (**C**); 2 cm (**D, E**). The minimum graduation of the rulers in **A, B** represents 1 mm.

Notes. Besides Assam tea, *C. taliensis* is another tea source plant that occurs in Thailand. Ming (1992) recognized *C. irrawadiensis* as a heterotypic synonym of *C. taliensis*. Chang et al. (1996) disagreed with Ming (1992) and suggested that

C. irrawadiensis could be distinguished from *C. taliensis* by its abaxially punctate (vs. glabrous) and caffeine-free (vs. present) leaves, shorter pedicel (7–8 mm vs. 12–14 mm), larger sepals (5–7 mm vs. 2–4 mm) and smaller flowers (4 cm vs. 5–6 cm in diam.). Ming (2000) trivialized the differences and retained *C. irrawadiensis* in the synonymy of *C. taliensis*. The morphological differences between them listed in Chang et al. (1996) are, however, either inaccurate (e.g., the leaves of *C. irrawadiensis* are not abaxially punctate) or so trivial and overlapped (e.g., the size of pedicel, sepals and flowers) so that should be treated as an infraspecific variation. The claim of caffeine-free for *C. irrawadiensis* in Chang et al. (1996) was referred to Sealy's (1958: 127) report. Sealy (1958) wrote that "…Dr. E.A.H. Roberts and Dr. D.J. Wood (both of the Indian Tea Association) tell me that chemically it [*C. irrawadiensis*] is clearly distinct from both, notably in that it does not contain caffeine." Nevertheless, Nagata and Sakai (1985) analysed two samples of *C. irrawadiensis* and found that they contained 0.02% and less than 0.01% caffeine, whereas the content of caffeine in *C. taliensis* was 2.28%. However, the variation of chemical contents may be common in the plants of *C.* sect. *Thea* (L.) Griff. For instance, Ye et al. (1997) investigated 22 samples of *C. ptilophylla* Hung T. Chang and suggested that all individuals contained 0.57%–6.84% theobromine; and 18 of the samples were caffeine-free, while the remaining contained 3.02%–4.94% caffeine. Therefore, the single difference of the content of caffeine may be insufficient to warrant separation of *C. irrawadiensis* from *C. taliensis* at specific rank, and Ming's (2000) treatment of them is followed here.

Keng (1972: 146) listed a single collection, *Smitinand 4331A* at BKF (Fig. 10A, B), under *C. pleurocarpa* in "Flora of Thailand". However, the collection actually represents *C. taliensis*. *Camellia pleurocarpa* is native to Vietnam and bears an abaxially punctate leaf, 5–8 persistent bracteoles, abaxially sericeous perianth and glabrous ovary, whereas *C. taliensis* has a glabrous leaf, 2–4 caducous bracteoles, abaxially glabrous perianth and pubescent ovary.

Discussion

Among nine taxa–seven species and two varieties–of *Camellia* in Thailand, only two species are endemic to the country: *C. connata* and *C. suddeeana*. As stated above, *C. pleurocarpa* and *C. tenii* in Keng's (1972) account of *Camellia* are excluded from the flora of Thailand. The former was a misidentification of *C. taliensis* and the latter was frequently used to indicate *C. suddeeana*. *Camellia thailandica* was described based on a specimen collected from Thailand (Chang and Ren 1991); it is, however, a heterotypic synonym of *C. kissi* (Zhao 2022c). *Camellia oleifera* C. Abel listed in Smitinand (1975) is actually *C. kissi* and the former is absent in the natural flora of Thailand. *Camellia sinensis* provided in Gardner et al. (2000) is merely cultivated in Thailand.

Most taxa of *Camellia* occur in northern and north-eastern Thailand (Fig. 2). This region geographically nears the current diversity centre of the genus—southern and south-western China and northern Vietnam (Chang 1981; Ming 2000). However, previous specimens were intensively collected from several provinces such as Chiang Mai, Loei, Mae Hong Son, Phayao, and Phitsanulok. Some under-collected gaps in the mountains of Chiang Rai, Mukdahan, Nan, and Nong Bua Lamphu could be searched in future to comprehensively understand the diversity of *Camellia* in Thailand (Fig. 2).

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Additional information

Conflict of interest

The author has declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

The author solely contributed to this work.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Taxonomic notes on the genus *Itea* (Iteaceae)

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Abstract

The genus *Itea* (Iteaceae) is recognised as a genus with about 21 extant species of shrubs and trees. Within the genus, most species have oblong to elliptical leaves. The lanceolate and obolanceolate leaves are only found in three species, vix *Itea amoena* Chun, *Itea riparia* Collett & Hemsl. and *Itea tenuinervia* S. Y. Liu. The results of our examination of literature, specimens and living plants in the wild have shown that *Itea tenuinervia* is conspecific with *Itea riparia* and is here reduced to a synonym of the latter species. The morphological description, colour pictures, voucher specimens, distribution map of *Itea riparia* and its related *Itea amoena*, together with the morphological comparisons between the two species, are provided in this study.

Key words: China, lectotypification, synonym, taxonomy

Introduction

Itea L. (Iteaceae) was first described based on the species *I. virginica* L. from eastern North America (Linnaeus 1753) and later it was reported in Asia, for example, *I. macrophylla* Wall. from tropical Asia (Wallich 1824), *I. nutans* Royle from western Himalaya (Royle 1835) and *I. japonica* Oliv. from Japan (Oliver 1865). *Itea* was previously divided into two sections based on its deciduous character, i.e. sect. *Deciduae* Engl. (= sect. *Itea*) and sect. *Sempervirentes* Engl. (Engler 1891). The former section comprises only two species with deciduous leaves, *I. virginica* and *I. japonica*, and the latter includes the other species with evergreen leaves. Recently, *Choristylis rhamnoides* Harv. (Harvey 1842) from southeastern Africa was transferred to *Itea* as the third section, i.e. sect. *Choristylis* (Harv.) Jordaan (Kubitzki 2007; Jordaan 2012). Thus, *Itea* was considered as an unusual genus with an East Asian-eastern North American-southeastern African disjunction pattern (Kubitzki 2007; Tian et al. 2021). The genus comprises about 21 extant species of shrubs and trees, including one in Africa, one in North America and 19 species in temperate, subtropical and tropical Asia (Tian et al. 2021; POWO 2023).

The leaf shapes of the genus *Itea* are usually oblong to elliptical, while the lanceolate and oblanceolate leaves only appear in three species, including *I. riparia* Collett & Hemsl. (Collett and Hemsley 1890), *I. amoena* Chun (Chun 1934) and *I. tenuinervia* S.Y. Liu (Liu 2001; Tian et al. 2021). *Itea riparia* was first published based on specimens collected on river-banks from Shan Hills, southern Shan States, Myanmar and it was characterised by narrow leaves, straight branches and erect racemes (Collett and Hemsley 1890). Gagnepain (1916) originally described *I. thorelii* based two gatherings from Vietnam and Laos and considered that it is very similar to *I. riparia*, but is different from the latter in the leaf width, the shape of anthers and the length of inflorescence, flower, stamen and ovary. Craib (1931) observed that some specimens of *I. riparia* from Thailand match *I. thorelii* in some respects. In China, *I. riparia* was recorded in Yunnan and *I. thorelii* was reported in Yunnan and Guangxi (Wu 1977; Fang and Qin 1985; Jin 1995), but the two species were merged in the Flora of China due to absence of obvious different characters (Jin and Ohba 2001). The earlier name *I. riparia* was adopted as its accepted name (Jin and Ohba 2001; Esser 2005; Chen and Liu 2015). The species grows on river-banks or near streams.

Chun (1934) described another *Itea* species with narrow leaves, *Itea amoena,* based on specimens from southern Guangxi, China and noted that it is well characterised by narrow, long-acuminate leaves and by long lanceolate calyx lobes. The species was previously identified as "*Itea riparia* var. *auminata* Hu var. nov.", based on *Ren-Chang Ching 8059* (Chun 1934) and recognised as "*Itea lanceolata* Merr. n. sp." based on *Kuan-Kwang Tsoong 1868* (Jin 1995). However, the latter two names have never been validly published. This species grows near streams, just like *I. riparia* (Fig. 5). Besides the habitat, *I. amoena* and *I. riparia* are also similar in the habit of evergreen shrubs, the lanceolate leaves and terminal inflorescences. Liu (2001) described *Itea tenuinervia* on the basis of a flowering collection found near streams in Shuolong Town, Daxin County, southwestern Guangxi, i.e. *Shou-Yang Liu 2893* (Fig. 1A) and it was morphologically compared with *I. riparia* and *I. thorelii* in the protologue. However, our examination of literature and specimens showed that there are no obvious differences between *I. tenuinervia* and *I. riparia* (including *I. thorelii*). Thus, this study treats *Itea tenuinervia* as a new synonym of *I. riparia* and discusses the morphological differences between *I. riparia* and *I. amoena*.

Materials and methods

The specimens of the genus *Itea* kept in the Herbaria HITBC, IBSC and KUN have been examined by visiting these Herbaria and the images of *Itea* specimens deposited in the Herbaria E, GXMG, GXMI, IBK, IMDY, L, MW, N, NAS, NF, P, PE, SZ, TCD and US were also studied through the databases of specimens, such as Chinese Virtual Herbarium (CVH, https://www.cvh.ac.cn), Global Biodiversity Information Facility (GBIF, https://www.gbif.org), RBGE Herbarium Catalogue (https://data.rbge.org.uk/search/herbarium/), Naturalis BioPortal (https://bioportal.naturalis.nl/), Muséum National D'Histoire Naturelle (https://science.mnhn.fr/all/search) and Smithsonian National Museum of Natural History (https://collections.nmnh.si.edu/search/botany). Acronyms for the herbaria follow the Index Herbariorum (Thiers 2023). We also observed the living plants of the relevant species in the wild, including in the type localities of *I. tenuinervia* and *I. amoea*, as well as multiple localities of *I. riparia*.

Taxonomic treatment

1. *Itea riparia* Collett & Hemsl., J. Linn. Soc., Bot. 28: 57. 1890.

Figs 1–4

= *Itea thorelii* Gagnep., Notul. Syst. (Paris) 3: 222.1916. Type. Laos. Luang-prabang, 1866–1868, *Thorel 3474* (lectotype: P00709632, photo!, designated by Lecompte 1965: 40; isolectotypes: P00709633 photo!, P00709634 photo!).
= *Itea tenuinervia* S. Y. Liu, Guihaia 21(1): 35. 2001. Type. China. Guangxi Province, Daxin County, Shuolong Town, by stream, 14 Jan 2000, *Shou-Yang Liu 2893* (holotype: GXCM; isotype: IBK00190789!), syn. nov.

Type. Myanmar. Southern Shan States, Shan hills, on river-banks, 2000–4000 feet (ca. 700–1400 m) elev., *H. Collett s.n.* (holotype, K).

Description. Shrub, evergreen, usually 0.5–2 m tall, sometimes up to 7 m. Stipules subulate, 0.2–0.7 mm long, caducous. Leaves alternate, both surfaces glabrous, chartaceous, lanceolate or oblanceolate, 3.5–13 cm long, 1–5 cm wide, length/width ratio is 2.6–5.2 (mean = 3.6), acute or slightly acuminate at apex, cuneate at base, distantly shallowly subglandular crenate-serrate along upper margin; mid-vein raised on both surfaces, lateral veins in 4–7 pairs, arcuate ascending, lateral and reticulate veins visible and impressed above surface; petiole 0.4–1.2 cm long, raised above. Pseudoracemes, terminal or sometimes also axillary, usually solitary, sometimes with short branches at base, 4–18 cm long, rachis puberulous, usually 2- or 3-flowered per node; bracts at base of pedicel, subulate, 2–3 mm long, 0.3–0.5 mm wide, deciduous. Flowers white; pedicel erect, puberulous, 3–11 mm long; calyx shallowly cupular; calyx lobes 5, triangular, green, 1.5–2 mm long, 1.2–1.5 mm wide at base, puberulous; petals 5, white, triangular-lanceolate, acute at apex, widest at base, ca. 5 mm long, 1.5–1.9 mm wide at base, glabrous, erect-spreading at anthesis, becoming green and thickened at fruiting; stamens 5, alternating with the petals, shorter than petals, 3.3–3.6 mm long; filaments glabrous, ca. 0.8 mm wide; anthers oblong, ca. 0.6 mm long, 0.4 mm wide; floral disc annular, fleshy, slightly yellow; ovary semi-inferior, consisting of two carpels diverging in the middle and united at the top; stigma capitate. Capsule glabrous, 5–8 mm long, consisting of two obviously divergent carpels, with persistent sepals and petals, turning brown and dehiscing along the ventral suture at mature. Seed numerous, white at immature and brown at mature, 1–1.7 mm across; testa slightly granular.

Distribution. The species is distributed in China, Laos, Myanmar, Thailand and Vietnam (Fig. 6). It usually occurs near streams under forests, with elevation range from 200 to 1400 m.

Specimens examined. China. Guangxi: Daxin, 15 May 2008, *Guangxi Exped. Inst. Bot. 498* (IBK00278403), 17 Sept 2004, *Shou-Yang Liu F000749* (GXMI014126), 400 m elev., 9 Jun 2023, 22.854261°N, 106.725634°E, *Zhu-Qiu Song et al. JZ20230549* (IBSC); Jingxi, 457 m elev., 30 June 2013, *En-De Liu 3996* (KUN1241727), 500 m elev., 10 May 2023, 22.991658°N, 106.674116°E, *Bu-Yun Zhang et al. JZ20230371* (IBSC), 500 m elev., 9 Jun 2023, 23.009193°N, 106.659319°E, *Zhu-Qiu Song et al. JZ20230553* (IBSC); Napo, 450 m elev., 18 May 1943, *Pu-Chin Tsoong & Ko-Zen Kuang 356* (PE00865551, PE00865552), 15 Apr 1977, *Yuan Lin et al. 3-5104* (GXMI014127, GXMI014128). Yunnan:

Cangyuan, 700 m elev., 29 May 1974, *Yan-Hui Li 11737* (HITBC015745, HITBC015750, IBSC0273493, KUN0477791, KUN0540565, KUN0540567), 790 m elev., 15 May 1979, *Yan-Hui Li 20907* (HITBC015744, HITBC015751, KUN0540559, KUN0540568); Jinghong, 540 m elev., 7 May 1955, *Kuo-Mei Feng 20754* (IBSC0273491, KUN0477788, KUN0477789, PE00865549, SZ00179768), 30 Aug 2019, *Yun-Hong Tan ML56* (XSBN002276); Malipo, 1100 m elev., 21 Jun 1940, *Chi-Wu Wang 86321* (KUN0477792, PE00865553), 1000 m elev., 3 Feb 1940, *Chi-Wu Wang 86599* (KUN0477790); Mengla, 17 Jan 1976, *Lai-Yun Xiao 11269* (HITBC099861, IBSC0273492), 680 m elev., 18 Dec 1986, *Shao-Rong Guo 592* (IMDY0008066), 850 m elev., 11 Feb 1960, *Yan-Hui Li 2813* (HITBC015743, IBK00170997, IBSC0273495, KUN0477787), 560 m elev., 14 Apr 1961, *Yan-Hui Li 3049* (HITBC015746), 11 May 1961, *Yan-Hui Li 3222* (HITBC015747, IBSC0273494, KUN0477785), Jun 1967, *Yunnan First Section 138* (PE00865550), 600 m elev., 2 Sept 2023, 21.989364°N, 101.368001°E, *Zhu-Qiu Song et al. JZ20231022* (IBSC); Zhenkang, 12 Apr 1976, *Yan-Hui Li 20116* (HITBC015748, HITBC015749, KUN0477786). **Laos.** Champasak: Paksong, 29 Apr 2013, H*ang Sun et al. sunhang16056* (KUN1256568, KUN1256569); Luang Namtha: Nateuy, 1130 m elev., 21 Apr 2006, *En-De Liu 1686* (KUN1204594); Luang Prabang: 1866–1868, *Thorel 3474* (P00709632, P00709633, P00709634); Phongsal: 30 Apr 1993, *Guo-Da Tao et al. 930162* (HITBC059236, HITBC059244); Vientiane: Mt. Phu Kao Kwai, 700–800 m elev., 31 Dec 1993, *N. Fukuoka & H. Koyama L-65039* (L4134635); Without precise locality, *H. Bon s.n.* (P03179260). **Myanmar.** Maymyo: 760 m elev., 21 Apr 1916, *A. Rodger 510* (NAS00337458), 1066 m elev., 8 May 1912, *J. H. Lace 5802* (E00397666), 1066 m elev., 4 May 1912, *J. H. Lace s.n.* (E00397667); Taunggyi: 1219 m elev., Apr 1939, *F. G. Dickason 8273* (E01033109). **Thailand.** Chaiyaphum: Phu Khieo, 600–700 m elev., 1972, *K. Larsen et al. 31288* (L1861211), Ban Nam Phrom, 600 m elev., 24 May 1974, *R. Geesink et al. 6886* (L1861215, P00392452); Chiang Mai: Thawatchai, Kasem, 700 m elev., 7 May 1991, *Guo-Da Tao et al. 653* (KUN0540552), Me Ka Pak Bank, 1300 m elev., 21 Apr 1928, *H. B. Garret 505* (L1861224, L1861225, P03179261), Mae Rim District, 600 m elev., 12 Jun 2009, *J. F. Maxwell 09-162* (L2058714, P00911865), Doi Sutep, Mae Sa Falls, 10 Apr 1989, *J. F. Maxwell 89-446* (L1861217), Doi Intson National Park, 650 m elev., 4 May 1997, *J. F. Maxwell 97-443* (L4160466), Doi Inthanon, 1400 m elev., 3 Jan 1975, *R. Geesink et al. 8048* (L1861214, P03371228), Doi Inthanon, 920–960 m elev., 21 Jul 1988, *S. Tsugaru T-61686* (L4161221), 18 Aug 1970, *Voravut 8* (L1861218); Kanchanaburi: Sangklaburi, Toong Yai Narssuan Wildlife Reserve, 200 m elev., 12 Jan 1994, *J. F. Maxwell 94-10* (L4134592), near Khwae Noi River, Pompee Village, 250 m elev., 25 Mar 1968, *C. F. van Beusekom & C. Phengkhlai 108* (L1861220), 800 m elev., 30 Apr 2004, *M. van de Bult 796* (L4160559); Nakhon Ratchasima: Khao Yai, 800 m elev., 25 Mar 1968, *B. Hansen et al. 11340* (L1861219, L1861221); Phrae: Mae Bhaem stream, 440 m elev., 5 Jan 1972, *C. F. van Beusekom et al. 4661* (L1861223); Tak: Pha Charoen Waterfall National Park, 20 June 2005, *Pooma et al. 5329* (L4160075), Lansang National Park, 600 m elev., 21 Jul 1973, *G. Murata et al. 16617* (L1861212, P03179258), Lan Sang National Park, 250–400 m elev., 30 Aug 1967, *M. Tagawa et al. 8558* (L1861213), Larn Sarng Nat. Park, 350 m elev., 29 May 1973, *R. Geesink et al. 5532* (L1861222, P03179259); Without precise locality, Apr 1921, *A. F. G. Kerr 5273* (TCD0016587), Mar 1924, *A. F. G. Kerr 8763* (TCD0016588). **Vietnam.** Dak Lak: Lak, Chu Yang Sin National Park, 900 m elev., 23 Mar 2013, *M.S. Nuraliev 724* (MW0738997); Hoa

Figure 1. *Itea riparia* **A** isotype of *Itea tenuinervia* (*Shou-Yang Liu 2893*, IBK00190789, https://www.cvh.ac.cn/spms/detail.php?id=c1cf1dd4) **B** topotype of *Itea tenuinervia* (*Shou-Yang Liu F000749*, GXMI014126), showing two divergent carpels per fruit **C** specimen of *Itea riparia* from Myanmar (*J. H. Lace s.n.*, E00397667, https://data.rbge.org.uk/herb/E00397667), showing two divergent carpels per fruit **D** lectotype of *Itea thorelii* (*Thorel 3474*, P00709632, https://science.mnhn.fr/institution/mnhn/collection/p/item/p00709632), showing two divergent carpels per fruit.

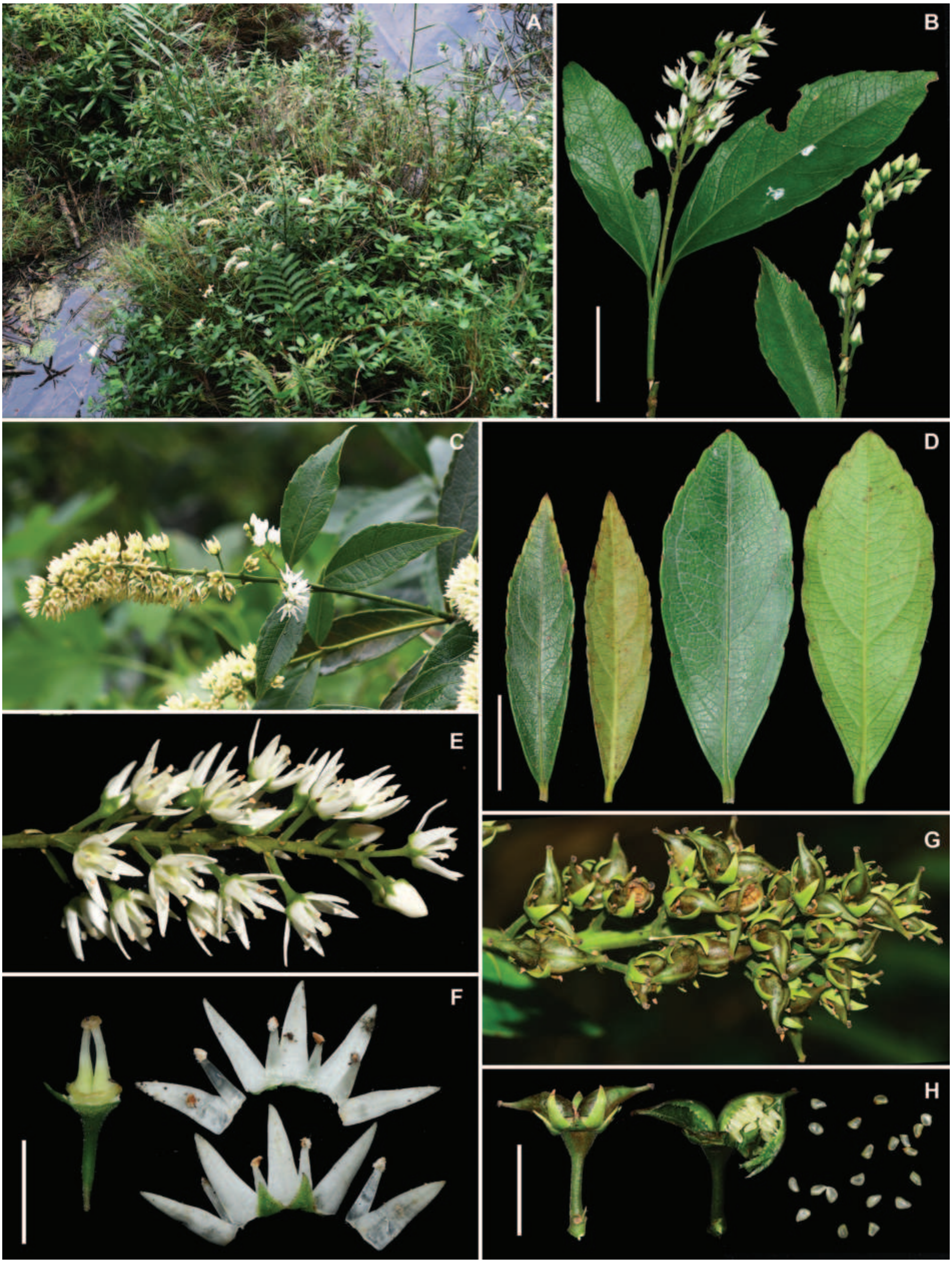

Figure 2. *Itea riparia* from Jingxi County, Guangxi, China **A** habitat **B–C** terminal inflorescences **D** leaves in adaxial and abaxial views **E** inflorescences **F** flowers with the different parts separated **G** infructescence, showing two divergent carpels per fruit and persistent sepals and petals **H** fruits and seeds. Voucher specimens: *Bu-Yun Zhang et al. JZ20230371* (fl., IBSC), *Zhu-Qiu Song et al. JZ20230553* (fr., IBSC). Scale bars: 2 cm (**B, D**); 5 mm (**F**); 1 cm (**H**).

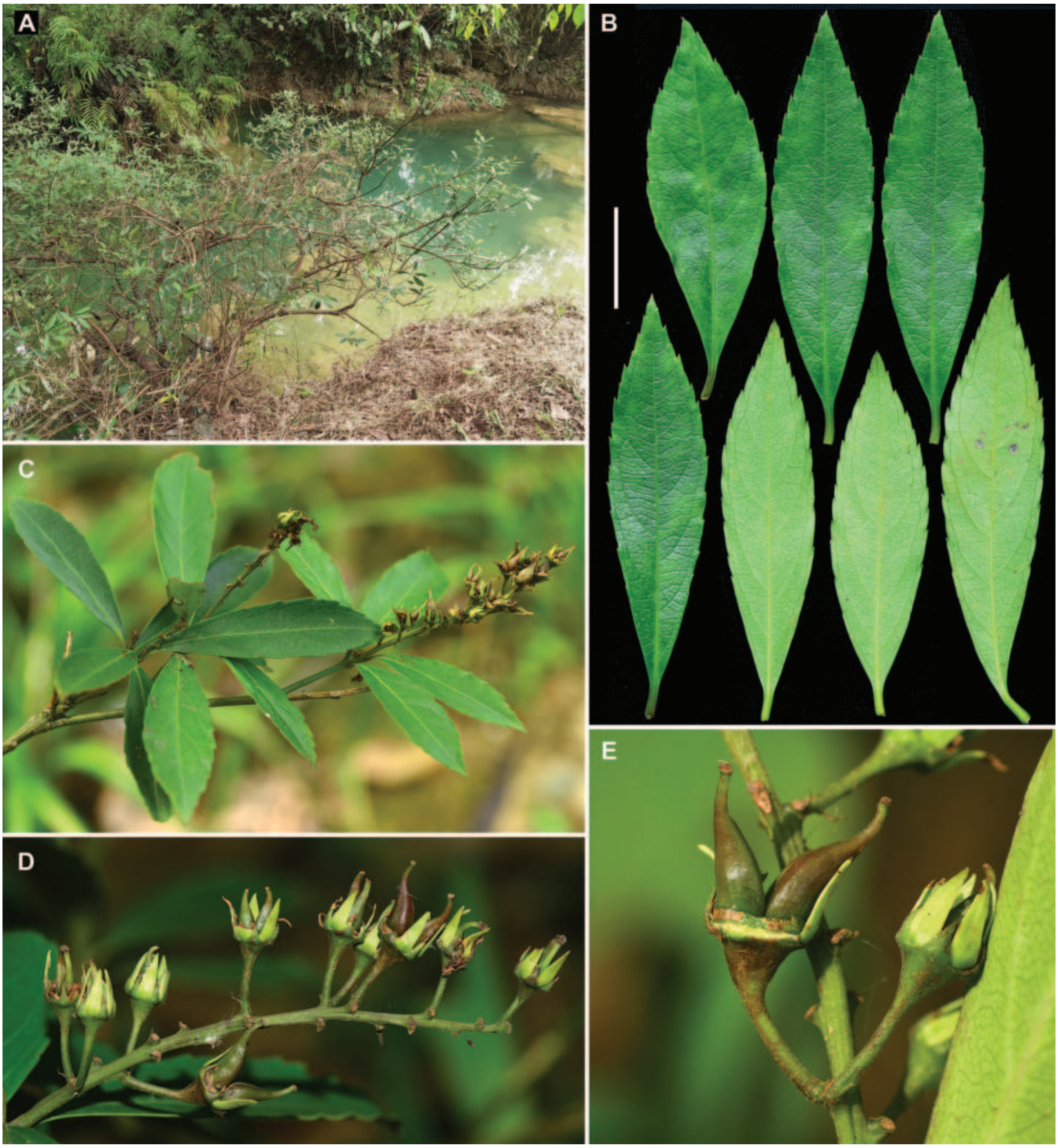

Figure 3. *Itea riparia* from Daxin County, Guangxi, China **A** habitat **B** leaves in adaxial and abaxial views **C** fruiting branchlets **D** infructescence **E** fruits, showing two divergent carpels per fruit and becoming green and thickened petals and persistent sepals and petals. Voucher specimens: *Zhu-Qiu Song et al. JZ20230549* (IBSC). Scale bar: 2 cm (**B**).

Binh: Yen Thuy, Cuc Phuong National Park, 12 Sept 2002, *M. V. Xinh MVX 241* (L1861216), Barrage de Cho-bo (Rivière Noire), sur les roches calcaires atteintes par les hautes eaux, 18 Oct 1888, *Balansa 3152* (P00709635).

Taxonomic notes. In the protologue, Liu (2001) considered that *I. tenuinervia* is distinguished from *I. riparia* in the height (1–2 m vs. 6 m), leaf shape (long elliptical, rarely oblanceolate vs. oblong, elliptical to lanceolate), pedicel length (10 mm vs. 3–5 mm) and petal length (6 mm vs. 4 mm) and it is distinguished from *I. thorelii* in the leaf shape (long elliptical, rarely oblanceolate vs.

oblanceolate), inflorescence type (racemes vs. racemose panicles), bract shape (triangular-lanceolate vs. linear-lanceolate), petal shape (narrowly lanceolate var. oblong-triangular) and pedicel length (10 mm vs. 4–6 mm). Subsequently, the species was accepted by Chen and Liu (2015). However, our examination of literature and specimens showed that there are no obvious differences between *I. tenuinervia* and *I. riparia* (including *I. thorelii*) in the characters above (see Table 1, Fig. 1). In the protologue, Liu (2001) did not describe the fruits of

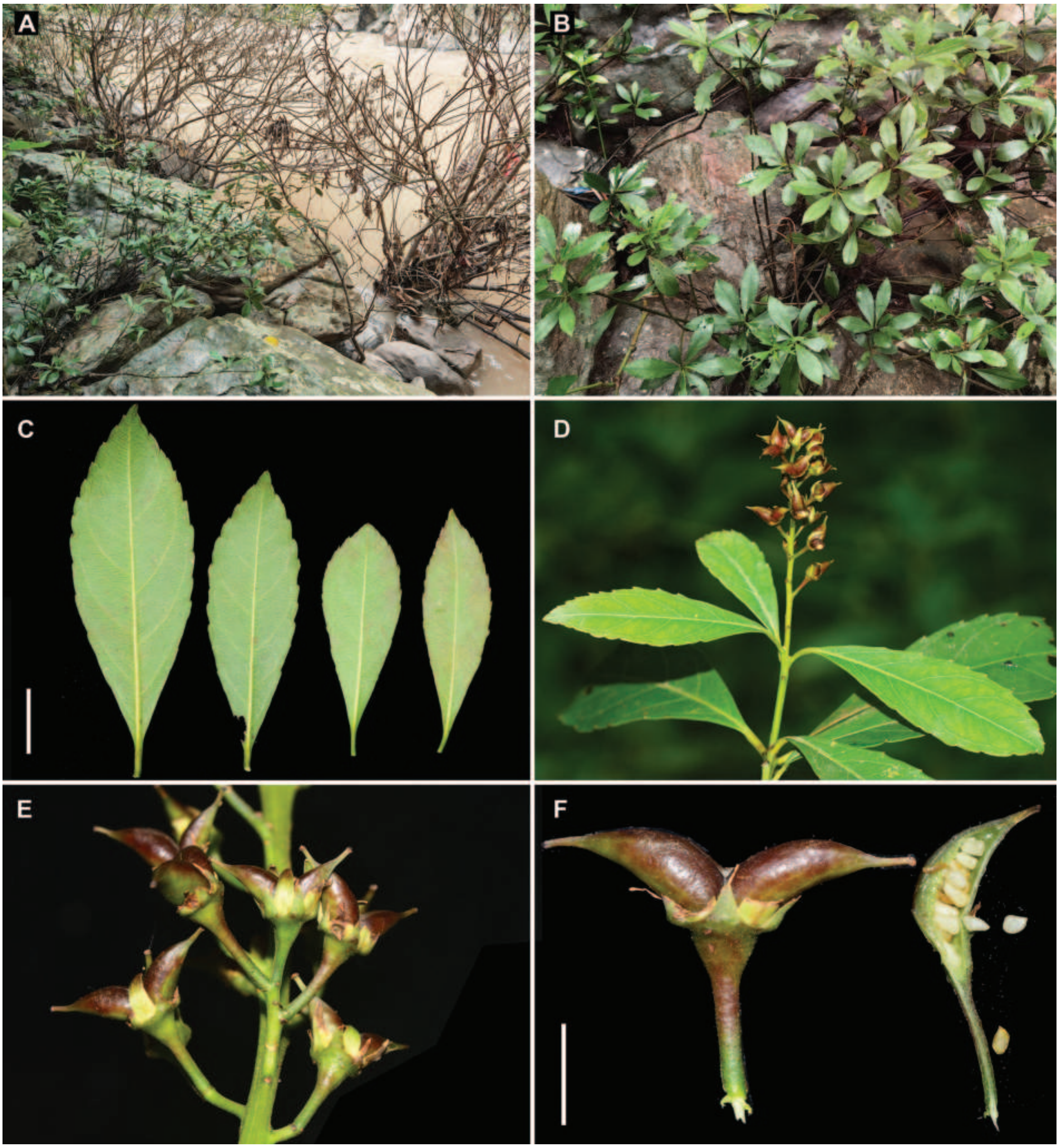

Figure 4. *Itea riparia* from Mengla County, Yunnan, China **A** habitat **B** habit **C** leaves **D** fruiting branchlet **E** part of infructescence **F** fruits and seeds, showing two divergent carpels per fruit. Voucher specimens: *Zhu-Qiu Song et al. JZ20231022* (IBSC). Scale bars: 2 cm (**C**); 5 mm (**F**).

I. tenuinervia, but he collected a fruiting gathering at the type locality in 2004, i.e. *Shou-Yang Liu F000749*, which shows two obviously divergent carpels per fruit (Fig. 1B). The fruits with two obviously divergent carpels are very special in the genus *Itea*, because most species bear two partly or completely fused carpels before dehiscence (Jordaan 2012) and only *Itea riparia* (including *I. thorelii*) was found to have two obviously divergent carpels (see Lecompte (1965: Pl. IV 8–10); Wu (1977: Pl. 26)). Thus, in the fruit character, *I. tenuinervia* is very similar to *I. riparia* as well. Furthermore, our observations of living plants in the wild, including in the type locality of *I. tenuinervia*, also showed that *I. tenuinervia* is consistent with *I. riparia* in the morphological characters and habit (Figs 2–4).

Table 1. Comparison between *Itea tenuinervia* and *Itea riparia*.

Characters	***Itea tenuinervia***	***Itea riparia***
Habit	shrubs 1–2 m	shrubs 1–6 m tall
Branchlet	green, striate, glabrous	yellow-green, striate, glabrous
Leaf arrangement	alternate, usually crowded at upper and lower parts of branchlets	alternate, usually crowded at apex of branchlets, subclustered
Leaf texture	thinly leathery	thinly leathery
Leaf hairiness	glabrous	both surfaces glabrous
Leaf shape	long elliptic, rarely oblanceolate, base cuneate, apex acuminate, margin incurved glandular dentate	elliptic to lanceolate or obovate-elliptic, base cuneate, apex acute or acuminate, margin curved cartilaginous glandular dentate
Leaf size	5–9 × 1.7–2.2 cm	5–13 × 1.5–5 cm
Lateral veins	4–5 pairs, confluent near margin, raised abaxially, slightly sunken adaxially	4–7 pairs, arcuate, confluent near margin, slightly raised abaxially, obscure adaxially
Tertiary veins	invisible above and visible below	reticulate, invisible above
Petiole	5 mm, glabrous	4–12 mm, glabrous
Stipules	ca. 1.5 mm long, caducous	0.2–0.7 mm long
Inflorescence	racemes terminal, 8–14 cm; rachis puberulous; flowers numerous, rather crowded, often 2–3-clustered	racemes terminal, 4–18 cm; rachis puberulous; flowers numerous, rather crowded, often 3-clustered
Bracts and bracteoles	bracts triangular-lanceolate, 3–5 mm; bracteoles 1–1.5 mm long	bracts ca. 3 by 0.5 mm, caducous, bracteoles to 1 mm long, similar
Pedicels	(6–) 10 mm	3–6 mm, puberulous
Calyx	shallowly cupular; lobes triangular, ca. 2 mm	shallowly cupular; lobes erect at anthesis, triangular-lanceolate, 1.5–4 mm
Petals	5, white, sometimes slightly pink, narrowly lanceolate, ca. 6 mm long, erect at anthesis	5, white, distinctly larger than the sepals, 4–5 by 1.5–2 mm, erect
Stamens	5, situated opposite the calyx lobes; filaments 5 mm long, slightly wider below the middle, glabrous; anthers ovoid, dorsifixed.	5, situated opposite the calyx lobes; filaments 2.5–3 mm long, glabrous; anthers ca. 1 mm long, dorsifixed, ovoid.
Disc	Ring-like, yellow	Ring-like
Ovary	semi-inferior, consisting of two carpels diverging above the base at the end of flowering, with a capitate stigma	superior or semi-inferior, glabrous, consisting of two carpels diverging in the middle and united at the top in a short style, surmounted by a capitate stigma
Fruit	capsules ovoid-conical, with very divergent carpels, except at the base; dehiscence by a slit corresponding to the ventral suture (based on a topotype, *Shou-Yang Liu F000749*, Fig. 1B)	capsules ovoid-conical, ca. 5 mm, glabrous, with very divergent carpels, except at the base; dehiscence by a slit corresponding to the ventral suture
Phenology	Fl. Jan., fr. Sept.	Fl. and fr. May–Feb.
Distribution	Guangxi, China	Myanmar, Thailand, Laos, Vietnam, China (Guangxi, Yunnan)
References	Liu (2001)	Lecompte (1965), Jin and Ohba (2001), Esser (2005)

2. *Itea amoena* Chun, Sunyatsenia 1(4): 238. 1934.

Fig. 5

Type. China. Guangxi Province, Shangsi County, Shup-man-tai Shan [Shi Wan Da Shan], in shaded ravine, about 1200 ft. (ca. 400 m), 29 Jul 1933, *Ching-Lieh Tso 23439* (lectotype, designated here: IBSC0004326, isolectotypes: IBSC0004324, IBSC0004325, PE00864804).

Description. Shrub, evergreen, usually 0.2–0.5 m, sometimes up to 2 m tall, glabrous, except puberulent on inflorescences. Stipules subulate, ca. 2 mm long, caducous. Leaves alternate, both surfaces glabrous, thinly leathery, narrowly lanceolate, 6.5–13.9 cm long, 1.2–2.2 cm wide, length/width ratio is 4.1–9.5 (mean = 6.5), acuminate or gradually acute at apex, cuneate or subobtuse at base, distantly shallowly subglandular crenate-serrate along upper margin; mid-vein raised on both surfaces, lateral veins in 6–8 pairs, arcuate ascending, lateral and reticulate veins obviously visible and prominently elevated above surface; petiole 1–1.5 cm long, narrowly grooved above. Pseudoracemes, terminal or sometimes also axillary, solitary, 6–24 cm long, rachis puberulous, usually 2- or 3-flowered per node; bracts at base of pedicel, subulate, ca. 1–2 mm long, deciduous. Flowers white; pedicel erect, puberulous, 5–9 mm long; calyx shallowly cupular; calyx lobes 5, narrowly lanceolate, green, 2–2.5 mm long, 0.8–1 mm wide at base, puberulous; petals 5, white, reflexed at anthesis, deciduous at fruiting, triangular-lanceolate, acute at apex, widest at base, ca. 5 mm long, ca. 1.5 mm wide at base, glabrous; stamens 5, alternating with the petals, shorter than petals, ca. 4 mm long; filaments glabrous, ca. 0.3–0.4 mm wide; anthers oblong, ca. 0.5 mm long, 0.3 mm wide; floral disc annular, fleshy, slightly yellow; ovary semi-inferior, narrowly grooved, consisting of two united carpels; stigma capitate. Capsule suboblong-conical, 5–6 mm, glabrous, turning brown and dehiscing septicidally at mature, with persistent sepals. Seed numerous.

Distribution. The species is only found in Guangxi, southern China (Fig. 6). It usually occurs near streams under evergreen forests, with elevation range from 90 to 800 m.

Specimens examined. China. Guangxi: Dongxing City, Malu, 107°58'56"E, 21°41'8"N, 90 m elev., 12 Oct 2018, *Dongxing Exped. 450681181012069LY* (GXMG0206492, IBK00418425), 21 Jun 1919, *Kuan-Kwang Tsoong 1868* (PE00864807), 26 Sept 1973, *Chou-Fen Liang 33611* (IBK00170636); Fangchenggang City, Pingwang, 15 Jul 2007, *Feng-Juan Mou 127* (IBSC0712193), Banba, 15 Oct 1973, *Chou-Fen Liang 33875* (IBK00170634), Nangui, 11 Nov 1958, *Chao-Chien Chang* 13197 (IBK00170635, IBSC0272608), Naliang, 24–31 Jul 1936, *Wai-Tak Tsang 26510* (IBSC0272609, P03179693), Naliang, 105 m elev., 13 Apr 1956, *Hepu Pl. Exped. 2365* (IBSC0272605, PE00864802), Naliang, 107°47.563'E, 21°47.218'N, 140 m elev., 13 Jan 2016, *Pu Zou & Kai Xu zp57* (IBSC0824452); Nalungou, 350 m elev., 21 Jul 1982, *Peng-Cheng Huang 216* (NF2011745, NF2011746); Shangsi County, Shi Wan Da Shan, 325 m elev., 9 Nov 1958, *Chao-Chien Chang* 12233 (IBSC0272601), Wangle, 107°49'36"E, 21°53'24"N, 221 m elev., 1 Apr 2009, *Wei-Bin Xu et al. liuyan0208* (KUN0906334, KUN0902457), Shi Wan Da Shan, 8 Jul 1937, *H. Y. Liang 69500* (IBK00170632, IBK00170633, IBSC0272602, PE00864803), Shi Wan Da Shan, 11–30 Jul 1934, *Wai-Tak Tsang 23804* (IBSC0272603), 15–24 Aug 1936, *Wai-Tak Tsang* 26675

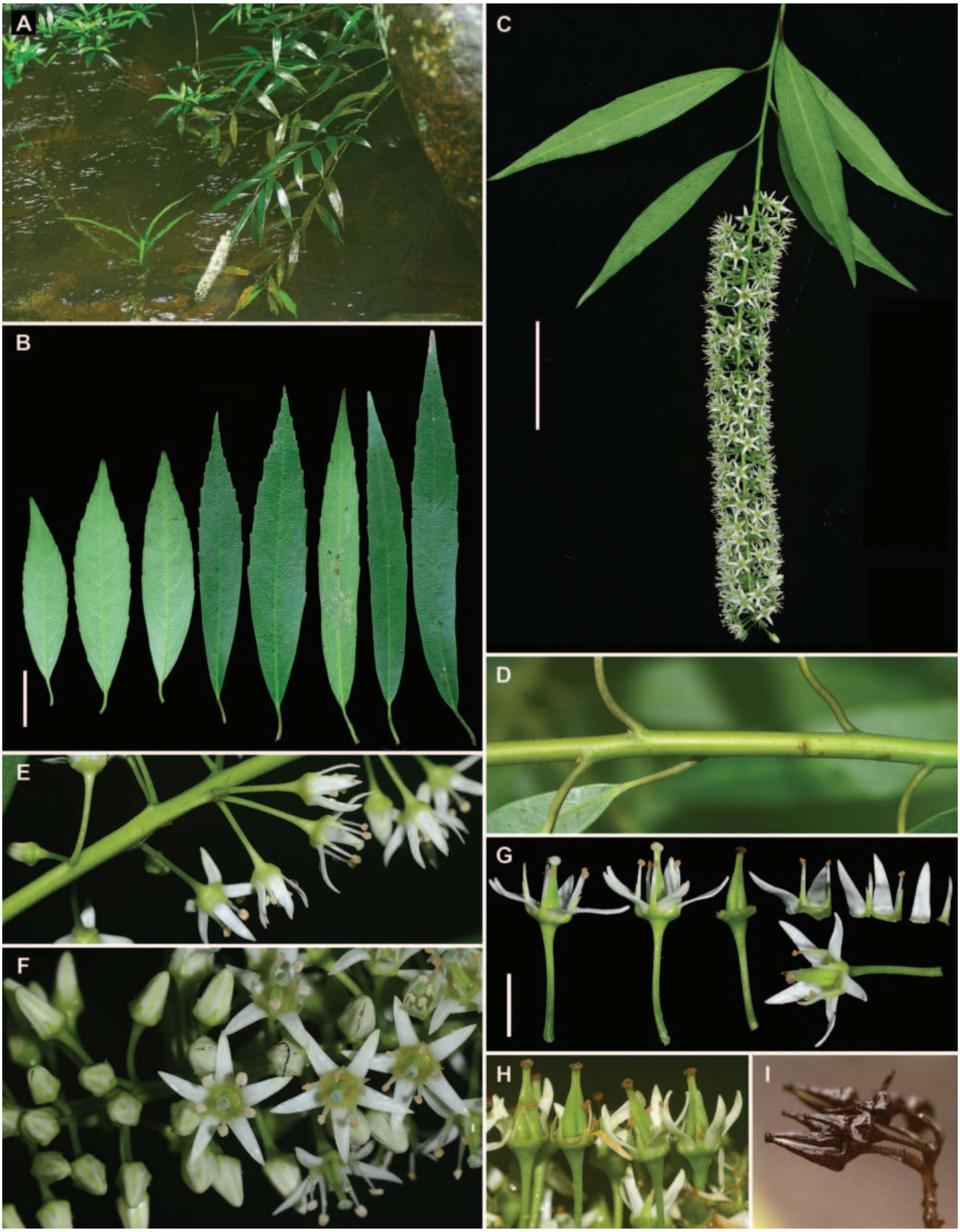

Figure 5. *Itea amoena* from Shangsi County, Guangxi, China **A** habitat **B** leaves in adaxial and abaxial views **C** flowering branchlet **D** branchlet **E** part of inflorescences, showing usually 2 or 3 flowers per node **F** part of inflorescences, showing floral petals reflexed at anthesis **G** flowers with the different parts separated **H** flowers at the end of flowering, showing two fused carpels per fruit and deciduous petals **I** mature fruits. Voucher specimens: *Zhu-Qiu Song et al. JZ20230531*, *JZ20230537* (IBSC). Scale bars: 2 cm (**B**); 4 cm (**C**); 5 mm (**G**).

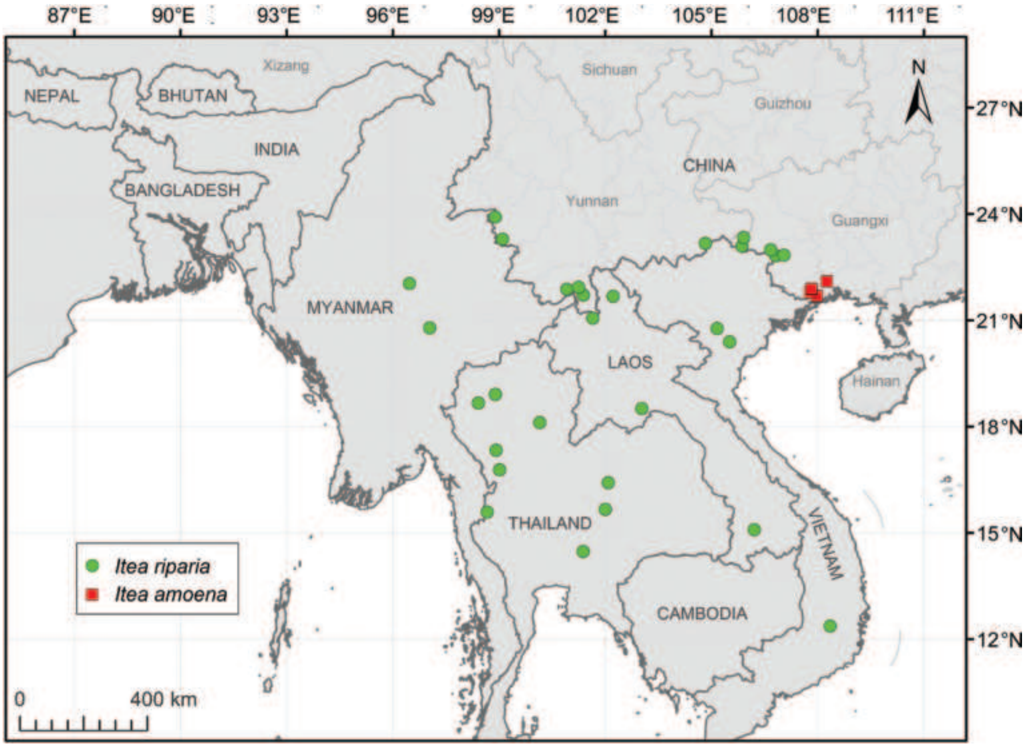

Figure 6. Distribution map of *Itea riparia* (green circles) and *Itea amoena* (red squares).

(IBSC0272604, P03179692), Seh-feng Dar Shan [Shi Wan Da Shan], 2500 feet (ca. 800 m) elev., 21 Oct 1928, *Ren-Chang Ching* 8059 (IBSC0272600, N117066318, PE00864805, PE00864806, US03684023), 250 m elev., 14 Aug 1986, *Beijing Youth Exped. 718* (PE01869678), 90 m elev., 23 Dec 1943, *S. H. Chun 3304* (IBSC0272607), 170–300 m elev., 24 May 1944, *Shao-Hing Chun* 5209 (IBSC0272606), 140 m elev., 8 Jun 2023, 21.097495°N, 108.257582°E, *Zhu-Qiu Song et al. JZ20230531* (IBSC), 320 m elev., 8 Jun 2023, 21.882874°N, 107.8346332°E, *Zhu-Qiu Song et al. JZ20230537* (IBSC).

Taxonomic notes. *Itea amoena* can be readily distinguished from *I. riparia* in its long narrower leaves (length: width = 4.1–9.5 and ratio mean = 6.5 vs. 2.6–5.2 and 3.6), raised lateral and reticulate veins in the adaxial leaf surface (vs. impressed veins), floral petals reflexed at anthesis (vs. floral petals erect at anthesis), floral petals deciduous at fruiting (vs. becoming green and thickened at fruiting), lanceolate calyx lobes (vs. triangular calyx lobes) and fruits with two fused carpels (vs. two obviously divergent carpels). In distribution, *I. amoena* is restricted to southern Guangxi and it does not overlap with *I. riparia* (Fig. 6).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: ZQS. Investigation: ZQS, BYZ. Methodology: ZQS, BYZ. Writing – original draft: ZQS.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

An updated infrageneric classification of the pantropical species-rich genus *Garcinia* L. (Clusiaceae) and some insights into the systematics of New Caledonian species, based on molecular and morphological evidence

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Abstract

Garcinia L. is a pantropically distributed genus comprised of at least 250 species of shrubs and trees and has centers of diversity located in Africa/Madagascar, Australasia, and Southeast Asia. The genus is notable due to its extreme diversity of floral form, common presence in lowland tropical rainforests worldwide, and potential pharmacological value. Across its entire geographic range, *Garcinia* lacks a recent taxonomic revision, with the last genus-level taxonomic treatment of *Garcinia* conducted over 40 years ago. In order to provide an evolutionary-based framework for a revised infrageneric classification of the genus and to investigate in more detail the systematics of New Caledonian species, we conducted molecular phylogenetic analyses using DNA sequence data for the nuclear ITS region on all samples, and for three chloroplast intergenic spacers (*psbM-trnD*, *trnQ-rps16* and *rps16-trnK*) on a subset of our overall sampling. Our phylogenetic analyses are the most comprehensive to date for the genus, containing 111 biogeographically and morphologically diverse *Garcinia* species. The analyses support a broad circumscription of *Garcinia*, including several previously segregated genera (e.g. *Allanblackia*, *Clusianthemum*, *Ochrocarpos* p.p., *Pentaphalangium*, *Rheedia*, and *Tripetalum*). We recovered nine major clades falling within two major lineages, and we delimit 11 sections. We discuss each of the clades, assign them sectional names, discuss their distinguishing morphological features, compare our taxonomic treatment with the most recent sectional treatment, list representative species, note geographic distribution, and highlight some questions that deserve future investigations. We propose nine new nomenclatural combinations, four new names, and three new lectotypes. In New Caledonia (NC), a total of ten, all endemic, species are recognized and were included in our phylogenetic analyses, with several replicates per species (with the exception of *G. virgata* and *G. urceolata*, represented by a single accession each). New Caledonian species were retrieved within three separate clades, respectively including 1) *G. balansae*; 2) *G. comptonii*, *G. neglecta*, *G. urceolata*, *G. virgata*; and 3) *G. amplexicaulis*, *G. densiflora*, *G. pedicellata*, *G. puat*, *G. vieillardii*. Within NC, the phylogenies did not support the distinction between a putative undescribed species and *G. balansae*. However, it confirmed the distinction between NC species and both *G. vitiensis* (found in Fiji and Vanuatu) and *G. adinantha* (found in Fiji), suggesting that all NC species should be considered as endemics.

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Introduction

Species rich, morphologically diverse genera can benefit from the delimitation of natural infrageneric groups, which can help to facilitate future monographic work, ecological and evolutionary research, and conservation efforts (van Welzen et al. 2009; Moonlight et al. 2018; Atkins et al. 2021). *Garcinia* L. is a large genus with centers of species diversity located in Africa/Madagascar, Australasia, and Southeast Asia. The genus exhibits extreme diversity of floral morphology, particularly in the androecium and is of high ecological significance with many species forming an important component of the lower strata of lowland tropical forests worldwide. *Garcinia* is also of high economic significance since many species have edible fruits (especially *G. mangostana*) and/or possible medicinal properties (e.g., Pedraza-Chaverri et al. 2008; Espirito Santo et al. 2020).

Recent phylogenetic and biogeographic studies (e.g. Sweeney 2008; Ruhfel et al. 2011; Ruhfel et al. 2016) support a broad circumscription of *Garcinia* that justifies the inclusion of several previously segregated genera (e.g. *Ochrocarpos* Thouars p.p., *Pentaphalangium* Warb., *Rheedia* L., and *Tripetalum* K. Schum.). When broadly circumscribed, the genus contains at least 250 species (Stevens 2007) and maybe as many as ca. 400 (POWO 2023). While some of these molecular studies (Sweeney 2008) revealed major clades with suites of shared morphological characters, no recent genus-wide infrageneric classification of the genus has been attempted.

Infrageneric taxonomy and classification of *Garcinia*

The taxonomy and systematics of *Garcinia* is made challenging due to several factors including the large number of species, dioecy, extreme floral diversity in the paleotropics (particularly in the androecium), poor preservation state of some features (e.g. fruits and flowers) on herbarium specimens, and numerous geographic sites harboring sympatric species. Several valuable efforts have been made to bring taxonomic order to the genus, at various geographic and taxonomic scales.

Previous taxonomic treatments over the past 200 years have resulted in more than 50 infrageneric taxa (Jones 1980). In the most recent worldwide taxonomic treatment of the genus and the benchmark against which more recent genus-level taxonomic work has been evaluated, Jones (1980) recognized 14 sections (Table 1). This treatment relied heavily on staminate flower and pollen morphology to classify upwards of 345 named species. Prior to Jones (1980), the most recent taxonomic treatment of the genus was that of Engler (1894, 1925), which recognized 34 sections. That work was an elaboration of Pierre (1883), who produced the first monograph of *Garcinia* (excluding *Ochrocarpos* and *Rheedia*) and used largely flower and inflorescence characters to classify 149 species into 37 sections that were organized into six groups. The only other monograph of the genus is that of Vesque (1893) who used floral morphology and leaf anatomy to classify 180 species (excluding *Rheedia*) into three subgenera and nine sections. The first major, global treatment of *Garcinia* (but narrowly circumscribed and not including the segregate genera *Discostigma*, *Ochrocarpos*, *Rheedia*, and *Xanthochymus*) was that of Planchon and Triana (1860), who used mostly floral characters to group 32 species into six sections.

In addition to the above-mentioned works that are global in scope, there have been several noteworthy publications that have dealt with the genus at narrower geographic or taxonomic scales. These studies include work on species in Africa (Sosef and Dauby 2012), Australia (Cooper 2013), Brazil (Mouzinho et al. 2022), China (Li et al. 2007), Colombia (Medellín Zabala 2015), India (Maheshwari 1964; Singh 1993; Mohanan et al. 2023), and Madagascar (Sweeney and Rogers 2008; Rogers et al. 2011).

Two notable recently published works dealing with the infrageneric classification of *Garcinia* are that of Nazre et al. (2018), who provided a monograph for section *Garcinia* and the molecular phylogenetic study of Sweeney (2008) who evaluated Jones' (1980) classification in relation to phylogeny and morphology. Some major findings of Sweeney (2008) were that some segregated genera should be included within *Garcinia*, and while partly congruent with phylogeny, the infrageneric sectional classification of Jones (1980) needs revision.

Taxonomy of New Caledonian *Garcinia* species

In contrast to other regions cited above, and in spite of the observed diversity within *Garcinia* in New Caledonia (NC), an archipelago that is well-known for its high overall levels of botanical diversity and endemism (Morat et al. 2012; Munzinger et al. 2023), the genus has not been recently and thoroughly studied in this territory. Only one species (*G. amplexicaulis*) was included in the phylogeny of Sweeney (2008). One species was recently described (Munzinger et al. 2021), leading to a total of ten –all presumed endemic– species, but the circumscription of some species is unclear and some questions remain about the conspecificity or, at least, the close evolutionary relationships between some non-NC and NC species that appear morphologically similar.

A taxon resembling *G. balansae* grows on the ultramafic massifs in the northwest of NC, but it displays linear, erect leaves and a very cracked greyish bark compared to the brownish and smoother bark of *G. balansae* (Fig. 1). This putative new taxon (*G.* sp. "JT814") is restricted to three massifs (Boulinda, Koniambo and Tiébaghi) and should be considered as Endangered (Lowry and Munzinger 2015), but its taxonomic rank remains unresolved. In addition, the Fijian *G. vitiensis* (A. Gray) Seem. is cited in NC by Sebert and Pancher (1874), but the material of this species is then assigned by Pierre to his endemic species: *G. balansae* Pierre. Strangely, Pierre (1883: XXXVI) states "that he has never seen material of *G. vitiensis*, appearing close to *G. balansae*" (our translation). The conspecificity or non conspecificity between the two taxa remains to be tested. The presence of *G. sessilis* Seem. in NC is also mentioned at the end of the 19th and in the early 20th century (Sebert and Pancher 1874; Hemsley 1895), while subsequent authors considered this species as a Fijian endemic (Smith and Darwin 1974; Smith 1981) without discussion about its potential occurrence in NC. *Garcinia sessilis* was later split into two species, with the description of *G. adinantha* A.C.Sm. & S.P.Darwin (Smith and Darwin 1974), but the evolutionary relationship between the New Caledonian and these two Fijian species remains unknown.

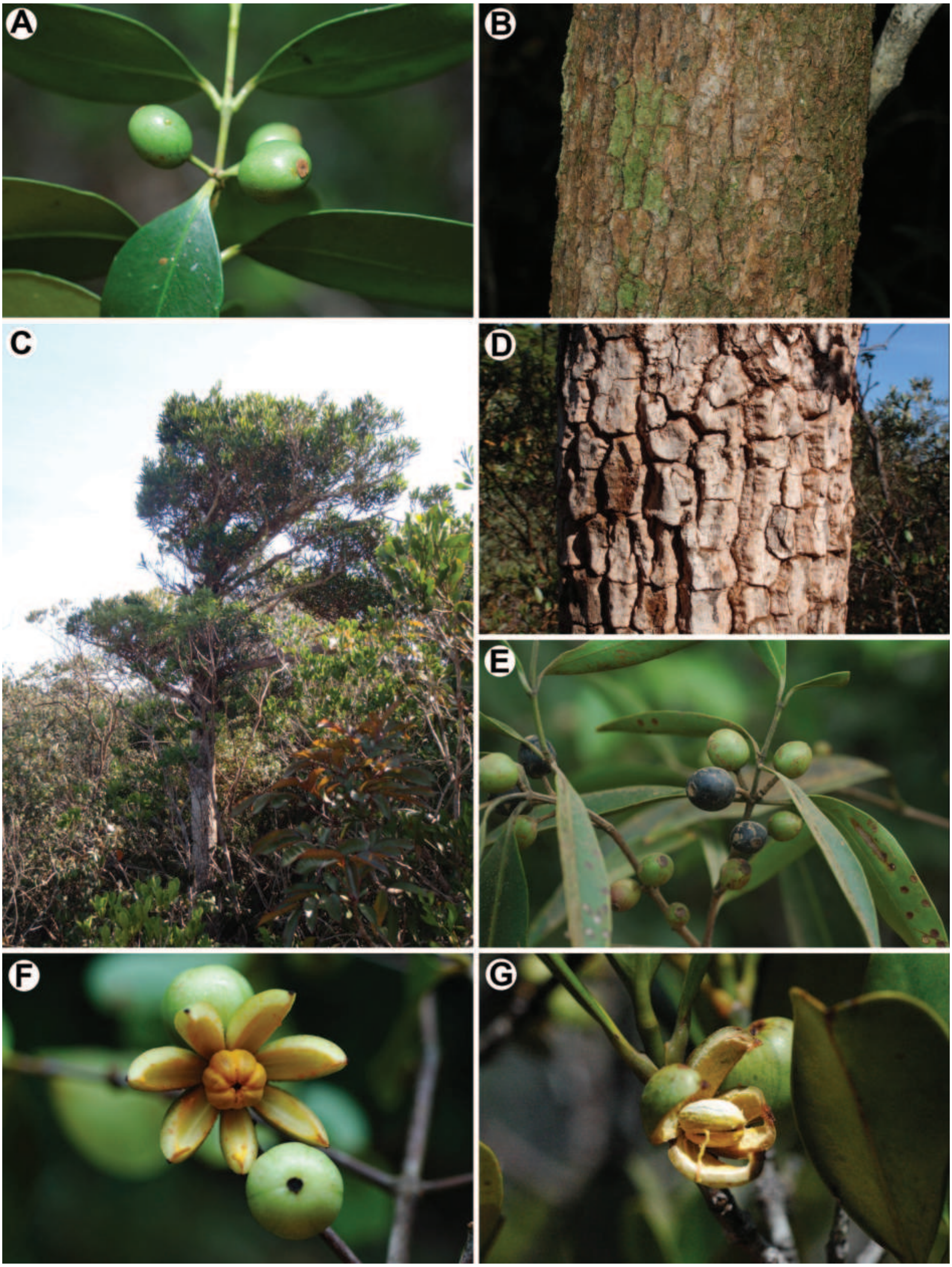


Figure 1. Some *Garcinia* New Caledonian species (except E from Fiji) and morphological features **A** *G. balansae* (Munzinger 4916), fruiting branch **B** *G. balansae* (Munzinger 4916), bark **C** *G.* sp. "JT814" (Munzinger 7282), habit **D** *G.* sp. "JT814" (Munzinger 7282), bark **E** *G. vitiensis* (Munzinger 7377), fruiting branch **F** *G. neglecta* (Munzinger 2690), fruit **G** *G. comptonii* (sin voucher), fruit.

Based on an enlarged taxonomic sampling compared to Sweeney (2008), and an important sampling effort in the Pacific Ocean region and NC in particular (including several samples per morphologically delimited species), our goal is to provide an updated molecular phylogeny of the genus in order: 1) to offer a way forward on a revised infrageneric classification of *Garcinia* considering both morphological and molecular evidence; and 2) to provide insight into the systematics of NC species.

Materials and methods

Taxonomic sampling

This study was based on both published and newly generated sequences, leading to a total of 160 samples representing 121 species (including ten outgroups) and two putative new species (*G.* sp. "JT814" from NC and *G.* sp. Munzinger 7380 from Fiji; Suppl. material 1). Published sequences included sequences from Sweeney (2008; 57 sequences), in addition to 25 sequences downloaded from Genbank and three sequences taken from Nazre (2006). New ITS sequences were generated from both herbarium and silica-dried leaf material collected in the field. They included a total of 72 samples representing 39 species and two unidentified taxa, among which were 32 samples representing 10 species and one unidentified taxon from NC (Suppl. material 1). The sampling comprised representatives of all major *Garcinia* clades based on Sweeney (2008) and *Allanblackia*, and covered both the morphological diversity and biogeographic range of *Garcinia*. The outgroup included seven genera: *Lorostemon* Ducke, *Montrouziera* Pancher ex Planch. & Triana, *Moronobea* Aubl., *Pentadesma* Sabine and *Symphonia* L.f. from the Symphonieae tribe, and *Arawakia* L.Marinho and *Clusia* L. from the Clusieae tribe. A subset of this sampling was used to generate a fully original chloroplast DNA dataset: it comprised 67 samples representing 45 species (among which was one outgroup) and two putative new species (see above), covering all *Garcinia* clades based on Sweeney (2008) and including nine out of the ten NC *Garcinia* species.

DNA sequencing

DNA extraction was performed with the DNeasy Plant Mini Kit (QIAGEN, Courtaboeuf, France), following the manufacturer's protocol except for a slight modification: we added 30 µL CTAB and 30 µL proteinase K for the initial digestion, which lasted 24h at 42 °C. The nuclear ribosomal ITS region included the two transcribed intergenic spacers ITS1 and ITS2, separated by the 5.8S gene. It was sequenced using either the primers ITS4 and ITS5 (White et al. 1990) or the newly designed primers ITS4Garci (5'-CCTGACCTGGGGTCGC-3') and ITS5Garci (5'-AACCTGCGGAAGGATCATTG-3') that were more specific to *Garcinia* or at least to angiosperms, minimizing the risk of false positive due to fungi amplification when the amount of plant DNA was too low as a PCR template. Three chloroplast intergenic spacers were also sequenced: *psbM-trnD*, *trnQ-rps16* and *rps16-trnK*. PCR primers were psbMF and trnD^{GUC}R for *psbM-trnD* (Shaw et al. 2005), trnQ^{UUG} and rps16x1 for *trnQ-rps16* (Shaw et al. 2007) and rpS16x2F2 and trnK^{UUU}x1 for *rps16-trnK* (Shaw et al. 2007). All PCRs were performed in 25 µL including 1X Taq Buffer, 2.5 mM $MgCl_2$, 1M betaine, 0.25 mM of each dNTP, 0.4 µM of each primer, 0.6U Taq polymerase and 1 µL template DNA. PCR conditions were: 94 °C for 5 min, followed by 40 cycles of: 94 °C 30 sec, Tm 45 sec, 72 °C 1 min, and a final extension step of 10 min at 72 °C. Tm was 48 °C for ITS and *psbM*-trnD, 44 °C for *trnQ-rps16*, and 46 °C for *rps16-trnK*. PCR products were sequenced in both directions by Eurofins (Evry, France), using the same primers as for the PCRs. Sequences were automatically aligned in MUSCLE v3.6 (Edgar 2004) before the alignments were manually revised in BioEdit v.7.2.5 (Hall 1999). Indels were coded following the simple coding method of Simmons and Ochoterena (2000) implemented in SeqState (Müller 2005). Vouchers details are listed in Suppl. material 1.

Phylogenetic reconstructions

First, individual analyses were carried out on each DNA region. Bayesian inferences (BI) were performed using MrBayes v.3.1.2 (Ronquist et al. 2011). For each region, the best-fitting model of nucleotide substitution was identified under the Akaike information criterion in MrModelTest v.2.3 (Nylander 2004): GTR + I + Γ for the ITS region and psbM-trnD intergenic spacer, and GTR + Γ for the trnQ-rps16 and rps16-trnK intergenic spacers (using distinct models for ITS1, ITS2 and 5.8S did not make any difference in the resulting tree). For indels, we used the restriction site (binary) model, with the option lset coding = variable. Two independent but parallel analyses were conducted using flat priors, starting from random trees and consisting of four chains each. The analyses were run for 6 million generations, sampling every 1000 generations and with a 25% burn-in. Analysis of output parameters, in Tracer v.1.6 (Rambaut et al. 2014), confirmed the convergence of chains and adequate burn-in length. Post-burn-in trees were pooled and a 50% majority-rule consensus tree was computed with posterior probability (PP) estimates for all nodes. Maximum likelihood (ML) was also used to estimate phylogenetic relationships. The ML analysis was performed in raxmlGUI 1.5.1 (Silvestro and Michalak 2012; Stamatakis 2014), using the same partitions and models of nucleotide evolution as for the BI. We performed 1000 rapid bootstrap (BS) replicates and searched for the best-scoring ML tree. The topologies inferred by BI analyses from each chloroplast marker were visually compared to identify potential incongruence among them (Suppl. materials 2–4). Since no major incongruence was highly supported, the three chloroplast sequences for each sample were then combined to maximise the number of characters analysed in the BI and ML analyses. Also, a BI analysis was performed by merging the nuclear and chloroplast datasets on the reduced sampling (Suppl. material 5).

Results

Large-scale infrageneric phylogeny

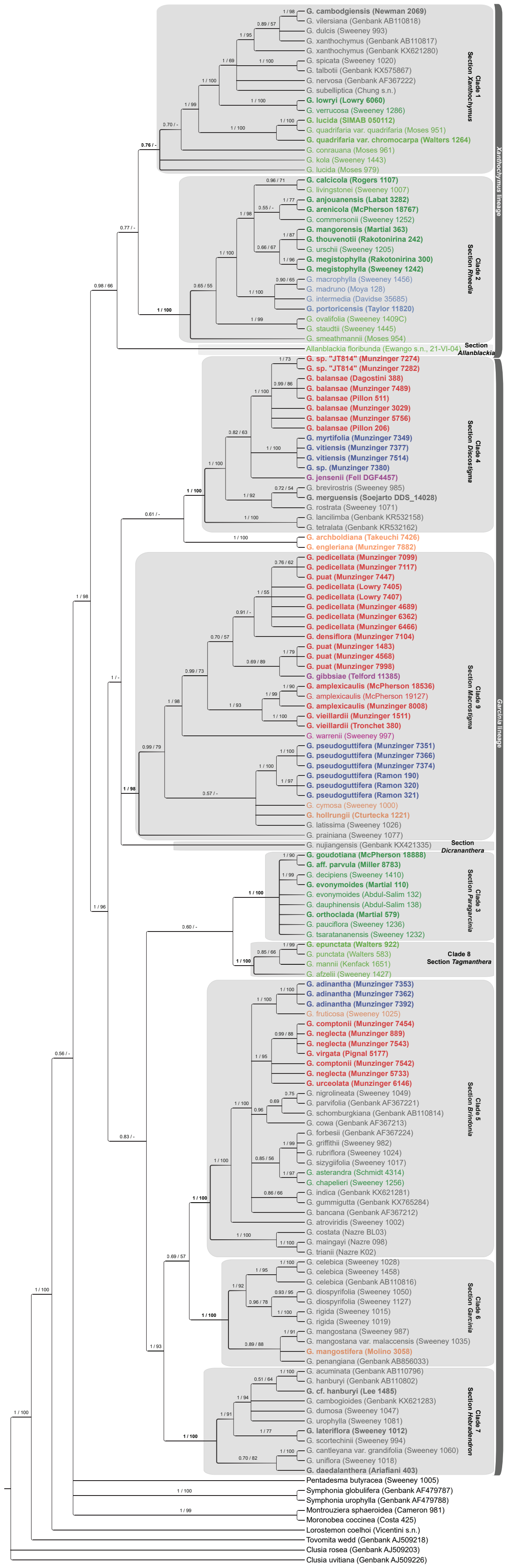
The ITS alignment was 773 base pairs (bp) long and 91 indels were coded, whereas the cpDNA alignment was 2484 bp long (795 bp for psbM-trnD, 674 bp for trnQ-rps16 and 1015 bp for rps16-trnK) and 167 indels were coded. Only minor differences were identified among trees using BI and ML, and no conflict was supported. Because both resolution and support were higher using BI, we chose to present the resulting BI topologies, on which we also indicated the support values obtained from the ML analyses (Figs 2, 3).

Based on ITS, we recovered mostly the same two major lineages and nine clades as Sweeney (2008). The allied genera *Allanblackia*, *Ochrocarpos*, *Pentaphalangium*, *Rheedia*, and *Tripetalum* were again retrieved within *Garcinia*. We retrieved a clade containing clade 1 and clade 2, which corresponds to Lineage A in Sweeney (2008). Its support was PP = 0.77 (vs. 0.99 in Sweeney 2008) and it was not retrieved in ML. Nevertheless, the clade consisting of lineage A of Sweeney (2008) and *Allanblackia floribunda* was more strongly supported (PP = 0.98, BS = 66). Clade 1 was not highly supported in BI (PP = 0.76 vs. 0.98 in Sweeney 2008) and not fully retrieved in ML. This was due to three species: *G. conrauana*, *G. kola* and *G. lucida*. The support of clade 1 excluding these three species reached PP = 1 and BS = 99. Compared to Sweeney (2008), nine new species were assigned to this clade (five downloaded from Genbank, three newly sequenced and *G. conrauana*). Clade 2 was strongly supported (PP = 1, BS = 100). Seven newly sequenced species were assigned to this clade. A clade corresponding to Lineage B of Sweeney (2008) consisted of clades 3 to 9 and three additional species, *G. engleriana*, *G. archboldiana* and *G. nujiangensis*, which were not included in any major clade. The Lineage B clade was highly supported (PP = 1, BS = 96) and all major subclades also received strong support (all PP = 1 and all BS = 100 except for clade 9, BS = 98). They included one (in clade 8) to 15 (in clade 5) additional species each compared to Sweeney (2008). Relationships between clades remained largely unresolved. No grouping was supported except the one including clades 5, 6 and 7 (PP = 1, BS = 93), as was observed by Sweeney (2008).

Based on the combined chloroplast dataset, the same nine clades were retrieved with high support (all PP = 1 and BS from 93 to 100). The only allied genus included in the analysis was *Pentaphalangium*, which was retrieved within *Garcinia* in agreement with the ITS phylogeny. *Garcinia archboldiana* and *G. engleriana* were again sister species, and not included in any major clade. Clades 1 and 2 grouped together (PP = 1, BS = 81), as did clades 3 and 8 (PP = 0.99, BS = 81), which were sister to clade 4 (PP = 1, BS = 95). Clades 5, 6 and 7 grouped together (PP = 1, BS = 78) and this clade grouped with clade 9 and *G. archboldiana* and *G. engleriana* (PP = 1, BS = 99).

Focus on the New Caledonian species

New Caledonian species were retrieved within three distinct clades: *G. balansae* and *G.* sp. “JT814” were recovered in clade 4; *G. comptonii*, *G. neglecta*, *G. urceolata* and *G. virgata* were placed in clade 5, within which they formed a highly supported subclade (PP = 1 and BS = 95 in the more densely sampled ITS phylogeny); and *G. amplexicaulis*, *G. densiflora*, *G. pedicellata*, *G. puat* and *G. vieillardii* were recovered in clade 9, grouped in a subclade that also included the Australian *G. gibbsiae* (PP = 0.99, BS = 73 in the ITS phylogeny). Together with *G. warrenii*, they formed a strongly supported clade (PP = 1, BS = 98). Within clade 4, the two accessions of *G.* sp. “JT814” formed a subclade based on ITS, but were scattered among the *G. balansae* accessions based on cpDNA. Similarly, the NC species grouped within clades 5 and 9 did not appear reciprocally


G. cambodgiensis (Newman 2069)
G. vilersiana (Genbank AB110818)
G. dulcis (Sweeney 993)
G. xanthochymus (Genbank AB110817)
G. xanthochymus (Genbank KX621280)
G. spicata (Sweeney 1020)
G. talbotii (Genbank KX575867)
G. nervosa (Genbank AF367222)
G. subelliptica (Chung s.n.)
G. lowryi (Lowry 6060)
G. verrucosa (Sweeney 1286)
G. lucida (SIMAB 050112)
G. quadrifaria var. quadrifaria (Moses 951)
G. quadrifaria var. chromocarpa (Walters 1264)
G. conrauana (Moses 961)
G. kola (Sweeney 1443)
G. lucida (Moses 979)
Clade 1
Section Xanthochymus
G. calcicola (Rogers 1107)
G. livingstonei (Sweeney 1007)
G. anjouanensis (Labat 3282)
G. arenicola (McPherson 18767)
G. commersonii (Sweeney 1252)
G. mangorensis (Martial 363)
G. thouvenotii (Rakotonirina 242)
G. urschii (Sweeney 1205)
G. megistophylla (Rakotonirina 300)
G. megistophylla (Sweeney 1242)
G. macrophylla (Sweeney 1456)
G. madruno (Moya 128)
G. intermedia (Davidse 35685)
G. portoricensis (Taylor 11820)
G. ovalifolia (Sweeney 1409C)
G. staudtii (Sweeney 1445)
G. smeathmannii (Moses 954)
Clade 2
Section Rheedia
Allanblackia floribunda (Ewango s.n., 21-VI-04)
Section Allanblackia
Xanthochymus lineage
G. sp. "JT814" (Munzinger 7274)
G. sp. "JT814" (Munzinger 7282)
G. balansae (Dagostini 388)
G. balansae (Munzinger 7489)
G. balansae (Pillon 511)
G. balansae (Munzinger 3029)
G. balansae (Munzinger 5756)
G. balansae (Pillon 206)
G. myrtifolia (Munzinger 7349)
G. vitiensis (Munzinger 7377)
G. vitiensis (Munzinger 7514)
G. sp. (Munzinger 7380)
G. jensenii (Fell DGF4457)
G. brevirostris (Sweeney 985)
G. merguensis (Soejarto DDS_14028)
G. rostrata (Sweeney 1071)
G. lancilimba (Genbank KR532158)
G. tetralata (Genbank KR532162)
Clade 4
Section Discostigma
G. archboldiana (Takeuchi 7426)
G. engleriana (Munzinger 7882)
G. pedicellata (Munzinger 7099)
G. pedicellata (Munzinger 7117)
G. puat (Munzinger 7447)
G. pedicellata (Lowry 7405)
G. pedicellata (Lowry 7407)
G. pedicellata (Munzinger 4689)
G. pedicellata (Munzinger 6362)
G. pedicellata (Munzinger 6466)
G. densiflora (Munzinger 7104)
G. puat (Munzinger 1483)
G. puat (Munzinger 4568)
G. puat (Munzinger 7998)
G. gibbsiae (Telford 11385)
G. amplexicaulis (McPherson 18536)
G. amplexicaulis (McPherson 19127)
G. amplexicaulis (Munzinger 8008)
G. vieillardii (Munzinger 1511)
G. vieillardii (Tronchet 380)
G. warrenii (Sweeney 997)
G. pseudoguttifera (Munzinger 7351)
G. pseudoguttifera (Munzinger 7366)
G. pseudoguttifera (Munzinger 7374)
G. pseudoguttifera (Ramon 190)
G. pseudoguttifera (Ramon 320)
G. pseudoguttifera (Ramon 321)
G. cymosa (Sweeney 1000)
G. hollrungii (Cturtecka 1221)
G. latissima (Sweeney 1026)
G. prainiana (Sweeney 1077)
Clade 9
Section Macrostigma
G. nujiangensis (Genbank KX421335)
Section Dicrananthera
G. goudotiana (McPherson 18888)
G. aff. parvula (Miller 8783)
G. decipiens (Sweeney 1410)
G. evonymoides (Martial 110)
G. evonymoides (Abdul-Salim 132)
G. dauphinensis (Abdul-Salim 138)
G. orthoclada (Martial 579)
G. pauciflora (Sweeney 1236)
G. tsaratananensis (Sweeney 1232)
Clade 3
Section Paragarcinia
G. epunctata (Walters 922)
G. punctata (Walters 583)
G. mannii (Kenfack 1651)
G. afzelii (Sweeney 1427)
Clade 8
Section Tagmanthera
G. adinantha (Munzinger 7353)
G. adinantha (Munzinger 7362)
G. adinantha (Munzinger 7392)
G. fruticosa (Sweeney 1025)
G. comptonii (Munzinger 7454)
G. neglecta (Munzinger 889)
G. neglecta (Munzinger 7543)
G. virgata (Pignal 5177)
G. comptonii (Munzinger 7542)
G. neglecta (Munzinger 5733)
G. urceolata (Munzinger 6146)
G. nigrolineata (Sweeney 1049)
G. parvifolia (Genbank AF367221)
G. schomburgkiana (Genbank AB110814)
G. cowa (Genbank AF367213)
G. forbesii (Genbank AF367224)
G. griffithii (Sweeney 982)
G. rubriflora (Sweeney 1024)
G. sizygiifolia (Sweeney 1017)
G. asterandra (Schmidt 4314)
G. chapelieri (Sweeney 1256)
G. indica (Genbank KX621281)
G. gummigutta (Genbank KX765284)
G. bancana (Genbank AF367212)
G. atroviridis (Sweeney 1002)
G. costata (Nazre BL03)
G. maingayi (Nazre 098)
G. trianii (Nazre K02)
Clade 5
Section Brindonia
G. celebica (Sweeney 1028)
G. celebica (Sweeney 1458)
G. celebica (Genbank AB110816)
G. diospyrifolia (Sweeney 1050)
G. diospyrifolia (Sweeney 1127)
G. rigida (Sweeney 1015)
G. rigida (Sweeney 1019)
G. mangostana (Sweeney 987)
G. mangostana var. malaccensis (Sweeney 1035)
G. mangostifera (Molino 3058)
G. penangiana (Genbank AB856033)
Clade 6
Section Garcinia
G. acuminata (Genbank AB110796)
G. hanburyi (Genbank AB110802)
G. cf. hanburyi (Lee 1485)
G. cambogioides (Genbank KX621283)
G. dumosa (Sweeney 1047)
G. urophylla (Sweeney 1081)
G. lateriflora (Sweeney 1012)
G. scortechinii (Sweeney 994)
G. cantleyana var. grandifolia (Sweeney 1060)
G. uniflora (Sweeney 1018)
G. daedalanthera (Ariafiani 403)
Clade 7
Section Hebradendron
Garcinia lineage
Pentadesma butyracea (Sweeney 1005)
Symphonia globulifera (Genbank AF479787)
Symphonia urophylla (Genbank AF479788)
Montrouziera sphaeroidea (Cameron 981)
Moronobea coccinea (Costa 425)
Lorostemon coelhoi (Vicentini s.n.)
Tovomita wedd (Genbank AJ509218)
Clusia rosea (Genbank AJ509203)
Clusia uvitiana (Genbank AJ509226)
1 / 98
0.89 / 57
1 / 95
1 / 69
1 / 100
1 / 100
1 / 99
1 / 100
0.70 / -
1 / 100
1 / 100
0.76 / -
0.96 / 71
1 / 77
0.55 / -
1 / 98
1 / 87
0.66 / 67
1 / 100
1 / 96
0.77 / -
0.90 / 65
0.98 / 66
0.65 / 55
1 / 100
1 / 100
1 / 99
1 / 73
0.99 / 86
1 / 100
0.82 / 63
1 / 100
1 / 100
0.72 / 54
1 / 100
1 / 92
0.61 / -
1 / 100
1 / 100
0.76 / 62
1 / 55
1 / 98
0.91 / -
0.70 / 57
1 / 79
0.69 / 89
0.99 / 73
1 / -
1 / 98
1 / 90
1 / 99
1 / 93
1 / 100
0.99 / 79
1 / 100
1 / 100
1 / 97
1 / 98
0.57 / -
1 / 90
1 / 99
1 / 100
1 / 96
0.60 / -
1 / 99
0.85 / 66
1 / 100
1 / 100
1 / 100
0.99 / 88
0.56 / -
1 / 95
0.75
1 / 100
0.69
0.96
0.83 / -
1 / 99
1 / 100
0.85 / 56
1 / 97
0.86 / 66
1 / 100
1 / 100
1 / 100
0.69 / 57
1 / 100
1 / 95
1 / 100
1 / 92
0.93 / 95
0.96 / 78
1 / 100
1 / 100
1 / 91
0.89 / 88
1 / 93
1 / 100
0.51 / 64
1 / 94
1 / 100
1 / 91
1 / 77
1 / 100
1 / 100
0.70 / 82
1 / 100
1 / 99

monophyletic, neither in the ITS nor in the cpDNA trees (combined analyses, including both ITS and cpDNA data, did not allow a better discrimination). The only exceptions were *G. vieillardii* (two samples from the same locality; PP = 1 and BS = 100 both based on ITS and on cpDNA) and *G. amplexicaulis* (three samples, PP = 1 and BS = 99 based on ITS; only one sample in cpDNA). *Garcinia vieillardii* and *G. amplexicaulis* were also sister species with high support based on ITS (PP = 1 and BS = 93), but not based on cpDNA. Both the ITS and (to a lesser extent) the cpDNA trees show that *G. vitiensis* from Fiji, although belonging to clade 4, was distinct from any of the NC taxa and more related to others Fijian species and to the *G. vitiensis* accession from Vanuatu. In clade 5, *Garcinia adinantha* was also closer to *G. fruticosa* (based on the ITS phylogeny, which was more densely sampled) than to NC species.

Discussion

The previous most comprehensive phylogeny for *Garcinia* (*sensu lato*) included 53 species (Sweeney 2008), and the present study increases this number to 111 and includes a biogeographically and morphologically diverse set of species. This more dense and diverse sampling allows for a robust evaluation of the infrageneric classification of the genus, in relation to the morphology-based sections delineated by Jones (1980). Additionally, the inclusion of 32 samples representing the ten species endemic to New Caledonia provides an opportunity to explore in more depth the evolution and taxonomy of New Caledonian *Garcinia*.

Taxonomy: proposal for an updated infrageneric classification of Garcinia

This study, like others (e.g. Sweeney 2008; Ruhfel et al. 2011; Ruhfel et al. 2016), supports a broad circumscription of *Garcinia* that justifies the inclusion of several previously segregated genera (e.g. *Allanblackia*, *Ochrocarpos* p.p., *Pentaphalangium*, *Rheedia*, and *Tripetalum*). The phylogenetic analyses in this paper and in Sweeney (2008) reveal nine major clades falling within two major lineages and provide a framework for a revised sectional classification of the genus. Seven of the major clades roughly correspond to sections recognized by Jones (1980; Table 1. Of the two remaining major clades, one (clade 2) is a morphologically cohesive group that is comprised chiefly of species that Jones (1980) placed into sections *Rheedia*, *Rheediopsis*, and *Teracentrum*. The other remaining major clade (clade 9) contains primarily species that were placed by Jones (1980)

Figure 2. Molecular phylogeny of *Garcinia* L. based on ITS sequences and Bayesian inference. Posterior probabilities (PP) and bootstrap support values (BS), obtained respectively by the Bayesian inference and Maximum Likelihood (ML) analysis, are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. The lineages/sections discussed in the text are highlighted, and species names appear in colors depending on their native distribution areas: light blue, Central and South America; light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) geographic region was used. Accessions in bold were newly sequenced in this study.

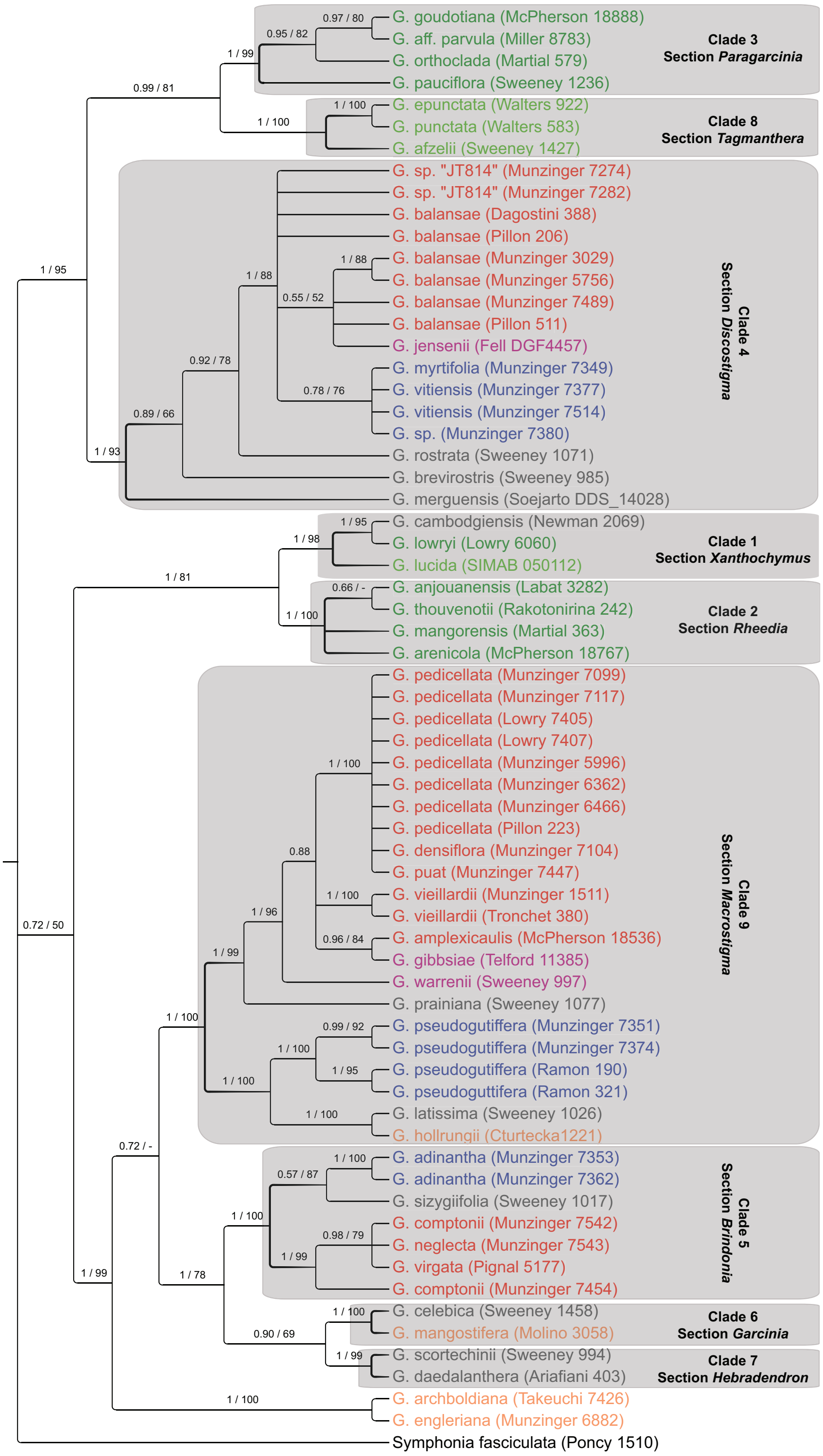


Figure 3. Molecular phylogeny of *Garcinia* L. based on a combined chloroplast DNA dataset and Bayesian inference. Posterior probabilities (PP) and bootstrap support values (BS), obtained respectively by the Bayesian inference and Maximum Likelihood (ML) analysis, are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. The lineages/sections discussed in the text are highlighted, and species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used. All accessions were newly sequenced in this study.

Table 1. Sections and numbers of species recognized by Jones (1980) and their correspondence to sections and clades recognized in this study. *Allanblackia* was treated as separate from *Garcinia* by Jones (1980).

Section sensu Jones (1980)	No. spp. (sensu Jones 1980)	Clade	Section in this study
Xanthochymus (Roxb.) Pierre	42	1	*Xanthochymus* (Roxb.) Pierre
Tetraphalangium Engl.	2		
Rheediopsis Pierre	20	2	*Rheedia* (L.) S.W.Jones ex P.W.Sweeney
Rheedia (L.) S.W.Jones, *nom. inval.*	21		
Teracentrum Pierre	4		
Paragarcinia (Baillon) Vesque	10	3	*Paragarcinia* (Baillon) Vesque
Discostigma (Haask.) Hook.f. subsection *Discostigma*	53	4	*Discostigma* (Haask.) Hook.f.
Brindonia (Thouars) Choisy	78	5	*Brindonia* (Thouars) Choisy
Garcinia L.	46	6	*Garcinia* L.
Hebradendron (Graham) Planch. & Triana	35	7	*Hebradendron* (Graham) Planch. & Triana
Tagmanthera Pierre	18	8	*Tagmanthera* Pierre
Mungotia Pierre	9	9	*Macrostigma* Pierre
Tripetalum (K. Schum.) S.W.Jones, 1980, *nom. inval.*	1		
Macrostigma Pierre	7		
Discostigma subsection *Dicrananthera* (Pierre) S.W.Jones, *nom. inval.*	2	–	*Dicrananthera* Pierre

into sections *Macrostigma*, *Mungotia*, and *Tripetalum*. Below we discuss each of these clades, providing their distinguishing characteristics and assigning them sectional names, with the aim of laying the foundation for a phylogenetically informed infrageneric classification of *Garcinia*. The distinguishing sectional characters below are taken from the literature and from examination of physical and digitized herbarium specimens (A, BO, CNS, G, GH, K, KEP, KLU, L, MEL, MO, NY, P, PE, SCA, SING, TAN, TEF, US, YU) and plants in the field. We refer readers to Jones (1980) for a detailed account of previous infrageneric classifications of *Garcinia*, along with sectional synonymy. Informed by an examination of specimens, protologues, and Jones' (1980) sectional assignments, we assign accepted species to sections. In cases where protologue descriptions or specimens were insufficient for determining sectional assignment, species were unplaced.

Taxonomic account

Genus *Garcinia* L. Sp. Pl. 1: 443 (1753).

Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

Synonyms. *Rheedia* L., Sp. Pl. 2: 1193 (1753). Type. *Rheedia lateriflora* L. [=*Garcinia humilis* (Vahl.) C.D.Adams, Phytologia 20(5): 312 (1970); non *Garcinia lateriflora* Blume, Bijdr. Fl. Ned. Ind. 5: 214 (1825)].

Cambogia L., Gen. Pl., ed. 5: 225 (1754). Type. *Cambogia gummi-gutta* L., Gen. Pl., ed. 5: 225 (1754) [≡*Garcinia gummi-gutta* (L.) N.Robson, Brittonia 20: 103 (1968)].

Coddampuli Adans., Fam. Pl. (Adanson) 2: 445 (1763), *nom. illeg. superfl.* Type: *Cambogia gummi-gutta* L., Gen. Pl., ed. 5: 225 (1754) [≡*Garcinia gummi-gutta* (L.) N.Robson, Brittonia 20: 103 (1968)].

Mangostan Garcin ex Adans., Fam. Pl. (Adanson) 2: 445 (1763), *nom. illeg. superfl.* Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

Biwaldia Scop., Intr. Hist. Nat. 232 (1777), *nom. illeg. superfl.* Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

Stalagmitis Murray, Commentat. Soc. Regiae Sci. Gott. 9: 173 (1789). Type. *Stalagmitis cambogioides* Murray, Commentat. Soc. Regiae Sci. Gott. 9: 173 (1789) [≡*Garcinia cambogioides* (Murray) Headland, Man. Mater. Med. Therap. [Royle], ed. 3. 339 (1856)].

Oxycarpus Lour., Fl. Cochinch. 2: 647 (1790). Type. *Oxycarpus cochinchinensis* Lour., Fl. Cochinch. 2: 648 (1790) [≡*Garcinia cochinchinensis* (Lour.) Choisy, Prodr. [A. P. de Candolle] 1: 561 (1824)].

Mangostana Rumph. ex Gaertn., Fruct. Sem. Pl. ii. 105. t. 105. (1791), *nom. illeg. superfl.* Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

Verticillaria Ruiz & Pav., Fl. Peruv. Prodr. 81, t. 15 (1794). Type. *Verticillaria acuminata* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 140 (1798) [=*Garcinia madruno* (Kunth) Hammel, Ann. Missouri Bot. Gard. 76: 928 (1989)].

Ochrocarpos Noronha ex Thouars, Gen. Nov. Madagasc. 15 (1805). Type. *Ochrocarpos madagascarensis* Choisy, Prodr. [A. P. de Candolle] 1: 560 (1824) [non *Ochrocarpos madagascariensis* Planchon & Triana, Ann. Sci. Nat. Bot., sér. 4, 14: 364 (1860)], see Sprague (1934) and Sweeney and Rogers (2008) for discussions about original material of *Ochrocarpos madagascarensis* and the type species of *Ochrocarpos*.

Xanthochymus Roxb., Pl. Coromandel 2(4): 51, t. 196 (1805). Type. *Xanthochymus pictorius* Roxb. [≡*Garcinia xanthochymus* Hook.f. ex T. Anderson Fl. Brit. India [J. D. Hooker] 1(2): 269 (1874)].

Brindonia Thouars, Dict. Sci. Nat. [F. Cuvier] 5: 339 (1806). Type. *Brindonia oxycarpa* Thouars, Hist. Veg. Isles Austr. Afr. ed. 2 t. 27 (1805) [≡*Garcinia oxycarpa* (Thouars) P.W.Sweeney comb. nov.]. See commentary under Section *Brindonia* for details about the status of *B. oxycarpa*.

Chloromyron Pers., Syn. Pl. [Persoon] 2(1): 73 (1806). Type. *Chloromyron verticillatum* Pers., Syn. Pl. [Persoon] 2(1): 73 (1806) [≡*Verticillaria acuminata* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 140 (1798); =*Garcinia madruno* (Kunth) Hammel, Ann. Missouri Bot. Gard. 76: 928 (1989)].

Hebradendron Graham, Companion Bot. Mag. 2: 199 (1837), *nom. illeg. superfl.* (Art. 58.1). Type. *Stalagmitis cambogioides* Murray, Commentat. Soc. Regiae Sci. Gott. Ix. 1787-88 (1789) 173. [≡*Garcinia cambogioides* (Murray) Headland, Man. Mater. Med. Therap. [Royle], ed. 3. 339 (1856); ≡*Hebradendron cambogioides* (Murray) Graham, Companion Bot. Mag. 2: 199, t. 27 (1837)].

Discostigma Hassk., Flora 25(2, Beibl.): 33 (1842). Type. *Discostigma rostratum* Hassk., Flora 25(2, Beibl.): 33 (1842) [≡*Garcinia rostrata* (Hassk.) Miq., Ann. Mus. Bot. Lugduno-Batavi 1(7): 209 (1864)].

Terpnophyllum Thwaites, Hooker's J. Bot. Kew Gard. Misc. 6: 70, t. 2 C (1854). Type. *Terpnophyllum zeylanicum* Thwaites, Hooker's J. Bot. Kew Gard. Misc. 6: 70, t. 2. F. 1 (1854) [≡*Garcinia terpnophylla* Thwaites, Enum. Pl. Zeyl. [Thwaites] 406 (1864)].

Rhinostigma Miq., Fl. Ned. Ind., Eerste Bijv. Pt. 3: 495 (1861). Type. *Rhinostigma parvifolium* Miq., Fl. Ned. Ind., Eerste Bijv. Pt. 3: 495 (1861) (lectotype, designated here) [≡*Garcinia parvifolia* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 1(7): 208 (1864)].

Clusianthemum Vieill., Bull. Soc. Linn. Normandie 9: 338 (1865). Type. *Clusianthemum pedicellatum* Vieill., Bull. Soc. Linn. Normandie 9: 339 (1865).

Allanblackia Oliv., Gen. Pl. [Benth. & Hook.f.] 1(3): 980 (1867), J. Linn. Soc., Bot. 10: 43 (1867). Type. *Allanblackia floribunda* Oliv., J. Linn. Soc., Bot. 10: 43 (1867).

Pentaphalangium Warb., Bot. Jahrb. Syst. 13(3–4): 382 (1891). Type. *Pentaphalangium crassinerve* Warb., Bot. Jahrb. Syst. 13(3–4): 382 (1891) [≡*Garcinia crassinervis* (Warb.) Kosterm., Ceylon J. Sci., Biol. Sci. 12(1): 68 (1976)].

Tripetalum K.Schum., Fl. Kais. Wilh. Land [K.M. Schumann & M.U. Hollrung] 51 (1889). Type. *Tripetalum cymosum* K.Schum., Fl. Kais. Wilh. Land [K.M. Schumann & M.U. Hollrung] 51 (1889) [≡*Garcinia cymosa* (K.Schum.) I.M.Turner & P.F.Stevens, Gard. Bull. Singapore 51(2): 176 (1999)].

Tsimatimia Jum. & H.Perrier, Ann. Sci. Nat., Bot. sér. 9, 11: 256 (1910). Type. *Tsimatimia pedicellata* Jum. & H.Perrier, Ann. Sci. Nat., Bot. sér. 9, 11: 265 (1910) (lectotype, designated here) [≡*Garcinia tsimatimia* P.W.Sweeney & Z.S.Rogers, Novon 18(4): 535 (2008)].

Septogarcinia Kosterm., Reinwardtia 6: 167 (1962). Type. *Septogarcinia sumbawaensis* Kosterm., Reinwardtia 6: 167 (1962) [≡*Garcinia septogarcinia* I.M. Turner & L.V.S. Jenn; non *Garcinia sumbawensis* Lauterb., Bot. Jahrb. Syst. 58(1): 26 (1922)].

Xanthochymus Lineage

Leaves with prismatic crystals in the mesophyll (this character is unstudied in *Allanblackia*) (Vesque 1889, 1893). ***Flowers*** with nectariferous antesepalous appendages or intrastaminal rings and disks (sometimes manifested as lobe-like antesepalous appendages that alternate with staminodes) (Sweeney 2008, 2010; Mathew et al. 2009, Fig. 1). Staminate flowers lacking pistillodes (rarely present and then rudimentary) and anthers with globose to widely elliptic thecae.

The *Xanthochymus* lineage is comprised of Lineage A in Sweeney (2008) and *Allanblackia*. It contains three sections as circumscribed below.

1. *Garcinia* section *Xanthochymus* (Roxb.) Pierre, Fl. Forest. Cochinch. 1, Fasc. 5, 3 (1883). Clade 1

Figs 2, 3

Basionym. *Xanthochymus* Roxb., Pl. Coromandel 2(4): 51, t. 196 (1805).

Type. *Xanthochymus pictorius* Roxb. [≡*Garcinia xanthochymus* Hook.f. ex T. Anderson Fl. Brit. India [J. D. Hooker] 1(2): 269 (1874)].

Distinguishing sectional characters. ***Flowers*** usually five-merous (rarely four-merous). Staminate flowers with stamens united into fascicles with filaments united for at least ½ (usually considerably more) of their length. Pollen five- to seven-colporate (Jones 1980). Ovaries with five (rarely four) locules and a single ovule per locule, placentation axile. Afrotropics, Indomalaya, and tropical Australasia.

This section largely corresponds section *Xanthochymus* sensu Jones (1980); however, based on molecular data [this study and Sweeney (2008)] and morphology, we exclude *G. hollrungii* Lauterb. and *G. prainiana* King (and the closely allied *G. phuongmaiensis* V.S.Dang, H.Toyama & D.L.A.Tuan). We also include here *G. conrauana* Engl. and *G. giadidii* De Wild. [=*G. kola* Heckel] – the only two species that Jones (1980) placed into section *Tetraphalangium* Engl., Bot. Jahrb. Syst. 40(4): 562 (1908), Type. *Garcinia conrauana* Engl.

Species. *Garcinia cambodgiensis* Vesque; *G. capuronii* Z.S.Rogers & P.W.Sweeney; *G. conrauana* Engl.; *G. densivenia* Engl.; *G. dulcis* (Roxb.) Kurz; *G. gamblei* Shameer, T.Sabu & N.Mohanan; *G. gerrardii* Harv. ex Sim; *G. kola* Heckel; *G. letestui* Pellegr.; *G. longifolia* Blume; *G. lowryi* Z.S.Rogers & P.W.Sweeney; *G. lucida* Vesque; *G. nervosa* (Miq.) Miq.; *G. petiolaris* Pierre; *G. pushpangadaniana* T.Sabu, N.Mohanan, Krishnaraj & Shareef; *G. quadrifaria* (Oliv.) Baill. ex Pierre; *G. spectabilis* Pierre; *G. spicata* (Wight & Arn.) Hook.f.; *G. subelliptica* Merr.; *G. talbotii* Raizada ex Santapau; *G. thwaitesii* Pierre; *G. verrucosa* Jum. & H.Perrier; *G. vidalii* Merr.; *G. vilersiana* Pierre; *G. volkensii* Engl.; *G. vriesiana* Pierre; *G. warburgiana* A.C.Sm.; *G. xanthochymus* Hook.f. ex T.Anderson.

2. *Garcinia* section *Rheedia* (L.) S.W.Jones ex P.W.Sweeney, comb. & stat. nov. Clade 2

urn:lsid:ipni.org:names:77338399-1
Figs 2, 3

Basionym. *Rheedia* L., Sp. Pl. 2: 1193 (1753).

Type. *Rheedia lateriflora* L. [=*Garcinia humilis* (Vahl.) C.D.Adams, Phytologia 20(5): 312 (1970); non *Garcinia lateriflora* Blume, Bijdr. Fl. Ned. Ind. 5: 214 (1825)].

Distinguishing sectional characters. ***Flowers*** usually with four petals (sepal number varies from two to five). Staminate flowers with stamens free or united into fascicles with filaments united up to ½ (rarely up to 2/3) of their length. Pollen tri-colporate with long ectoaperatures and endocolpi (Jones 1980). Ovaries with two to four locules and a single ovule per locule, placentation axile. Vesque (1893:288) noted that the leaves of species included in this section (i.e., species placed in the genus *Rheedia* and *Garcinia* subgenus *Rheediopsis* in his monograph) have sunken stomata with raised papilla-like protuberances arising from the accessory cells and partially covering the stomatal opening. Neotropics and Afrotropics.

This section includes species placed by Jones (1980) into sections *Rheedia* (L.) S.W.Jones *nom. inval.* (Art. 30.9, Turland et al. 2018); *Rheediopsis* Pierre, Fl. Forest. Cochinch. 1, Fasc. 5, 2 (1883), Type. *G. smeathmannii* (Planch. & Triana) N.Robson ex Spirl. (lectotype, designated here); and *Teracentrum* Pierre, Fl. Forest. Cochinch. 1, Fasc. 5, 1 (1883), Type. *G. livingstonei* T. Anderson. This section includes species that were formerly placed into the genus *Rheedia* L.

Species. *Garcinia albuquerquei* (M.E.Berg) Bittrich; *G. ambrensis* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. anjouanensis* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. aphanophlebia* Baker; *G. apostoloi* Mouzinho; *G. arenicola* (Jum. & H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. aristata* (Griseb.) Borhidi; *G. bakeriana* (Urb.) Borhidi; *G. barkeriana* (Urb. & Ekman) Alain; *G. benthamiana* (Planch. & Triana) Pipoly; *G. brasiliensis* Mart.; *G. calcicola* (Jum. & H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. cincta* (Urb.) Borhidi; *G. clarensis* Borhidi; *G. commersonii* (Planch. & Triana) Vesque; *G. cubensis* (Borhidi) Borhidi; *G. dalleizettei* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. decussata* C.D.Adams; *G. floribunda* Miq.;

G. fluviatilis Mouzinho & L.Marinho; *G. gabonensis* Sosef & Dauby; *G. gardneriana* (Planch. & Triana) Zappi; *G.* × *guacopary* (S.Moore) M.Nee; *G. hessii* (Britton) Alain; *G. humilis* (Vahl) C.D.Adams; *G. intermedia* (Pittier) Hammel; *G. kingaensis* Engl.; *G. leptophylla* Bittrich; *G. livingstonei* T.Anderson; *G. macrophylla* Mart.; *G. madruno* (Kunth) Hammel; *G. magnifolia* (Pittier) Hammel; *G. magnophylla* (Cuatrec.) Hammel; *G. mangorensis* (R.Vig. & Humbert) P.W.Sweeney & Z.S.Rogers; *G. martinii* (Maguire) Govaerts; *G. megistophylla* P.W.Sweeney & Z.S.Rogers; *G. moaensis* (Bisse) Borhidi; *G. obliqua* Sosef & Dauby; *G. ophiticola* (Borhidi) Borhidi; *G. ovalifolia* Oliv.; *G. pachyclada* N.Robson; *G. parviflora* Benth.; *G. pervillei* (Planch. & Triana) Vesque; *G. polyneura* (Urb.) Borhidi; *G. portoricensis* (Urb.) Alain; *G. pulvinata* (Planch. & Triana) Hammel; *G. pungens* Borhidi; *G. revoluta* (Urb.) Borhidi; *G. robsoniana* Bamps; *G. ruscifolia* (Griseb.) Borhidi; *G. semseii* Verdc.; *G. serpentini* Borhidi; *G. smeathmannii* (Planch. & Triana) Oliv.; *G. spruceana* (Engl.) Mouzinho; *G. staudtii* Engl.; *G. thouvenotii* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. tsimatimia* P.W.Sweeney & Z.S.Rogers; *G. urschii* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. verticillata* Alain.

3. *Garcinia* section *Allanblackia* (Oliv.) P.W. Sweeney, comb. & stat. nov.

urn:lsid:ipni.org:names:77338400-1

Basionym. *Allanblackia* Oliv., Gen. Pl. [Benth. & Hook.f.] 1(3): 980 (1867), J. Linn. Soc., Bot. 10: 43 (1867).

Type. *Allanblackia floribunda* Oliv., J. Linn. Soc., Bot. 10: 43 (1867) [≡*Garcinia oleosperma* P.W. Sweeney, nom. nov.; non *Garcinia floribunda* Miq., Stip. Surin. Sel. 39, non *Garcinia floribunda* Mast. ex Vesque, Monogr. Phan. [A.DC. & C.DC.] 8: 488 (1893)]

Distinguishing sectional characters. ***Flowers*** five-merous. Staminate flowers with stamens united into five phalanges, anthers subsessile, two-thecous. Pollen 4-colporate (Jones 1980). Ovaries incompletely five-locular containing multiple ovules per carpel/locule, placentation parietal. Afrotropics.

Note. There are nine currently accepted species in the genus *Allanblackia* Oliv., all native to Africa (Bamps 1969; Stevens 2007; POWO 2023). Here we create the section *Allanblackia* (Oliv.) P.W. Sweeney for these species when they are treated as *Garcinia* and below provide names for them in *Garcinia*.

Species:

***Garcinia guineensis* P.W.Sweeney, nom. nov.**

urn:lsid:ipni.org:names:77338401-1

Allanblackia parviflora A.Chev., Vég. Ut. Afr. Trop. Franç. 5: 163 (1909). Type. Côte d'Ivoire: Alépé, *Chevalier 16239*.

Note. A replacement name ("nom. nov."), *Garcinia guineensis*, is created here for *Allanblackia parviflora*, because the epithet *parviflora* was used previously in *Garcinia* for a different species. The epithet *guineensis* is chosen to reflect the distribution of this species in the Upper Guinean Forest region of West Africa.

Garcinia kisonghi **(Vermoesen) P.W.Sweeney, comb. nov.**
urn:lsid:ipni.org:names:77338402-1

Allanblackia kisonghi Vermoesen, Man. Ess. Forest. Congo: 11 (1923). Type. Democratic Republic of the Congo: Mpse, *Van Naemen in Gillet s.n.*

Garcinia kimbiliensis **(Spirlet) P.W.Sweeney, comb. nov.**
urn:lsid:ipni.org:names:77338403-1

Allanblackia kimbiliensis Spirlet, Bull. Jard. Bot. État Bruxelles 29: 357 (1959). Type. Democratic Republic of the Congo: Kimbili, *Michelson 766*.

Garcinia marienii **(Staner) P.W.Sweeney, comb. nov.**
urn:lsid:ipni.org:names:77338404-1

Allanblackia marienii Staner, Bull. Jard. Bot. État Bruxelles 13: 110 (1934). Type. Democratic Republic of the Congo: Haute Nsele, *De Groof s.n.*

Garcinia ngouniensis **P.W.Sweeney, nom. nov.**
urn:lsid:ipni.org:names:77338405-1

Allanblackia gabonensis (Pellegr.) Bamps, Bull. Jard. Bot. Natl. Belg. 39: 356 (1969). Type. Gabon: between Moubighou and Nzoundou, *Le Testu 6001*.

Note. A replacement name, *Garcinia ngouniensis*, is created here for *Allanblackia gabonensis*, because the epithet *gabonensis* was used previously in *Garcinia* for a different species. The epithet *ngouniensis* is in reference to Gabon's Ngounié province, an area where many specimens of this species have been collected.

Garcinia oleosperma **P.W.Sweeney, nom. nov.**
urn:lsid:ipni.org:names:77338406-1

Allanblackia floribunda Oliv., J. Linn. Soc., Bot. 10: 43 (1867). Type. Cameroon: Cameroon River, *Mann 2193*.

Note. A replacement name, *Garcinia oleosperma*, is created here for the type species (*A. floribunda*) of the genus *Allanblackia*, because the epithet *floribunda* was used previously in *Garcinia* for a different species. The epithet *oleosperma* is in reference to the seeds that have a high oil content and are an important source of vegetable oil in tropical western Africa (Crockett 2015).

Garcinia staneriana **(Exell & Mendonça) P.W.Sweeney, comb. nov.**

urn:lsid:ipni.org:names:77338407-1

Allanblackia staneriana Exell & Mendonça, J. Bot. 74(Suppl.): 20 (1936). Type. Angola: Belize, *Grossweiler 8221*.

Garcinia stuhlmannii **(Engl.) P.W.Sweeney, comb. nov.**

urn:lsid:ipni.org:names:77338408-1

Allanblackia stuhlmannii (Engl.) Engl., H.G.A.Engler & K.A.E.Prantl, Nat. Pflanzenfam., Nachtr. 1: 249 (1897). Type. Tanzania: Usambara, *Holst 2296*.

Garcinia ulugurensis **(Engl.) P.W.Sweeney, comb. nov.**

urn:lsid:ipni.org:names:77338409-1

Allanblackia ulugurensis Engl., Bot. Jahrb. Syst. 28: 435 (1900). Type. Tanzania: Sudost Uluguru, *Stuhlmann 8773*.

Garcinia Lineage

Leaves with druse crystals in the mesophyll (Vesque 1889, 1893). ***Flowers*** without nectariferous antesepalous appendages or intrastaminal rings and disks (Sweeney 2010). Staminate flowers in many sections with pistillodes (but usually absent in sections *Brindonia*, *Hebradendron*, and *Macrostigma*) and anthers of various shapes.

The *Garcinia* lineage contains eight sections as circumscribed below and corresponds to Lineage B in Sweeney (2008).

4. *Garcinia* section *Paragarcinia* (Baillon) Vesque, Monogr. Phan. [A. DC. & C. DC.] 8: 254 (1893). Clade 3

Figs 2, 3

Type. *Ochrocarpos decipiens* Baill., Adansonia 11: 370 (1876) [≡*Garcinia decipiens* (Baill.) Vesque, Monogr. Phan. [A.DC. & C.DC.] 8: 482 (1893)].

Distinguishing sectional characters. ***Flowers*** with two (usually) sepals, fused in bud. Staminate flowers with a pistillode, stamens arranged into four (up to eight) fascicles with sessile to subsessile, two-thecous anthers. Ovaries four locular, stigmas weakly lobed. ***Fruits*** with smooth walls. ***Inflorescences*** terminal or axillary with few to many flowers. Afrotropics (Madagascar and Comoros).

This section contains the *Garcinia* species that were formerly placed into the segregate genus *Ochrocarpos*. The twelve species in this section are endemic to Madagascar and Comoros (Sweeney and Rogers 2008).

Species. *Garcinia cerasifer* (H.Perrier) P.F.Stevens; *G. dauphinensis* P.W.Sweeney & Z.S.Rogers; *G. decipiens* Vesque; *G. evonymoides* (Planch. & Triana)

P.W.Sweeney & Z.S.Rogers; *G. goudotiana* (Planch. & Triana) P.W.Sweeney & Z.S.Rogers; *G. madagascariensis* (Planch. & Triana) Pierre; *G. multifida* (H. Perrier) P.W.Sweeney & Z.S.Rogers; *G. orthoclada* Baker; *G. parvula* (H. Perrier) P.W.Sweeney & Z.S.Rogers; *G. pauciflora* Baker; *G. tsaratananensis* (H. Perrier) P.W.Sweeney & Z.S.Rogers.

5. *Garcinia* section *Discostigma* (Haask.) Hook.f., Gen. Pl. [Benth. & Hook.f.] 1: 174 (1862). Clade 4

Figs 2, 3

Basionym. *Discostigma* Hassk., Flora 25(2, Beibl.): 33 (1842).

Type. *Discostigma rostratum* Hassk., Flora 25(2, Beibl.): 33 (1842) [≡*Garcinia rostrata* (Hassk.) Miq., Ann. Mus. Bot. Lugduno-Batavi 1(7): 209 (1864)].

Distinguishing sectional characters. ***Flowers*** with four sepals and petals. Staminate flowers with a pistillode, stamens arranged into four fascicles that are distally covered with sessile to subsessile, two-thecous anthers. Ovaries bilocular (or unilocular; four-locular in *G. yunnanensis*), stigmas unlobed and smooth. ***Fruits*** with a smooth surface and capped with a conspicuous discoid stigma, sepals caducous in fruits. ***Inflorescences*** terminal or axillary with few to many flowers. Indomalaya, tropical Australasia, and Oceania.

Sweeney (2008) noted that there were two groups of species placed into section *Discotigma* by Jones (1980) that differed from typical members of the section by their androecial morphology. One group of species differs by having their stamens fused to the petals and includes *G. balansae*, *G. lanessanii* Pierre, *G. terpnophylla* Thwaites, and *G. warrenii* F.Muell. The position of *G. warrenii* in the trees presented here and in Sweeney (2008) suggests that some of these species may be better placed within section *Macrostigma* (clade 9); however, our molecular analyses find strong support for placement of *G. balansae* within *Discostigma*. The second group of species is restricted to New Guinea, the Philippines, and Taiwan and includes *G. dives* Pierre, *G. hunsteinii* Lauterb., *G. linii* C. E. Chang, *G. luzoniensis* Merrill, and *G. palawanensis* Elmer (Jones 1980). This latter group is reported to have peltate anthers, like species of section Hebradendron (sensu Jones 1980); however, Jones (1980) placed them into section *Discostigma* because they share the same stamen arrangement and pollen apertures as typical members of the section. Species representing the *G. dives* group have not yet been included in molecular phylogenetic analyses. *Garcinia anomala* was placed into Section *Garcinia* by Jones (1980), but excluded from that section by Nazre et al. (2018), due to its possession of axillary inflorescences in thyrses and stamens being united into an unlobed annular mass. Fruit characters suggest that this species belongs to Section Discostigma; however, the stamens are arranged into a ring.

In our ITS phylogeny, two species not treated by Jones (1980), *G. archboldiana* A.C. Sm. and *G. engleriana* A.C.Sm., are weakly supported as sister to section *Discostigma*; however, in the chloroplast phylogeny these two species are shown as sister to a larger clade comprised of sections *Brindonia*, *Garcinia*, *Hebradendron*, and *Macrostigma*. The staminate flowers of *G. archboldiana* and *G. engleriana* lack pistillodes and they have deeply branched fascicles with numerous subpeltate anthers (Smith 1941). We leave these species unplaced.

Future molecular and morphological work may warrant the placement of these species into their own section.

Species. *Garcinia apetala* Pierre; *G. balansae* Pierre; *G. balica* Miq.; *G. binnendijkii* Pierre; *G. boerlagii* Pierre; *G. brevirostris* Scheff.; *G. cadelliana* King; *G. calophylla* Pierre; *G. calophyllifolia* Ridl.; *G. caudiculata* Ridl.; *G. cordata* Merr.; *G. cuneifolia* Pierre; *G. cuspidata* King; *G. diversifolia* King; *G. dives* Pierre; *G. dryobalanoides* Pierre; *G. enthaematoeides* Lauterb.; *G. gitingensis* Elmer; *G. grandifolia* (Choisy) Pierre; *G. hasskarlii* Pierre; *G. havilandii* Stapf; *G. holttumii* Ridl.; *G. hunsteinii* Lauterb.; *G. jensenii* W.E.Cooper; *G. keenania* Pierre; *G. kwangsiensis* Merr. ex F.N.Wei; *G. lanceola* Ridl.; *G. lancilimba* C.Y.Wu ex Y.H.Li; *G. lanessanii* Pierre; *G. linearis* Pierre; *G. linii* C.E. Chang; *G. luzoniensis* Merr.; *G. memecyloides* Ridl.; *G. merguensis* Wight; *G. microphylla* Merr.; *G. minimiflora* Ridl.; *G. minutiflora* Ridl.; *G. monantha* Ridl.; *G. multiflora* Champ. ex Benth.; *G. murtonii* Whitmore; *G. myrtifolia* A.C.Sm.; *G. novoguineensis* Vesque; *G. picrorhiza* Miq.; *G. rostrata* (Hassk.) Miq.; *G. salakensis* Pierre; *G. sampitana* Diels; *G. santisukiana* Ngerns. & Suddee; *G. sarawhensis* Pierre; *G. scaphopetala* B.L.Burtt; *G. tauensis* Lauterb.; *G. terpnophylla* Thwaites; *G. tetralata* C.Y.Wu ex Y.H.Li; *G. travancorica* Bedd.; *G. treubii* Pierre; *G. umbonata* Lauterb.; *G. versteegii* Lauterb.; *G. vitiensis* (A. Gray) Seem.; *G. wollastonii* Ridl.; *G. zichii* W.E.Cooper.

6. *Garcinia* section *Brindonia* (Thouars) Choisy, Mém. Soc. Hist. Nat. Paris 1: 230 (1823). Clade 5

Figs 2, 3

Basionym. *Brindonia* Thouars, Dict. Sci. Nat. [F. Cuvier] 5: 339 (1806).

Type. *Brindonia oxycarpa* Thouars, Hist. Veg. Isles Austr. Afr. Ed. 2 t. 27 (1805) [≡*Garcinia oxycarpa* (Thouars) P.W.Sweeney, comb. nov.; *Garcinia indica* (Thours) Choisy Mém. syn. nov.]. The copy of *Histoire des végétaux recueillis dans les isles australes d'Afrique* ed. 2 at Kew bears the date 1805 (Baker 1894) and contains six plates (25–30) that do not have accompanying text in the main body of the publication (see also Hiern 1900). Plate 27 is labeled "*Brindonia oxycarpa*" and it depicts two flowering branches, fruit, and dissected flowers (pers. obs). This suffices as an illustration with analysis and thus *Brindonia oxycarpa* is validly published as per Articles 38.1, 38.7, and 38.8 of the ICN (Turland et al. 2018). Some (e.g. Hiern 1900) have considered *B. oxycarpa* a synonym of *Garcinia indica* (Thours) Choisy Mém. Soc. Hist. Nat. Paris 1: 230 (1823) [≡*Brindonia indica* Thouars, Dict. Sci. Nat. [F. Cuvier] 5: 340 (1806)]; however, if these two taxa are considered synonymous, the epithet *oxcycarpa* would have priority.

Distinguishing sectional characters. ***Flowers*** with four sepals and petals. Staminate flowers without a pistillode (usually), stamens united into a single central bundle (or ring when pistillode present), anthers four-thecous (but in some species two-thecous). Ovaries multilocular, stigmas divided into distinct rays and usually papillate. ***Fruits*** in many species with furrows or grooves along the septal radii. ***Inflorescence***s terminal or axillary with one to many flowers. Afrotropics (Madagascar), Indomalaya, tropical Australasia, and Oceania.

Three species treated as section *Garcinia* by Jones (1980) (i.e., *G. costata* Hemsl. ex King, *G. maingayi* Hook.f., and *G. trianii* Pierre) form a clade sister to clade 5, the latter largely corresponding to section *Brindona* sensu Jones (1980). While they share some features (e.g. tendency to have furrowed/grooved (very shallow in *G. maingayi* and *G. trianii*), multilocular fruits) with *Brindonia* sensu Jones (1980), they have other features (i.e., pistillodes, stamens arranged into a ring, and two-thecous anthers) that are not typical of the section. While it would be tempting to recognize a separate section for these species, pistillodes and stamens arranged into a ring are also shared by *G. atroviridis* Griff. ex T.Anderson and *G. pedunculata* Roxb. ex Buch.-Ham., two species that were included in section *Brindonia* by Jones (1980). It is noteworthy that *G. atroviridis* is the first branching lineage within clade 5, which together with the *G. costata*/*G. maingayi*/*G. trianii* clade form a basal grade within section *Brindonia* (as circumscribed here).

Garcinia usually has an indehiscent drupe or berry (Stevens 2007). The genus *Clusianthemum* Vieill. was established by Vieillard for a new Caledonian species having a capsular fruit (*C. pedicellatum* Vieill.). Later, another capsular genus, *Septogarcinia* was established by Kostermans (1962) for *S. sumbawaensis* Kosterm., from Sumbawa (Indonesia), obviously not knowing about Vieillard's *Clusianthemum*. Notably, several species of NC *Garcinia*, viz. *G. virgata* Vieill. ex Guillaumin, *G. neglecta* Vieill. and *G. comptonii* Baker f. have capsular fruits (Fig. 1). Jones (1980) did not mention *Clusianthemum* in her treatment but included *Septogarcinia* in *Garcinia* sect. *Brindonia*. Jones (1980) does not cite any NC capsular species. The newly described *G. urceolata* is also suspected of having dehiscent fruits (Munzinger et al. 2021). All these species are morphologically similar and could result from *in situ* (within NC) diversification, and all sampled species with dehiscent fruit are found in a strongly supported subclade within clade 5. We do not have sequence material of *G. septogarcinia* I.M. Turner & L.V.S. Jenn. to determine whether that character is an autapomorphy of a dehiscent fruit clade, or if it evolved at least twice, in New Caledonia and Sumbawa. Staminate floral morphology supports placement of *G. septogarcinia* I.M. Turner & L.V.S. Jenn. into section *Brindona* (Medellín-Zabala and Marinho 2015).

Species. *Garcinia adinantha* A.C.Sm. & S.P.Darwin; *G. amabilis* Kaneh. & Hatus.; *G. amboinensis* Spreng.; *G. angustifolia* A.C. Sm.; *G. assamica* J.Sarma, Shameer & N.Mohanan; *G. assugu* Lauterb.; *G. asterandra* Jum. & H.Perrier; *G. atroviridis* Griff. ex T.Anderson; *G. balimensis* A.C. Sm.; *G. bancana* Miq.; *G. beccarii* Pierre; *G. bicolorata* Elmer; *G. binucao* (Blanco) Choisy; *G. borneensis* Pierre; *G. chapelieri* (Planch. & Triana) H.Perrier; *G. cochinchinensis* (Lour.) Choisy; *G. comptonii* Baker f.; *G. conicarpa* Wight; *G. corallina* Vieill.; *G. costata* Hemsl. ex King; *G. cowa* Roxb. ex DC.; *G. crassiflora* Jum. & H.Perrier; *G. dallmannensis* Kaneh. & Hatus.; *G. delpyana* Pierre; *G. dhanikhariensis* S.K.Srivast.; *G. dioica* Blume; *G. emarginata* Lauterb.; *G. erythrosepala* Y.H.Li; *G. esculenta* Y.H.Li; *G. fruticosa* Lauterb.; *G. fusca* Pierre; *G. griffithii* T.Anderson; *G. gummi-gutta* (L.) N.Robson; *G. horsfieldiana* Pierre; *G. hygrophila* Lauterb.; *G. indica* (Thouars) Choisy; *G. klinkii* Lauterb.; *G. korthalsii* Pierre; *G. lanceifolia* Roxb.; *G. lauterbachiana* A.C.Sm.; *G. ledermannii* Lauterb.; *G. leggeae* W.E.Cooper; *G. loheri* Merr.; *G. macgregorii* Merr.; *G. macrantha* A.C.Sm.; *G. maingayi* Hook. f.; *G. maluensis* Lauterb.; *G. mestonii* F.M.Bailey; *G. microstigma* Kurz; *G. minahassensis* Pierre; *G. miquelii* Pierre; *G. myristicifolia* Pierre; *G. nigrolineata* Planch. ex T.Anderson; *G. oblongifolia* Champ. ex Benth.; *G. oligophlebia* Merr.; *G. oliveri* Pierre; *G. oreophila* Lauterb.; *G. oxycarpa* (Thours) P.W.Sweeney; *G. pachyantha* A.C.Sm.; *G. pachypetala* Lauterb.; *G. pallida* Lauterb.; *G. parvifolia* (Miq.) Miq.; *G. pedunculata* Roxb.

ex Buch.-Ham.; *G. ponapensis* Lauterb.; *G. quaesita* Pierre; *G. ramosii* Merr.; *G. riparia* A.C.Sm.; *G. rubra* Merr.; *G. rubriflora* Boerl.; *G. sabangensis* Lauterb.; *G. samarensis* Merr.; *G. schomburgkiana* Pierre; *G. segmentata* Kosterm.; *G. septogarcinia* I.M.Turner & L.V.S.Jenn.; *G. siripatanadilokii* Ngerns., Meeprom, Boonth., Chamch. & Sinbumr.; *G. solomonensis* A.C.Sm.; *G. sopsopia* (Buch.-Ham.) Mabb.; *G. stigmacantha* Pierre; *G. succifolia* Kurz; *G. sulphurea* Elmer; *G. tetrandra* Pierre; *G. teysmanniana* Scheff.; *G. trianii* Pierre; *G. urceolata* Munzinger, Bruy & M.Pignal; *G. valetoniana* Lauterb.; *G. vidua* Ridl.; *G. virgata* Vieill. ex Guillaumin; *G. viridiflora* Ridl.; *G. wallichii* Choisy; *G. xishuanbannaensis* Y.H.Li; *G. zeylanica* Roxb.

7. *Garcinia* L. section *Garcinia*. Clade 6

Figs 2, 3

Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

Distinguishing sectional characters. ***Flowers*** with four sepals and four petals. Staminate flowers often with a pistillode, stamens united into a single four-lobed or four-angled bundle, anthers two-thecous. Ovaries multilocular and stigmas with or without lobes and smooth or corrugated. ***Fruits*** with a smooth surface. ***Inflorescences*** terminal and comprised of simple cymes (Nazre et al. 2018). Indomalaya and tropical Australasia.

This section was recently monographed by Nazre et al. (2018) who recognized 13 species in the section and noted that species in the section share terminal inflorescences of simple cymes, stamens united into a single four-lobed or four-angled bundle, and fruits with a smooth surface. Based on morphological and molecular data he excluded several species that were included in this section by Jones (1980); our molecular results fully support his decisions (see discussion under clade 5).

Species. *Garcinia acuticosta* Nazre; *G. celebica* L.; *G. diospyrifolia* Pierre; *G. discoidea* Nazre; *G. exigua* Nazre; *G. harmandii* Pierre; *G. mangostana* L.; *G. mangostifera* Kaneh. & Hatus.; *G. nitida* Pierre; *G. ochracea* Nazre; *G. penangiana* Pierre; *G. rigida* Miq.; *G. sangudsangud* Nazre; *G. sibeswarii* Shameer, J.Sarma, N.Mohanan & A.Begum; *G. venulosa* (Blanco) Choisy.

8. *Garcinia* section *Hebradendron* Planch. & Triana, Ann. Sci. Nat., Bot. sér. 4, 14: 349 (1860). Clade 7

Figs 2, 3

Basionym. *Hebradendron* Graham, Companion Bot. Mag. 2: 199 (1837), *nom. illeg. superfl.* The genus name *Hebradendron* is illegitimate (superfluous as per Article 52.1, Turland et al. 2018) because Graham (1837) included within it *Stalagmitis cambogioides* Murray, Commentat. Soc. Regiae Sci. Gott. ix. 1787-88 (1789) 173 [≡*Hebradendron cambogioides* (Murray) Graham, Companion Bot. Mag. 2: 199, t. 27 (1837)], the type of *Stalagmitis* Murray, Commentat. Soc. Regiae Sci. Gott. 9: 173 (1789). Later, Planchon and Triana (1860) published *Garcinia* section *Hebradendron* Planch. & Triana, Ann. Sci. Nat., Bot. sér. 4, 14: 349 (1860), which according to Article 58.1 (Turland et al. 2018) can be considered a replacement name.

Type. *Stalagmitis cambogioides* Murray, Commentat. Soc. Regiae Sci. Gott. 9: 173 (1789) [≡*Garcinia cambogioides* (Murray) Headland, Man. Mater. Med. Therap. [Royle], ed. 3. 339 (1856); ≡*Hebradendron cambogioides* (Murray) Graham, Companion Bot. Mag. 2: 199, t. 27 (1837)]. See Shameer and Mohanan (2020) for a discussion about the priority of *G. cambogioides* (Murray) Headland over *G. morella* (Gaertn.) Desr.

Distinguishing sectional characters. ***Flowers*** sessile to subsessile and with four sepals and four petals. Staminate flowers without a pistillode, stamens united into a single central bundle, anthers unilocular and peltate with circumscissile dehiscence or with multiple chambers that dehisce via pores. Ovaries multilocular, stigmas lobed and variously ornamented, often papillate. ***Fruits*** with smooth surface, pedicels thick in fruit. ***Inflorescences*** axillary with one to a few flowers. Indomalaya and tropical Australasia.

Species. *Garcinia acuminata* Planch. & Triana; *G. blumei* Pierre; *G. bonii* Pit.; *G. burkillii* Whitmore; *G. calycina* Kurz; G. *cambogioides* (Murray) Headland; *G. cantleyana* Whitmore; *G. choisyiana* (Choisy) Wall. ex Planch. & Triana; *G. daedalanthera* Pierre; *G. desrousseauxii* Pierre; *G. dumosa* King; *G. fuscopetiolata* Lauterb.; *G. garciae* Elmer; *G. gaudichaudii* Planch. & Triana; *G. gjellerupii* Lauterb.; *G. grahamii* Pierre; *G. hanburyi* Hook.f.; *G. hendersoniana* Whitmore; *G. heterandra* Wall. ex Planch. & Triana; *G. hopii* H.Toyama & V.S.Dang; *G. idenburgensis* A.C.Sm.; *G. imberti* Bourd.; *G. jaweri* Lauterb.; *G. lateriflora* Blume; *G. microcarpa* Pierre; *G. microtropidiiformis* Kaneh. & Hatus.; *G. mindanaensis* Merr.; *G. murdochii* Ridl.; *G. oligantha* Merr.; *G. poilanei* Gagnep.; *G. pullei* Lauterb.; *G. rheedei* Pierre; *G. schlechteri* Lauterb.; *G. scortechinii* King; *G. subtilinervis* F.Muell.; *G. timorensis* Zipp. ex Span.; *G. uniflora* King; *G. urophylla* Scort. ex King; *G. wightii* T.Anderson.

9. *Garcinia* section *Tagmanthera* Pierre, Fl. Forest. Cochinch. Vol. 1, Fasc. 6, 17 (1883). Clade 8

Figs 2, 3

Type. *Garcinia punctata* Oliv., Fl. Trop. Afr. 1: 167 (1868).

Distinguishing sectional characters. ***Staminate flowers*** with a pistillode, stamens arranged into four (rarely two) strap-shaped fascicles each with a single row of sessile, recurved, and sometimes multilocellate anthers at the end. Ovaries four locular, stigmas weakly lobed. ***Fruits*** with smooth surface. ***Inflorescences*** terminal or axillary with one to a few flowers. Afrotropics.

Species. *Garcinia acutifolia* N.Robson; *G. afzelii* Engl.; *G. bifasciculata* N.Robson; *G. buchananii* Baker; *G. buchneri* Engl.; *G. elliotii* Engl.; *G. epunctata* Stapf; *G. huillensis* Welw. ex Oliv.; *G. lujae* de Wild.; *G. mannii* Oliv.; *G. preussii* Engl.; *G. punctata* Oliv.; *G. tanzaniensis* Verdc.

10. *Garcinia* section *Macrostigma* Pierre, Fl. Forest. Cochinch. Vol. 1, Fasc. 6, 36 (1883). Clade 9

Figs 2, 3

Type. *Garcinia latissima* Miq., Ann. Mus. Bot. Lugduno-Batavi 1: 209 (1864).

Distinguishing sectional characters. ***Staminate flowers*** lacking pistillode (usually, but rudimentary or well-developed pistillode present in some species), stamens united into central column (sometimes lobed with lobes equaling number of petals) or into completely separate antepetalous fascicles, androecium often adnate to the petals to varying degrees, anthers two-thecous. Ovaries four (three) to eight locular, stigmas unlobed and smooth or divided and papillose. ***Fruits*** with smooth walls or faintly to deeply furrowed/grooved. ***Inflorescences*** axillary or terminal with one to many flowers. Indomalaya, tropical Australasia, and Oceania.

This section includes chiefly species that were included in Jones' (1980) sections *Macrostigma*, *Mungotia*, and *Tripetalum*. This is perhaps the most heterogenous of the sections recognized here and it is difficult to point to a single character shared by all of the species in the section. Many species, especially those that were placed into sections *Macrostigma* and *Tripetalum*, often have stamen bundles adnate to the petals. It has been suggested that highly branched, anastomosing exudate-containing canals on the adaxial leaf surface may be a synapomorphy for this clade (Sweeney 2008); however, this has not been comprehensively studied across the genus and may not be a reliable character for determining sectional placement (see Cooper 2013). Many species possess leaves with elliptic, elliptic-obovate, or obovate leaves with thin, closely spaced (ca. <5 mm) secondary veins. Other possible features uniting species in the group include the presence of an exotegmen and non-garcinioid type seed germination (see Brandza 1908; Stevens 2007). Further study is needed to confirm the distribution/presence of these characters.

In the phylogeny, this clade includes three species that have been variously placed into other sections by other authors (Lauterbach 1922; Jones 1980): *G. hollrungii*, *G. prainiana*, and *G. warrenii*. In addition to molecular data, these species have morphology that supports their placement into section *Macrostigma*.

Species. *Garcinia amplexicaulis* Vieill. ex Pierre; *G. branderhorstii* Lauterb.; *G. brassii* C.T.White; *G. carolinensis* (Lauterb.) Kosterm.; *G. crassifolia* Seeth.; *G. crassinervis* (Warb.) Kosterm.; *G. cymosa* (K.Schum.) I.M.Turner & P.F.Stevens; *G. densiflora* Pierre; *G. gibbsiae* S.Moore; *G. hollrungii* Lauterb.; *G. latissima* Miq.; *G. moselleyana* Pierre; *G. multibracteolata* Merr.; *G. mungotia* Planch. ex Pierre; *G. nuntasaenii* Ngerns. & Suddee; *G. pachycarpa* (A.C.Sm.) Kosterm.; *G. pancheri* Pierre; *G. pedicellata* (G.Forst.) Seem.; *G. phuongmaiensis* V.S.Dang, H.Toyama & D.L.A.Tuan; *G. platyphylla* A.C.Sm.; *G. prainiana* King; *G. pseudoguttifera* Seem.; *G. puat* (Montrouz.) Guillaumin; *G. quadrilocularis* Seeth.; *G. russellii* W.E.Cooper; *G. sessilis* (G. Forst.) Seem.; *G. smithii* Kosterm.; *G. vieillardii* Pierre; *G. warrenii* F.Muell.

11. *Garcinia* section *Dicrananthera* Pierre, Fl. Forest. Cochinch. 1, Fasc. 6, 8 (1883).

Type. *Garcinia thorelii* Pierre, Fl. Forest. Cochinch. t. 62.

Distinguishing sectional characters. ***Leaves*** with prominent stipuliform structures. Staminate flowers with a pistillode, stamens united into an annular mass encircling and attached to the pistillode, anthers two-thecous. Ovaries one to two locular, stigmas unlobed and smooth. ***Fruits*** with smooth walls. ***Inflorescences*** axillary or terminal with three to many flowers. Indomalaya.

Garcinia nujiangensis C.Y.Wu & Y.H.Li occupies an isolated position in the phylogeny, in a polytomy with clades 4 and 9. We resurrect Pierre's section *Dicrananthera* for a morphologically coherent group of species that was designated the "*Garcinia stipulata*" group in Sweeney et al. (2022). Jones (1980) treated this group, using Pierre's sectional name, as a subsection of *Discostigma* (*Garcinia* section *Discostigma* subsection *Dicrananthera* (Pierre) S.W.Jones *nom. inval.* Art. 30.9, Turland et al. 2018). Species in this group collectively range from eastern India and Bhutan, east to southwest China, and south to Myanmar and Laos. In addition to *G. nujiangensis*, the section contains *G. yaatapsap* K. Armstr. & P.W. Sweeney, *G. paucinervis* Chun & F.C.How (1956: 12), *G. stipulata* T.Anderson, and *G. thorelii* Pierre (1882: t. [plate] 62). These species all share prominent stipuliform structures (rare in Clusiaceae, Stevens 2007), leaves with prominent, widely spaced, curved secondary veins and percurrent tertiaries, staminate flowers with numerous stamens united into an annular mass encircling and attached to the pistillode (in *G. paucinervis* and *G. nujiangensis* the stamens are described as being in four bundles (Chun and How 1956; Li 1981)), and ellipsoid fruits with a discoid stigma and one to two seeds. Future molecular phylogenetic analyses will confirm if species of the 'stipulata' group are monophyletic and whether they will remain a distinct clade separate from clade 4/section *Discostigma*.

Species. *Garcinia nujiangensis* C.Y.Wu & Y.H.Li; *G. paucinervis* Chun & F.C.How; *G. stipulata* T.Anderson; *G. thorelii* Pierre; *G. yaatapsap* K.Armstr. & P.W.Sweeney.

Unplaced species

Garcinia anomala Planch. & Triana; *G. archboldiana* A.C.Sm.; *G. blancoi* Pierre; *G. bracteata* C.Y.Wu ex Y.H.Li; *G. busuangaensis* Merr.; *G. caloneura* Boerl.; *G. ceramica* Boerl.; *G. clusiifolia* Ridl.; *G. engleriana* A.C.Sm.; *G. erythrosperma* Lauterb.; *G. fagraeoides* A.Chev.; *G. graminea* Kosterm.; *G. ituman* Merr.; *G. jelinckii* Kurz; *G. klossii* Ridl.; *G. linearifolia* Elmer; *G. longipedicellata* Kosterm.; *G. lucens* Pierre; *G. mammeoides* Kosterm.; *G. matsudae* Kaneh.; *G. montana* Ridl.; *G. moszkowskii* Lauterb.; *G. moulmeinensis* Pierre ex Vesque; *G. nubigena* Lauterb.; *G. pacifica* Merr.; *G. pallide-sanguinea* Lauterb.; *G. plena* Craib; *G. propinqua* Craib; *G. qinzhouensis* Y.X.Liang & Z.M.Wu; *G. ramulosa* Lauterb.; *G. rhizophoroides* Elmer; *G. rumiyo* Kaneh.; *G. rupestris* Lauterb.; *G. schraderi* Lauterb.; *G. squamata* Lauterb.; *G. subfalcata* Y.H.Li & F.N.Wei; *G. torensis* Lauterb.; *G. tuberculata* Lauterb.; *G. whitfordii* Merr.; *G. wichmannii* Lauterb.

Taxonomy of the NC *Garcinia* species

The phylogenetic framework estimated in this study does not support the distinction between *G.* sp. "JT814" and *G. balansae* within NC, nor recover four species with multiple accessions as monophyletic (viz. *G. pedicellata*, *G. puat*, *G. comptonii*, *G. neglecta*), but confirms the distinction between NC species and both *G. vitiensis* and *G. adinantha* found in Fiji. Therefore, all NC species should still be considered as endemics. Also, *G. balansae* (belonging to clade 4/section *Discostigma*) appears more closely related to species from Fiji (*G. myrtifolia*, *G. vitiensis*), Australia (*G. jensenii*) and southeast Asia (*G. brevirostris*, *G. merguensis*, *G. rostrata*, *G. lancilimba*, *G. tetralata*) than to any other NC species.

The four species with capsular fruits (*G. comptonii*, *G. neglecta*, *G. urceolata* and *G. virgata*; retrieved in clade 5/section *Brindonia*) cannot be distinguished based on the present molecular data, but they form two pairs of species based on morphology and ecology. *Garcinia urceolata* and *G. virgata* have small leaves and were confused for a long time but differ by their flowers (green urceolate versus yellowish cup-like corolla), leaves and fruits. Both occur in dense humid forest on non-ultramafic substrates, but *G. urceolata* grows at higher elevation and in wetter conditions than *G. virgata*. *G. comptonii* appears restricted to maquis or forest edges on ultramafic substrates, while *G. neglecta* is mostly a forest tree on ultramafic and non-ultramafic substrates.

In the other NC clade (included in clade 9/section *Macrostigma*), *G. vieillardii* is restricted to the northeast dense humid forest on non-ultramafic soils, above 550 m a.s.l., while *G. densiflora* occurs in the same area and also on non-ultramafic substrates but at lower elevation. In addition, it is more a rupicolous species. The three other species can be found on both substrates (ultramafic and non-ultramafic). *Garcinia puat* is restricted to dense humid forest at low elevations, while *G. pedicellata* is a coastal (including small islands) to medium elevation tree, growing in drier conditions than the three previously cited species. Finally, *G. amplexicaulis* is the species with the widest ecological amplitude, growing in open maquis to closed humid forest, from low to 900 m a.s.l., throughout all the main island.

Conclusions

This study offers a way forward on a revised infrageneric classification of the species-rich genus *Garcinia*, based on both evolutionary history (as informed by molecular phylogenies) and morphology. We recognize eleven sections within *Garcinia*, list representative species and document distinctive morphological features for each. This classification provides an evolutionary-based foundation for future, much needed monographic work within the genus. Although additional phylogenetic analyses are warranted, by including more species and increasing the phylogenetic resolution, our phylogenetic results are a major contribution to the understanding of the evolutionary history of the genus and they provide a starting point for more ecological and evolutionary investigations as well as conservation planning and taxonomic work. Future revisionary efforts focused on some of the more speciose sections/clades recognized here (*Brindonia*, *Discostigma*, and *Hebradendron*) will certainly result in many species being reduced to synonymy and some new species being described. This was the case with a recent revision of Section *Garcinia* (Nazre et al. 2018). And, as more detailed taxonomic work is done, some species section reassignments are inevitable as are the erection of new sections to accommodate newly discovered clades with distinct suites of morphological characters.

One area that is particularly attractive for future research concerns the biogeographic history of the genus. A more complete knowledge of the spatio-temporal history of *Garcinia* would allow for a better understanding of the events that lead to the present geographic distribution of the genus. This would contribute to a growing body of knowledge about the biogeography of pantropically distributed clades and would provide additional data for exploring hypotheses about intercontinental disjunctions (e.g. Clayton et al. 2009; Couvreur et al. 2011; Baker and Couvreur 2013; Ruhfel et al. 2016; Torke et al. 2022). At a smaller scale, studying the origin of the ten endemic NC *Garcinia* species would also be valuable. Species diversification probably occurred after colonization of the territory by long-distance colonization and recent studies on other plant groups showed that in addition to the closest and largest landmass that is Australia, diverse geographic origins could be revealed (e.g. Duangjai et al. 2009; Del Rio et al. 2017; Samuel et al. 2019).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: PS, JM, MG. Data curation: JM, PS, MG. Formal analysis: MG, PS. Funding acquisition: MG. Investigation: PS, MG. Writing - original draft: MG, PS, JM.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

List of taxa and accessions used in this study

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: xlsx

Explanation note: The origin of DNA sequences is indicated, together with information on the herbarium voucher and distribution area of the taxon. In cases where the accepted name that was used in this study differed from the name provided in the original study that generated a sequence or voucher, the original name is provided (under “Prior determination”) along with a reference for the taxonomic decision. Accessions that were newly sequenced in this study have boldface text. All accessions were included in the nuclear DNA phylogenetic analysis (except three samples, as indicated in the first column) and a subset was included in the chloroplast DNA phylogenetic analysis, as indicated in the corresponding column.

Link: https://doi.org/10.3897/phytokeys.239.112563.suppl1

Supplementary material 2

Molecular phylogeny of *Garcinia* L. based on *psbM-trnD* and Bayesian inference

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: jpeg

Explanation note: Posterior probabilities (PP) are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. Species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used. All accessions were newly sequenced in this study.

Link: https://doi.org/10.3897/phytokeys.239.112563.suppl2

Supplementary material 3

Molecular phylogeny of *Garcinia* L. based on *trnQ-rps16* and Bayesian inference

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: jpeg

Explanation note: Posterior probabilities (PP) are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. Species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used. All accessions were newly sequenced in this study.

Link: https://doi.org/10.3897/phytokeys.239.112563.suppl3

Supplementary material 4

Molecular phylogeny of *Garcinia* L. based on *rps16-trnK* and Bayesian inference

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: jpeg

Explanation note: Posterior probabilities (PP) are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. Species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used. All accessions were newly sequenced in this study.

Link: https://doi.org/10.3897/phytokeys.239.112563.suppl4

Supplementary material 5

Molecular phylogeny of *Garcinia* L. based on a combined ITS and chloroplast DNA (*psbM-trnD, trnQ-rps16* and *rps16-trnK*) dataset and Bayesian inference

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: jpeg

Explanation note: Posterior probabilities (PP) are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. Species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used.

Link: https://doi.org/10.3897/phytokeys.239.112563.suppl5

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Checklist

Beyond nutmeg, mace, and cloves: Checklist of the liverworts and hornworts of Maluku Islands (Moluccas), Indonesia

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Abstract

The first ever liverwort and hornwort checklist is provided for the Maluku Islands (Moluccas/Spice Islands) of Indonesia. We report 355 accepted and 16 doubtful species and reject 22 species previously reported for Maluku Islands. The list is based on the specimens housed in the Herbarium Bogoriense (BO) and reports from over 500 literature references, including monographs, regional studies, and molecular investigations. The Maluku Islands are part of the Wallacea Biodiversity Hotspot with many unique species found only in Wallacea. Publications focusing on liverworts and hornworts of Maluku Islands are few and scattered. Considering regionally widespread species that have been recorded elsewhere, we predict that further fieldwork exploring the diversity of habitats coupled with collections unveiled from regional herbaria, a number of new records remain to be reported.

Key words: Checklist, hornworts, Indonesia, liverworts, Maluku, Moluccas

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Introduction

The Maluku Islands (Moluccas) is an island archipelago of over 1,000 islands situated in eastern Indonesia south of the Philippine island of Mindanao and east of Sulawesi, scattered in a series of irregular arcs spanning the Maluku, the Banda, and the Seram Seas (Zerner 1994; Leunufna and Evans 2014). The Maluku Islands were also formerly known as the Spice Islands because the archipelago held great geopolitical significance due to the abundance in spices as a commodity (Van Gils and Cox 1994). For instance, the spice nutmeg (*Myristica fragrans* Houtt.) a small-holder's crop, with 3500 years of antiquity, is indigenous to the Banda Islands, and is now grown in about 12 countries including some secondary centers of domestication (Peter 2001; Sasikumar 2021).

The biogeographical region of Maluku Islands (Fig. 1) encompasses the Indonesian geopolitical provinces of North Moluccas (Maluku Utara Province) and part of South Moluccas (Maluku Province) (Rutgrink et al. 2018). The major island groups in the north Moluccas are Halmahera, Bacan, Morotai, Obi, Sula,

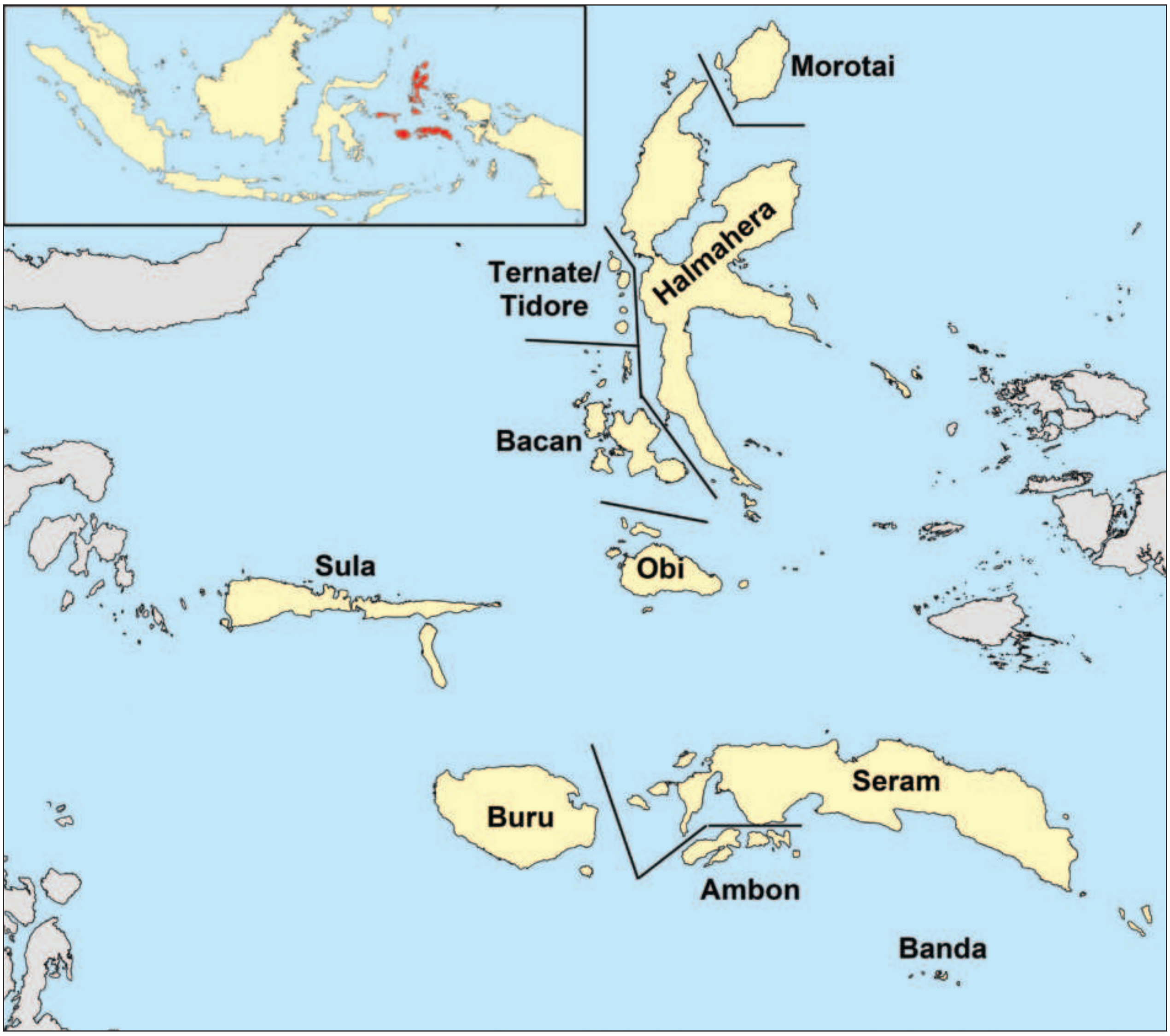

Figure 1. Moluccas in the Indonesian archipelago (inset) as defined in the present paper and the islands and archipelagos here used.

Ternate, and Tidore whereas Seram (previously known as Ceram), Buru, Banda, and Ambon are situated in the south. Many of the islands of Maluku are comprised of fragments of continental crusts (Monk et al. 1997) and are one of the most complex biogeographical and oceanographic areas on Earth (Pitriana et al. 2020). The island groups have experienced considerable, but very different tectonic displacements. During the last 10 million years, the North Moluccas moved westwards along the north coast of New Guinea to their current position. The Southern Moluccas moved northwards from Australia, west of New Guinea (Rutgrink et al. 2018). Not surprisingly the flora shows a marked similarity to those of New Guinea and Australia but also includes many endemic species and at least two endemic genera (*Parakibara* Philipson and *Siphokentia* Burret) (Burret 1927; Philipson 1985).

Famously, western exploration of the natural history of the Maluku Islands dates back to the 17th century, starting with Georg Everhard Rumphius, and later, for example, Alfred Russel Wallace (Strack 1993; Lamoureux 1990). Notably, Wallace (1863), proposed a sharp boundary of the Indo-Australian Archipelago based upon land-mammal and land-bird distributions. It has since achieved iconic status and today its significance is recognized well beyond the confines of the biogeography community (Ali and Heaney 2021). Yet, it is noteworthy that the application in recent years of modern analytical techniques has not led to a consensus view on where the lines/areas should run/be placed (Ali and Heaney 2021). The Maluku Islands are part of what is termed as the Wallacea Biodiversity Hotspot, a region that covers an area of 338 thousand square kilometers with thousands of islands supporting highly diverse biological communities with many unique species found only in Wallacea (van Welzen et al. 2005; CEPF 2014). Wallacea was identified as one of the original 25 biodiversity hotspots in the world (Myers et al. 2000).

Maluku Islands are situated in the “Tropical and Subtropical Moist Broadleaved Forests” biome (Olson et al. 2001) and contribute approximately 24% of forest cover of the Wallacea land surface. The archipelago as here defined is separated into four ecoregions, eastern part of “Sulawesi Lowland Rainforests”, “Buru Rainforests”, “Halmahera Rainforests” and “Seram Rainforests” (Fig. 3, https://www.oneearth.org/bioregions/sulawesi-maluku-islands-au14/) and is considered home to much endemic flora (CEPF 2014). The Maluku Islands are one of the few places in the Indonesian archipelago where it is possible to find a complete altitudinal sequence of vegetation, with few places elsewhere in the tropics providing a comparable range (Edwards et al. 1993). Many of the forests in Maluku are lowland evergreen and semi-evergreen forests (Fig. 2), especially on Halmahera and adjacent islands, tropical montane forests, limestone (karst) geologies, and ultrabasic (serpentine) geologies (Ellen 1997; Abdo 2017).

Liverworts and hornworts are, together with mosses, commonly referred to as bryophytes. They represent three early diverging clades of land plants forming the second largest group of green land plants after flowering plants and are of critical biological, ecological, and phylogenetic significance. Bryophytes serve as the “macrophytes,” providing a matrix where many microscopic organisms live, including tardigrades, mites, rotifers, micro-molluscs, microalgae, microfungi, and prokaryotes (Gerson 1982; Huttunen et al. 2017; Muggia and Grube 2018). They also play an important role as possible indicators of climate change (e.g., Lindo et al. 2013; Ruklani et al. 2021), in nutrient cycling (Rieley et al. 1979) and through their water retention reducing soil nutrient loss and flooding risk (Anderson et al. 2010). Because of their physiological properties they have therefore been used extensively as ecological indicators (e.g., Pakeman et al. 2019; Déleg et al. 2021). Resolving relationships among bryophytes and their relationships to the remaining land plants is critical for understanding the evolution of fundamental innovations within land plants (Leebens-Mack et al. 2019).

Historically, relatively few publications have focused on plant collections from the Maluku Islands, despite the significance of the flora. Approximately 4,442 species of plants and fungi were recorded from Maluku Islands until 2017 (Retnowati and Rugayah 2019). Herbarium Amboinense, a classic work by Rumphius (1741–1755), contains descriptions of plants commonly found in Ambon and the surrounding islands. However, the floristic knowledge of liverworts and hornworts remains poor, especially compared to seed plants, and has scarcely been published. Seram and Ambon have been the most investigated areas for liverworts and hornworts and have been reported by several authors

Figure 2. Vegetation of the Aketajawe-Lolobata National Park in Halmahera. Photo: Ida Haerida.

(e.g. Akiyama 2009; Doei 1987a, 1987b; Hasegawa 1986; Hattori 1986b; Inoue 1986; Mizutani 1986a). One of the most significant contributions to bryophytes of the Maluku Islands is the checklist of bryophytes from Seram and Ambon by Akiyama (2009) who recorded as many as 226 species of liverworts. One species, *Lepidozia integrifolia* Doei, is an endemic species of Seram (Doei 1987a).

We here present the first ever checklist of liverworts and hornworts for Maluku Islands in an effort to further promote bryological research, especially in the eastern part of Indonesia. The checklist complements recently published checklists for Indonesia including Söderström et al. (2010) for Java and Nadhifah et al. (2021) for the Lesser Sunda Islands. The significance of check-

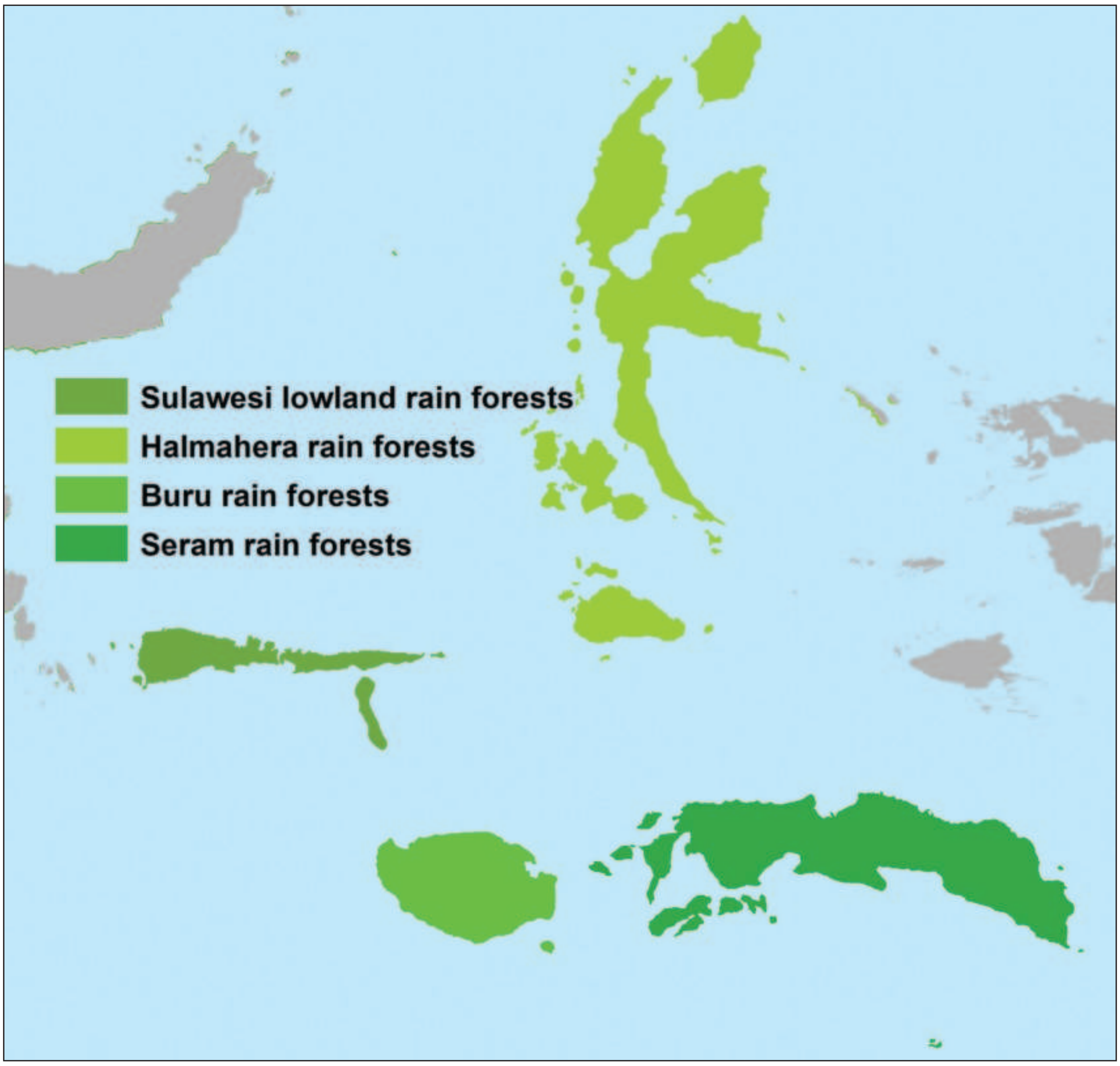

Figure 3. Ecoregions of the Moluccas Islands.

lists is summarized by Söderström et al. (2008), including outlining the utility of checklists as powerful and important tools, and their applicability to taxonomy, systematics, and conservation.

Liverwort types from Maluku

Not less than 113 names (9 of them invalid) have original material from the Maluku Islands. Of the validly published names, 13 have holotypes and 47 of the rest are lectotypified. However, 43 names remain to be typified. Here we designate lectotypes, or validate earlier unsuccessful lectotypifications, for 13 names. For a discussion on lectotypification procedures, including the concept of inadvertent lectotypifications, see Söderström and Hentschel (2023). In the list below we cite the lectotypification source and indicate where further typifications are needed.

Chandonanthus gracilis **Herzog, *Hedwigia* 66 (6): 341, 1926 (Herzog 1926b).**

Original citation. Ceram: Hoale-Paß, ca. 1600 m, leg. E. Stresemann, 1911.

Lectotype (here designated, cf. Váňa et al. 2013: 30 as "holotype"). Indonesia, Moluccas, Seram, Hoale Pass, 1600 m., 1911, *Stresemann s.n.* (JE04005601, https://je.jacq.org/JE04005601).

Note. Only one specimen has been located but it cannot be ruled out that there exist duplicates elsewhere. Váňa et al. (2013: 30) call it "holotype" but this is too late for an inadvertent lectotypification. The specimen is also annotated as holotype by K. Amamoto in 2020. In case duplicates are found, we here formally designate it as a lectotype.

Currently accepted name. *Plicanthus hirtellus* (F.Weber) R.M.Schust. (see Váňa et al. 2013).

Lepidozia longifolia **Steph., *Sp. Hepat. (Stephani)* 3: 606, 1909 (Stephani 1909a).**

Original citation. Hab. *Amboina* (Karsten).

Lectotype (here designated). Indonesia, Moluccas, Ambon, *Karsten* (G00069659 https://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=123550&lang=en).

Note. The lectotype is annotated "type" by Mizutani in Feb. 1975.

Lophocolea deningeri **Herzog, *Beih. Bot. Centralbl.* 38 (2): 321, 1921 (Herzog 1921).**

Original citation. Buru: Im Urwald des Kapalamadang, leg. Dr. K. Deninger †, 1906.

Lectotype (here designated). Indonesia, Moluccas, Buru, Im Urwald des Kapalamadang, *Deninger* 1906 (JE04005314 https://je.jacq.org/JE04005314).

Note. JE04005314 is marked as "holotype" by R. Grolle. We are not aware of any other type material.

Lopholejeunea sagrana **var. *dentistipula*** **Schiffn. ex P.Syd., *Just's Bot. Jahresber.* 19 (1): 246, 1894 (Sydow 1894) ('*sagraeana*').**

Original citation. Ins. Amboina, in iisdem locis ac typica, pauca tantum frustula sed c. per. et ♂ inventa sunt (7. 6. 75).

Lectotype (here designated, Zhu and Gradstein 2005: 85 as "holotype"). Indonesia, Moluccas, Ambon, 7 Jun 1875, *D. Naumann* (FH).

Note. Zhu and Gradstein (2005: 85) call it "holotype" but this is too late for an inadvertent lectotypification.

Currently accepted name. *Caudalejeunea reniloba* (Gottsche) Steph. (see Zhu and Gradstein 2005).

Madotheca crenilobula **Herzog, *Beih. Bot. Centralbl.* 38 (2): 328, 1921 (Herzog 1921).**

Original citation. Buru: Im Urwald des Kapalamadang, leg. Dr. K. Deninger †, 1906.

Lectotype (here designated). Indonesia, Moluccas, Buru, Im Urwald des Kapalamadang, 1906, *K. Deninger* (JE04001514 https://je.jacq.org/JE04001514, isotype JE04001515 https://je.jacq.org/JE04001515).

Note. The lectotype was annotated "Type!" and the isotype "isotype" by S. Hattori in 1968 but has apparently never been published.

Currently accepted name. *Porella javanica* (Gottsche) Inoue (see Hattori 1975e).

Mastigobryum deningeri **Herzog, *Beih. Bot. Centralbl.* 38 (2): 322, 1921 (Herzog 1921).**

Original citation. Buru: In den Bergen Mittelburus, ca. 1500 m, leg. Dr. K. Deninger †, 1911.

Lectotype (here designated). Indonesia, Moluccas, Buru, Mittelburu, ca. 1500 m, 1911, *Deninger 10* (JE04006158 https://je.jacq.org/JE04006158, isolectotype JE04006157 https://je.jacq.org/JE04006157).

Note. The selected lectotype is richer than the isolectotype and has a label in Herzog's handwriting marked "n.sp.". The isolectotype is marked "Typus" and annotated as type and syn. to *Bazzania longicaulis* by Kitagawa 18 Nov 1978 but no typification seems to have been published.

Currently accepted name. *Bazzania longicaulis* (Sande Lac.) Schiffn., syn. nov.

Mastigobryum nigricans **Herzog, *Beih. Bot. Centralbl.* 38 (2): 322, 1921 (Herzog 1921).**

Original citation. Buru: Im Urwald des Kapalamadang, leg. Dr. K. Deninger †, 1906.

Lectotype (here designated). Indonesia, Moluccas, Buru, Kapalamadang, 1906, *K. Deninger 112* (JE04006129 https://je.jacq.org/JE04006129).

Note. The lectotype is marked "n.sp." on the label and annotated by N. Kitagawa 1991 as type.

Mastigobryum stresemannii **Herzog, *Beih. Bot. Centralbl.* 38 (2): 324, 1921 (Herzog 1921).**

Original citation. Ceram: Paßhöhe zwischen Mansela und Wolu (Useahánpaß), ca. 1750 m, leg. E. Stresemann, 1911.

Lectotype (here designated). Indonesia, Moluccas, Seram, between Mansela and Wolu ca. 1750 m, 1911, *E. Stresemann 110*, (JE04005944 https://je.jacq.org/JE04005944).

Note. The lectotype is marked "n.sp." on the label by Herzog and annotated as type by N. Kitagawa in 1978.

Currently accepted name. *Bazzania stresemannii* (Herzog) N.Kitag.

Mastigobryum vermiculare **Herzog, *Hedwigia* 66 (6): 339, 1926 (Herzog 1926b).**

Original citation. Ceram: Hoale, ca.1100m, leg. E. Stresemann, 1911.

Lectotype (here designated). Indonesia, Moluccas, Seram, Hoale, ca. 1100 m, 1911, *Stresemann* (JE04006130 https://je.jacq.org/JE04006130).

Note. Only one specimen is online in JE and without any annotation.

Pycnolejeunea ventricosa **Schiffn. ex P.Syd., *Just's Bot. Jahresber.* 19 (1): 246, 1894 (Sydow 1894).**

Original citation. In insula Amboina cum aliis Lejeuniis parcissime, cum fl. ♀ et periantbiis vetustis (7. 6. 75) [cf. Schiffner 1890: 32].

Lectotype (here designated, cf. Zhu and Lai 2005: 200 as "holotype"). Indonesia, Moluccas, Ambon, Gazellen Expedition, 7.6.1875, *Naumann* (FH00284228 https://kiki.huh.harvard.edu/databases/specimen_search.php?mode=details&id=206370).

Note. "Holotype" by Zhu and Lai (2005: 200) is too late to be an inadvertent lectotype (cf. ICN2018 Art. 7.11) and is here designated as lectotype.

Currently accepted name. *Cheilolejeunea ventricosa* (Schiffn. ex P.Syd.) Xiao L.He

***Schistochila amboinensis* Steph., *Sp. Hepat. (Stephani)* 4: 77, 1909 (Stephani 1909c).**

Original citation. Hab. *Amboina*.

Lectotype (here designated, cf. So 2003a: 87 as "holotype"). Indonesia, Moluccas, Ambon, 1883, *Luerssen 1270* (G00067852 https://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=131418&lang=en).

Note. So (2003a: 87 as "holotype") is too late for an inadvertent lectotypification.

Currently accepted name. *Schistochila beccariana* (De Not.) Trevis. (see So 2003a).

***Schistochila inversa* Herzog, *Hedwigia* 66 (6): 342, 1926 (Herzog 1926b).**

Original citation. Ceram: Hoale-Paß, ca. 1600 m, leg. E. Stresemann, 1911; in Bruchstücken aus *Lepidozia ceramensis* und *L. Ferdinandi Mülleri* herausgelesen.

Lectotype (here designated, cf. So 2003a: 98 as "holotype"). Indonesia, Moluccas, Seram, Hoale-Pass, ca. 1600 m, 1911, *E. Stresemann s.n.* (JE04002842 https://je.jacq.org/JE04002842).

Note. So (2003a: 98 as "holotype") is too late to be an inadvertent lectotypification.

Currently accepted name. *Schistochila sciurea* (Nees) Schiffn. (see So 2003a).

***Schistochila purpurascens* Herzog, *Hedwigia* 66 (6): 341, 1926 (Herzog 1926b).**

Original citation. Ceram: Hoale-Paß, ca. 1600 m, leg. E. Stresemann, 1911.

Lectotype (here designated, cf. So 2003a: 80 as "holotype"). Indonesia, Moluccas, Seram, Hoale-Pass, ca. 1000 m, Mar-Aug 1911, *E. Stresemann 201* (JE04002840 https://je.jacq.org/JE04002840, isotype L-937.235.12 https://data.biodiversitydata.nl/naturalis/specimen/L%20%200444630).

Note. "holotype" by So (2003a: 80) is too late for an inadvertent lectotypification.

Currently accepted name. *Schistochila acuminata* Steph. (see So 2003a).

Materials and methods

Nomenclature and taxonomy follow the world checklist of hornworts and liverworts (Söderström et al. 2016) with some updates from recent literature. Sources include more than 500 publications found through the work with Early Land Plants Today (ELPT) database of liverwort taxonomy and distribution, and with some consultation with taxonomic experts. In addition, we also examined the specimens collected from the Maluku Islands in the Herbarium Bogoriense (BO). The checklist follows a similar format of a series of previous liverwort and hornwort regional checklists by the authors, e.g., Java, Lesser Sunda Islands (Söderström et al. 2010; Nadhifah et al. 2021). References citing primary reports (citing specimens or material seen by the author) are given in bold. Secondary references not citing any material seen are given in normal font. In cases where we are not aware of any primary source, or the earliest report is a secondary source without any clear connection to a primary source published later, we comment on the situation. In the current checklist we note under which name a taxon is reported except when it is reported under the currently accepted name.

We here accept reports of 355 species from the area in addition to 16 reported species that we consider as doubtful and 21 species reported whose occurrence we reject from the islands. Species number known varies a lot between the islands/archipelagos (Table 1, Fig. 4). We are not aware of a single report from Sula while 258 species are known from Seram. Thus, we expect that with further investigations the number of species will rise considerably for many of the islands in the region.

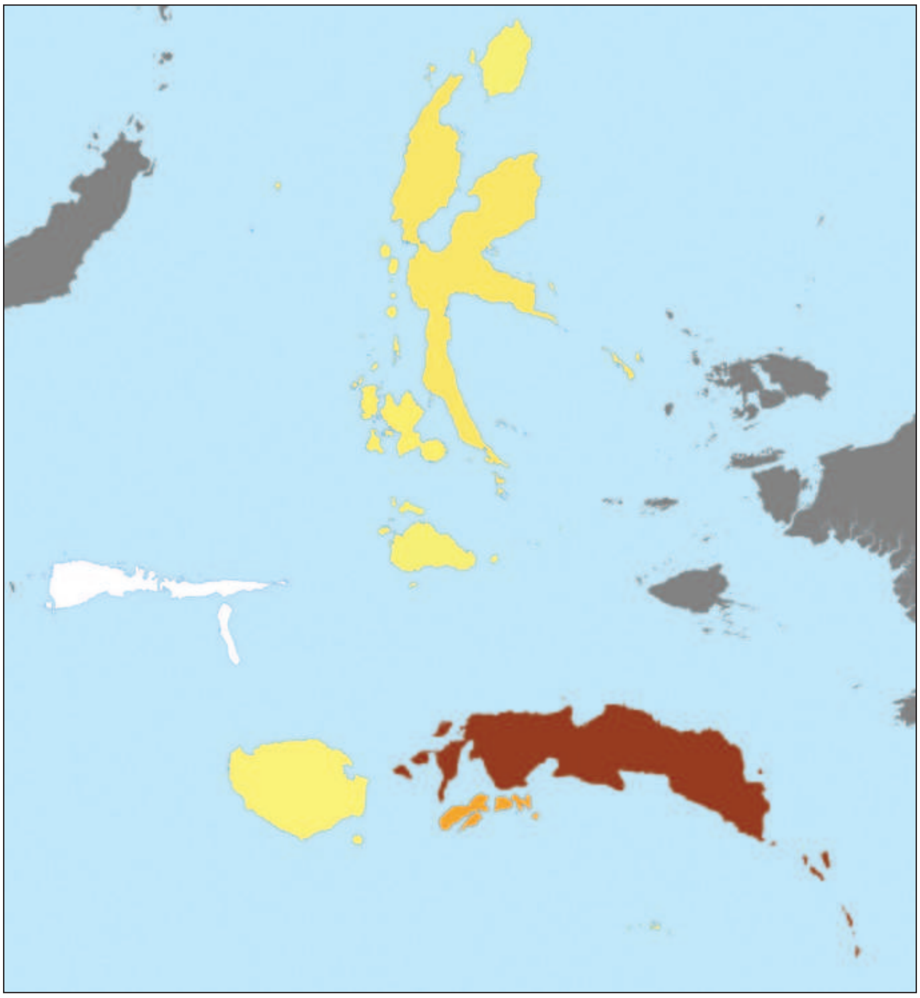

Figure 4. Species richness on the different islands/archipelagos of Moluccas. The darker the more species known (cf. Table 1). White (Sulu I) means that no liverwort or hornwort species are known from the area.

Table 1. Number of accepted, doubtful and rejected species of liverworts and hornworts from Moluccas and the recognized areas (islands/archipelagos) within the Moluccas.

Area	Accepted	Doubtful	Rejected
Ambon	143	11	10
Bacan	26	0	0
Banda	7	2	0
Buru	13	0	2
Halmahera	31	3	0
Morotai	2	0	0
Obi	2	0	0
Seram	258	7	5
Sulu	0	0	0
Ternate/Tidore	22	0	2
Moluccas	355	16	22

Taxa accepted for Moluccas

Anthocerotophyta

Dendroceros Nees

Dendroceros acutilobus Steph. **MOLUCCAS**: AMBON: **LECTOTYPE** [Piippo 1993a: 44], **LECTOTYPE** of *Dendroceros karstenii* [to be designated], **Schiffner 1898** as *Dendroceros karstenii*, **Stephani 1909b, Stephani 1917** as *Dendroceros karstenii*, Stephani 1917, **Bonner 1965** also as *Dendroceros karstenii*, **Hasegawa 1980**, 1982, 1986, 2002, Piippo 1993a, **Peñalosa et al. 2019**. SERAM: A**kiyama 1986, Hasegawa 1986**, 2002, **Akiyama 2009**.

Dendroceros cavernosus J.Haseg. **MOLUCCAS**: SERAM: **Akiyama 1986, Hasegawa 1986**, 2002, **Akiyama 2009**.

Dendroceros crispus (Sw.) Nees. **MOLUCCAS**: Amélio et al. 2021. AMBON: **Schiffner 1893b**.

Dendroceros foliicola J.Haseg. **MOLUCCAS**: SERAM: **Akiyama 1986, Hasegawa 1986** as *Dendroceros* '*foliicala*', **Akiyama 2009**.

Dendroceros javanicus (Nees) Nees. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009, Hasegawa 1986**.

Dendroceros pedunculatus Steph. **MOLUCCAS**: AMBON: **LECTOTYPE** [Hasegawa 1980: 306], **Stephani 1909b**, 1917, **Bonner 1965**, Hasegawa 1980, Piippo 1993a, **Peñalosa et al. 2019**.

Dendroceros seramensis J.Haseg. **MOLUCCAS**: SERAM: **HOLOTYPE, Akiyama 1986, 2009, Hasegawa 1986, Engel 1993, Crosby and Engel 2006, Peñalosa et al. 2019**.

Folioceros D.C.Bharadwaj

Folioceros amboinensis (Schiffn.) Piippo. **MOLUCCAS**: AMBON: **Schiffner 1890, 1898** both as *Anthoceros amboinensis*, **Sydow 1894** as *Anthoceros amboinensis*, Stephani 1916 as *Aspiromitus amboinensis*, Meijer 1954 as *Anthoceros amboinensis*, **Bonner 1962b** as *Aspiromitus amboinensis* and *Anthoceros amboinensis*, Hasegawa 1993 as *Anthoceros amboinensis*.

Folioceros appendiculatus (Steph.) J.Haseg. **MOLUCCAS**: Seram: **Akiyama 1986, Hasegawa 1986**, 2002 as *Anthoceros appendiculatus*, **Akiyama 2009**.

Folioceros glandulosus (Lehm. et Lindenb.) D.C.Bharadwaj. **MOLUCCAS**: Inoue and Miller 1965 as *Anthoceros glandulosus*, Inoue 1965 as *Anthoceros glandulosus*, Miller et al. 1983 as *Anthoceros glandulosus*, Bapna and Kachroo 2000a. Banda: **Meijer 1957** as *Anthoceros glandulosus*. ?Seram: Piippo 1993a. Note: we are not aware of any first hand report from Seram.

Megaceros Campb.

Megaceros flagellaris (Mitt.) Steph. **MOLUCCAS**: Ambon: **Schiffner 1893b, 1898** both as *Anthoceros grandis*, Merrill 1906 as *Anthoceros grandis*, Miller et al. 1983 as *Megaceros grandis*. Seram: **Akiyama 1986, 2009, Hasegawa 1986**.

Phaeoceros Prosk.

Phaeoceros carolinianus (Michx.) Prosk. **MOLUCCAS**: Seram: **Akiyama 1986, 2009** both as *Phaeoceros laevis* subsp. *carolinianus*, **Hasegawa 1986** as *Phaeoceros laevis* subsp. *carolinianus*.

Phaeomegaceros R.J.Duff, J.C.Villarreal, Cargill et Renzaglia

Phaeomegaceros hirticalyx (Steph.) R.J.Duff, J.C.Villarreal, Cargill et Renzaglia. **MOLUCCAS**: Ambon: **Hasegawa 1986** as *Phaeoceros polyandrus*, Campbell and Hasegawa 1993 as *Phaeoceros hirticalyx*, **Akiyama 2009** as *Phaeoceros polyandrus*.

Marchantiophyta

Acrolejeunea (Spruce) Steph.

Acrolejeunea fertilis (Reinw., Blume et Nees) Schiffn. **MOLUCCAS**: **LECTOTYPE** of *Ptychocoleus tener* [Gradstein 1975: 86], Bapna and Kachroo 2000b, Singh et al. 2010. Ambon: **Sande Lacoste 1864** as *Phragmicoma fertilis*, **Schiffner 1898, Gradstein 1975**.

Acrolejeunea pycnoclada (Taylor) Schiffn. **MOLUCCAS**: Mizutani 1977, Bapna and Kachroo 2000b, Haerida et al. 2010, Siregar et al. 2014, Siregar 2015. Ambon: Verdoorn 1934a, **1934b** both as *Ptychocoleus pycnocladus*, Swanson and Miller 1969 as *Ptychocoleus pycnocladus*, Kamimura 1974 as *Ptychocoleus pycnocladus*, Miller et al. 1983 also as *Ptychocoleus pycnocladus*. Seram: **Mizutani 1986a, Akiyama 2009**.

— subsp. *pycnoclada*. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Acrolejeunea rostrata* [Gradstein 1975: 109], **LECTOTYPE** of *Ptychocoleus brunneus* [Gradstein 1975: 109 as “holotype”], **ORIGINAL MATERIAL** of *Acrolejeunea rostrata* var. *major*, **ORIGINAL MATERIAL** of *Acrolejeunea rostrata* var. *minor*, **Schiffner 1890** as *Acrolejeunea rostrata* and its var. *major* and var. *minor*, **Bonner 1962b** as *Acrolejeunea rostrata* and its var. *Major* and var. *minor*, **Gradstein 1975**, Miller et al. 1983 as *Ptychocoleus brunneus*, **Geissler and Bischler 1987** as *Lejeunea rostrata* var. *Minor*, **Geissler and Bischler 1989** as *Ptychocoleus brunneus*.

Acrolejeunea securifolia (Nees) Steph. **MOLUCCAS**: Seram: **Mizutani 1986a** as *Acrolejeunea securifolia*, **Akiyama 2009**.

— subsp. *hartmannii* (Steph.) Gradst. **MOLUCCAS**: Ambon: **Gradstein 1975**, Bonner 1977, Gradstein et al. 2002, Piippo et al. 2002.

***Acromastigum* A.Evans**

Acromastigum aurescens A.Evans. **MOLUCCAS**: Ambon: **Grolle 1978**.

Acromastigum bancanum (Sande Lac.) A.Evans. **MOLUCCAS**: Ambon: **Grolle 1978** as *Acromastigum bidenticulatum*.

Acromastigum divaricatum (Nees) A.Evans ex Reimers. **MOLUCCAS**: Ambon: **Schiffner 1893b, 1898** both as *Bazzania divaricata*, **Evans 1934**, Brown and Renner 2014. Seram: **Akiyama 1986, 2009**.

Acromastigum echinatiforme (De Not.) A.Evans. **MOLUCCAS**: Ambon: **Schiffner 1893b, 1898** as *Bazzania echinatiformis*, **Stephani 1909a** as *Mastigobryum echinatiforme*, **Evans 1934**, Bonner 1962b, 1963a as *Bazzania echinatiformis*, Grolle 1965, 1978, Pócs 1971, Miller et al. 1983, Piippo 1991, Schuster 2000a. Seram: **Grolle 1978**, Miller et al. 1983, Piippo 1991.

Acromastigum inaequilaterum (Lehm. et Lindenb.) A.Evans. **MOLUCCAS**: Ambon: **Evans 1934**, Jovet-Ast 1958, Bonner 1962b, Sharma and Srivastava 1993, Schuster 2000a.

Acromastigum lobuliferum A.Evans. **MOLUCCAS**: Ambon: **Grolle 1978**.

***Acroscyphella* N.Kitag. et Grolle**

Acroscyphella tjiwideiensis (Sande Lac.) N.Kitag. et Grolle. **MOLUCCAS**: Piippo 1985 as *Clasmatocolea tjiwideiensis*. Ambon: **LECTOTYPE** of *Chiloscyphus falcifolius* [Bonner 1963b: 733], **Stephani 1907c** as *Chiloscyphus falcifolius*, **Bonner 1963b** as *Chiloscyphus falcifolius*, **Grolle 1984** as *Clasmatocolea tjiwideiensis*, **1986**, Enroth 1991 as *Clasmatocolea tjiwideiensis*.

***Allorgella* Tixier**

Allorgella semperiana (Steph.) Bechteler, G.E.Lee, Schäf.-Verw. et Heinrichs. **MOLUCCAS**: Seram: **Mizutani 1986a** as *Otolejeunea semperiana*, **Akiyama 2009** as *Otolejeunea semperiana*.

Allorgella zantenii (Grolle) Bechteler, G.E.Lee, Schäf.-Verw. et Heinrichs. **MOLUCCAS**: Seram: **Bi et al. 2019**.

***Anastrophyllopsis* (R.M.Schust.) Váňa et L.Söderstr.**

Anastrophyllopsis revoluta (Steph.) Váňa et L.Söderstr. **MOLUCCAS**: Ah-Peng et al. 2010 as *Anastrophyllum revolutum*. Seram: **Akiyama 1986** as *Anastrophyllum revolutum*, Váňa and Piippo 1989b as *Anastrophyllum revolutum*, Váňa 1991b as *Anastrophyllum revolutum*, **Akiyama 2009** as *Anastrophyllum revolutum*.

***Anastrophyllum* (Spruce) Steph.**

Anastrophyllum piligerum (Nees) Steph. **MOLUCCAS**: Váňa and Engel 2013. HALMAHERA: **Váňa and Piippo 1989b**, Váňa 1991b.

***Aneura* Dumort.**

Aneura amboinensis Steph. **MOLUCCAS**: AMBON: **LECTOTYPE** [Bonner 1962b: 86], **Stephani 1899b, Bonner 1962b**.

Aneura pinguis (L.) Dumort. **MOLUCCAS**: AMBON: **Schiffner 1893b** as *Aneura pinguis* f. *normalis*, **1898** as *Riccardia pinguis*.

***Balantiopsis* Mitt.**

Balantiopsis ciliaris S.Hatt. subsp. *novoguineensis* S.Hatt. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009**.

***Bazzania* Gray**

Bazzania asymmetrica (Steph.) N.Kitag. **MOLUCCAS**: SERAM: **Herzog 1926b** as *Mastigobryum asymmetricum*.

Bazzania cadens N.Kitag. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009**.

Bazzania cincinnata (De Not.) Trevis. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009**.

Bazzania commutata (Lindenb. et Gottsche) Schiffn. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009**.

Bazzania conophylla (Sande Lac.) Schiffn. **MOLUCCAS**: AMBON: **LECTOTYPE** of *Mastigobryum longidens* [Kitagawa 1973: 263 as "type"], **Stephani 1886a**, 1886b, **1908c** all as *Mastigobryum longidens*, **Schiffner 1893b, 1898** as *Bazzania longidens*, Bonner 1963a as *Bazzania longidens*, Kitagawa 1973. SERAM: **Akiyama 1986, 2009**.

Bazzania crassitexta Steph. **MOLUCCAS**: AMBON: **LECTOTYPE** [Bonner 1963a: 340], **Stephani 1893c, 1908c** as *Mastigobryum crassitextum*, **Schiffner 1898, Bonner 1963a**, Kitagawa 1979b.

Bazzania distans (Nees) Trevis. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009**.

Bazzania erosa (Reinw., Blume et Nees) Trevis. **MOLUCCAS**: Del Rosario 1975b. HALMAHERA: **Meijer 1960**, Kitagawa 1978, Miller et al. 1983, Meagher 2015, Lestari and Ariyanti 2017, Siregar et al. 2018, Haerida et al. 2023. SERAM: **Akiyama 1986, 2009**.

Bazzania fallax (Sande Lac.) Schiffn. **MOLUCCAS**: AMBON: **Stephani 1908c** as *Mastigobryum fallax*.

Bazzania horridula Schiffn. **MOLUCCAS**: Geissler and Bischler 1985 as *Mastigobryum horridulum*. AMBON: **LECTOTYPE** [Kitagawa 1967: 254], **Schiffner 1893b, 1898, Stephani 1908d** as *Mastigobryum horridulum*, **Bonner 1963a, Kitagawa 1967**, Grolle 1968b, Del Rosario 1975b, He et al. 2013, Cheah and Yong 2016, Lestari and Ariyanti 2017.

Bazzania insignis (De Not.) Trevis. **MOLUCCAS**: AMBON: **Schiffner 1893b, 1898, Stephani 1908c** as *Mastigobryum insigne*, Evans 1932, Del Rosario 1975b. SERAM: **Akiyama 1986, 2009**.

Bazzania intermedia (Gottsche et Lindenb.) Trevis. **MOLUCCAS**: Ambon: **Schiffner 1893b, 1898, Stephani 1908c** as *Mastigobryum intermedium*, **1908d** as *Mastigobryum concinnum*, Bonner 1963a also as *Bazzania concinna*, Inoue and Miller 1965, Pócs et al. 1967, Pócs 1968, Tixier 1971, Miller et al. 1983 as *Bazzania concinna*, Bapna and Kachroo 2000a. ?Banda: Pócs 1968. Note: we are not aware of any first hand report from Banda,

— var. *sarawakiana* (De Not.) Schiffn. **MOLUCCAS**: ?Ambon: Bonner 1963a. Note: we are not aware of any first hand report of this variety from **Moluccas** and we are do not know if it is worth recognizing.

Bazzania irregularis (Steph.) Schiffn. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Mastigobryum irregulare* [to be designated], Stephani 1886b, **1908c** both as *Mastigobryum irregulare*, **Schiffner 1898**, Bonner 1963a.

Bazzania javanica (Sande Lac.) Schiffn. **MOLUCCAS**: Khotimperwati et al. 2018. Seram: **Sande Lacoste 1864** as *Mastigobryum javanicum*, **Schiffner 1898, Stephani 1908e** as *Mastigobryum javanicum*, **Meijer 1960**, Kitagawa 1967, Del Rosario 1975b, Miller et al. 1983, Meagher 2015.

Bazzania kernii Steph. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**.

Bazzania kokawana N.Kitag. et T.Kodama. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**.

Bazzania longicaulis (Sande Lac.) Schiffn. **MOLUCCAS**: Buru: **LECTOTYPE** of *Mastigobryum deningeri* [here designated], **Herzog 1921** as *Mastigobryum deningeri*, Herzog 1926a as *Mastigobryum deningeri*. Seram: **Akiyama 1986, 2009**.

Bazzania loricata (Reinw., Blume et Nees) Trevis. **MOLUCCAS**: Kitagawa 1967, Siregar and Pasaribu 2019. Seram: **Akiyama 1986, 2009**.

Bazzania merrillana (Steph.) Inoue ex Bonner. **MOLUCCAS**: ?Buru: Herzog 1926a as *Mastigobryum merrillanum*. Seram: **Herzog 1921** as *Mastigobryum* '*Merillanum*'. Note: we are not aware of any first hand report from Buru.

Bazzania parvitexta Steph. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**.

Bazzania pectinata (Lindenb. et Gottsche) Schiffn. **MOLUCCAS**: Siregar and Pasaribu 2019. Ambon: **Schiffner 1893b, 1898**, Stephani 1908c as *Mastigobryum pectinatum*, Evans 1932, Bonner 1963a, 1977, Sari 2014, Khotimperwati et al. 2018. Seram: **Akiyama 1986, 2009**.

Bazzania praerupta (Reinw., Blume et Nees) Trevis. **MOLUCCAS**: Khotimperwati et al. 2018. Seram: **Meijer 1960**, Miller et al. 1983.

Bazzania spiralis (Reinw., Blume et Nees) Meijer. **MOLUCCAS**: Halmahera: **Meijer 1960**, Miller et al. 1983. Seram: **Akiyama 1986, 2009**.

Bazzania stresemannii (Herzog) N.Kitag. **MOLUCCAS**: Seram: **LECTOTYPE** of *Mastigobryum stresemannii* [here designated], **Herzog 1921**, 1926a both as *Mastigobryum stresemannii*, Kitagawa 1979b.

Bazzania subtilis (Sande Lac.) Trevis. **MOLUCCAS**: Ambon: **Stephani 1908d** as *Mastigobryum subtile*, Meijer 1960 [with doubt], Bonner 1963a, Del Rosario 1975b, **Meagher 2010**, Sari 2014, Thouvenot et al. 2018.

Bazzania tridens (Reinw., Blume et Nees) Trevis. var. *tridens*. **MOLUCCAS**: Khotimperwati et al. 2018, Siregar and Pasaribu 2019. Ambon: **LECTOTYPE** of *Mastigobryum amboinense* [Kitagawa 1972: 449 as "type"], **Stephani 1924** as *Mastigobryum amboinense*, **Kitagawa 1972** as *Bazzania oshimensis*, Miller et al. 1983 as *Bazzania australis* and *Bazzania intermedia*, Sharma and Srivastava 1993. ?Banda: Pócs 1969b. Seram: **Sande Lacoste 1864** as *Mastigobryum tridens*, **Schiffner 1898**, Stephani 1908c as *Mastigobryum tridens*, Evans 1932, **Meijer 1960**, Bonner 1963a, Inoue and Miller 1965, Inoue 1965, Mizutani 1967, Hattori 1968, Del Rosario 1975b, Pócs 1971, Kamimura 1975, Miller et al. 1983, **Akiyama 1986, Akiyama 2009, 2009** both also as *Bazzania australis*, Sharma and Srivastava 1993, Bapna and Kachroo 2000a, Khotimperwati et al. 2018.

Bazzania uncigera (Reinw., Blume et Nees) Trevis. **MOLUCCAS**: AMBON: **Schiffner 1893b, 1898**, Stephani 1908e as *Mastigobryum uncigerum*, Bonner 1963a, Hattori 1975b, Miller et al. 1983.

Bazzania vittata (Gottsche) Trevis. **MOLUCCAS**: ?AMBON: Stephani 1909a as *Mastigobryum vittatum*, Hattori 1951, Miller et al. 1983, Sari 2014, Siregar et al. 2018. SERAM: **Akiyama 1986, 2009**. Note: we are not aware of any first hand report from Ambon.

Bazzania wallichiana (Lindenb.) Trevis. **MOLUCCAS**: AMBON: **Stephani 1908d** as *Mastigobryum wallichianum*, Hattori 1951.

Calatholejeunea K.I.Goebel

Calatholejeunea paradoxa (Schiffn.) K.I.Goebel. **MOLUCCAS**: AMBON: **LECTOTYPE** of *Lejeunea paradoxa* [Mizutani 1984: 331 as "holotype"], **Schiffner 1893b** as *Lejeunea paradoxa*, **1898** as *Colurolejeunea paradoxa*, Stephani 1916 as *Colura paradoxa*, **Jovet-Ast 1954, Bischler 1961**, Bonner 1963a, 1963b as *Colura paradoxa*, Grolle 1966a, Schuster 1969, **Mizutani 1984**, Gradstein 1985, Piippo 1992.

Calypogeia Raddi

Calypogeia goebelii (Schiffn.) Steph. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009**.

Caudalejeunea Schiffn.

Caudalejeunea cristiloba (Steph.) Gradst. **MOLUCCAS**: Mizutani 1977 as *Caudalejeunea circinata*. ?AMBON: Thiers and Gradstein 1989, Gradstein et al. 2002, Sass-Gyarmati 2003. SERAM: Verdoorn 1934a as *Caudalejeunea circinata*, **1934b** as *Caudalejeunea circinata*, Jovet-Ast 1958 as *Caudalejeunea circinata*, Miller et al. 1983 as *Caudalejeunea circinata*, **Mizutani 1986a** as *Caudalejeunea circinata*, **Akiyama 2009** as *Caudalejeunea circinata*. Note: we are not aware of any first hand report from Ambon.

Caudalejeunea reniloba (Gottsche) Steph. **MOLUCCAS**: Mizutani 1977, Siregar 2015. AMBON: **LECTOTYPE** of *Lopholejeunea sagrana* var. *dentistipula* [here designated], **Sande Lacoste 1864** as *Phragmicoma reniloba*, **Schiffner 1890** as *Lopholejeunea 'Sagraeana'* var. *dentistipula*, **1898** as *Lopholejeunea dentistipula* and *Thysananthus renilobus*, **Sydow 1894** as *Lopholejeunea 'Sagraeana'* var. *dentistipula*, Miller et al. 1983 also as *Thysananthus renilobus*, **Geissler and Bischler 1987** as *Lejeunea sagrana* var. *dentistipula*, **Mizutani 1988**, Bapna and Kachroo 2000b, **Zhu and Gradstein 2005** as *Lopholejeunea dentistipula*, Siregar et al. 2014, Rosyanti et al. 2018. SERAM: **Sande Lacoste 1864** as *Lejeunea recurvistipula* and *Phragmicoma reniloba*, **Schiffner 1898** as *Caudalejeunea recurvistipula* and *Thysananthus renilobus*, Verdoorn 1934a, **1934b**, Jovet-Ast 1958, Miller 1968, Swanson and Miller 1969, Tixier 1970a, 1970b as *Caudalejeunea 'renilyba'*, Miller et al. 1983 also as *Thysananthus renilobus*, **Mizutani 1986a, Mizutani 1988** also as *Caudalejeunea recurvistipula*, Bapna and Kachroo 2000b, **Akiyama 2009**, Siregar et al. 2014, Siregar 2015, Rosyanti et al. 2018, Ginting and Batubara 2019.

***Cephalozia* (Dumort.) Dumort.**

Cephalozia stolonacea (Herzog) Váňa. **MOLUCCAS**: Ambon: **Váňa 1993** as *Metahygrobiella stolonacea*, Schuster 2002 as *Metahygrobiella stolonacea*.

***Ceratolejeunea* (Spruce) J.B.Jack et Steph.**

Ceratolejeunea belangeriana (Gottsche) Steph. **MOLUCCAS**: Seram: **Mizutani 1986a**, Zhu et al. 2005, **Akiyama 2009**.
Ceratolejeunea moniliata Herzog. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009**.

***Cheilolejeunea* (Spruce) Steph.**

Cheilolejeunea ceylanica (Gottsche) R.M.Schust. et Kachroo. **MOLUCCAS**: Mizutani 1978. Bacan: **Hoffmann 1935** as *Pycnolejeunea ceylanica*. Ambon: **Schiffner 1893b** as *Lejeunea connivens*, **1898** as *Pycnolejeunea ceylanica*, Tixier 1967b, 1972, 1973b, Kamimura 1974, Miller et al. 1983 also as *Xenolejeunea ceylanica*, **Braggins et al. 2014**. Seram: **Mizutani 1986a**, 2009.
Cheilolejeunea falsinervis (Sande Lac.) R.M.Schust. et Kachroo. **MOLUCCAS**: Bacan: **Zwickel 1932** as *Pycnolejeunea falsinervis*, **Hoffmann 1935** as *Pycnolejeunea falsinervis*.
Cheilolejeunea gigantea (Steph.) R.M.Schust. et Kachroo. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Pycnolejeunea gigantea* [Thiers 1992: 16 as "holotype"], **Stephani 1896b** as *Pycnolejeunea gigantea*, **Schiffner 1898** as *Pycnolejeunea gigantea*, Stephani 1914 as *Pycnolejeunea gigantea*, **Hoffmann 1935** as *Pycnolejeunea gigantea*, **Thiers 1992**.
Cheilolejeunea incisa (Gottsche) R.M.Schust. et Kachroo. **MOLUCCAS**: Bacan: **Hoffmann 1935** as *Pycnolejeunea incisa*.
Cheilolejeunea intertexta (Lindenb.) Steph. **MOLUCCAS**: Ambon: **Grolle 1979b**, Mizutani 1982, Miller et al. 1983, Asthana et al. 1995, Zhu and So 1999, Piippo et al. 2002. Seram: **Mizutani 1986a**, **Akiyama 2009**.
Cheilolejeunea lindenbergii (Gottsche) Mizut. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Euosmolejeunea integristipula* [Bonner 1965: 153], **Stephani 1896b** as *Euosmolejeunea integristipula*, **Schiffner 1898** as *Euosmolejeunea integristipula*, **Bonner 1965** as *Euosmolejeunea integristipula*, **Mizutani 1972**, Pócs et al. 1994, Szabó 1997.
Cheilolejeunea longidens (Steph.) R.M.Schust. et Kachroo. **MOLUCCAS**: Ambon: **Thiers 1986** as *Pycnolejeunea demissa*.
Cheilolejeunea occlusa (Herzog) T.Kodama et N.Kitag. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009**.
Cheilolejeunea trapezia (Nees) Kachroo et R.M.Schust. **MOLUCCAS**: Ambon: **Schiffner 1893b** as *Lejeunea trapezia*, **1898** as *Pycnolejeunea trapezia*, **Hoffmann 1935** as *Pycnolejeunea meyeniana*, Zhu and Grolle 2004. Seram:

Mizutani 1986a as *Cheilolejeunea meyeniana* and *Cheilolejeunea imbricata*, **Akiyama 2009** as *Cheilolejeunea imbricata* and *Cheilolejeunea meyeniana*.

Cheilolejeunea trifaria (Reinw., Blume et Nees) Mizut. **MOLUCCAS**: Mizutani 1977. Ternate/Tidore: **LECTOTYPE** of *Lejeunea heterophylla* [to be designated], **Sande Lacoste 1856a, 1856b** both as *Lejeunea heterophylla*, **Schiffner 1898** as *Euosmolejeunea heterophylla*, Bonner 1965 as *Euosmolejeunea heterophylla*. Ambon: **Schiffner 1890** as *Euosmolejeunea trifaria*, **1898** as *Lejeunea trifaria*, **Sydow 1894** as *Euosmolejeunea trifaria*, Miller et al. 1983. Seram: **Sande Lacoste 1864** as *Lejeunea heterophylla*, **Schiffner 1898** as *Euosmolejeunea heterophylla*, Bonner 1965 as *Euosmolejeunea heterophylla*.

Cheilolejeunea ventricosa (Schiffn. ex P.Syd.) Xiao L.He. **MOLUCCAS**: Furuki and Yamaguchi 2005, Pócs et al. 2013. Ambon: **LECTOTYPE** of *Pycnolejeunea ventricosa* [here designated], **Schiffner 1890, 1898** both as *Pycnolejeunea ventricosa*, **Sydow 1894** as *Pycnolejeunea ventricosa*, Stephani 1914 as *Pycnolejeunea ventricosa*, **Zhu et al. 2002, Zhu and Lai 2005**, Pócs and Streimann 2006, **Renner 2011**.

Cheilolejeunea vittata (Steph. ex G.Hoffm.) R.M.Schust. et Kachroo. **MOLUCCAS**: Seram: **Mizutani 1986a**, Zhu and So 1999, Zhu et al. 2002, **Akiyama 2009**.

***Chiastocaulon* Carl**

Chiastocaulon braunianum (Nees) S.D.F.Patzak, M.A.M.Renner, Schäf.-Verw. et Heinrichs. **MOLUCCAS**: Halmahera: **Sande Lacoste 1864** as *Plagiochila brauniana*, **Schiffner 1898**, 1900 both as *Plagiochila brauniana*, Hattori 1952 as *Plagiochilion* '*Braunianus*', Miller et al. 1983 as *Plagiochilion braunianum*.

Chiastocaulon dendroides (Nees) Carl. **MOLUCCAS**: Jovet-Ast 1951, Grolle 1965. Bacan: **Carl 1931a**. Ternate/Tidore: **New to Ternate:** Ternate Piek v. Ternate Oosthelling (Ake abdas), 1951.09.02, *D.R. Pleyte 33* (BO11333). Ambon: **Stephani 1903a** as *Plagiochila dendroides*, Bonner 1963b, Miller et al. 1983. Seram: **Inoue 1986** as *Plagiochila dendroides*, **Akiyama 2009** as *Plagiochila dendroides*.

Chiastocaulon oppositum (Reinw., Blume et Nees) S.D.F.Patzak, M.A.M.Renner, Schäf.-Verw. et Heinrichs. **MOLUCCAS**: Ternate/Tidore: **LECTOTYPE** of *Plagiochila opposita* γ *filiformis* [to be designated], **Reinwardt et al. 1824** as *Jungermannia opposita*, **Lindenberg 1843** as *Plagiochila opposita* γ *filiformis*, Gottsche et al. 1844 as *Plagiochila opposita* γ *filiformis*, **Sande Lacoste 1856a** as *Plagiochila opposite* and *Plagiochila opposita* γ *filiformis*, **1864** as *Plagiochila opposita*, **Schiffner 1898** as *Plagiochila opposite* and *Plagiochila opposita* var. *filiformis*, Hattori 1942 as *Plagiochila opposita*, Inoue 1958 as *Noguchia opposita*, Miller et al. 1983 as *Plagiochilion oppositum*, Zheng et al. 2005 as *Plagiochilion oppositum*. Ambon: **Sande Lacoste 1864** as *Plagiochila opposita*, **Schiffner 1893b, 1898** both as *Plagiochila opposita*, Stephani 1904b as *Plagiochila opposita*, Hattori 1942 as *Plagiochila opposita*, Inoue 1958 as *Noguchia opposita*, Miller et al. 1983 as *Plagiochilion oppositum*, Bapna and Kachroo 2000b as *Plagiochilion oppositum*, Zheng et al. 2005 as *Plagiochilion oppositum*. Seram: **Herzog 1921** as *Plagiochila opposita*, **Carl 1931b** as *Plagiochila opposita*, **Akiyama 1986, Akiyama 2009** both as *Plagiochilion* '*oppositus*'.

Cladoradula **(Spruce) M.A.M.Renner, Gradst., Ilk.-Borg. et F.R.Oliveira-da-Silva**

Cladoradula campanigera (Mont.) M.A.M.Renner, Gradst., Ilk.-Borg. et F.R.Oliveira-da-Silva. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009** both as *Radula campanigera*, Yamada 1989 as *Radula campanigera*.

Cololejeunea **(Spruce) Steph.**

Cololejeunea aequabilis (Sande Lac.) Schiffn. **MOLUCCAS**: Inoue and Miller 1965 as *Cololejeunea yulensis*, Miller et al. 1983 as *Cololejeunea yulensis*. SERAM: **Mizutani 1986a** as *Cololejeunea yulensis*, **Akiyama 2009** as *Cololejeunea yulensis*.

Cololejeunea angustiflora (Steph.) Mizut. **MOLUCCAS**: SERAM: **Mizutani 1986a** as *Cololejeunea crenulata* and *Cololejeunea javanica*, **Akiyama 2009** as *Cololejeunea javanica* and *Cololejeunea crenulata*.

Cololejeunea dozyana (Sande Lac.) Schiffn. **MOLUCCAS**: Bonner 1963b, Mizutani 1977, Tixier 1980, Pócs and Piippo 2011. BACAN: **Benedix 1953**. SERAM: **Mizutani 1986a**, Zhu and So 1998b, Zhu and So 1999, **Akiyama 2009**, Müller et al. 2016.

Cololejeunea equialbi Tixier. **MOLUCCAS**: Pócs et al. 2011. SERAM: **Mizutani 1986a**, Pócs et al. 1994, Zhu and So 2001, Eggers 2006, **Akiyama 2009** as *Cololejeunea 'equalbi'*, Pócs and Piippo 2011, Pócs and Podani 2015.

Cololejeunea falcata (Horik.) Benedix. **MOLUCCAS**: SERAM: **Mizutani 1986a** as *Cololejeunea falcatoides*, **Akiyama 2009** as *Cololejeunea falcatoides*.

Cololejeunea floccosa (Lehm. et Lindenb.) Schiffn. **MOLUCCAS**: SERAM: **Mizutani 1986a**, **Akiyama 2009**.

Cololejeunea hamata Steph. **MOLUCCAS**: AMBON: **LECTOTYPE** [Bonner 1963b: 830], **Stephani 1895, Schiffner 1898**, Stephani 1916 as *Physocolea hamata*, **Bonner 1963b**.

Cololejeunea haskarliana (Lehm.) Schiffn. **MOLUCCAS**: SERAM: **Mizutani 1986a**, **Akiyama 2009** as *Cololejeunea 'hasskarliana'*.

Cololejeunea inflectens (Mitt.) Benedix. **MOLUCCAS**: Jovet-Ast and Tixier 1962 as *Cololejeunea ciliatilobula*, Tixier 1967b, 1971, 1979 all as *Cololejeunea ciliatilobula*, Mizutani 1975 as *Campylolejeunea inflectens*, Bapna and Kachroo 2000b as *Campylolejeunea inflectens*. AMBON: Stephani 1916 as *Physocolea ciliatilobula*, **Benedix 1953** as *Cololejeunea ciliatilobula*, **Bischler 1961** as *Campylolejeunea ciliatilobula*, Bonner 1963a as *Campylolejeunea ciliatilobula*, 1963b as *Cololejeunea ciliatilobula*. SERAM: **Mizutani 1986a** as *Cololejeunea peculiaris*, **Akiyama 2009** as *Cololejeunea peculiaris*.

Cololejeunea koponenii (Pócs) Pócs. **MOLUCCAS**: SERAM: **Bi et al. 2019**.

Cololejeunea lanciloba Steph. **MOLUCCAS**: SERAM: **Mizutani 1986a**, Pócs et al. 1994, **Akiyama 2009**.

Cololejeunea metzgeriopsis (K.I.Goebel) Gradst., R.Wilson, Ilk.-Borg. et Heinrichs. **MOLUCCAS**: Miller et al. 1983 as *Metzgeriopsis pusilla*. BACAN: Schiffner 1893a as *Metzgeriopsis pusilla*, **Schiffner 1893c** as *Lejeunea pusilla*, **1898** as *Metzgeriopsis pusilla*, Stephani 1916 as *Metzgeriopsis pusilla*, Gradstein et al. 2006. SERAM: **Mizutani 1986a** as *Metzgeriopsis pusilla*, Gradstein et al. 2006, **Akiyama 2009** as *Metzgeriopsis pusilla*.

Cololejeunea obliqua (Nees et Mont.) Schiffn. **MOLUCCAS**: SERAM: **Mizutani 1986a** as *Cololejeunea nymannii*, **Akiyama 2009** as *Cololejeunea 'nymanii'*.

Cololejeunea papillosa (K.I.Goebel) Mizut. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009**.

Cololejeunea plagiophylla Benedix. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009**.

Cololejeunea planissima (Mitt.) Abeyw. var. *planissima*. **MOLUCCAS**: Seram: **Mizutani 1986a** as *Cololejeunea planissima*, **Akiyama 2009** as *Cololejeunea planissima*.

Cololejeunea raduliloba Steph. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009**.

Cololejeunea stephanii Schiffn. ex Benedix. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009**.

Cololejeunea triapiculata (Herzog) Tixier. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009**.

Cololejeunea trichomanis (Gottsche) Besch. **MOLUCCAS**: Seram: **Mizutani 1986a** as *Cololejeunea goebelii*, **Akiyama 2009** as *Cololejeunea goebelii*.

***Colura* (Dumort.) Dumort.**

Colura acroloba (Prantl) Jovet-Ast. **MOLUCCAS**: Seram: **Mizutani 1986a**, Eggers et al. 1998, **Akiyama 2009**.

Colura amboinensis Steph. **MOLUCCAS**: Ambon: **LECTOTYPE** [to be designated], ORIGINAL MATERIAL of *Colurolejeunea superba* var. *typica*, **Schiffner 1890** as '*Coluro-Lejeunea*' *superba* var. *typica*, **Stephani 1916**, Bonner 1963b, Miller et al. 1983 as *Colurolejeunea superba*.

Colura ari (Steph.) Steph. **MOLUCCAS**: Halmahera: **Jovet-Ast 1953**, Bonner 1963b, Grolle 1965, Pócs et al. 1967, Tixier 1967a, Onraedt 1979, Miller et al. 1983. Seram: **Mizutani 1986a**, **Akiyama 2009**.

Colura conica (Sande Lac.) K.I.Goebel. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009**.

Colura imperfecta Steph. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009**.

Colura karstenii K.I.Goebel. **MOLUCCAS**: Ambon: **LECTOTYPE** [Jovet-Ast 1953: 230, Bonner 1963b: 869], **Stephani 1896b** as *Colurolejeunea karstenii*, 1916, **Schiffner 1898** as *Colurolejeunea karstenii*, Schiffner and Stephani 1901 as *Colurolejeunea karstenii* var. *latifolia*, **Jovet-Ast 1953, Bonner 1963b**, Tixier 1970a, **Zhu and So 2001**, Pócs 2013, **Sangrattanaprasert et al. 2018**.

Colura maxima Jovet-Ast. **MOLUCCAS**: Halmahera: **LECTOTYPE** [to be designated], **Jovet-Ast 1953, Bonner 1963b**.

Colura ornata K.I.Goebel. **MOLUCCAS**: Pócs and Ninh 2012. Seram: **Mizutani 1986a**, Pócs et al. 1994, **Akiyama 2009**.

Colura superba (Mont.) Steph. **MOLUCCAS**: Reiner-Drehwald 1999 as *Lejeunea superba* var. *typica*. Ambon: Bonner 1963b as *Colurolejeunea superba*, **Geissler and Bischler 1987** as *Lejeunea superba* var. *typica*. Seram: **Mizutani 1986a**, **Akiyama 2009**.

***Conoscyphus* Mitt.**

Conoscyphus trapezioides (Sande Lac.) Schiffn. **MOLUCCAS**: Seram: **Akiyama 1986, Akiyama 2009**.

Cryptolophocolea L.Söderstr., Crand.-Stotl., Stotler et Váňa

Cryptolophocolea costata (Nees) L.Söderstr. **MOLUCCAS**: Seram: **Akiyama 1986, 2009** both as *Lophocolea giulianettii*.

Cuspidatula **Steph.**

Cuspidatula contracta (Reinw., Blume et Nees) Steph. **MOLUCCAS**: Ambon: **Schiffner 1893b, 1898** both as *Anastrophyllum contractum*, Schiffner 1900 as *Anastrophyllum contractum*, **Stephani 1901c**, Bonner 1962b as *Anastrophyllum contractum*, Bonner 1963b, Kitagawa 1970, Grolle 1971, Bizot and Pócs 1974, Miller et al. 1983, Engel and Glenny 2008. Seram: **Akiyama 1986** as *Jamesoniella contracta*, **Akiyama 2009** as *Jungermannia contracta*.

Cuspidatula flaccida (Steph.) K.Feldberg, Váňa, Hentschel et Heinrichs. **MOLUCCAS**: Seram: **Akiyama 1986, 2009** both as *Anomacaulis flaccidus*.

Cuspidatula flexicaulis (Nees) Váňa et L.Söderstr. **MOLUCCAS**: Miller et al. 1983 as *Jamesoniella flexicaulis*. Ambon: **Grolle 1971** as *Jamesoniella flexicaulis*. Seram: **Akiyama 1986, 2009** both as *Jungermannia flexicaulis*.

Denotarisia **Grolle**

Denotarisia linguifolia (De Not.) Grolle. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Jungermannia ovifolia* [Grolle 1971: 11 as “holotype”], **Schiffner 1893b, 1898**, 1900 all as *Jamesoniella ovifolia*, **Stephani 1901b** as *Jamesoniella ovifolia*, Grolle 1966a as *Jamesoniella ovifolia*, **1971, Bonner 1976** as *Jungermannia ovifolia*, Miller et al. 1983 also as *Jamesoniella ovifolia* and *Jungermannia ovifolia*, Váňa and Piippo 1989b, Váňa 1991b. Seram: **Akiyama 1986, 2009**.

Dinckleria **Trevis.**

Dinckleria singularis (Schiffn.) M.A.M.Renner, Schäf.-Verw. et Heinrichs. **MOLUCCAS**: Ternate/Tidore: **Gottsche et al. 1844** as *Plagiochila trapezoidea* β *tenera*, **Sande Lacoste 1856a**, 1856b both as *Plagiochila trapezoidea* β *tenera*, **Schiffner 1898** as *Plagiochila trapezoidea* var. *tenera*. Seram: **So 2000a, 2001a, 2001b** all as *Plagiochila singularis*, Renner et al. 2016.

Diplasiolejeunea **(Spruce) Schiffn.**

Diplasiolejeunea cavifolia Steph. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009**.

Diplasiolejeunea patelligera Herzog. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009**.

Drepanolejeunea **(Spruce) Steph.**

Drepanolejeunea blumei Steph. var. *angustistipa* Herzog. **MOLUCCAS**: Bonner 1965. Bacan: **Herzog 1936**.

Drepanolejeunea dactylophora (Nees, Lindenb. et Gottsche) J.B.Jack et Steph. **MOLUCCAS**: Mizutani 1961 as *Drepanolejeunea dactylophora*, Inoue 1965, Kamimura 1974, Mizutani 1975 as *Drepanolejeunea dactylophora*, Mizutani 1977 as *Drepanolejeunea dactylophora*, Mizutani 1978 as *Drepanolejeunea dactylophora*. Bacan: **Schiffner 1893c**. ?Ambon: Stephani 1913 as *Drepanolejeunea dactylophora*, Tixier 1962 as *Drepanolejeunea dactylophora*, 1972, Bonner 1965 as *Drepanolejeunea dactylophora*, Pócs et al. 1967, Miller et al.

1983 as *Drepanolejeunea dactylophora*, Zhu and So 2001 as *Drepanolejeunea dactylophora*. Seram: **Mizutani 1986a** as *Drepanolejeunea dactylophora*, Zhu and So 2001 as *Drepanolejeunea dactylophora*, **Akiyama 2009**. Note: we are not aware of any first hand report from Ambon.

Drepanolejeunea foliicola Horik. **MOLUCCAS**: Seram: **Mizutani 1986a** as *Leptolejeunea foliicola*.

Drepanolejeunea grandis Herzog. **MOLUCCAS**: **LECTOTYPE** [to be designated], **Herzog 1939, Bonner 1965**, Pócs et al. 1995, Pócs et al. 2019a. Seram: **Mizutani 1986a**, **Akiyama 2009**.

Drepanolejeunea hampeana Steph. **MOLUCCAS**: Ambon: Stephani 1913, Bonner 1965, Miller et al. 1983.

Drepanolejeunea intermedia Zwickel. **MOLUCCAS**: O'Shea et al. 1997. Bacan: **Grolle 1976**. Seram: **Mizutani 1986a**, **Akiyama 2009**.

Drepanolejeunea levicornua Steph. **MOLUCCAS**: Seram: **Mizutani 1986a** as *Drepanolejeunea levicornua* var. *levicornua*, **1990**, Streimann 1991, Szabó 1997, Eggers et al. 1998, Zhu and So 2001, **Akiyama 2009** as *Drepanolejeunea levicornua* var. *levicornua*, Siregar et al. 2017, Pócs et al. 2019b, Susilo et al. 2023.

Drepanolejeunea longicornua (Herzog) Mizut. **MOLUCCAS**: Seram: **Mizutani 1986a** as *Drepanolejeunea levicornua* var. *longicornua*, **1990, Akiyama 2009** as *Drepanolejeunea levicornua* var. *longicornua*.

Drepanolejeunea longicruris (Steph.) Grolle et R.L.Zhu. **MOLUCCAS**: Seram: **Mizutani 1986a** as *Rhaphidolejeunea longicruris*, Grolle and Zhu 2000, **Akiyama 2009** as *Rhaphidolejeunea longicruris*.

Drepanolejeunea lyrata Grolle. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009**.

Drepanolejeunea moluccensis Herzog. **MOLUCCAS**: Bacan: **LECTOTYPE** [Nadhifah et al. 2021: 6], **Herzog 1934, Nadhifah et al. 2021**.

Drepanolejeunea obliqua Steph. **MOLUCCAS**: Pócs et al. 1967. Bacan: **Herzog 1939**.

Drepanolejeunea pentadactyla (Mont.) Steph. **MOLUCCAS**: Jovet-Ast 1958 as *Drepanolejeunea micholitzii*, Jovet-Ast and Tixier 1962 as *Drepanolejeunea micholitzii* var. *genuina*, Bonner 1965 as *Drepanolejeunea micholitzii* var. *genuina*, Miller 1968 as *Drepanolejeunea micholitzii*, Tixier 1970b as *Drepanolejeunea micholitzii*, Kitagawa 1981 as *Drepanolejeunea micholitzii*, Miller et al. 1983 as *Drepanolejeunea micholitzii*. Bacan: **ORIGINAL MATERIAL** of *Drepanolejeunea micholitzii* var. *genuina*, **Herzog 1934** as *Drepanolejeunea micholitzii* var. *genuina*. Seram: **Mizutani 1986a** as *Drepanolejeunea micholitzii*, Zhu and So 2001, **Akiyama 2009** as *Drepanolejeunea micholitzii*, Asthana and Shukla 2009, Dey et al. 2013, Susilo et al. 2023.

— var. *dactylophoroides* (Herzog) Pócs. ?**MOLUCCAS**: Tixier 1979 as *Drepanolejeunea micholitzii* var. *dactylophoroides*. Note: we are not aware of any first hand report of this variety from Moluccas although it is reported to occur on neighbouring islands.

Drepanolejeunea spinosocornuta Steph. **MOLUCCAS**: Seram: **Mizutani 1986a**, **1990, Akiyama 2009**, Pócs et al. 2019a.

Drepanolejeunea tenera K.I.Goebel. **MOLUCCAS**: Jovet-Ast 1958, Bonner 1965 as *Drepanolejeunea tenera* var. *genuina*, Pócs 1969a, Tixier 1974b. Bacan: **ORIGINAL MATERIAL** of *Drepanolejeunea tenera* var. *genuina*, **Herzog 1934** as *Drepanolejeunea tenera* var. *genuina*. Seram: **Mizutani 1986a**, **Akiyama 2009**.

Drepanolejeunea ternatensis (Gottsche) Schiffn. **MOLUCCAS**: Inoue 1965, Miller 1968, Pócs 1969a, Kamimura 1974, Mizutani 1975, 1977, 1978, Udar and Awasthi 1982 as *Drepanolejeunea ternatensis* var. *ternatensis*, Bapna and Kachroo 2000b as *Drepanolejeunea ternatensis* var. *ternatensis*, Xiong and Cao 2018, Siregar et al. 2020a. Bacan: **Herzog 1939** as *Drepanolejeunea ternatensis* var. *ternatensis* as *Drepanolejeunea ternatensis*. Ternate/Tidore: **LECTOTYPE** of *Lejeunea ternatensis* [to be designated], **Gottsche et al. 1845b** as *Lejeunea ternatensis*, **Sande Lacoste 1856a**, 1856b both as *Lejeunea ternatensis*, **Stephani 1890b** as *Lejeunea ternatensis*, **Schiffner 1898, Mizutani 1961**, Miller et al. 1983 as *Lejeunea ternatensis*, *Microlejeunea ternatensis* and *Drepanolejeunea ternatensis*, **Zhu and So 2001, Dey et al. 2013**. Seram: **Mizutani 1986a** as *Drepanolejeunea ternatensis*, Zhu and So 2001, **Akiyama 2009**, Dey et al. 2013, Siregar et al. 2017, Susilo et al. 2023.

Drepanolejeunea thwaitesiana (Mitt.) Steph. var. *thwaitesiana*. **MOLUCCAS**: Seram: **Mizutani 1990**, Zhu and So 2001, Haerida 2009, Siregar et al. 2017, Susilo et al. 2023.

Drepanolejeunea tricornua Herzog. **MOLUCCAS**: Seram: **LECTOTYPE** [Bonner 1965: 105], **Herzog 1936, Bonner 1965**, Tixier 1979, Mizutani 1990, **Pócs et al. 2011**, Pócs et al. 2013, Pócs et al. 2014, Siregar et al. 2017, **Samarakkody et al. 2018**, Kasiani et al. 2019.

Dumortiera Nees

Dumortiera hirsuta (Sw.) Nees. **MOLUCCAS**: Ambon: **Sopacua et al. 2020** as *Dumortiera* '*hirsute*' [Saparua I]. Note: we are not aware of any first hand report from **Moluccas** although it is reported to occur on neighbouring islands.

Frullania Raddi

Frullania akiyamae S.Hatt. **MOLUCCAS**: Seram: HOLOTYPE, **Hattori 1986b, Engel 1993, Crosby and Engel 2006, Akiyama 2009**.

Frullania apiculata (Reinw., Blume et Nees) Nees. **MOLUCCAS**: Verdoorn 1930, Inoue and Miller 1965, Inoue 1965, Pócs et al. 1967, Miller 1968, Swanson and Miller 1969, Tixier 1972, Haerida et al. 2023. Halmahera: **Sande Lacoste 1864, Schiffner 1898, Umagap 2019**. Ambon: **Schiffner 1890, 1898, Sydow 1894**. Seram: **Sande Lacoste 1864, Schiffner 1898, Hattori 1986b, Akiyama 2009**.

— var. *apiculata*. **MOLUCCAS**: Ambon: Schiffner 1893b, Miller et al. 1983. Seram: Miller et al. 1983.

— var. *goebelii* Schiffn. **MOLUCCAS**: Tixier 1971. Ambon: **LECTOTYPE** of *Frullania karstenii* [to be designated], **Schiffner 1893b, 1898** both as *Frullania karstenii*, Stephani 1911 as *Frullania karstenii*, **Bonner 1965** as *Frullania karstenii*.

Frullania armatifolia Verd. **MOLUCCAS**: Seram: **Hattori 1986b, Akiyama 2009**.

Frullania attenuata Steph. **MOLUCCAS**: Seram: **Hattori 1986b, Akiyama 2009**.

Frullania berthoumieui Steph. **MOLUCCAS**: Ambon: **Hattori 1975a**, 1976, Hattori et al. 1977, Bapna and Kachroo 2000b.

Frullania claviloba Steph. **MOLUCCAS**: Ambon: **LECTOTYPE** [Bonner 1965: 266], **Stephani 1911, Verdoorn 1930, Bonner 1965**, Pócs et al. 1967, Kamimura 1974, Hattori 1975a, **1975d**, 1976, 1982, Hattori et al. 1977, **Sukkharak 2018**.

Frullania cordistipula (Reinw., Blume et Nees) Nees. **MOLUCCAS**: Halmahera: **Sande Lacoste 1864**, **Schiffner 1898**, Merrill and Merritt 1910, Hattori 1977, Miller et al. 1983.

— var. *dentistipula* S.Hatt. **MOLUCCAS**: Seram: **HOLOTYPE**, **Hattori 1986b, Engel 1993, Crosby and Engel 2006, Akiyama 2009**.

Frullania ericoides (Nees) Mont. **MOLUCCAS**: Verdoorn 1930 as *Frullania squarrosa* var. *planescens*, Bonner 1965 as *Frullania squarrosa* f. *campanuloides*, Bai 2002 as *Frullania ericoides* var. *planescens*, Haerida et al. 2023. Seram: **Sande Lacoste 1864** as *Frullania squarrosa*, **Schiffner 1898** as *Frullania squarrosa*, Miller et al. 1983 as *Frullania squarrosa*, **Hattori 1986b, Akiyama 2009**.

Frullania fallax Gottsche. **MOLUCCAS**: Halmahera: **Sande Lacoste 1864**, **Schiffner 1898**, Hattori 1975a as *Frullania fallax* var. *fallax*.

Frullania gaudichaudii (Nees et Mont.) Nees et Mont. **MOLUCCAS**: Ambon: **Schiffner 1893b**, Schiffner and Stephani 1901, **Verdoorn 1930**, Bonner 1965, Swanson and Miller 1969, Kamimura 1971, Miller et al. 1983, Haerida et al. 2023. Seram: **Hattori 1986b, Akiyama 2009**.

Frullania gracilis (Reinw., Blume et Nees) Nees. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Frullania lacerifolia* [Bonner 1965: 345], **Stephani 1911** as *Frullania lacerifolia*, Verdoorn 1930 as *Frullania gracilis* var. *lacerifolia*, **Bonner 1965** as *Frullania gracilis* var. *lacerifolia* and *Frullania lacerifolia*, Kamimura 1974, Miller et al. 1983. Seram: **Hattori 1986b**.

— var. *gracilis*. **MOLUCCAS**: Seram: **Akiyama 2009**.

— var. *vittata* S.Hatt. **MOLUCCAS**: Seram: **HOLOTYPE, Hattori 1986b, Engel 1993, Crosby and Engel 2006, Akiyama 2009**.

Frullania grandistipula Lindenb. **MOLUCCAS**: Bacan: **Verdoorn 1930**. Halmahera: **Sande Lacoste 1864** as *Frullania rugosa*, **Schiffner 1898** as *Frullania rugosa*, Pócs et al. 1967, Hattori 1974b, 1975a, 1976 as *Frullania grandistipula* var. *grandistipula*, 1979, 1982, Miller et al. 1983, Hattori and Piippo 1986.

Frullania hasskarliana Lindenb. **MOLUCCAS**: Haerida et al. 2023.

— var. *gracilis* S.Hatt. **MOLUCCAS**: Seram: **HOLOTYPE, Hattori 1986b, Engel 1993, Crosby and Engel 2006, Akiyama 2009**.

— var. *hasskarliana*. **MOLUCCAS**: Seram: **Hattori 1986b, Akiyama 2009**.

— var. *parvidentata* S.Hatt. **MOLUCCAS**: Seram: **HOLOTYPE, Hattori 1986b, Engel 1993, Crosby and Engel 2006, Akiyama 2009**.

Frullania heteromorpha Schiffn. **MOLUCCAS**: Seram: **Hattori 1986b, Akiyama 2009**.

Frullania integristipula (Nees) Nees

— var. *emarginata* Verd. **MOLUCCAS**: Halmahera: **Verdoorn 1930, Hattori 1980,** Hattori 1982, Hattori and Piippo 1986.

— var. *integristipula*. **MOLUCCAS**: Halmahera: **Hattori 1980** as *Frullania integristipula*.

Frullania intermedia (Reinw., Blume et Nees) Nees. **MOLUCCAS**: Inoue and Miller 1965, Bapna and Kachroo 2000b. Seram: Miller et al. 1983.

— subsp. *intermedia*. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Frullania amboinensis* [Bonner 1965: 228], **LECTOTYPE** of *Frullania billardiereana* [Bonner 1965: 248], **Montagne 1843, 1856** both as *Frullania billardiereana*, **Gottsche et al. 1845b** as *Frullania billardiereana*, **Schiffner 1890, 1898** both as *Frullania amboinensis*, **1898** as *Frullania billardiereana*, **Sydow 1894** as *Frullania amboinensis*, Schiffner and Stephani 1901 as *Frullania amboinensis*, Stephani 1911 as *Frullania amboinensis*, Verdoorn 1930 as *Frullania intermedia* f. '*billardieriana*', **Verdoorn 1930** as *Frullania intermedia* var. *amboinensis*, **Bonner 1965** as *Frullania intermedia* f. '*billardieriana*', Bonner 1965 as *Frullania intermedia* var. a*mboinensis*, *Frullania amboinensis* and *Frullania billardiereana*, Hattori 1976 as *Frullania intermedia* f. '*billardieriana*', **1980** as *Frullania billardiereana*, 1982, 1986 both as *Frullania intermedia* f. '*billardieriana*', Miller et al. 1983 as *Frullania intermedia* f. '*billardierana*'. SERAM: **Sande Lacoste 1864** as *Frullania billardiereana*, **Schiffner 1898** as *Frullania billardiereana*, **Verdoorn 1930** as *Frullania intermedia* f. '*billardieriana*', Bonner 1965 as *Frullania intermedia* f. '*billardieriana*', Hattori 1976 as *Frullania intermedia* f. '*billardieriana*', 1980 as *Frullania billardiereana*, 1982, 1986 both as *Frullania intermedia* f. '*billardieriana*', Miller et al. 1983 as *Frullania intermedia* f. '*billardierana*'.

Frullania junghuhniana Gottsche

— var. *junghuhniana*. **MOLUCCAS**: SERAM: **Hattori 1986b, Akiyama 2009**.

— var. *tenella* (Sande Lac.) Grolle et S.Hatt. **MOLUCCAS**: SERAM: **Hattori 1986b, Akiyama 2009**.

Frullania multilacera Steph. **MOLUCCAS**: SERAM: **Hattori 1986b, Akiyama 2009**.

Frullania nepalensis (Spreng.) Lehm. et Lindenb. **MOLUCCAS**: BACAN: **Verdoorn 1930**, Hattori 1952, 1973b, Kamimura 1961, Pócs et al. 1967.

Frullania nigricaulis (Reinw., Blume et Nees) Nees. **MOLUCCAS**: HALMAHERA: **Verdoorn 1930**, Hattori 1974b, 1975c, Hattori et al. 1977.

Frullania nobilis Steph. var. *cochleata* (Steph.) S.Hatt. **MOLUCCAS**: SERAM: **Hattori 1986b, Akiyama 2009**.

Frullania nodulosa (Reinw., Blume et Nees) Nees. **MOLUCCAS**: Verdoorn 1930 as *Frullania nodulosa* β *plana*, *Frullania nodulosa* f. *dapitana* and *Frullania nodulosa* f. *irreflexa*, Kamimura 1943 as *Frullania nodulosa* f. *dapitana*, Bonner 1965 as *Frullania nodulosa* f. *dapitana*, Bonner 1965 as *Frullania nodulosa* f. *irreflexa*, Miller et al. 1983 as *Frullania dapitana* and *Frullania nodulosa* f. *irreflexa*, Haerida et al. 2023. MOROTAI: **Hattori 1975a, Hattori 1980** as *Frullania nodulosa* var. *nodulosa*, Miller et al. 1983. AMBON: **LECTOTYPE** of *Frullania nodulosa* β *plana* [to be designated], **Sande Lacoste 1864** also as *Frullania thuillieri*, **Schiffner 1890** as *Frullania nodulosa* var. *nodulosa* and *Frullania nodulosa* β *plana*, **1893b, 1898** also as *Frullania replicate* and *Frullania nodulosa* β *plana*, **Sydow 1894** as *Frullania nodulosa* β *plana*, **Verdoorn 1930, 1932** as *Frullania nodulosa* f. *irreflexa*, Hattori 1951, **Bonner 1965** as *Frullania nodulosa* β *plana*, Swanson and Miller 1969, **Hattori 1975a, 1980** as *Frullania nodulosa* var. *nodulosa*, Miller et al. 1983. SERAM: **Sande Lacoste 1864, Verdoorn 1930**, Hattori 1951, Swanson and Miller 1969, **Hattori 1980** as *Frullania nodulosa* var. *nodulosa*, **1986b**, Miller et al. 1983, **Akiyama 2009**.

Frullania orientalis Sande Lac. **MOLUCCAS**: Bapna and Kachroo 2000b, Haerida et al. 2023. SERAM: **Hattori 1986b, Akiyama 2009**.

Frullania ornithocephala (Reinw., Blume et Nees) Nees. **MOLUCCAS**: Haerida 2015. AMBON: Merrill and Merritt 1910, **Verdoorn 1930**, Bonner 1965, Hattori 1974c, 1975c, 1976, Hattori et al. 1977. SERAM: **Verdoorn 1930**, Bonner 1965, Hattori 1974c, 1975c, 1976, Hattori et al. 1977.

— var. *major* (Nees) Schiffn. **MOLUCCAS**: AMBON: **Schiffner 1893b, 1898**.

— var. *ornithocephala*. **MOLUCCAS**: AMBON: Hattori 1974a, 1975a. SERAM: Hattori 1974a, 1975a as *Frullania ornithocephala*.

Frullania pauciramea Steph. **MOLUCCAS**: Seram: **Hattori 1986b, Akiyama 2009**.

Frullania piptophylla S.Hatt. var. *minor* S.Hatt. **MOLUCCAS**: Seram: **HOLOTYPE, Hattori 1986b, Engel 1993, Crosby and Engel 2006, Akiyama 2009**.

Frullania pulogensis Steph. **MOLUCCAS**: Seram: **Hattori 1986b, Akiyama 2009**.

Frullania ramuligera (Nees) Mont. **MOLUCCAS**: Seram: **Hattori 1986b, Akiyama 2009**.

Frullania reflexistipula Sande Lac. var. *reflexistipula* **MOLUCCAS**: Haerida et al. 2023. Seram: **Sande Lacoste 1864**, **Schiffner 1898, Verdoorn 1930**, Hattori 1973b, 1974a, 1974c, 1975a, 1976, 1982, **1986b**, Miller et al. 1983, Hattori and Piippo 1986, **Akiyama 2009**.

Frullania repandistipula Sande Lac. **MOLUCCAS**: Ambon: Stephani 1911, Verdoorn 1930 [rejecting Stephani's reports], Bonner 1965, Hattori 1973a [rejecting earlier reports], Bizot et al. 1978. Seram: **Hattori 1986b, Akiyama 2009**. Note: the only report from Ambon is rejected as *Frullania tricarinata* by Verdoorn (1930).

Frullania serrata Gottsche. **MOLUCCAS**: Pócs 1971, Hattori 1974a, Miller et al. 1983. Bacan: **Verdoorn 1930**.

— var. *ceramensis* S.Hatt. **MOLUCCAS**: Seram: **HOLOTYPE, Hattori 1986b, Engel 1993, Crosby and Engel 2006, Akiyama 2009**.

— var. *hamatispina* (S.Hatt.) S.Hatt. **MOLUCCAS**: Seram: **Hattori 1986b, Akiyama 2009**.

— var. *serrata*. **MOLUCCAS**: Seram: **Hattori 1986b** as *Frullania serrata* f. *crispulo-dentata*, **Akiyama 2009** as *Frullania serrata* f. *crispulo-dentata*.

Frullania subcaduca S.Hatt. **MOLUCCAS**: Seram: **Hattori 1986b, Akiyama 2009**.

Frullania sublignosa Steph. **MOLUCCAS**: Seram: **Hattori 1986b, Akiyama 2009**.

Frullania subnigricaulis S.Hatt. var. *subtruncata* S.Hatt. **MOLUCCAS**: Seram: **Hattori 1986b, Akiyama 2009**.

Frullania subocellata S.Hatt. **MOLUCCAS**: Seram: **HOLOTYPE, Hattori 1986b**, 1988, **Engel 1993, Crosby and Engel 2006, Akiyama 2009**, Pócs et al. 2014.

Frullania ternatensis Gottsche. **MOLUCCAS**: Haerida 2015, Haerida et al. 2023. Bacan: **Verdoorn 1930**, Tixier 1962, Kamimura 1974. Ternate/Tidore: **LECTOTYPE** [Bonner 1965: 451], **Gottsche et al. 1846, Sande Lacoste 1856a,** 1856b, **Schiffner 1898, Verdoorn 1930**, Tixier 1962, 1970a, 1971, 1972, Kamimura 1974, Miller et al. 1983. Ambon: **Verdoorn 1932**. Seram: **Verdoorn 1932**, Miller et al. 1983.

— var. *non-appendiculata* S.Hatt. **MOLUCCAS**: Seram: **Hattori 1986b, Akiyama 2009**.

— var. *ternatensis*. **MOLUCCAS**: Ternate/Tidore: Hattori 1974a. Seram: **Hattori 1975a**.

Frullania tricarinata Sande Lac. **MOLUCCAS**: Ambon: **Schiffner 1893b, 1898**, Verdoorn 1930.

Frullania trichodes Mitt. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Frullania picta* [Bonner 1965: 400; here affirmed], **Stephani 1894a** as *Frullania picta*, **Schiffner 1898** as *Frullania picta*, **Verdoorn 1930** as *Frullania picta*, Svihla 1955, 1959 both as *Frullania picta*, Kamimura 1961, 1974 both as *Frullania tenuicaulis*, Arnell 1965 as *Frullania picta*, **Bonner 1965** as *Frullania picta*, Kitagawa 1969 as *Frullania picta*, Tixier 1973b as *Frullania tenuicaulis*, 1974b as *Frullania picta*.

Frullania vaginata (Sw.) Nees. **MOLUCCAS**: Ternate/Tidore: **Reinwardt et al. 1824** as *Jungermannia vaginata*, **Nees 1830** as *Jungermannia vaginata*. Ambon: **Sande Lacoste 1864** [Saparoea I], **Verdoorn 1930**, Hattori 1975a, 1975c 1982, Hattori and Piippo 1986.

Gottschelia **Grolle**

Gottschelia schizopleura (Spruce) Grolle. **MOLUCCAS**: Váňa and Piippo 1989b, Váňa 1991b, Schuster 2002, Long and Váňa 2007. HALMAHERA: **Sande Lacoste 1864** as *Jungermannia flexicaulis* β *microphylla*. TERNATE/TIDORE: **Schiffner 1898** as *Jamesoniella flexicaulis* var. *microphylla*, 1900 as *Jamesoniella microphylla*, **Stephani 1901b** as *Jamesoniella microphylla*, Bonner 1966 as *Jamesoniella microphylla*, **Grolle 1968a**, Bizot and Pócs 1974, Miller et al. 1983. SERAM: **Sande Lacoste 1864** as *Jungermannia flexicaulis* β *microphylla*, **Schiffner 1898** as *Jamesoniella flexicaulis* var. *microphylla*, 1900 as *Jamesoniella microphylla*, **Stephani 1901b** as *Jamesoniella microphylla*, Bonner 1966 as *Jamesoniella microphylla*, **Grolle 1968a**, Miller et al. 1983, Bapna and Kachroo 2000b.

Hattoriolejeunea **Mizut.**

Hattoriolejeunea akiyamae Mizut. **MOLUCCAS**: SERAM: **HOLOTYPE, Mizutani 1986a, Engel 1993, Crosby and Engel 2006, Akiyama 2009**.

Herbertus **Gray**

Herbertus longifissus Steph. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009**.

Herbertus longispinus J.B.Jack et Steph. **MOLUCCAS**: AMBON: **Schiffner 1893b** as '*Herberta longispina*' [but represents *Herbertus pilifer*], **1898** as "*Herberta longispina*' [but citing only the type of *Herbertus pilifer*]. SERAM: **Akiyama 1986, 2009**.

Herbertus pilifer (Steph.) H.A.Mill. **MOLUCCAS**: AMBON: **LECTOTYPE** of *Schisma pilifera* [Miller 1965: 327], Stephani 1909c as *Schisma pilifera*, **Miller 1965** as '*Herberta pilifera*', Miller et al. 1983 as *Herbertus pilifer* and *Schisma piligerum*, **Piippo 1984a** as *Herbertus pilifer*, **So 2003b** as *Herbertus pilifer*, **Juslén 2006** as *Herbertus pilifer*.

Herbertus ramosus (Steph.) H.A.Mill. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009** both as *Herbertus javanicus*.

Herbertus sendtneri (Nees) Lindb. **MOLUCCAS**: SERAM: **LECTOTYPE** of *Schisma divaricatum* [Miller 1965: 325 as "type"], **Herzog 1921**, 1926a both as *Schisma divaricatum*, **Miller 1965** as '*Herberta divaricata*', Del Rosario 1975a as '*Herberta divaricata*', **Piippo 1984a** as *Herbertus armitanus*, **Akiyama 1986, 2009** both as *Herbertus armitanus*, **Gao 2003** as *Herbertus divaricatus*, **So 2003b** as *Herbertus armitanus*, **Juslén 2006** as *Herbertus armitanus*.

Heteroscyphus **Schiffn.**

Heteroscyphus amboinensis (Schiffn.) Schiffn. **MOLUCCAS**: AMBON: **LECTOTYPE** of *Chiloscyphus endlicherianus* δ *amboinensis* [to be designated], **Schiffner 1890** as *Chiloscyphus endlicherianus* δ *amboinensis*, **1898** as *Chiloscyphus amboinensis*, **Stephani 1907** as *Chiloscyphus amboinensis*, **Bonner 1963b** as *Chiloscyphus decurrens* var. *amboinensis* [error for *C. endlicherianus* δ *amboinensis*] and *Chiloscyphus amboinensis*, Miller et al. 1983 as *Chiloscyphus endlicherianus* δ *amboinensis*.

Heteroscyphus argutus (Reinw., Blume et Nees) Schiffn. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009**.

Heteroscyphus aselliformis (Reinw., Blume et Nees) Schiffn. **MOLUCCAS**: Ambon: **Schiffner 1893b, 1898** both as *Chiloscyphus aselliformis*, Stephani 1907 as *Chiloscyphus aselliformis*, Bonner 1963b as *Chiloscyphus aselliformis* and *Gamoscyphus aselliformis*, Grolle 1965 as *Chiloscyphus aselliformis*, Inoue 1965, Bonner 1966, 1976 as *Jungermannia aselliformis*, Kitagawa 1979a as *Chiloscyphus aselliformis*, Miller et al. 1983, Piippo 1985, 1989b, Yamada and Hayashi 2003. Seram: **Akiyama 1986, 2009**.

Heteroscyphus coalitus (Hook.) Schiffn. var. *coalitus* **MOLUCCAS**: Ambon: **Sande Lacoste 1864** as *Chiloscyphus coalitus*, **Schiffner 1890, 1898** both as *Chiloscyphus coalitus*, **Sydow 1894** as *Chiloscyphus coalitus*, Inoue and Miller 1965 as *Heteroscyphus* '*coaltitus*', Miller et al. 1983, Piippo 1985, 1989b, 1993b. Seram: **Akiyama 1986, 2009**.

Heteroscyphus splendens (Lehm. et Lindenb.) Grolle. **MOLUCCAS**: Halmahera: **Sande Lacoste 1864** as *Chiloscyphus decurrens*, De Notaris 1874 as *Chiloscyphus decurrens*, **Schiffner 1898** as *Chiloscyphus decurrens*, Pócs 1971 as *Heteroscyphus decurrens*, Miller et al. 1983 as *Heteroscyphus decurrens*. Ambon: **Schiffner 1893b, 1898** both as *Chiloscyphus decurrens*, Grolle 1965 as *Chiloscyphus decurrens*, Pócs 1971 as *Heteroscyphus decurrens*, Kitagawa 1979a as *Chiloscyphus decurrens*, Miller et al. 1983 as *Heteroscyphus decurrens*, Piippo 1985, 1989b, 1993b, Piippo and Tan 1992, Bapna and Kachroo 2000b as *Chiloscyphus decurrens*, Yamada and Hayashi 2003, Hayashi and Yamada 2004. Seram: **Sande Lacoste 1864** as *Chiloscyphus decurrens*, **Schiffner 1898** as *Chiloscyphus decurrens*, **Herzog 1921** as *Chiloscyphus decurrens*, Grolle 1965 as *Chiloscyphus decurrens*, Pócs 1971 as *Heteroscyphus decurrens*, Kitagawa 1979a as *Chiloscyphus decurrens*, Miller et al. 1983 as *Heteroscyphus decurrens*, Piippo 1985, **Akiyama 1986**, Piippo 1989b, 1993b, Piippo and Tan 1992, 1993b, Yamada and Hayashi 2003, Hayashi and Yamada 2004, **Akiyama 2009**.

Heteroscyphus zollingeri (Gottsche) Schiffn. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**.

Kurzia **G.Martens**

Kurzia geniculata Mizut. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**.

Kurzia gonyotricha (Sande Lac.) Grolle. **MOLUCCAS**: Del Rosario 1971, 1975b both as *Microlepidozia gonyotricha*, Pócs et al. 2011. Seram: **Akiyama 1986, 2009**.

Leiomitra **Lindb.**

Leiomitra breviseta (Steph.) R.M.Schust. **MOLUCCAS**: Seram: **Akiyama 1986, 2009** both as *Trichocolea breviseta*.

Lejeunea **Lib.**

Lejeunea albescens (Steph.) Mizut. **MOLUCCAS**: Miller et al. 1983. Bacan: **Eifrig 1936** as *Taxilejeunea albescens*. Seram: **Mizutani 1986a**, **Akiyama 2009, Lee 2013**.

Lejeunea anisophylla Mont. **MOLUCCAS**: Ambon: **Pócs 2010, Lee 2013**. Seram: **Mizutani 1986a** as *Lejeunea catanduana*, **Akiyama 2009** as *Lejeunea catanduana*.

Lejeunea discreta Lindenb. **MOLUCCAS**: Mizutani 1971, Tixier 1973a, 1979 both as *Hygrolejeunea discreta*, Mizutani 1975, 1977, Miller et al. 1983, Long and Grolle 1990, Parihar et al. 1994, Zhu and So 1999, Bapna and Kachroo 2000b, Chantanaorrapint et al. 2003, 2004, Alam and Srivastava 2009, Haerida 2009, Lee et al. 2010. BACAN: **Eifrig 1936** as *Hygrolejeunea discreta*.

Lejeunea exilis (Reinw., Blume et Nees) Grolle. **MOLUCCAS**: Pócs et al. 2011. AMBON: **LECTOTYPE** of *Harpalejeunea exigua* [Grolle & Reiner-Drehwald 1999: 41 as "holotype"], **Stephani 1913** as *Harpalejeunea exigua*, **Grolle 1988** as *Lejeunea microstipula*, **Grolle and Reiner-Drehwald 1999** as *Microlejeunea microstipula*. SERAM: **Mizutani 1986a**, **Akiyama 2009**.

Lejeunea fissistipula (Steph.) Steph. **MOLUCCAS**: AMBON: **LECTOTYPE** of *Eulejeunea fissistipula* [Bonner 1965: 138], **Stephani 1896b** as *Eulejeunea fissistipula*, 1915, **Schiffner 1898** as *Eulejeunea fissistipula*, **Bonner 1965** as *Eulejeunea fissistipula*, Miller et al. 1983 also as *Eulejeunea fissistipula*. SERAM: **Mizutani 1986a**, **Akiyama 2009**.

Lejeunea flava (Sw.) Nees subsp. *orientalis* R.M.Schust. **MOLUCCAS**: **LECTOTYPE** of *Jungermannia indica* [to be designated]. TERNATE/TIDORE: **Reinwardt and Nees 1823** as *Jungermannia indica*.

Lejeunea lumbricoides (Nees) Nees. **MOLUCCAS**: AMBON: **LECTOTYPE** of *Taxilejeunea karstenii* [to be designated], **Schiffner 1893b, 1898** as *Taxilejeunea lumbricoides*, **Stephani 1914** as *Taxilejeunea karstenii*, **Eifrig 1936** as *Taxilejeunea lumbricoides*, Kamimura 1974, Lee et al. 2014. SERAM: **Mizutani 1986a**, **Akiyama 2009, Lee 2013**.

Lejeunea microloba Taylor. **MOLUCCAS**: SERAM: **Mizutani 1986a**, Zhu and Reiner-Drehwald 2004 as *Lejeunea chalmersii*, **Akiyama 2009, Lee 2013**.

Lejeunea sordida (Nees) Nees. **MOLUCCAS**: Mizutani 1977, Miller et al. 1983 also as *Hygrolejeunea parkinsonii*, Pócs et al. 2011. AMBON: **LECTOTYPE** of *Hygrolejeunea amboinensis* [to be designated], **Schiffner 1890, 1898** both as *Hygrolejeunea amboinensis*, **Sydow 1894** as *Hygrolejeunea amboinensis*, Stephani 1914 as *Hygrolejeunea amboinensis*, **Eifrig 1936** as *Taxilejeunea laxiretis* and *Taxilejeunea sordida*, Miller et al. 1963, 1968 both as *Hygrolejeunea sordida*, Mizutani 1964 as *Taxilejeunea sordida*, Inoue and Miller 1965 as *Hygrolejeunea sordida*, Swanson and Miller 1969 as *Hygrolejeunea sordida*, Miller et al. 1983 also as *Hygrolejeunea sordida* and *Hygrolejeunea amboinensis*, **Thiers 1986, Lee 2013**. SERAM: **Mizutani 1986a**, **Akiyama 2009**.

Lejeunea stenodentata M.A.M.Renner et Pócs. **MOLUCCAS**: Mizutani 1977 as *Drepanolejeunea dentata*, Thouvenot 2015, Pócs et al. 2019a. AMBON: **LECTOTYPE** of *Drepanolejeunea dentata* [Bonner 1965: 82], **Stephani 1896b**, 1913 both as *Drepanolejeunea dentata*, **Schiffner 1898** as *Drepanolejeunea dentata*, **Bonner 1965** as *Drepanolejeunea dentata*, **Mizutani 1972** as *Drepanolejeunea dentata*, Pócs et al. 1995 as *Stenolejeunea dentata*, Schuster 2000b as *Stenolejeunea dentata*, **Renner et al. 2013**.

Lejeunea umbilicata (Nees) Nees. **MOLUCCAS**: TERNATE/TIDORE: **Sande Lacoste 1856a, 1956b** both as *Omphalanthus umbilicatus*, **Schiffner 1898** as *Hygrolejeunea umbilicata*.

Lepicolea Dumort.

Lepicolea rara (Steph.) Grolle. **MOLUCCAS**: Pócs et al. 2011. Seram: **Akiyama 1986, 2009**.

Lepicolea yakusimensis (S.Hatt.) S.Hatt. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**.

Lepidolejeunea R.M.Schust.

Lepidolejeunea bidentula (Steph.) R.M.Schust. **MOLUCCAS**: Geissler and Bischler 1989 as *Pycnolejeunea decurvifolia*. Ambon: **LECTOTYPE** of *Hygrolejeunea decurvifolia* [Mizutani 1978: 133], **Stephani 1896b**, 1910a both as *Hygrolejeunea decurvifolia*, **Hoffmann 1935** as *Pycnolejeunea decurvifolia*, Bonner 1966 as *Hygrolejeunea decurvifolia*, **Mizutani 1978** as *Pycnolejeunea badia*, Miller et al. 1983 as *Hygrolejeunea decurvifolia*. Seram: **Mizutani 1986a**, **Akiyama 2009**.

Lepidozia (Dumort.) Dumort.

Lepidozia borneensis Steph. **MOLUCCAS**: Seram: **Akiyama 1986, 2009, Doei 1987b**.

Lepidozia brotheri Steph. **MOLUCCAS**: Seram: **Doei 1987b, Akiyama 2009**.

Lepidozia ceramensis Herzog. **MOLUCCAS**: Seram: **LECTOTYPE** [to be designated], **Herzog 1926b**, Doei 1987b.

Lepidozia cladorhiza (Reinw., Blume et Nees) Nees. **MOLUCCAS**: Seram: **Akiyama 1986, 2009, Doei 1987b**.

Lepidozia ferdinandii-muelleri Steph. **MOLUCCAS**: Halmahera: Engel 1987. Seram: Herzog 1926a as *Lepidozia* '*Friderici Mülleri*', **1926b** as *Lepidozia* '*Ferdinandi Mülleri*', Grolle 1968b as *Lepidozia* '*fernandi-muelleri*'], Mizutani 1968b, 1974, Miller et al. 1983, Piippo 1984b, **Akiyama 1986, 2009** as *Lepidozia* '*ferdinandii*-muelleri', Doei **1987b**, Enroth 1991, Schuster 2000a.

Lepidozia griseola Herzog. **MOLUCCAS**: Seram: **LECTOTYPE** [to be designated], **Herzog 1926b**, Doei 1987b.

Lepidozia haskarliana (Gottsche, Lindenb. et Nees) Steph. **MOLUCCAS**: Siregar et al. 2018. Seram: **Akiyama 1986, 2009** as *Lepidozia* '*hasskarliana*', **Doei 1987b** as *Lepidozia* '*hasskarliana*', von Konrat et al. 2014, Siregar and Pasaribu 2019.

Lepidozia integrifolia Doei. **MOLUCCAS**: Seram: **HOLOTYPE, Doei 1987a, 1987b, Engel 1993, Crosby and Engel 2006, Akiyama 2009**.

Lepidozia longifolia Steph. **MOLUCCAS**: Ambon: **LECTOTYPE** [here designated], **Stephani 1909a**, Miller et al. 1983.

Lepidozia massartiana Schiffn. ex Steph. **MOLUCCAS**: Ambon: **Stephani 1909a**, Kitagawa 1973, Miller et al. 1983, **Geissler and Bischler 1985**.

Lepidozia subintegra Lindenb. **MOLUCCAS**: Inoue and Miller 1965, Mizutani 1968a, 1976, Del Rosario 1975b, Miller et al. 1983, Bapna and Kachroo 2000a, Bakalin et al. 2021. Seram: **Akiyama 1986**, 2009 [misidentification of *Lepidozia subtrichodes* fide Doei (1987b: 525).].

Lepidozia subtrichodes Steph. **MOLUCCAS**: Seram: **Herzog 1926b, 2009, Doei 1987b**.

Lepidozia trichodes (Reinw., Blume et Nees) Nees. **MOLUCCAS**: Ambon: **Schiffner 1893b, 1898**, Mizutani 1968a, 1974, Pócs 1968, Del Rosario 1975b, Kamimura 1975 as *Lepidozia* '*tricodes*'], Miller et al. 1983, Piippo 1984b, Doei 1987b, Siregar et al. 2018. Seram: **Akiyama 1986, 2009, Doei 1987b**.

***Leptolejeunea* (Spruce) Steph.**

Leptolejeunea dentistipula Steph. **MOLUCCAS**: Seram: **Mizutani 1986a**, **Akiyama 2009** as '*Lepidolejeunea*' *dentistipula*.

Leptolejeunea elliptica (Lehm. et Lindenb.) Besch. **MOLUCCAS**: Dey et al. 2009. Seram: **Mizutani 1986a**, **Akiyama 2009** as '*Lepidolejeunea*' *elliptica*.

Leptolejeunea epiphylla (Mitt.) Steph. **MOLUCCAS**: Bapna and Kachroo 2000b. Seram: **Mizutani 1986a**, **Akiyama 2009** as '*Lepidolejeunea*' *epiphylla*.

Leptolejeunea foliicola Steph. **MOLUCCAS**: Tixier 1974b, Parihar et al. 1994, Bapna and Kachroo 2000b. Seram: **Akiyama 2009** as '*Lepidolejeunea*' *foliicola*.

Leptolejeunea maculata (Mitt.) Schiffn. **MOLUCCAS**: Vanden Berghen 1977, Haerida 2009, Siregar et al. 2020a. Seram: **Mizutani 1986a**, **Akiyama 2009** as '*Lepidolejeunea*' *maculata*.

Leptolejeunea schiffneri (Steph. ex Schiffn.) Steph. **MOLUCCAS**: Tixier 1972 as *Leptolejeunea schiffneri*, Mizutani 1975 as *Leptolejeunea schiffneri*, Miller et al. 1983 as *Leptolejeunea schiffneri*, **Geissler and Bischler 1985** as *Leptolejeunea schiffneri* f. *angustifolia*, Bapna and Kachroo 2000b. Bacan: **Herzog 1942** as *Leptolejeunea schiffneri* var. *genuina*.

Leptolejeunea vitrea (Nees) Schiffn. **MOLUCCAS**: Jovet-Ast 1958, Jovet-Ast and Tixier 1962, Tixier 1970a, 1970b, 1971, 1973a, 1977, 1979, 1980, Miller et al. 1983, Pócs et al. 1994, Eggers 2006, Siregar et al. 2020a. Bacan: **Herzog 1942**.

***Lobatiriccardia* (Mizut. et S.Hatt.) Furuki**

Lobatiriccardia coronopus (De Not.) Furuki. **MOLUCCAS**: Seram: **Furuki 1996** as *Lobatiriccardia lobata*, Furuki 2006.

— subsp. *coronopus*. **MOLUCCAS**: Seram: Preussing et al. 2010.

***Lophocolea* (Dumort.) Dumort.**

Lophocolea deningeri Herzog. **MOLUCCAS**: Buru: **LECTOTYPE** [here designated], **Herzog 1921**.

Lophocolea kurzii Sande Lac. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**.

***Lopholejeunea* (Spruce) Steph.**

Lopholejeunea applanata (Reinw., Blume et Nees) Schiffn. **MOLUCCAS**: Ternate/ Tidore: **Sande Lacoste 1864** as *Lejeunea* '*adplanata*', **Schiffner 1898**. Ambon: **Sande Lacoste 1864** as *Lejeunea* '*adplanata*', Miller et al. 1983. Seram: **Sande Lacoste 1864** as *Lejeunea* '*adplanata*', **Schiffner 1898**, Miller et al. 1983.

Lopholejeunea eulopha (Taylor) Schiffn. **MOLUCCAS**: Haerida et al. 2010, Siregar et al. 2020a. Halmahera: Verdoorn 1934a, **1934b**, Hattori 1951, Kamimura

1974, Miller et al. 1983. Ternate/Tidore: **Mizutani 1979**, Miller et al. 1983, **Zhu and Gradstein 2005**. Ambon: **Schiffner 1890** as *Lopholejeunea eulopha*, **Sydow 1894**, Verdoorn 1934a, **1934b**, Hattori 1951, Kamimura 1974, Miller et al. 1983. Seram: **Mizutani 1979, 1986a**, Miller et al. 1983, **Akiyama 2009**.

Lopholejeunea horticola Schiffn. **MOLUCCAS**: Haerida et al. 2010, Siregar et al. 2014, Siregar 2015. Seram: **Mizutani 1986a**, **Akiyama 2009**.

Lopholejeunea nigricans (Lindenb.) Schiffn. **MOLUCCAS**: Mizutani 1994, Haerida et al. 2010, Siregar et al. 2014, Siregar et al. 2020a. Ternate/Tidore: **Verdoorn 1934b**. Seram: **Mizutani 1986a**, **Akiyama 2009** also as *Lopholejeunea javanica*.

Lopholejeunea subfusca (Nees) Schiffn. **MOLUCCAS**: Mizutani 1994, Haerida 2009, Haerida et al. 2010, Siregar et al. 2014, 2020a, Siregar 2015, Rosyanti et al. 2018. Ambon: **Schiffner 1893b** as *Lejeunea* '*Sagraeana*', **1898** as *Lopholejeunea sagrana* var. *subfusca*, **Stephani 1912b** as *Lopholejeunea pyriflora*, Verdoorn 1934a, **1934b**, Hattori 1951, Jovet-Ast 1958, Inoue and Miller 1965, Tixier 1966, 1967a, 1967b, Pócs et al. 1967, Swanson and Miller 1969, Miller et al. 1983 also as *Lopholejeunea pyriflora* and *Lopholejeunea sagrana*, **Geissler and Bischler 1985** as *Lopholejeunea pyriflora*, Bapna and Kachroo 2000b, Gradstein et al. 2002, **Zhu and Gradstein 2005**. Banda: **Verdoorn 1934b**, Jovet-Ast 1958, Tixier 1966, 1967a, Swanson and Miller 1969. Seram: **Mizutani 1986a**, Zhu and Gradstein 2005, **Akiyama 2009**.

Lopholejeunea wiltensii Steph. **MOLUCCAS**: Haerida et al. 2010, Siregar 2015. Halmahera: **Umagap 2019**. Ternate/Tidore: **Mizutani 1979**, Zhu and Gradstein 2005. Seram: **Mizutani 1979, Zhu and Gradstein 2005**, Siregar et al. 2014, Siregar 2015.

Marchantia L.

Marchantia emarginata Reinw., Blume et Nees. **MOLUCCAS**: Siregar et al. 2013, Siregar 2015, Ginting and Batubara 2019, Siregar et al. 2020b, Ruklani and Rubasinghe 2022. Ternate/Tidore: Bischler and Piippo 1991. Seram: Bischler and Piippo 1991.

— subsp. *emarginata*. **MOLUCCAS**: **Bischler 1989**, Singh and Singh 2013. Ternate/Tidore: **Bischler-Causse 1989**. Ambon: **LECTOTYPE** of *Marchantia amboinensis* [Bischler-Causse 1989: 183 as "type", second-step lectotypification needed], **Montagne 1838, 1856** both as *Marchantia amboinensis*, **Gottsche et al. 1846** as *Marchantia amboinensis*, **Schiffner 1898** as *Marchantia amboinensis*, **Stephani 1899a** as *Marchantia amboinensis*, Miller et al. 1983 as *Marchantia amboinensis*, **Bischler-Causse 1989**, Bischler and Piippo 1991. Seram: **Bischler-Causse 1989**.

Marchantia geminata Reinw., Blume et Nees. **MOLUCCAS**: Halmahera: **Umagap 2019**.

Marchantia polymorpha L. **MOLUCCAS**: Ambon: **Sopacua et al. 2020** [Saparua I].

Marchantia rubribarba Steph. **MOLUCCAS**: Ambon: **Bischler-Causse 1989**, Bischler and Piippo 1991.

Mastigophora Nees

Mastigophora diclados (Brid. ex F.Weber) Nees. **MOLUCCAS**: Buru: **Herzog 1921**. Halmahera: **LECTOTYPE** of *Sendtnera vrieseana* [to be designated],

Sande Lacoste 1864 as *Sendtnera diclados* β *calcarata* and *Sendtnera vrieseana*, **Schiffner 1898** also as *Mastigophora vrieseana*, Stephani 1909c as *Mastigophora vrieseana*, Inoue and Miller 1965, Miller et al. 1983. Ternate/Tidore: **Sande Lacoste 1864** as *Sendtnera diclados* α *scorpioides*, **Schiffner 1898** as *Mastigophora diclados* var. *scorpioides*, Inoue and Miller 1965, Miller et al. 1983. Ambon: **Schiffner 1898**, Inoue and Miller 1965, Miller et al. 1983. Seram: **Herzog 1921**, **Akiyama 1986, 2009**.

— var. *borneensis* (De Not.) Schiffn. **MOLUCCAS**: Ambon: **Schiffner 1893b, 1898**.

— var. *diclados*. **MOLUCCAS**: Ambon: **Schiffner 1893b** as *Mastigophora diclados*.

Metalejeunea **Grolle**

Metalejeunea cucullata (Reinw., Blume et Nees) Grolle. **MOLUCCAS**: **Grolle 1995**. Ambon: **SYNTYPE** of *Microlejeunea parallela* [lectotype to be designated], **Schiffner 1890** as *Microlejeunea parallela*, 1898 as *Eulejeunea parallela*, **Sydow 1894** as *Microlejeunea parallela*, Stephani 1915 as *Microlejeunea parallela*. Seram: **Mizutani 1986a** as *Lejeunea cucullata*, **Akiyama 2009** as *Lejeunea cucullata*.

Metzgeria **Raddi**

Metzgeria ciliata Raddi. **MOLUCCAS**: Halmahera: **Umagap 2019** as *Metzgeria decipiens*.

Metzgeria foliicola Schiffn. **MOLUCCAS**: Ternate/Tidore: **So 2003c**. Seram: **Akiyama 1986, 2009**.

Metzgeria furcata (L.) Corda. **MOLUCCAS**: Halmahera: **Umagap 2019**.

Metzgeria leptoneura Spruce var. *leptoneura* **MOLUCCAS**: Engel 1976, Schuster 1983. Buru: **So 2003c**. Ambon: **LECTOTYPE** of *Metzgeria hamatiformis* [to be designated], **Schiffner 1893b, 1898** both as *Metzgeria hamatiformis*, **Stephani 1899d** as *Metzgeria hamatiformis*, **Kuwahara 1966** as *Metzgeria hamata*, 1984, Schuster 1992, **Engel 1978**, Miller et al. 1983, **So 2003c, Costa 2008**. Seram: **Akiyama 1986, 2009**.

Microlejeunea **(Spruce) Steph.**

Microlejeunea filicuspis (Steph.) Heinrichs, Schäf.-Verw., Pócs et S.Dong. **MOLUCCAS**: **Grolle 1979a** as *Harpalejeunea filicuspis*, Miller et al. 1983 as *Drepanolejeunea filicuspis*. Ambon: **Grolle 1979a** as *Harpalejeunea filicuspis*.

Mnioloma **Herzog**

Mnioloma fuscum (Lehm.) R.M.Schust. **MOLUCCAS**: Seram: **Akiyama 1986, 2009** both as *Calypogeia fusca*.

Neolepidozia **Fulford et J.Taylor**

Neolepidozia cuneifolia (Steph.) Fulford et J.Taylor. **MOLUCCAS**: Ambon: **Engel and Smith Merrill 2004** as *Telaranea cuneifolia*, von Konrat et al. 2014.

Neolepidozia papulosa (Steph.) Fulford et J.Taylor. **MOLUCCAS**: Seram: **Akiyama 1986, 2009** both as *Lepidozia papulosa*, **Doei 1987b** as *Lepidozia papulosa*.

Neolepidozia wallichiana (Gottsche) Fulford et J.Taylor. **MOLUCCAS**: Ambon: **Sande Lacoste 1864** as *Lepidozia wallichiana*, De Notaris 1874 as *Lepidozia wallichiana*, **Schiffner 1893b, 1898** both as *Lepidozia wallichiana*, Hattori and Mizutani 1958 as *Lepidozia wallichiana*, Inoue and Miller 1965 as *Lepidozia wallichiana*, Swanson and Miller 1969, Mizutani 1974, 1976 both as *Lepidozia wallichiana*, Del Rosario 1975b as *Lepidozia wallichiana*, Kamimura 1975 as *Lepidozia wallichiana*, Miller et al. 1983, Piippo 1984b as *Lepidozia wallichiana*, Doei 1987b as *Lepidozia wallichiana*, Sharma and Srivastava 1993 as *Lepidozia wallichiana*, Bapna and Kachroo 2000a as *Lepidozia wallichiana*, Engel and Smith Merrill 2004 as *Telaranea wallichiana*. Seram: **Doei 1987b** as *Lepidozia wallichiana*, **Akiyama 2009** as *Lepidozia wallichiana*.

***Pallavicinia* Gray**

Pallavicinia ambigua (Mitt.) Steph. **MOLUCCAS**: Seram: **Grolle and Piippo 1986**, Koponen et al. 2000, Furuki 2002.

Pallavicinia lyellii (Hook.) Gray. **MOLUCCAS**: Inoue and Miller 1965, Swanson and Miller 1969, Miller et al. 1983, Bapna and Kachroo 2000b, Manju et al. 2015. Halmahera: **Umagap 2019**.

***Plagiochila* (Dumort.) Dumort.**

Plagiochila abietina (Nees) Mont. et Nees. **MOLUCCAS**: Ambon: **Stephani 1903b**, Bonner 1962a, Miller et al. 1983.

Plagiochila akiyamae Inoue. **MOLUCCAS**: Seram: **HOLOTYPE, Inoue 1986, Engel 1993, Grolle and So 1998, Grolle and So 1999, So and Grolle 2000, So 2001b, Crosby and Engel 2006, Akiyama 2009**, Singh and Rawat 2020.

Plagiochila amboynensis Taylor. **MOLUCCAS**: **Geissler and Bischler 1989** [type, Amboina], **So and Grolle 2000** [type, Amboina]. Ambon: **LECTOTYPE** [So and Grolle 2000: 201 as "**holotype**"], T**aylor 1846, Gottsche et al. 1847** as *Plagiochila* '*amboinensis*', **Schiffner 1898** as *Plagiochila* '*amboinensis*', **Stephani 1904a** as *Plagiochila* '*amboinensis*', **Bonner 1962a, Inoue 1984, So 2001c**, Schuster 2021.

Plagiochila arbuscula (Brid. ex Lehm. et Lindenb.) Lindenb. **MOLUCCAS**: Halmahera: **Sande Lacoste 1864** as *Plagiochila belangeriana*, **Schiffner 1898** as *Plagiochila belangeriana*, Miller et al. 1983. Ternate/Tidore: **Sande Lacoste 1864** as *Plagiochila belangeriana*, Miller et al. 1983. Ambon: **Sande Lacoste 1864** as *Plagiochila belangeriana* [Saparoea I], **Schiffner 1893b, 1898** both as *Plagiochila belangeriana*, Miller et al. 1983. Seram: **Inoue 1986, So 2001b, Akiyama 2009**.

Plagiochila bantamensis (Reinw., Blume et Nees) Mont. **MOLUCCAS**: Seram: **Inoue 1986, Akiyama 2009**.

Plagiochila bicornuta Steph. **MOLUCCAS**: Pócs et al. 2011. Ambon: **Stephani 1903a**, Bonner 1962a, Inoue 1981, Miller et al. 1983, **So 2000a, 2001a**, Schuster 2021. Seram: So 2000a, 2001a.

Plagiochila blepharophora (Nees) Lindenb. **MOLUCCAS**: Ternate/Tidore: **Schiffner 1898**, 1900, Stephani 1903c, Miller et al. 1983.

Plagiochila chauviniana Mont. **MOLUCCAS**: SERAM: **Inoue 1986** as *Plagiochila novae-guineae*, **Akiyama 2009** as *Plagiochila novae-guineae*.

Plagiochila frondescens (Nees) Lindenb. **MOLUCCAS**: AMBON: **Sande Lacoste 1864** as *Plagiochila frondescens* γ *rigida*, **Schiffner 1893b, 1898** 1900 all as *Plagiochila frondescens* var. *tenerrima*, **1898** as *Plagiochila frondescens* γ *rigida*, **Stephani 1903a**, Swanson and Miller 1969, Miller et al. 1983, Piippo 1989a. SERAM: **Inoue 1986, Akiyama 2009**.

Plagiochila gymnoclada Sande Lac. **MOLUCCAS**: Singh Deo and Singh 2014. BURU: **Herzog 1921, Carl 1931b, Inoue 1984**, Inoue 1989. TERNATE/TIDORE: **Sande Lacoste 1864**, **Schiffner 1898**, 1900, Stephani 1903b. SERAM: **Inoue 1986** as *Plagiochila pseudaberrans*, **Akiyama 2009** as *Plagiochila pseudaberrans*.

Plagiochila hampeana Gottsche. **MOLUCCAS**: SERAM: **Inoue 1986** as *Plagiochila gedeana*, So and Grolle 2001, **Akiyama 2009** as *Plagiochila gedeana*.

Plagiochila junghuhniana Sande Lac. **MOLUCCAS**: AMBON: **So 2000b, 2001b**.

Plagiochila kuhliana Sande Lac. **MOLUCCAS**: SERAM: **Sande Lacoste 1864**, **Schiffner 1898**, 1900, **Stephani 1903d**, Bonner 1962a, **Geissler and Bischler 1989**.

Plagiochila kurzii Steph. **MOLUCCAS**: SERAM: **Sande Lacoste 1864** as *Plagiochila bantamensis* var. *denticulata*, **Schiffner 1898** as *Plagiochila bantamensis* var. *denticulata*, Bonner 1962a as *Plagiochila bantamensis* var. *denticulata*.

Plagiochila massalongoana Schiffn. **MOLUCCAS**: SERAM: **Inoue 1986, Akiyama 2009**.

Plagiochila pulvinata Steph. **MOLUCCAS**: **So and Grolle 1999**. SERAM: **HOLOTYPE** of *Plagiochila ceramica*, **Inoue 1986** as *Plagiochila ceramica*, **Engel 1993** as *Plagiochila ceramica*, **So and Grolle 2000, Crosby and Engel 2006** as *Plagiochila ceramica*, **Akiyama 2009** as *Plagiochila ceramica*.

Plagiochila renitens (Nees) Lindenb. **MOLUCCAS**: ?HALMAHERA: Schiffner 1900, Stephani 1903b. SERAM: **Inoue 1984, 1986**, 1989, Piippo 1989a, **Akiyama 2009**, Schuster 2021. Note: we are not aware of any first hand report from Halmahera.

Plagiochila salacensis Gottsche. **MOLUCCAS**: SERAM: **Inoue 1986, Akiyama 2009**.

Plagiochila sandei Dozy. **MOLUCCAS**: **So and Grolle 1999**. TERNATE/TIDORE: Schiffner and Stephani 1901 as *Plagiochila blepharophora* var. *major*. AMBON: **Sande Lacoste 1864** [Saparoea I], **Schiffner 1898**, 1900 [both Saparoea I], Stephani 1903d [Saparoea I], **Grolle 1968b** as *Plagiochila seemannii*, Miller et al. 1983 as *Plagiochila seemannii*, Inoue 1986 as *Plagiochila seemannii*, Piippo 1989a as *Plagiochila seemannii*. SERAM: **Sande Lacoste 1864**, Stephani 1903d, **Inoue 1986** also as *Plagiochila seemannii*, 1989, Müller and Schäfer-Verwimp 1999, **Akiyama 2009** also as *Plagiochila seemannii*.

Plagiochila sciophila Nees. **MOLUCCAS**: ?AMBON: Pócs 1971 as *Plagiochila acanthophylla*. SERAM: **Inoue 1986** also as *Plagiochila decidua*, 1989, **Akiyama 2009** also as *Plagiochila decidua*. Note: we aree not aware of any first hand report from Ambon.

Plagiochila teysmannii Sande Lac. **MOLUCCAS**: **So and Grolle 1999**. BACAN: **LECTOTYPE** of *Plagiochila batjanensis* [Inoue 1984: 90 as "type"], **Herzog 1938** as *Plagiochila batjanensis*, **Bonner 1962a** as *Plagiochila batjanensis*, **Inoue 1984, Geissler and Bischler 1989** as *Plagiochila batjanensis*, Piippo 1989a, **So and Grolle 2000**. AMBON: **Schiffner 1893b, 1898** both as *Plagiochila semialata*. SERAM: **Inoue 1986**, 1989, **Akiyama 2009** as *Plagiochila* '*teysmanii*'.

Plagiochila trabeculata Steph. **MOLUCCAS**: SERAM: **So 2001b**.

***Pleurozia* Dumort.**

Pleurozia conchifolia (Hook. et Arn.) Austin. **MOLUCCAS**: Pócs et al. 2011. Ambon: **Schiffner 1898** *Pleurozia* '*conchaefolia*', Miller et al. 1983.

Pleurozia gigantea (F.Weber) Lindb. **MOLUCCAS**: Ambon: **Schiffner 1893b, 1898**, Horikawa 1935, Pócs et al. 1967, Tixier 1973b, 1974b, Bizot and Pócs 1974, Miller et al. 1983, **Thiers 1993**. Seram: **Akiyama 1986, 2009**.

***Plicanthus* R.M.Schust.**

Plicanthus hirtellus (F.Weber) R.M.Schust. **MOLUCCAS**: Seram: **LECTOTYPE** of *Chandonanthus gracilis* [here designated], **Herzog 1921** as *Chandonanthus hirtellus*, 1926a as *Chandonanthus gracilis*, **Herzog 1926b, 1926b** both as *Chandonanthus hirtellus*, **Bonner 1963b** as *Chandonanthus gracilis*, **Akiyama 1986, 2009** both as *Chandonanthus hirtellus*, **Váňa et al. 2013**.

***Podomitrium* Mitt.**

Podomitrium malaccense (Steph.) Campb. **MOLUCCAS**: Ambon: Troll 1930 as *Hymenophyton malaccense*, Grolle 1966a, Schuster 1969 as *Podomitrium* '*mallacense*', Miller et al. 1983, **Grolle and Piippo 1986**. Seram: **Akiyama 1986, 2009**.

***Porella* L.**

Porella acutifolia (Lehm. et Lindenb.) Trevis. var. *acutifolia* **MOLUCCAS**: Halmahera: **Sande Lacoste 1864** as *Madotheca acutifolia*, **Schiffner 1898** as *Madotheca acutifolia*, **Hattori 1970** as *Porella acutifolia* var. *subligulifera*.

Porella geheebii (Steph.) S.Hatt. **MOLUCCAS**: Seram: **Bi et al. 2019**.

Porella javanica (Gottsche) Inoue. **MOLUCCAS**: Hattori 1978, Miller et al. 1983. Buru: **LECTOTYPE** of *Madotheca crenilobula* [here designated], **Herzog 1921**, 1926a both as *Madotheca crenilobula*.

***Psiloclada* Mitt.**

Psiloclada clandestina Mitt. subsp. *clandestina* **MOLUCCAS**: Ambon: **LECTOTYPE** of *Psiloclada unguligera* [to be designated], **Schiffner 1893a**, 1893b, **1898** all as *Psiloclada unguligera*, **Stephani 1909a**, Herzog 1953, Arnell 1955, **Fulford and Taylor 1959** as *Psiloclada unguligera*, Arnell 1963, Mizutani 1974, 1976, Schuster 1980, Hürlimann 1983, Miller et al. 1983. Seram: **Akiyama 1986, 2009**.

— subsp. *melanesica* R.M.Schust. ?**MOLUCCAS**: Ambon: Miller 1985, Schuster 2000a with a "?"], Engel and Glenny 2008. Note: we are not aware of any positively identified specimen of this subspecies from **Moluccas**.

***Ptychanthus* Nees**

Ptychanthus striatus (Lehm. et Lindenb.) Nees var. *striatus*. **MOLUCCAS**: Mizutani 1977, Miller et al. 1983 as *Ptychanthus moluccensis*, Haerida et al. 2010, Siregar et al. 2014, Siregar 2015, Siregar et al. 2020a. Buru: **Herzog**

1921, 1926a both as *Ptychanthus moluccensis*. Halmahera: **Sande Lacoste 1864** as *Ptychanthus javanicus*, **Schiffner 1898** as *Ptychanthus javanicus*, **Verdoorn** 1934a, **1934b, Umagap 2019**. Ambon: **LECTOTYPE** of *Ptychanthus squarrosus* [to be designated], **Lehmann 1844** as *Ptychanthus squarrosus*, **Gottsche et al. 1845a** as *Ptychanthus squarrosus*, **Montagne 1856** as *Ptychanthus squarrosus*, **Stephani 1890a, Schiffner 1898**, Verdoorn 1933 as *Ptychanthus moluccensis*, 1934a, Mizutani 1961, Tixier 1971, Kamimura 1974, Miller et al. 1983, Bapna and Kachroo 2000b. Seram: **SYNTYPE** of *Ptychanthus moluccensis* [**lectotype** to be designated], **Sande Lacoste 1864** as *Ptychanthus moluccensis*, **Schiffner 1898** as *Ptychanthus moluccensis*, **Verdoorn** 1933 as *Ptychanthus moluccensis*, **1934b**, Miller et al. 1983 as *Ptychanthus striatus*, **Mizutani 1986a**, **Akiyama 2009**.

Pycnolejeunea **(Spruce) Schiffn.**

Pycnolejeunea cavistipula (Steph.) Mizut. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Strepsilejeunea cavistipula* [Mizutani 1972: 161 as "type"], **Stephani 1896b** as *Strepsilejeunea cavistipula*, 1913 as *Trachylejeunea cavistipula*, **Schiffner 1898** as *Strepsilejeunea cavistipula*, **Mizutani 1972, Thiers 1986**.

Pycnolejeunea connivens Schiffn. ex P.Syd. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Pycnolejeunea connivens* [to be designated], **Schiffner 1890** as *Pycnolejeunea connivens*, **Sydow 1894**.

Radula **Dumort.**

Radula anceps Sande Lac. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**, Yamada 1989, Bapna and Kachroo 2000b.

Radula densifolia Castle. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**, Yamada and Piippo 1989, Yamada 1989, Yamada 2002.

Radula formosa (C.F.W.Meissn. ex Spreng.) Nees. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Radula pycnolejeuneoides* [Castle 1950: 267; second-step lectotypification needed], **Schiffner 1893b, 1898** both as *Radula pycnolejeuneoides*, Stephani 1910b also as *Radula pycnolejeuneoides*, Jovet-Ast 1949, **Castle 1950**, 1968, Steere 1953, Inoue and Miller 1965, Grolle 1966a, **Kitagawa 1979a** as *Radula formosa* var. *pycnolejeuneoides*, Miller et al. 1983 also as *Radula pycnolejeuneoides*, **So 2006**. ?Seram: Yamada 1979, 1989, Miller et al. 1983, Siregar 2015, Ginting and Batubara 2019. Note: we are not aware of any first hand report from Seram.

Radula javanica Gottsche. **MOLUCCAS**: Buru: New to Moluccas: Buru, E hoe, 1921.09, *Toxopens 299a*, det. H. Castle (BO4137]. Seram: **LECTOTYPE** of *Radula ceramensis* [to be designated], **LECTOTYPE** of *Radula ovalifolia* [Castle 1966: 68; second-step lectotypification needed)], **Stephani 1884** as *Radula ovalifolia* and *Radula ceramensis*, **Schiffner 1898** as *Radula ceramensis* and *Radula ovalifolia*, **Stephani** 1910b, **1924** both as *Radula ceramensis*, **Castle 1966** as *Radula wallichiana*, Miller et al. 1983 as *Radula ceramensis*, **Akiyama 1986, 2009, Yamada 1989**.

Radula multiflora Gottsche ex Schiffn. **MOLUCCAS**: Seram: **Akiyama 1986**.

Radula nymannii Steph. **MOLUCCAS**: Ambon: Swanson and Miller 1969, Miller et al. 1983. Seram: **Akiyama 1986, 2009** as *Radula 'nymanii'*, Yamada 1989 as *Radula 'nymanii'*.

Radula reflexa Nees et Mont. **MOLUCCAS**: Ambon: **LECTOTYPE** [Castle 1965: 374], **Montagne 1843**, 1846, **1856, Gottsche et al. 1845a, Schiffner 1898, Castle 1965, 1968, Yamada 1976, 1979**, 2002, Miller et al. 1983, **So 2005, 2006**. Seram: **LECTOTYPE** of *Radula subsimilis* [Castle 1965: 376 as "type"], **Sande Lacoste 1864, Stephani 1884** as *Radula subsimilis*, **Schiffner 1898** also as *Radula subsimilis*, Stephani 1910b as *Radula subsimilis*, **Castle 1965, 1968** both as *Radula subsimilis*, Yamada 1979 as *Radula subsimilis*, 1987, Miller et al. 1983 also as *Radula subsimilis*, Yamada and Piippo 1989, Streimann 1991 as *Radula subsimilis*, Piippo et al. 2002, **So 2006**, Siregar 2015.

Radula sumatrana Steph. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**, Yamada 1989.

Radula tjibodensis K.I.Goebel. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**, Yamada 1989, Zhu 1999, Zhu and So 2001.

Radula van-zantenii K.Yamada. **MOLUCCAS**: Seram: **Akiyama 1986, 2009** as *Radula* '*vanzantenii*', Yamada and Piippo 1989.

Radula vrieseana Sande Lac. **MOLUCCAS**: Siregar 2015. Obi: **Yamada 1979**. Banda: **Sande Lacoste 1864**, **Schiffner 1898**. Seram: **LECTOTYPE** [Castle 1965: 372], **Sande Lacoste 1864**, **Schiffner 1898**, Stephani 1910b as *Radula* '*vriesei*', **Castle 1965, 1968** both as *Radula* '*Vriesei*', **Yamada 1974** as *Radula* '*vriesei*', **1979, Akiyama 1986, 1989, 2009, Yamada and Piippo 1989**, Bapna and Kachroo 2000b, Siregar 2015.

Riccardia Gray

Riccardia albomarginata (Steph.) Schiffn. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Aneura albomarginata* [Bonner 1962b: 85, cf. also Furuki 1995: 112 as "holotype"], **Stephani 1893a**, 1893b, **1899c** all as *Aneura* '*albo-marginata*', **Schiffner 1898, Bonner 1962b** as *Aneura albomarginata*, Grolle 1967, 1968b, Miller et al. 1983 also as *Aneura albomarginata*, **Furuki 1995**, Thouvenot et al. 2018.

Riccardia aspera (Steph.) Grolle. **MOLUCCAS**: Seram: **Furuki 1998**.

Riccardia karstenii (Steph.) Schiffn. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Aneura karstenii* [Bonner 1962b: 114], **Stephani 1893a**, 1893b, **1899c** all as *Aneura karstenii*, **Schiffner 1898, Bonner 1962b** as *Aneura karstenii*.

Riccia L.

Riccia amboinensis Schiffn. **MOLUCCAS**: Ambon: **LECTOTYPE** [to be designated], **Schiffner 1890, 1898, Sydow 1894, Stephani 1898**, Campbell 1915 as *Riccia* '*amboiniana*'.

Riccia billardierei Mont. et Nees. **MOLUCCAS**: Bapna and Kachroo 2000b, Chaudhary et al. 2006. Halmahera: **Meijer 1958,** Jovet-Ast 2000, 2003. Banda: **Jovet-Ast 2003**.

Riccia junghuhniana Nees et Lindenb. **MOLUCCAS**: Ambon: **Xiang et al. 2022**.

Saccogynidium Grolle

Saccogynidium muricellum (De Not.) Grolle. **MOLUCCAS**: Miller et al. 1983, Enroth 1991. Bacan: **Grolle and Schultze-Motel 1972**. ?Ambon: Piippo 1985, 1989b, Gao et al. 2001. Seram: **Akiyama 1986, 2009**. Note: we are not aware of any first hand report from Ambon.

Saccogynidium rigidulum (Nees) Grolle. **MOLUCCAS**: Inoue and Miller 1965, **Grolle and Schultze-Motel 1972**, Miller et al. 1983, Enroth 1991. Ambon: **LECTOTYPE** of *Chiloscyphus granulatus* [to be designated], **Schiffner 1893b, 1898** as *Chiloscyphus granulatus*, **Stephani 1908a** as *Saccogyna rigidula*, Hattori 1951 as *Saccogyna rigidula*, **Bonner 1963b** as *Chiloscyphus granulatus*, Inoue and Miller 1965, **Grolle 1968b** as *Saccogynidium jugatum*, Miller et al. 1983 also as *Chiloscyphus granulatus*, Piippo 1985, 1989b, Gao et al. 2001.

***Sandeothallus* R.M.Schust.**

Sandeothallus radiculosus (Schiffn.) R.M.Schust. **MOLUCCAS**: Ambon: **Akiyama 2009**. Seram: **Akiyama 1986**.

***Schiffneria* Steph.**

Schiffneria hyalina Steph. **MOLUCCAS**: Engel 1987, Long and Grolle 1990, Piippo and Tan 1992, Váňa 1993, O'Shea et al. 1997, Bapna and Kachroo 2000a, Schuster 2002. Halmahera: Bacan: **LECTOTYPE** [Grolle and Piippo 1984: 305 ad "holotype"], **Stephani 1894b, 1908a, Schiffner 1898, Kitagawa 1973, Grolle and Piippo 1984, Asthana et al. 1994, Váňa et al. 2014**.

***Schiffneriolejeunea* Verd.**

Schiffneriolejeunea cumingiana (Mont.) Gradst. **MOLUCCAS**: Ambon: **Verdoorn** 1934a, **1934b** both as *Ptychocoleus cumingianus*, Tixier 1966, 1967b, 1972 all as *Ptychocoleus cumingianus*, Miller 1968 as *Ptychocoleus cumingianus*, Swanson and Miller 1969 as *Ptychocoleus cumingianus*, Kachroo 1970 as *Ptychocoleus cumingianus*, Miller et al. 1983, Bapna and Kachroo 2000b. Seram: **Verdoorn** 1934a, **1934b** both as *Ptychocoleus cumingianus*, Miller 1968 as *Ptychocoleus cumingianus*, Swanson and Miller 1969 as *Ptychocoleus cumingianus*, **Gradstein and Terken 1981**, Miller et al. 1983.

Schiffneriolejeunea pulopenangensis (Gottsche) Gradst. **MOLUCCAS**: Bapna and Kachroo 2000b, Siregar et al. 2020a. Ambon: **ORIGINAL MATERIAL** of *Acrolejeunea densifolia*, **Schiffner 1890** as *Acrolejeunea densifolia*, **1898** as *Acrolejeunea pulopenangensis*, **Sydow 1894** as *Acrolejeunea densifolia*, Stephani 1912b as *Ptychocoleus densifolius*, **Verdoorn 1934b** as *Ptychocoleus pulopenangensis*, **Bonner 1962b** as *Acrolejeunea densifolia*, Mizutani 1964 as *Ptychocoleus pulopenangensis*, Miller et al. 1983 also as *Acrolejeunea densifolia*, Hürlimann 1989.

Schiffneriolejeunea tumida (Nees) Gradst. **MOLUCCAS**: Ambon: **Gradstein and Terken 1981**. Seram: **Mizutani 1986a**, **Akiyama 2009**.

— var. *haskarliana* (Gottsche) Gradst. et Terken. **MOLUCCAS**: Mizutani 1977, 1978 both as *Schiffneriolejeunea 'hasskarliana'*. Ambon: **Schiffner 1893b** as *Lejeunea haskarliana*, **1898** as *Acrolejeunea haskarliana*, **Verdoorn** 1934a, **1934b** as *Ptychocoleus 'Hasskarlianus'*, Amakawa 1960 as *Ptychocoleus haskarlianus*, Miller et al. 1983 as *Acrolejeunea haskarliana* and *Schiffneriolejeunea haskarliana*.

Schistochila **Dumort.**

Schistochila acuminata Steph. **MOLUCCAS**: Seram: **LECTOTYPE** of *Schistochila purpurascens* [here designated, cf. So 2003a: 80 as "**holotype**")], **Herzog** 1926a, **1926b** both as *Schistochila purpurascens*, Grolle 1966b as *Schistochila purpurascens*, Hässel 1976 as *Schistochila purpurascens*, **So 2003a**.

Schistochila aligera (Nees et Blume) J.B.Jack et Steph. **MOLUCCAS**: Pócs 1971, Tixier 1972. Buru: **Herzog 1921**, 1926a also as *Schistochila graeffeana*, Miller et al. 1983 as *Schistochilaster graeffeanus* and *Schistochila graeffeana*, **So 2003a**. Bacan: **Buch 1939**. ?Halmahera: Miller et al. 1983 as *Schistochilaster aliger*. Ambon: **ORIGINAL MATERIAL** of *Schistochila philippinensis* var. *transiens*, **Schiffner 1893b** as '*Schistocheila*' *aligera*, **1898**, Stephani 1896a as '*Schistocheila' philippinensis*, 1909c, **Buch 1939** also as *Schistochila philippinensis*, Bonner 1966 as *Gottschea aligera*, Grolle 1966b also as *Schistochila philippinensis*, Grolle 1966b, Pócs 1968, 1971, Tixier 1972, Miller et al. 1983 as *Gottschea aligera*, *Schistochilaster aliger* and as *Schistochilaster philippinensis*, Piippo 1984a also *Schistochila philippinensis*, Bapna and Kachroo 2000b, **So 2003a**. Seram: **Akiyama 1986, 2009** both also as *Schistochila philippinensis* and *Schistochila recurvata*.

Schistochila beccariana (De Not.) Trevis. **MOLUCCAS**: Ambon: **LECTOTYPE** of *Schistochila amboinensis* [here designated, cf. So 2003a: 87 as "holotype"], **Stephani 1909c** as *Schistochila amboinensis*, **So 2003a**.

Schistochila blumei (Nees) Trevis. **MOLUCCAS**: Tixier 1974a. Halmahera: **Sande Lacoste 1864** as *Gottschea blumei*, **Schiffner 1898** as *Schistochila 'blumii'*, **Buch 1939**, Grolle 1966b, Pócs 1971, Kitagawa 1973, 1978, Miller et al. 1983, Piippo 1984a, Inoue 1985, Enroth 1991 as *Schistochila 'blumii'*. Ambon: **So 2003a**. Seram: **Akiyama 1986, 2009** both as *Schistochila formosana*.

Schistochila doriae (De Not.) Trevis. **MOLUCCAS**: Ambon: **Schiffner 1893b** as '*Schistocheila*' *doriae*, **1898**.

Schistochila reinwardtii (Nees) Schiffn. **MOLUCCAS**: Ambon: **So 2003a**.

Schistochila sciurea (Nees) Schiffn. var. *sciurea*. **MOLUCCAS**: Ambon: **Schiffner 1893b** as '*Schistocheila' sciurea* f. *robustior*, **1898**, Verdoorn 1937, Hattori 1968, Miller et al. 1983, So 2003a. Seram: **LECTOTYPE** of *Schistochila inversa* [here designated, cf. So 2003a: 98 as "holotype"], **Herzog 1926b** as *Schistochila inversa*, Grolle 1966b as *Schistochila inversa*, Hässel 1976 as *Schistochila inversa*, **Akiyama 1986, 2009, So 2003a**.

Schizophyllopsis **Váňa et L.Söderstr.**

Schizophyllopsis bidens (Reinw., Blume et Nees) Váňa et L.Söderstr. **MOLUCCAS**: Seram: **Akiyama 1986, 2009** both as *Anastrophyllum bidens*, Váňa and Piippo 1989b as *Anastrophyllum bidens* var. *bidens* as *Anastrophyllum bidens*, Váňa 1991b as *Anastrophyllum bidens*, Schill and Long 2003 as *Anastrophyllum bidens*, Eggers 2006 as *Anastrophyllum bidens*.

Solenostoma **Mitt.**

Solenostoma ariadne (Taylor) R.M.Schust. ex Váňa et D.G.Long. **MOLUCCAS**: Ambon: **Sande Lacoste 1864** as *Jungermannia ariadne*, **Schiffner 1898**, 1900 both as *Nardia ariadne*, **Stephani 1901a** as *Jungermannia ariadne*, Amakawa 1968 as *Jungermannia ariadne*, Swanson and Miller 1969 as *Jungermannia ariadne*, Váňa 1972 as *Jungermannia ariadne* [rejecting report by Sande Lacoste 1864 as *J. tetragona*], Bonner 1976 as *Jungermannia ariadne*, Miller et al. 1983 as *Plectocolea ariadne*, Váňa and Piippo 1989a as *Jungermannia ariadne*. Seram: **Akiyama 1986, 2009** both as *Jungermannia ariadne*, Váňa and Piippo 1989a as *Jungermannia ariadne*, Váňa 1991a as *Jungermannia ariadne*, Bapna and Kachroo 2000a as *Jungermannia ariadne*.

Solenostoma comatum (Nees) C.Gao var. *comatum*. **MOLUCCAS**: Ternate/Tidore: Sande **Lacoste 1856b** as *Plagiochila comata*, **Schiffner 1898**, 1900 both as *Nardia comata*, **Stephani 1901a** as *Jungermannia comata*, Hattori 1951 as *Plectocolea comata*, Bonner 1965 as *Eucalyx* '*comatus*', Váňa 1972 as *Jungermannia comata*, 1973 as *Jungermannia comata* [with a '?'], Miller et al. 1983 as *Jungermannia comata*, Váňa and Piippo 1989a as *Jungermannia comata*.

Solenostoma tetragonum (Lindenb.) R.M.Schust. ex Váňa et D.G.Long. **MOLUCCAS**: Ambon: **Váňa 1972**, 1973, 1975, 1991a all both as *Jungermannia tetragona*, Hattori 1975b as *Jungermannia tetragona*, Miller et al. 1983 as *Jungermannia tetragona*, Váňa and Piippo 1989a as *Jungermannia tetragona*, Bapna and Kachroo 2000a as *Jungermannia tetragona*, Srivastava and Sharma 2000 as *Jungermannia tetragona*, Easa 2003 as *Jungermannia tetragona*. Seram: **Akiyama 1986, 2009** both as *Jungermannia tetragona*, Váňa and Piippo 1989a as *Jungermannia tetragona*, Váňa 1991a as *Jungermannia tetragona*.

Solenostoma truncatum (Nees) R.M.Schust. ex Váňa et D.G.Long. **MOLUCCAS**: Halmahera: **Váňa and Piippo 1989a** as *Jungermannia truncata*, Váňa 1991a as *Jungermannia truncata*. Ambon: Váňa 1973, 1991a as *Jungermannia truncata*, Váňa and Piippo 1989a as *Jungermannia truncata*, Bapna and Kachroo 2000a as *Jungermannia truncata*, **Akiyama 2009** as *Jungermannia truncata*. Seram: **Akiyama 1986, 2009** both as *Jungermannia truncata*, Váňa and Piippo 1989a as *Jungermannia truncata*, Váňa 1991a as *Jungermannia truncata*.

Spruceanthus **Verd.**

Spruceanthus polymorphus (Sande Lac.) Verd. **MOLUCCAS**: Halmahera: **Umagap 2019**. Seram: **Mizutani 1986a**, **Akiyama 2009**.

Symphyogynopsis **Grolle**

Symphyogynopsis gottscheana (Mont. et Nees) Grolle. **MOLUCCAS**: Wigginton and Porley 2001, Schaumann et al. 2002. Seram: **Grolle and Piippo 1986** as *Symphyogynopsis filicum*, **Grolle 1987**, Enroth 1991, Furuki 2002 as *Symphyogynopsis filicum*.

Syzygiella **Spruce**

Syzygiella ovalifolia Inoue. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**, So and Grolle 2003.

Syzygiella securifolia (Nees) Inoue. **MOLUCCAS**: Halmahera: **Sande Lacoste 1864** as *Plagiochila variegata*, **Schiffner 1898**, 1900 as *Syzygiella variegata*, Miller et al. 1983 as *Syzygiella variegata*. Seram: **Akiyama 1986, 2009**.

***Telaranea* Spruce ex Schiffn.**

Telaranea major (Herzog) J.J.Engel et G.L.Merr. **MOLUCCAS**: Schuster 2000a as *Arachniopsis major*. Ambon: **Grolle 1968b** as *Arachniopsis major*. Seram: **Akiyama 1986, 2009** as *Arachniopsis major*, von Konrat et al. 2014.

Telaranea trisetosa (Steph.) Grolle. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**.

***Temnoma* Mitt.**

Temnoma setigerum (Lindenb.) R.M.Schust. **MOLUCCAS**: Seram: **Grolle 1967, Akiyama 1986, 2009**, Long and Grolle 1990, Bapna and Kachroo 2000a.

***Thysananthus* Lindenb.**

Thysananthus appendiculatus Steph. **MOLUCCAS**: Ambon: **Sukkharak 2015**. Seram: **Mizutani 1986a**, **Akiyama 2009**.

Thysananthus convolutus Lindenb. var. *convolutus*. **MOLUCCAS**: Haerida et al. 2010, Siregar et al. 2014, 2017, 2020a, Siregar 2015, Ginting and Batubara 2019. Buru: **Verdoorn 1934b**, Eggers and Schäfer-Verwimp 1987. Ambon: **Sukkharak 2011**. Seram: **Mizutani 1986a**, **Akiyama 2009**.

Thysananthus frauenfeldii Reichardt. **MOLUCCAS**: Thiers and Gradstein 1989 as *Mastigolejeunea undulata*, Gradstein et al. 2002 as *Mastigolejeunea undulata*, Sass-Gyarmati 2003 as *Mastigolejeunea undulata*, Sukkharak 2011 as *Thysananthus undulatus*. Seram: **Mizutani 1986a**, 1986b both as *Mastigolejeunea undulata*, **Akiyama 2009** as *Mastigolejeunea undulata*.

Thysananthus fruticosus (Lindenb. et Gottsche) Schiffn. **MOLUCCAS**: Mizutani 1977. Obi: **Verdoorn 1934b**. Banda: **Sande Lacoste 1864** as *Bryopteris fruticosa*, **Schiffner 1898**, Hattori 1951. Seram: **Sande Lacoste 1864** as *Bryopteris fruticosa*, **Verdoorn** 1934a, **1934b**, Hattori 1951, Miller et al. 1983, **Mizutani 1986a, 1987, Akiyama 2009**.

Thysananthus humilis (Gottsche) Sukkharak et Gradst. **MOLUCCAS**: Mizutani 1977 as *Mastigolejeunea humilis*. Ambon: Stephani 1912a as *Mastigolejeunea humilis*, **Verdoorn** 1934a, **1934b** both as *Mastigolejeunea humilis*, Miller et al. 1983 as *Mastigolejeunea humilis*, Awasthi and Udar 1984 as *Mastigolejeunea humilis*, Bapna and Kachroo 2000b as *Mastigolejeunea humilis* var. *humilis*. Banda: **Verdoorn 1934b** as *Mastigolejeunea humilis*, **Bonner 1963a** as *Brachiolejeunea molukkensis*, Tixier 1966 as *Mastigolejeunea humilis*, Bapna and Kachroo 2000b as *Mastigolejeunea humilis*. Seram: **LECTOTYPE** of *Brachiolejeunea molukkensis* [Bonner 1963a: 456], Awasthi and Udar 1984 as *Mastigolejeunea humilis*, **Mizutani 1986a, 1986b** both as *Mastigolejeunea humilis*, Bapna and Kachroo 2000b as *Mastigolejeunea humilis*, **Akiyama 2009** as *Mastigolejeunea humilis*.

Thysananthus ligulatus (Lehm. et Lindenb.) Sukkharak et Gradst. **MOLUCCAS**: Buru: **Verdoorn 1934b** as *Mastigolejeunea ligulata*, Swanson and Miller 1969 as *Mastigolejeunea ligulata*, Miller et al. 1983 as *Mastigolejeunea ligulata*.

Ambon: **Mizutani 1986b** as *Mastigolejeunea ligulata*. Seram: **Sande Lacoste 1864** as *Phragmicoma ligulata*, **Schiffner 1898** as *Mastigolejeunea ligulata*, Swanson and Miller 1969 as *Mastigolejeunea ligulata*, Miller et al. 1983 as *Mastigolejeunea ligulata*, **Mizutani 1986a, 1986b** both as *Mastigolejeunea ligulata*, **Akiyama 2009** as *Mastigolejeunea ligulata*, **Sukkharak and Gradstein 2014** as *Mastigolejeunea ligulata*.

Thysananthus repletus (Taylor) Sukkharak et Gradst. **MOLUCCAS**: Ambon: **Verdoorn 1934b** as *Mastigolejeunea atypos*, Grolle 1968b as *Mastigolejeunea atypos*, Miller et al. 1983 as *Mastigolejeunea atypos*. Seram: **Verdoorn 1934b** as *Mastigolejeunea atypos*, Grolle 1968b as *Mastigolejeunea atypos*, Miller et al. 1983 as *Mastigolejeunea atypos*.

Thysananthus spathulistipus (Reinw., Blume et Nees) Lindenb. **MOLUCCAS**: Mizutani 1977, Haerida et al. 2010, Siregar et al. 2014, Siregar 2015, Siregar et al. 2017. Ambon: **LECTOTYPE** of *Mastigolejeunea amboinensis* [to be designated], **LECTOTYPE** of *Mastigolejeunea amboinensis* var. *paucidentata* [to be designated], **Sande Lacoste 1864** [Saparoea I], **Schiffner 1890** as *Mastigolejeunea amboinensis*, **Schiffner 1890** as *Mastigolejeunea amboinensis* var. *paucidentata*, **1898, Sydow 1894** as *Mastigolejeunea amboinensis*, **Verdoorn 1934b** [also Saparoea I], Swanson and Miller 1969, Miller et al. 1983, Bapna and Kachroo 2000b. Seram: **Sande Lacoste 1864**, **Schiffner 1898, Verdoorn** 1934a, **1934b**, Grolle 1965, Swanson and Miller 1969, **Mizutani 1986a**, **Akiyama 2009** as *Thysananthus* '*spatulistipus*'.

Thysananthus truncatus (Mizut.) Sukkharak et Gradst. **MOLUCCAS**: Seram: **Mizutani 1986a, 1986b** both as *Mastigolejeunea truncata*, Pócs et al. 1994 as *Mastigolejeunea truncata*, **Akiyama 2009** as *Mastigolejeunea truncata*, **Sukkharak and Gradstein 2014** as *Mastigolejeunea truncata*.

Thysananthus virens Ångstr. **MOLUCCAS**: Haerida et al. 2010 as *Mastigolejeunea virens*, Siregar et al. 2014, 2020a both as *Mastigolejeunea virens*, Siregar 2015 as *Mastigolejeunea virens*, Ginting and Batubara 2019 as *Mastigolejeunea virens*, Siregar et al. 2020a as *Mastigolejeunea virens*. Seram: **Mizutani 1986a** as *Mastigolejeunea virens*, **Mizutani 1986b** as *Mastigolejeunea virens*, **Akiyama 2009** as *Mastigolejeunea virens*.

Treubia **K.I.Goebel**

Treubia insignis K.I.Goebel. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**.

Trichocolea **Dumort.**

Trichocolea pluma (Reinw., Blume et Nees) Mont. **MOLUCCAS**: Buru: **Herzog 1921** as *Trichocolea striolata*. Ambon: **Schiffner 1893b, 1898** both as *Trichocolea tomentella* var. *javanica*, **Katagiri et al. 2013**. Seram: **Akiyama 1986, 2009**.

Trichocolea tomentella (Ehrh.) Dumort. **MOLUCCAS**: Morotai: **New to Moluccas**: Morotai, Sangowo, *Exp. Kostermans*) (BO13087)]. Ambon: Miller et al. 1983 as *Trichocolea tomentella*, Bapna and Kachroo 2000a. Note: we are not aware of any first hand report from Ambon but it is here confirmed for Moluccas.

***Tricholepidozia* (R.M.Schust.) E.D.Cooper**

Tricholepidozia kogiana (Steph.) E.D.Cooper. **MOLUCCAS**: Seram: **Akiyama 1986, 2009** both as *Telaranea kogiana*.

Tricholepidozia neesii (Lindenb.) E.D.Cooper. **MOLUCCAS**: Halmahera: **Grolle 1966c** as *Telaranea neesii*, Pócs 1971 as *Telaranea neesii*, Mizutani 1974, 1976 both as *Telaranea neesii*, Engel 1978 as *Telaranea neesii*, Kitagawa 1978 as *Telaranea neesii*, Yamaguchi 1983 as *Telaranea neesii*, Miller 1986 as *Telaranea neesii*, Enroth 1991 as *Telaranea neesii*, Engel and Smith Merrill 2004 as *Telaranea neesii*. Seram: Piippo 1984b as *Telaranea neesii*, **Akiyama 1986, 2009** both as *Telaranea neesii*.

***Tuyamaella* S.Hatt.**

Tuyamaella serratistipa S.Hatt. **MOLUCCAS**: Seram: **Mizutani 1986a**, Zhu and So 1998a, 2000, **Akiyama 2009**.

***Wettsteinia* Schiffn.**

Wettsteinia inversa (Sande Lac.) Schiffn. **MOLUCCAS**: Seram: **Akiyama 1986, 2009**.

***Zantenia* (S.Hatt.) Váňa et J.J.Engel**

Zantenia borneensis (Herzog) Váňa et J.J.Engel. **MOLUCCAS**: Seram: **Váňa and Piippo 1989b** as *Anastrophyllum borneense*, Váňa 1991b as *Anastrophyllum borneense*.

Zantenia karstenii (Schiffn.) Váňa et J.J.Engel. **MOLUCCAS**: Herzog 1926a as *Anastrophyllum karstenii*. Ambon: **LECTOTYPE** of *Anastrophyllum karstenii* [Bonner 1962b: 73], **Schiffner** 1893a, **1893b, 1898** all as *Anastrophyllum karstenii*, **Stephani 1901c** as *Anastrophyllum karstenii*, **Bonner 1962b** as *Anastrophyllum karstenii*, Hattori 1966 as *Anastrophyllum karstenii*.

***Zoopsis* Hook.f. ex Gottsche, Lindenb. et Nees**

Zoopsis liukiuensis Horik. **MOLUCCAS: Grolle and Piippo 1984**. Ambon: **Grolle 1968b**, Schuster 1969, Miller et al. 1983, **Schuster 1999**, Engel and Glenny 2008. Seram: **Akiyama 1986, 2009**.

Zoopsis setigera K.I.Goebel. **MOLUCCAS**: Ambon: **LECTOTYPE** [Grolle and Piippo 1984: 303 as "neotype"], **Grolle and Piippo 1984, Schuster 1999**, Engel and Glenny 2008. Seram: **Akiyama 1986, 2009**.

Names not referred to any accepted taxon

We are not able to refer the following published names to any accepted taxon.

***Phaeoceros* Prosk.**

Phaeoceros velutinus J.Haseg. ex H.Akiyama *nom. inval.* **MOLUCCAS**: Ambon: **ORIGINAL MATERIAL**. Seram: Akiyama 1986. Note: we have not found the name *Phaeoceros velutinus* anywhere else than in Akiyama (1986) listing it from Moluccas, and we do not know where to refer it.

***Jungermannia* L.**

Jungermannia gigantea β *laxior* (Nees) Lindenb. **MOLUCCAS**: Ternate/Tidore: **SYNTYPE** of *Jungermannia gigantea* β *laxior* [lectotype to be designated], **ORIGINAL MATERIAL** of *Plagiochila trapezoidea* γ *major*, **Nees 1830, 1831** both as *Jungermannia gigantea* β *laxior*, **Lindenberg 1840** as *Plagiochila trapezoidea* γ '*maior*', **Schiffner 1898**, 1900 as *Plagiochila trapezoidea* var. *major*, **Geissler and Bischler 1987** as *Jungermannia gigantea* β *laxior*. Note: this name does have a confusing history and before someone really select and identify a **lectotype**, it is impossible to know what taxon it represents

Jungermannia tamarisci L. var. β *minus-ramosa* Schwägr. *nom. inval.* **MOLUCCAS**: **ORIGINAL MATERIAL, Gaudichaud 1828**. Note: *Frullania tamarisci* is a mainly Eurasian taxon and this name must refer to a tropical taxon

***Plagiochila* (Dumort.) Dumort.**

Plagiochila opposita (Reinw., Blume et Nees) Lindenb. β *falcata* (Nees) Schiffn. **MOLUCCAS**: Ternate/Tidore: **Sande Lacoste 1856b, Schiffner 1898**. Note: *Plagiochila opposita* is now *Chiastocaulon oppositum* but we are not sure if unranked β *falcata* also belong to that species and is worth recognizing.

Taxa doubtfully occurring in Moluccas

We doubt the identification of the following taxa or we are not aware of any first-hand report from Moluccas.

***Acromastigum* A.Evans**

Acromastigum echinatum (Gottsche) A.Evans. **MOLUCCAS**: Ambon: Stephani 1909a as *Mastigobryum echinatum*, Bonner 1962b, Swanson and Miller 1969, Miller et al. 1983. Note: we are not aware of any first hand report from Moluccas although it is reported to occur on neighbouring islands.

***Bazzania* Gray**

Bazzania ceylanica (Mitt.) Steph. **MOLUCCAS**: Ambon: Stephani 1902 as *Mastigobryum ceylanicum*. Note: we are not aware of any first hand report from Moluccas although it is reported to occur on neighbouring islands.

Bazzania japonica (Sande Lac.) Lindb. **MOLUCCAS**: Siregar and Pasaribu 2019. Note: we are not aware of any first hand report from Moluccas although it is reported to occur on neighbouring islands.

***Calypogeia* Raddi**

Calypogeia tosana (Steph.) Steph. **MOLUCCAS**: Halmahera: **Umagap 2019**. Note: a Sino-Himalayan taxon that seems unlikely to occur in the tropics.

Chiloscyphus Corda

Chiloscyphus ernstianus Steph. **MOLUCCAS**: Seram: **Akiyama 1986, 2009** both as *Lophocolea* aff. *ernstiana*. Note: we are not aware of any positively identified report from Moluccas. It is otherwise only known from the type from Sumatra and if worth recognizing it certainly belongs to some other genus.

Cololejeunea (Spruce) Steph.

Cololejeunea cordiflora Steph. **MOLUCCAS**: Ambon: Tixier 1962 as *Cololejeunea karstenii*. Note: we are not aware of any first hand report from Moluccas although it is reported to occur on neighbouring islands.

Cololejeunea verrucosa Steph. **MOLUCCAS**: Miller 1968, Pócs and Ninh 2012, Pócs 2012. Ambon: Miller et al. 1983. Note: we are not aware of any first hand report from Moluccas although it is reported to occur on neighbouring islands.

Cryptolophocolea L.Söderstr., Crand.-Stotl., Stotler et Váňa

Cryptolophocolea ciliolata (Nees) L.Söderstr., Crand.-Stotl., Stotler et Váňa. **MOLUCCAS**: Seram: **Akiyama 1986, 2009** both as *Lophocolea* aff. *ciliolata*. Note: we are not aware of any positively identified report from Moluccas although it is reported to occur on neighbouring islands.

Leptolejeunea (Spruce) Steph.

Leptolejeunea balansae Steph. **MOLUCCAS**: Ambon: Jovet-Ast 1958. Note: we are not aware of any first hand report from Moluccas although it is reported to occur on neighbouring islands.

Leptolejeunea subacuta Steph. ex A.Evans. **MOLUCCAS**: Inoue and Miller 1965, Miller 1968, Swanson and Miller 1969, Miller et al. 1983, Bapna and Kachroo 2000b. Note: we are not aware of any first hand report from Moluccas although it is reported to occur on neighbouring islands.

Mastigophora Nees

Mastigophora woodsii (Hook.) Nees. **MOLUCCAS**: Seram: **LECTOTYPE** of *Mastigophora ramentifissa* [to be designated], **Herzog** 1926a, **1926b** as *Mastigophora ramentifissa*, Inoue 1971. Note: Inoue (1971) synonymized *Mastigophora ramentifissa* with *Mastigophora woodsii* but doubted the origin of the type of the former as *Mastigophora woodsii* is unlikely to occur in the tropics.

Plagiochila (Dumort.) Dumort.

Plagiochila gracilis Lindenb. et Gottsche. **MOLUCCAS**: Miller et al. 1983. Note: we are not aware of any first hand report from Moluccas although it is reported to occur on neighbouring islands.

Radula **Dumort.**

Radula amentulosa Mitt. **MOLUCCAS**: SERAM: Yamada 1999. Note: we are not aware of any first-hand report from Moluccas.

Schistochila **Dumort.**

Schistochila schultzei Steph. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009** both as *Schistochila* aff. *schultzei*. Note: we are not aware of any positively identified specimen from Moluccas although it is reported from neighboring islands.

Spruceanthus **Verd.**

Spruceanthus semirepandus (Nees) Verd. **MOLUCCAS**: Haerida et al. 2010. Note: we are not aware of any positively identified specimen from Moluccas although it is reported from neighboring islands.

Thysananthus **Lindenb.**

Thysananthus auriculatus (Wilson et Hook.) Sukkharak et Gradst. **MOLUCCAS**: Haerida et al. 2010 as *Mastigolejeunea auriculata*, Singh et al. 2010 as *Mastigolejeunea auriculata*. Note: we are not aware of any positively identified specimen from Moluccas although it is reported from neighboring islands.

Taxa reported but rejected from Moluccas

The following taxa are reported to occur in Moluccas but the reports are rejected either earlier or here as misidentified or highly unlikely to occur in the area.

Cheilolejeunea **(Spruce) Steph.**

Cheilolejeunea mariana (Gottsche) B.M.Thiers et Gradst. **MOLUCCAS**: SERAM: **Mizutani 1986a** as *Spruceanthus marianus*, **Akiyama 2009** as *Spruceanthus marianus*. Note: a Pacific species frequently, but erroneously, reported from SE Asia and many other areas. Reports should mainly be referred to *Archilejeunea planiuscula*.

Chiastocaulon **Carl**

Chiastocaulon fimbriatum (Mitt.) S.D.F.Patzak, M.A.M.Renner, Schäf.-Verw. et Heinrichs. **MOLUCCAS**: SERAM: **Akiyama 1986, 2009** both as *Plagiochilion* aff. *fimbriatum*. Note: a Sino-Himalayan taxon very unlikely to occur in the tropics.

Conocephalum **Hill**

Conocephalum conicum (L.) Dumort. **MOLUCCAS**: AMBON: Sopacua et al. 2020 as '*Conocephelum*' *conicum* [Saparua I]. Note: presumably a mainly European taxon reported *sensu lato* from many other places. It is unlikely that the genus *Conocephalum* occurs in the tropics, but if it is a *Conocephalum* sp. it is probably more related to *Conocephalum salebrosum* than to *Conocephalum conicum*.

Cryptolophocolea **L.Söderstr., Crand.-Stotl., Stotler et Váňa**

Cryptolophocolea connata (Sw.) L.Söderstr. et Váňa. **MOLUCCAS**: **Gaudichaud 1828** as *Jungermannia connata*. Note: an American species and this old record must be rejected as either mis-identified or mis-labelled.

Dendroceros **Nees**

Dendroceros exalatus Steph. **MOLUCCAS**: AMBON: **LECTOTYPE** [Hasegawa 1980: 302], **Stephani 1909b**, 1917, **Bonner 1965**. Note: Stephani erroneously reported the type locality as "Amboina" but as this is a Brazilian species that must be due to mislabeling (cf. Hasegawa 1980).

Heteroscyphus **Schiffn.**

Heteroscyphus caledonicus (Steph.) Schiffn. **MOLUCCAS**: AMBON: Miller et al. 1983. Note a Pacific species possibly endemic to New Caledonia.

Lepicolea **Dumort.**

Lepicolea ochroleuca (Spreng.) Spruce. **MOLUCCAS**: SERAM: **Herzog 1921**. Note: an Afro-American species only once reported from SE Asia. This report must be an error.

Lepicolea scolopendra (Hook.) Dumort. ex Trevis. **MOLUCCAS**: SERAM: **Herzog 1926b**. Note: an Australian/New Zealandian species frequently, but erroneously, reported from many other places.

Lepidozia **(Dumort.) Dumort.**

Lepidozia microphylla (Hook.) Lindenb. **MOLUCCAS**: SERAM: Siregar and Pasaribu 2019. Note: a species endemic to New Zealand (cf. Engel and Schuster 2001) and all reports from other areas must be rejected.

Lepidozia rigida Steph. **MOLUCCAS**: BURU: **ORIGINAL MATERIAL** of *Lepidozia rigida* f. *minor*, **Herzog 1921** as *Lepidozia rigida* f. *minor*, Herzog 1926a as *Lepidozia rigida* var. *minor*. Note: a species from Vanuatu. Herzog's material must belong to another species.

Plagiochila **(Dumort.) Dumort.**

Plagiochila gigantea Lindenb. **MOLUCCAS**: TERNATE/TIDORE: **Nees 1830** as *Jungermannia gigantea*. Note: a New Zealand taxon.

Plagiochila trapezoidea Lindenb. **MOLUCCAS**: TERNATE/TIDORE: **Reinwardt et al. 1824** as *Jungermannia simplex* Web, Schiffner 1900, Bapna and Kachroo 2000b. Note: Inoue (1984) designated the only specimen from Java of *Jun-*

germannia simplex Web. that he could locate as a neotype of *Plagiochila trapezoidea* and *Plagiochila trapezoidea* β *tenera* is described as based on *Jungermannia simplex* Web. However, Inoue (1984) reject the report of β *tenera* in Gottsche et al. (1844; all other reports probably based on this) as *Plagiochila ciliata*. The occurrence of *Plagiochila trapezoidea* in Moluccas is therefore not confirmed and reports should be rejected following Inoue, until confirmed, although it occurs in most neighbouring islands.

***Podomitrium* Mitt.**

Podomitrium phyllanthus (Hook.) Mitt. **MOLUCCAS**: AMBON: **Schiffner 1890, 1898** as '*Hymenophytum' phyllanthus*, **Sydow 1894**. Note: this is an Australian/New Zealandian species.

***Porella* L.**

Porella nitens (Steph.) S.Hatt. **MOLUCCAS**: Long and Grolle 1990. Note: the second-hand reports from Malesia in Long and Grolle (1990) of this Sino-Himalayan species is due to supposed, but rejected, synonymy with *Porella javanica* (cf. also Hattori 1978).

***Pycnolejeunea* (Spruce) Schiffn.**

Pycnolejeunea schwaneckei (Steph.) Schiffn. ex P.Syd. **MOLUCCAS**: AMBON: **Schiffner 1890**, **Sydow 1894** as *Pycnolejeunea* '*schwaneckii*'. Note: this is a neotropical species.

***Radula* Dumort.**

Radula pinnulata Mitt. **MOLUCCAS**: Miller et al. 1983. Note: Yamada (2002) rejected all reports from Moluccas.

***Riccardia* Gray**

Riccardia latifrons (Lindb.) Lindb. **MOLUCCAS**: AMBON: **Schiffner 1890** as *Aneura latifrons*, **Sydow 1894** as *Aneura latifrons*. Note: a mainly boreal species and all reports from tropical areas should be rejected.

***Schistochila* Dumort.**

Schistochila neesii (Mont.) Lindb. **MOLUCCAS**: AMBON: **Schiffner 1893b, 1898**, Buch 1939, Hässel 1976 as *Paraschistochila neesii*. Note: an African species rejected from Moluccas by So (2003a).

***Symbiezidium* Trevis.**

Symbiezidium transversale (Sw.) Trevis. **MOLUCCAS**: **Gaudichaud 1828** as *Jungermannia transversalis*. Note: an American species.

Zoopsis Hook.f. ex Gottsche, Lindenb. et Nees

Zoopsis argentea (Hook.f. et Taylor) Gottsche, Lindenb. et Nees. **MOLUCCAS**: Ambon: Stephani 1908a, Del Rosario 1975b, Miller et al. 1983. Note: an Australian/New Zealandian species.

Zoopsis setulosa Leitg. **MOLUCCAS**: Miller et al. 1983 as *Zoopsis rigida*. Ambon: **Schiffner 1893b** as *Cephalozia setulosa*, **1898, Stephani 1908b**, Hattori 1951, Hodgson 1965, Schuster 1969. Note: an Australian/New Zealandian/New Caledonian species rejected from Asia as *Zoopsis setigera* by Grolle and Piippo (1984).

Synonyms

Acrolejeunea densifolia (Schiffn.) Schiffn. ex P.Syd. *nom. inval*. = *Schiffneriolejeunea pulopenangensis*

Acrolejeunea densifolia Schiffn. *nom. inval*. = *Schiffneriolejeunea pulopenangensis*

Acrolejeunea haskarliana (Gottsche) Schiffn. ≡ *Schiffneriolejeunea tumida* var. *haskarliana*

Acrolejeunea pulopenangensis (Gottsche) Schiffn. ≡ *Schiffneriolejeunea pulopenangensis*

Acrolejeunea rostrata Schiffn. *nom. inval*. = *Acrolejeunea pycnoclada* subsp. *pycnoclada*

Acrolejeunea rostrata var. α *minor* Schiffn. *nom. inval*. = *Acrolejeunea pycnoclada* subsp. *pycnoclada*

Acrolejeunea rostrata var. β *major* Schiffn. *nom. inval*. = *Acrolejeunea pycnoclada* subsp. *pycnoclada*

Acrolejeunea securifolia (Nees) Steph. *nom. inval*. ≡ *Acrolejeunea securifolia*

Acromastigum bidenticulatum A.Evans = *Acromastigum bancanum*

Anastrophyllum bidens (Reinw., Blume et Nees) Steph. ≡ *Schizophyllopsis bidens*

Anastrophyllum borneense Herzog ≡ *Zantenia borneensis*

Anastrophyllum contractum (Reinw., Blume et Nees) Steph. ≡ *Cuspidatula contracta*

Anastrophyllum karstenii Schiffn. ≡ *Zantenia karstenii*

Anastrophyllum revolutum Steph. ≡ *Anastrophyllopsis revoluta*

Aneura albomarginata Steph. ≡ *Riccardia albomarginata*

Aneura karstenii Steph. ≡ *Riccardia karstenii*

Aneura latifrons Lindb. ≡ *Riccardia latifrons*

Aneura pinguis f. *normalis* Schiffn. *nom. inval*. = *Aneura pinguis*

Anomacaulis flaccidus (Steph.) Grolle ≡ *Cuspidatula flaccida*

Anthoceros amboinensis Schiffn. ≡ *Folioceros amboinensis*

Anthoceros appendiculatus Steph. ≡ *Folioceros appendiculatus*

Anthoceros glandulosus Lehm. et Lindenb. ≡ *Folioceros glandulosus*

Anthoceros grandis Ångstr. = *Megaceros flagellaris*

Arachniopsis major Herzog ≡ *Telaranea major*

Aspiromitus amboinensis (Schiffn.) Steph. ≡ *Folioceros amboinensis*

Bazzania australis (Mont.) Trevis. = *Bazzania tridens*

Bazzania concinna (De Not.) Trevis. = *Bazzania intermedia*

Bazzania divaricata (Nees) Trevis. = *Acromastigum divaricatum*

Bazzania echinatiformis (De Not.) Trevis. ≡ *Acromastigum echinatiforme*

Bazzania intermedia auct. = *Bazzania tridens* var. *tridens*
Bazzania longidens (Steph.) Schiffn. = *Bazzania conophylla*
Bazzania oshimensis (Steph.) Horik. = *Bazzania tridens*
Brachiolejeunea molukkensis Steph. = *Thysananthus humilis*
Bryopteris fruticosa Lindenb. et Gottsche ≡ *Thysananthus fruticosus*
Calypogeia fusca (Lehm.) Steph. ≡ *Mnioloma fuscum*
Campylolejeunea ciliatilobula (Schiffn.) S.Hatt. = *Cololejeunea inflectens*
Campylolejeunea inflectens (Mitt.) Mizut. ≡ *Cololejeunea inflectens*
Caudalejeunea circinata Steph. = *Caudalejeunea cristiloba*
Caudalejeunea recurvistipula (Gottsche) Schiffn. = *Caudalejeunea reniloba*
Cephalozia setulosa (Leitg.) Spruce ≡ *Zoopsis setulosa*
Chandonanthus gracilis Herzog = *Plicanthus hirtellus*
Chandonanthus hirtellus (F.Weber) Mitt. ≡ *Plicanthus hirtellus*
Cheilolejeunea imbricata (Nees) S.Hatt. = *Cheilolejeunea trapezia*
Cheilolejeunea meyeniana (Nees, Lindenb. et Gottsche) R.M.Schust. et Kachroo = *Cheilolejeunea trapezia*
Chiloscyphus amboinensis (Schiffn.) Schiffn. ≡ *Heteroscyphus amboinensis*
Chiloscyphus aselliformis (Reinw., Blume et Nees) Nees ≡ *Heteroscyphus aselliformis*
Chiloscyphus coalitus (Hook.) Nees ≡ *Heteroscyphus coalitus*
Chiloscyphus decurrens (Reinw., Blume et Nees) Nees = *Heteroscyphus splendens*
Chiloscyphus decurrens var. *amboinensis* (Schiffn.) Schiffn. ex Bonner *nom. inval*. ≡ *Heteroscyphus amboinensis*
Chiloscyphus endlicherianus δ *amboinensis* Schiffn. ≡ *Heteroscyphus amboinensis*
Chiloscyphus falcifolius Steph. = *Acroscyphella tjiwideiensis*
Chiloscyphus granulatus Schiffn. = *Saccogynidium rigidulum*
Clasmatocolea tjiwideiensis (Sande Lac.) Grolle ≡ *Acroscyphella tjiwideiensis*
Cololejeunea ciliatilobula (Schiffn.) Schiffn. = *Cololejeunea inflectens*
Cololejeunea crenulata (Herzog) Benedix *nom. inval.* = *Cololejeunea angustiflora*
Cololejeunea falcatoides Benedix = *Cololejeunea falcata*
Cololejeunea goebelii (Gottsche ex Schiffn.) Schiffn. = *Cololejeunea trichomanis*
Cololejeunea javanica (Steph.) Mizut. = *Cololejeunea angustiflora*
Cololejeunea karstenii (Steph.) Benedix = *Cololejeunea cordiflora*
Cololejeunea nymannii (Steph.) Benedix = *Cololejeunea obliqua*
Cololejeunea peculiaris (Herzog) Benedix = *Cololejeunea inflectens*
Cololejeunea yulensis (Steph.) Benedix = *Cololejeunea aequabilis*
Colura paradoxa (Schiffn.) Steph. ≡ *Calatholejeunea paradoxa*
Colurolejeunea karstenii (K.I.Goebel) Steph. ≡ *Colura karstenii*
Colurolejeunea karstenii var. *latifolia* (Schiffn.) Schiffn. *nom. inval*. = *Colura karstenii*
Colurolejeunea paradoxa (Schiffn.) Schiffn. ≡ *Calatholejeunea paradoxa*
Colurolejeunea superba (Mont.) Steph. ≡ *Colura superba*
Colurolejeunea superba Schiffn. *nom. inval*. = *Colura amboinensis*
Colurolejeunea superba var. α *typica* Schiffn. *nom. inval*. = *Colura amboinensis*
Dendroceros karstenii Schiffn. ex Steph. = *Dendroceros acutilobus*
Drepanolejeunea dactylophora (Nees, Lindenb. et Gottsche) Schiffn. ≡ *Drepanolejeunea dactylophora*
Drepanolejeunea dentata Steph. ≡ *Lejeunea stenodentata*
Drepanolejeunea filicuspis Steph. ≡ *Microlejeunea filicuspis*

Drepanolejeunea levicornua var. *longicornua* Herzog ≡ *Drepanolejeunea longicornua*
Drepanolejeunea micholitzii Steph. = *Drepanolejeunea pentadactyla*
Drepanolejeunea micholitzii var. *dactylophoroides* Herzog ≡ *Drepanolejeunea pentadactyla* var. *dactylophoroides*
Drepanolejeunea micholitzii var. *genuina* Herzog *nom. illeg.* = *Drepanolejeunea pentadactyla*
Drepanolejeunea tenera var. *genuina* Herzog *nom. illeg.* = *Drepanolejeunea tenera*
Drepanolejeunea ternatensis (Gottsche) Steph. *nom. inval*. ≡ *Drepanolejeunea ternatensis*
Eucalyx comata (Nees) Verd. ≡ *Solenostoma comatum*
Eulejeunea fissistipula Steph. ≡ *Lejeunea fissistipula*
Eulejeunea parallela (Schiffn.) Schiffn. = *Metalejeunea cucullata*
Euosmolejeunea heterophylla (Sande Lac.) Schiffn. = *Cheilolejeunea trifaria*
Euosmolejeunea integristipula Steph. = *Cheilolejeunea lindenbergii*
Euosmolejeunea trifaria (Reinw., Blume et Nees) Steph. ≡ *Cheilolejeunea trifaria*
Frullania amboinensis Schiffn. = *Frullania intermedia* subsp. *intermedia*
Frullania billardiereana Nees et Mont. = *Frullania intermedia* subsp. *intermedia*
Frullania dapitana Steph. = *Frullania nodulosa*
Frullania ericoides var. *planescens* (Verd.) S.Hatt. = *Frullania ericoides*
Frullania gracilis var. *lacerifolia* (Steph.) Verd. = *Frullania gracilis*
Frullania intermedia f. *billardiereana* (Nees et Mont.) Verd. = *Frullania intermedia* subsp. *intermedia*
Frullania intermedia var. *amboinensis* (Schiffn.) Verd. = *Frullania intermedia* subsp. *intermedia*
Frullania karstenii Schiffn. = *Frullania apiculata* var. goebelii
Frullania lacerifolia Steph. = *Frullania gracilis*
Frullania nodulosa f. *dapitana* (Steph.) Verd. = *Frullania nodulosa*
Frullania nodulosa f. *irreflexa* Verd. = *Frullania nodulosa*
Frullania nodulosa β *plana* Schiffn. = *Frullania nodulosa*
Frullania picta Steph. = *Frullania trichodes*
Frullania replicata (Nees) Mont. = *Frullania nodulosa*
Frullania rugosa Mitt. = *Frullania grandistipula*
Frullania serrata f. *crispulo-dentata* Verd. = *Frullania serrata* var. *serrata*
Frullania squarrosa (Mont.) Nees = *Frullania ericoides*
Frullania squarrosa f. *campanuloides* Verd. = *Frullania ericoides*
Frullania squarrosa var. *planescens* Verd. = *Frullania ericoides*
Frullania tenuicaulis Mitt. = *Frullania trichodes*
Frullania thuillieri Nees = *Frullania nodulosa*
Gamoscyphus aselliformis (Reinw., Blume et Nees) Trevis. ≡ *Heteroscyphus aselliformis*
Gottschea aligera (Nees et Blume) Nees ≡ *Schistochila aligera*
Gottschea blumei (Nees) Nees ≡ *Schistochila blumei*
Harpalejeunea exigua Steph. = *Lejeunea exilis*
Harpalejeunea filicuspis (Steph.) Mizut. ≡ *Microlejeunea filicuspis*
Herbertus armitanus (Steph.) H.A.Mill. = *Herbertus sendtneri*
Herbertus divaricatus (Herzog) H.A.Mill. = *Herbertus sendtneri*
Herbertus javanicus (Steph.) H.A.Mill. = *Herbertus ramosus*
Herbertus javanicus (Steph.) Schiffn. *nom. inval.* = *Herbertus ramosus*

Heteroscyphus decurrens (Nees) Schiffn. = *Heteroscyphus splendens*
Hygrolejeunea amboinensis (Schiffn.) Schiffn. *nom. inval.* = *Lejeunea sordida*
Hygrolejeunea amboinensis (Schiffn.) Schiffn. ex P.Syd. = *Lejeunea sordida*
Hygrolejeunea decurvifolia Steph. = *Lepidolejeunea bidentula*
Hygrolejeunea discreta (Lindenb.) Schiffn. ≡ *Lejeunea discreta*
Hygrolejeunea discreta (Lindenb.) Steph. *nom. inval.* ≡ *Lejeunea discreta*
Hygrolejeunea parkinsonii Steph. = *Lejeunea sordida*
Hygrolejeunea sordida (Nees) Schiffn. ≡ *Lejeunea sordida*
Hygrolejeunea sordida (Nees) Steph. *nom. inval.* ≡ *Lejeunea sordida*
Hygrolejeunea umbilicata (Nees) Steph. *nom. inval.* ≡ *Lejeunea umbilicata*
Hymenophyton malaccense Steph. ≡ *Podomitrium malaccense*
Hymenophyton phyllanthus (Hook.) Steph. ≡ *Podomitrium phyllanthus*
Jamesoniella contracta (Reinw., Blume et Nees) N.Kitag. ≡ *Cuspidatula contracta*
Jamesoniella flexicaulis (Nees) Schiffn. ≡ *Cuspidatula flexicaulis*
Jamesoniella flexicaulis var. β *microphylla* (Nees) Schiffn. = *Gottschelia schizopleura*
Jamesoniella microphylla (Nees) Schiffn. = *Gottschelia schizopleura*
Jamesoniella ovifolia (Schiffn.) Schiffn. = *Denotarisia linguifolia*
Jungermannia ariadne Taylor ≡ *Solenostoma ariadne*
Jungermannia aselliformis Reinw., Blume et Nees ≡ *Heteroscyphus aselliformis*
Jungermannia comata Nees ≡ *Solenostoma comatum*
Jungermannia connata Sw. ≡ *Cryptolophocolea connata*
Jungermannia contracta Reinw., Blume et Nees ≡ *Cuspidatula contracta*
Jungermannia flexicaulis Nees ≡ *Cuspidatula flexicaulis*
Jungermannia flexicaulis β *microphylla* Gottsche, Lindenb. et Nees = *Gottschelia schizopleura*
Jungermannia gigantea Hook. *nom. illeg.* ≡ *Plagiochila gigantea*
Jungermannia gigantea β *laxior* Nees ≡ *Plagiochila gigantea laxior*
Jungermannia indica Nees = *Lejeunea flava* subsp. *orientalis*
Jungermannia opposita Reinw., Blume et Nees ≡ *Chiastocaulon oppositum*
Jungermannia ovifolia Schiffn. = *Denotarisia linguifolia*
Jungermannia simplex Weber *nom. illeg.* = *Plagiochila trapezoidea*
Jungermannia tetragona Lindenb. ≡ *Solenostoma tetragonum*
Jungermannia transversalis Sw. ≡ *Symbiezidium transversale*
Jungermannia truncata Nees ≡ *Solenostoma truncatum*
Jungermannia vaginata Sw. ≡ *Frullania vaginata*
Lejeunea applanata (Reinw., Blume et Nees) Nees ≡ *Lopholejeunea applanata*
Lejeunea catanduana (Steph.) H.A.Mill., Bonner et Bischl. = *Lejeunea anisophylla*
Lejeunea chalmersii (Steph.) Mizut. = *Lejeunea microloba*
Lejeunea connivens Gottsche = *Cheilolejeunea ceylanica*
Lejeunea cucullata (Reinw., Blume et Nees) Nees ≡ *Metalejeunea cucullata*
Lejeunea haskarliana (Gottsche) Spruce *nom. illeg.* ≡ *Schiffneriolejeunea tumida* var. *haskarliana*
Lejeunea heterophylla Sande Lac. = *Cheilolejeunea trifaria*
Lejeunea microstipula (Steph.) Prantl = *Lejeunea exilis*
Lejeunea paradoxa Schiffn. ≡ *Calatholejeunea paradoxa*
Lejeunea pusilla (K.I.Goebel) Schiffn. *nom. illeg.* = *Cololejeunea metzgeriopsis*
Lejeunea recurvistipula Gottsche = *Caudalejeunea reniloba*
Lejeunea rostrata var. α *minor* Schiffn. ex P.Geissler et Bischl. *nom. inval.* = *Acrolejeunea pycnoclada* subsp. *pycnoclada*

Lejeunea sagrana (Mont.) Gottsche, Lindenb. et Nees = *Lopholejeunea subfusca*
Lejeunea sagrana var. *dentistipula* Schiffn. = *Caudalejeunea reniloba*
Lejeunea superba var. α *typica* Schiffn. *nom. inval.* = *Colura superba*
Lejeunea ternatensis Gottsche ≡ *Drepanolejeunea ternatensis*
Lejeunea trapezia (Nees) Nees ≡ *Cheilolejeunea trapezia*
Lejeunea trifaria (Reinw., Blume et Nees) Nees ≡ *Cheilolejeunea trifaria*
Lepidozia papulosa Steph. ≡ *Neolepidozia papulosa*
Lepidozia rigida f. *minor* (Steph.) Herzog *nom. inval.* = *Lepidozia rigida*
Lepidozia rigida var. *minor* (Steph.) Herzog *nom. inval*. = *Lepidozia rigida*
Lepidozia wallichiana Gottsche ≡ *Neolepidozia wallichiana*
Leptolejeunea foliicola (Horik.) R.M.Schust. *nom. illeg.* ≡ *Drepanolejeunea foliicola*
Leptolejeunea schiffneri f. *angustifolia* Herzog *nom. inval*. = *Leptolejeunea schiffneri*
Leptolejeunea schiffneri var. *genuina* Herzog *nom. inval*. = *Leptolejeunea schiffneri*
Leptolejeunea schiffneri (Steph. ex Schiffn.) Steph. = *Leptolejeunea schiffneri*
Lobatiriccardia lobata (Schiffn.) Furuki = *Lobatiriccardia coronopus*
Lophocolea ciliolata (Nees) Gottsche ≡ *Cryptolophocolea ciliolata*
Lophocolea ernstiana (Steph.) N.Kitag. ≡ *Chiloscyphus ernstianus*
Lophocolea giulianettii Steph. = *Cryptolophocolea costata*
Lopholejeunea dentistipula (Schiffn.) Schiffn. = *Caudalejeunea reniloba*
Lopholejeunea eulopha (Taylor) Steph. *nom. inval*. ≡ *Lopholejeunea eulopha*
Lopholejeunea javanica (Nees) Schiffn. = *Lopholejeunea nigricans*
Lopholejeunea pyriflora Steph. = *Lopholejeunea subfusca*
Lopholejeunea sagrana (Mont.) Steph. = *Lopholejeunea subfusca*
Lopholejeunea sagrana var. *dentistipula* (Schiffn.) Schiffn. ex P.Syd. = *Caudalejeunea reniloba*
Lopholejeunea sagrana var. *dentistipula* Schiffn. *nom. inval*. = *Caudalejeunea reniloba*
Lopholejeunea sagrana var. β *subfusca* (Nees) Schiffn. ≡ *Lopholejeunea subfusca*
Madotheca acutifolia Lehm. et Lindenb. ≡ *Porella acutifolia*
Madotheca crenilobula Herzog = *Porella javanica*
Marchantia amboinensis Nees et Mont. = *Marchantia emarginata* subsp. *emarginata*
Mastigobryum amboinense Steph. = *Bazzania tridens*
Mastigobryum asymmetricum Steph. ≡ *Bazzania asymmetrica*
Mastigobryum ceylanicum Mitt. ≡ *Bazzania ceylanica*
Mastigobryum concinnum De Not. = *Bazzania intermedia*
Mastigobryum crassitextum (Steph.) Steph. ≡ *Bazzania crassitexta*
Mastigobryum deningeri Herzog = *Bazzania longicaulis*
Mastigobryum echinatiforme De Not. ≡ *Acromastigum echinatiforme*
Mastigobryum echinatum Gottsche ≡ *Acromastigum echinatum*
Mastigobryum fallax Sande Lac. ≡ *Bazzania fallax*
Mastigobryum horridulum (Schiffn.) Steph. ≡ *Bazzania horridula*
Mastigobryum insigne De Not. ≡ *Bazzania insignis*
Mastigobryum intermedium Gottsche et Lindenb. ≡ *Bazzania intermedia*
Mastigobryum irregulare Steph. ≡ *Bazzania irregularis*
Mastigobryum javanicum Sande Lac. ≡ *Bazzania javanica*
Mastigobryum longidens Steph. = *Bazzania conophylla*
Mastigobryum merrillanum Steph. ≡ *Bazzania merrillana*
Mastigobryum pectinatum (Nees) Lindenb. et Gottsche = *Bazzania pectinata*

Mastigobryum stresemannii Herzog ≡ *Bazzania stresemannii*
Mastigobryum subtile Sande Lac. ≡ *Bazzania subtilis*
Mastigobryum tridens (Reinw., Blume et Nees) Dumort. ≡ *Bazzania tridens*
Mastigobryum uncigerum (Reinw., Blume et Nees) Nees ≡ *Bazzania uncigera*
Mastigobryum vittatum Gottsche ≡ *Bazzania vittata*
Mastigobryum wallichianum Lindenb. ≡ *Bazzania wallichiana*
Mastigolejeunea amboinensis (Schiffn.) Schiffn. ex P.Syd. = *Thysananthus spathulistipus*
Mastigolejeunea amboinensis Schiffn. *nom. inval.* = *Thysananthus spathulistipus*
Mastigolejeunea amboinensis var. β *paucidentata* Schiffn. *nom. inval.* = *Thysananthus spathulistipus*
Mastigolejeunea atypos Schiffn. ex Sydow = *Thysananthus repletus*
Mastigolejeunea auriculata (Wilson et Hook.) Steph. ≡ *Thysananthus auriculatus*
Mastigolejeunea humilis (Gottsche) Schiffn. ≡ *Thysananthus humilis*
Mastigolejeunea ligulata (Lehm. et Lindenb.) Schiffn. ≡ *Thysananthus ligulatus*
Mastigolejeunea truncata Mizut. ≡ *Thysananthus truncatus*
Mastigolejeunea undulata Gradst. et Grolle = *Thysananthus frauenfeldii*
Mastigolejeunea virens (Ångstr.) Steph. ≡ *Thysananthus virens*
Mastigophora diclados var. β *scorpioides* (Reinw., Blume et Nees) Schiffn. = *Mastigophora diclados*
Mastigophora ramentifissa Herzog = *Mastigophora woodsii*
Mastigophora vrieseana (Sande Lac.) Schiffn. = *Mastigophora diclados*
Megaceros grandis (Ångstr.) Steph. = *Megaceros flagellaris*
Metahygrobiella stolonacea (Herzog) R.M.Schust. ≡ *Cephalozia stolonacea*
Metzgeria decipiens (C.Massal.) Schiffn. = *Metzgeria ciliata*
Metzgeria hamatiformis Schiffn. = *Metzgeria leptoneura* var. *leptoneura*
Metzgeriopsis pusilla K.I.Goebel = *Cololejeunea metzgeriopsis*
Microlejeunea microstipula Steph. = *Lejeunea exilis*
Microlejeunea parallela Schiffn. = *Metalejeunea cucullata*
Microlejeunea ternatensis (Gottsche) Herzog nom. inval. ≡ *Drepanolejeunea ternatensis*
Microlepidozia gonyotricha (Sande Lac.) Del Ros. ≡ *Kurzia gonyotricha*
Nardia ariadne (Taylor) Schiffn. ≡ *Solenostoma ariadne*
Nardia comata (Nees) Schiffn. ≡ *Solenostoma comatum*
Noguchia opposita (Reinw., Blume et Nees) Inoue ≡ *Chiastocaulon oppositum*
Omphalanthus umbilicatus (Nees) Nees ≡ *Lejeunea umbilicata*
Otolejeunea semperiana (Steph.) Grolle ≡ *Allorgella semperiana*
Paraschistochila neesii (Mont.) R.M.Schust. ≡ *Schistochila neesii*
Phaeoceros hirticalyx (Steph.) J.Haseg. ≡ *Phaeomegaceros hirticalyx*
Phaeoceros laevis subsp. *carolinianus* (Michx.) Prosk. ≡ *Phaeoceros carolinianus*
Phaeoceros polyandrus (Steph.) J.Haseg. = *Phaeomegaceros hirticalyx*
Phragmicoma fertilis (Reinw., Blume et Nees) Nees ex Mont. ≡ *Acrolejeunea fertilis*
Phragmicoma ligulata (Lehm. et Lindenb.) Gottsche, Lindenb. et Nees ≡ *Thysananthus ligulatus*
Phragmicoma reniloba Gottsche ≡ *Caudalejeunea reniloba*
Physocolea ciliatilobula (Schiffn.) Steph. = *Cololejeunea inflectens*
Physocolea hamata (Steph.) Steph. ≡ *Cololejeunea hamata*
Plagiochila acanthophylla Gottsche = *Plagiochila sciophila*
Plagiochila bantamensis var. γ *denticulata* Sande Lac. = *Plagiochila kurzii*

Plagiochila batjanensis Schiffn. ex Herzog = *Plagiochila teysmannii*
Plagiochila belangeriana Lindenb. = *Plagiochila arbuscula*
Plagiochila blepharophora var. *major* (Schiffn.) Bonner = *Plagiochila sandei*
Plagiochila brauniana (Nees) Lindenb. ≡ *Chiastocaulon braunianum*
Plagiochila ceramica Inoue = *Plagiochila pulvinata*
Plagiochila comata (Nees) Lindenb. ≡ *Solenostoma comatum*
Plagiochila decidua Inoue et Grolle = *Plagiochila sciophila*
Plagiochila dendroides (Nees) Lindenb. ≡ *Chiastocaulon dendroides*
Plagiochila frondescens var. *tenerrima* (Nees) Schiffn. = *Plagiochila frondescens*
Plagiochila frondescens α *tenerrima* (Nees) Lindenb. = *Plagiochila frondescens*
Plagiochila frondescens γ *rigida* (Nees) Lindenb. = *Plagiochila frondescens*
Plagiochila gedeana Schiffn. = *Plagiochila hampeana*
Plagiochila novae-guineae Sande Lac. = *Plagiochila chauviniana*
Plagiochila opposita (Reinw., Blume et Nees) Lindenb. ≡ *Chiastocaulon oppositum*
Plagiochila opposita var. β *falcata* (Nees) Schiffn. ≡ *Plagiochila conjugata* var. *falcata*
Plagiochila opposita var. γ *filiformis* (Lindenb.) Schiffn. = *Chiastocaulon oppositum*
Plagiochila opposita β *falcata* (Nees) Lindenb. ≡ *Plagiochila conjugata* var. *falcata*
Plagiochila opposita γ *filiformis* Lindenb. *nom. inval*. = *Chiastocaulon oppositum*
Plagiochila pseudaberrans Inoue et Grolle = *Plagiochila gymnoclada*
Plagiochila seemannii Mitt. = *Plagiochila sandei*
Plagiochila semialata Sande Lac. = *Plagiochila teysmannii*
Plagiochila singularis Schiffn. ≡ *Dinckleria singularis*
Plagiochila trapezoidea var. β *tenera* (Nees) Schiffn. = *Dinckleria singularis*
Plagiochila trapezoidea var. γ *major* (Lindenb.) Schiffn. = *Plagiochila gigantea laxior*
Plagiochila trapezoidea β *tenera* (Nees) Lindenb. = *Dinckleria singularis*
Plagiochila trapezoidea γ *major* Lindenb. *nom. illeg*. = *Plagiochila gigantea laxior*
Plagiochila variegata Lindenb. = *Syzygiella securifolia*
Plagiochilion braunianum (Nees) S.Hatt. ≡ *Chiastocaulon braunianum*
Plagiochilion fimbriatum (Mitt.) Inoue ≡ *Chiastocaulon fimbriatum*
Plagiochilion oppositum (Reinw., Blume et Nees) S.Hatt. ≡ *Chiastocaulon oppositum*
Plectocolea ariadne (Taylor) Mitt. ≡ *Solenostoma ariadne*
Plectocolea comata (Nees) S.Hatt. ≡ *Solenostoma comatum*
Porella acutifolia var. *subligulifera* S.Hatt. = *Porella acutifolia* var. *acutifolia*
Psiloclada unguligera Schiffn. = *Psiloclada clandestina* subsp. *clandestina*
Ptychanthus javanicus Nees = *Ptychanthus striatus* var. *striatus*
Ptychanthus moluccensis Sande Lac. = *Ptychanthus striatus* var. *striatus*
Ptychanthus squarrosus Mont. = *Ptychanthus striatus*
Ptychocoleus brunneus Steph. = *Acrolejeunea pycnoclada* subsp. *pycnoclada*
Ptychocoleus cumingianus (Mont.) Trevis. ≡ *Schiffneriolejeunea cumingiana*
Ptychocoleus densifolius (Schiffn. ex P.Syd.) Steph. *nom. illeg.* = *Schiffneriolejeunea pulopenangensis*
Ptychocoleus haskarlianus (Gottsche) Steph. ≡ *Schiffneriolejeunea tumida* var. *haskarliana*
Ptychocoleus pulopenangensis (Gottsche) Trevis. ≡ *Schiffneriolejeunea pulopenangensis*
Ptychocoleus pycnocladus (Taylor) Steph. ≡ *Acrolejeunea pycnoclada*
Ptychocoleus tener Steph. = *Acrolejeunea fertilis*

Pycnolejeunea badia Steph. = *Lepidolejeunea bidentula*
Pycnolejeunea ceylanica (Gottsche) Schiffn. ≡ *Cheilolejeunea ceylanica*
Pycnolejeunea ceylanica (Gottsche) Steph. *nom. inval*. ≡ *Cheilolejeunea ceylanica*
Pycnolejeunea connivens (Gottsche) Gottsche ex Schiffn. *nom. inval*. = *Pycnolejeunea connivens*
Pycnolejeunea decurvifolia (Steph.) Steph. = *Lepidolejeunea bidentula*
Pycnolejeunea demissa Steph. ex Kachroo et R.M.Schust. *nom. inval.* = *Cheilolejeunea longidens*
Pycnolejeunea falsinervis (Sande Lac.) Schiffn. ≡ *Cheilolejeunea falsinervis*
Pycnolejeunea gigantea Steph. ≡ *Cheilolejeunea gigantea*
Pycnolejeunea incisa (Gottsche) Schiffn. ≡ *Cheilolejeunea incisa*
Pycnolejeunea meyeniana (Nees, Lindenb. et Gottsche) Steph. *nom. inval*. = *Cheilolejeunea trapezia*
Pycnolejeunea schwaneckei Steph. nom. inval. = *Pycnolejeunea schwaneckei*
Pycnolejeunea trapezia (Nees) Schiffn. ≡ *Cheilolejeunea trapezia*
Pycnolejeunea ventricosa (Schiffn.) Schiffn. ex P.Syd. = *Cheilolejeunea ventricosa*
Pycnolejeunea ventricosa Schiffn. *nom. inval*. = *Cheilolejeunea ventricosa*
Radula campanigera Mont. ≡ *Cladoradula campanigera*
Radula ceramensis Steph. = *Radula javanica*
Radula formosa var. *pycnolejeuneoides* (Schiffn.) N.Kitag. = *Radula formosa*
Radula ovalifolia Steph. = *Radula javanica*
Radula pycnolejeuneoides Schiffn. = *Radula formosa*
Radula subsimilis Steph. = *Radula reflexa*
Radula wallichiana Lehm. = *Radula javanica*
Rhaphidolejeunea longicruris (Steph.) Herzog ≡ *Drepanolejeunea longicruris*
Riccardia pinguis (L.) Gray ≡ *Aneura pinguis*
Saccogyna rigidula (Nees) Schiffn. ≡ *Saccogynidium rigidulum*
Saccogynidium jugatum (Mitt.) Grolle = *Saccogynidium rigidulum*
Schiffneriolejeunea haskarliana (Gottsche) Gradst. ≡ *Schiffneriolejeunea tumida* var. *haskarliana*
Schisma divaricatum Herzog = *Herbertus sendtneri*
Schisma pilifera (Schiffn.) Steph. = *Herbertus pilifer*
Schisma piligerum Steph. *nom. inval*. = *Herbertus pilifer*
Schistochila amboinensis Steph. = *Schistochila beccariana*
Schistochila formosana Horik. = *Schistochila blumei*
Schistochila graeffeana J.B.Jack et Steph. = *Schistochila aligera*
Schistochila inversa Herzog = *Schistochila sciurea*
Schistochila philippinensis (Mont.) J.B.Jack et Steph. *nom. inval*. = *Schistochila aligera*
Schistochila philippinensis (Mont.) Steph. = *Schistochila aligera*
Schistochila philippinensis var. *transiens* H.Buch *nom. inval*. = *Schistochila aligera*
Schistochila purpurascens Herzog = *Schistochila acuminata*
Schistochila recurvata H.Buch *nom. inval*. = *Schistochila aligera*
Schistochila sciurea f. *robustior* Schiffn. = *Schistochila sciurea*
Schistochilaster aliger (Nees et Blume) H.A.Mill. ≡ *Schistochila aligera*
Schistochilaster graeffeanus (J.B.Jack et Steph.) H.A.Mill. = *Schistochila aligera*
Schistochilaster philippinensis (Mont.) H.A.Mill. = *Schistochila aligera*
Sendtnera diclados α *scorpioides* (Reinw., Blume et Nees) Nees = *Mastigophora diclados*

Sendtnera diclados β *calcarata* (Reinw., Blume et Nees) Gottsche, Lindenb. et Nees *nom. inval*. = *Mastigophora diclados*
Sendtnera vrieseana Sande Lac. = *Mastigophora diclados*
Spruceanthus marianus (Gottsche) Mizut. ≡ *Cheilolejeunea mariana*
Stenolejeunea dentata (Steph.) Pócs ≡ *Lejeunea stenodentata*
Strepsilejeunea cavistipula Steph. ≡ *Pycnolejeunea cavistipula*
Symphyogynopsis filicum (Nadeaud) Grolle = *Symphyogynopsis gottscheana*
Syzygiella variegata (Lindenb.) Spruce = *Syzygiella securifolia*
Taxilejeunea albescens Steph. ≡ *Lejeunea albescens*
Taxilejeunea karstenii Steph. = *Lejeunea lumbricoides*
Taxilejeunea laxiretis (Steph.) Eifrig = *Lejeunea sordida*
Taxilejeunea lumbricoides (Nees) Steph. ≡ *Lejeunea lumbricoides*
Taxilejeunea sordida (Nees) Eifrig ≡ *Lejeunea sordida*
Telaranea cuneifolia (Steph.) J.J.Engel et G.L.Merr. ≡ *Neolepidozia cuneifolia*
Telaranea kogiana (Steph.) Grolle ≡ *Tricholepidozia kogiana*
Telaranea neesii (Lindenb.) Fulford ≡ *Tricholepidozia neesii*
Telaranea wallichiana (Gottsche) R.M.Schust. ≡ *Neolepidozia wallichiana*
Thysananthus renilobus (Gottsche) Schiffn. ≡ *Caudalejeunea reniloba*
Thysananthus undulatus (Gradst. et Grolle) Sukkharak *nom. inval*. = *Thysananthus frauenfeldii*
Trachylejeunea cavistipula (Steph.) Steph. ≡ *Pycnolejeunea cavistipula*
Trichocolea breviseta Steph. ≡ *Leiomitra breviseta*
Trichocolea striolata Steph. = *Trichocolea pluma*
Trichocolea tomentella var. *javanica* (Reinw., Blume et Nees) Schiffn. = *Trichocolea pluma*
Xenolejeunea ceylanica (Gottsche) Tixier *nom. illeg*. ≡ *Cheilolejeunea ceylanica*
Zoopsis rigida Pearson = *Zoopsis setulosa*

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: MK, AN. Data curation: AH, LS. Formal analysis: LS. Methodology: MK. Resources: FSF, AN, IH. Visualization: LS. Writing - original draft: AN, MK. Writing - review and editing: AN, IH, AH, FSF, LS.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Dryopteris jinpingensis, a critically endangered diploid new species of Dryopteridaceae from Yunnan, China

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Abstract

Dryopteris jinpingensis, a new species of diploid, sexually reproductive ferns of Dryopteridaceae from Yunnan, southwestern China, is described and illustrated. Morphologically, *D. jinpingensis* is similar to *D. gaoligongensis* but unique in elongated lanceolate laminae, sessile or subsessile pinna stalks, and overlapping membranous scales adnate to stipe base. Phylogenetic analyses based on both plastome and the nuclear *AK1* gene sequences showed that *D. jinpingensis* is sister to *D. gaoligongensis*. A detailed taxonomic description with line drawings is provided, and its conservation status is evaluated to be critically endangered.

Key words: *Dryopteris* sect. *Diclisodon*, molecular phylogeny, new species, sexual diploid

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Introduction

Dryopteris Adans. (Dryopteridaceae) is one of the largest fern genera in the world, comprising approximately 350–400 species (Wu et al. 2013; Sessa et al. 2015; PPG I 2016). It exhibits a wide distribution across temperate region and tropical montane areas, with a primary center of diversity in eastern Asia (Fraser-Jenkins 1986; Sessa et al. 2015). In China, there are some 167 species classified into four subgenera (Wu et al. 2013). Within the genus, *Dryopteris* sect. *Diclisodon* (T. Moore) C. Chr. is of particular interest, as recent studies have revealed that many taxa in this section look similar in general appearance to their closely related known species, but actually exhibit significant difference in molecular data and close-up morphologies (Zuo et al. 2022a, b).

During our field work in Yunnan Province, China, we discovered a morphologically unique population of *Dryopteris* in Jinping County. The population exhibits a great similarity with *D. gaoligongensis* Z.Y. Zuo, Jin Mei Lu & D.Z. Li we described earlier (Zuo et al. 2022b). Through extensive morphological and phylogenetic studies, we have confirmed that this population represents a distinct species and accordingly we propose a new species within *D*. sect. *Diclisodon*.

Methods

Living plants of the potentially new taxon and *D. gaoligongensis* were observed in the field to conduct morphological comparisons. In particular, the scales, frond shape, and pinna stalks, were observed and counted. Additionally, specimens or photographs of specimens of related species of *D*. sect. *Diclisodon* deposited in the herbaria CSH, K, KUN, MICH, PE, and PYU were also examined.

Ploidy levels were estimated using flow cytometry (BD FACSCalibur, U.S.A.) by measuring nuclear DNA content (2C value) of young fresh leaves, with *Zea mays* L. (1C = 2.70 pg) (Bennett and Smith 1976) as reference standard. Reproductive mode was estimated by counting the spores in each sporangium, with 64 spores and 32 spores per sporangium representing sexual and apogamous reproduction, respectively (Walker 1979). At least ten intact sporangia were observed under a mini-microscopy (Yuantu 100×, China).

A young leaf of the potentially new taxon was collected from living plants in the field, and total genomic DNA was extracted from 30 mg of silica-gel dried leaf material using the modified 4× CTAB DNA extraction method (Doyle and Doyle 1987). For plastid genome (plastome), library preparation and Illumina sequencing were conducted at the Germplasm Bank of Wild Species, Kunming Institute of Botany (CAS). *De-novo* assemblies, connecting and annotation were constructed using GetOrganelle v.1.7.0 (Jin et al. 2020), Bandage 0.8.1 (Wick et al. 2015) and Geneious 9.1.4 (Kearse et al. 2012), respectively, based on the previously published plastome of *Dryopteris gaoligongensis* (NC_067598). The new obtained plastomes were uploaded to NCBI (Suppl. material 1).

The products of PCR amplification of the low-copy nuclear *AK1* gene (*AK4F*: 5'-GATGAAGCCATCAAGAAACCA-3'; *AKR2*: 5'-ATGGATCCAGCGACCAGTAA-3') (Hori et al. 2021) were cloned and sequenced at Tsingke Biotechnology Co., Ltd. Kunming, with at least six colonies for each sample (Suppl. material 2).

Two matrices were constructed for phylogenetic analyses. We extracted nine identical plastid regions from two newly obtained plastomes of the potentially new taxon, and added them to our previous combined plastid matrix (including 57 samples, Suppl. material 1, 3) (Zuo et al. 2022a, b). The second matrix consisted of 50 nuclear *AK1* sequences, two of which were newly obtained and the others from previous studies (Hori et al. 2021; Zuo et al. 2022a, b; Wei et al. 2024). The two matrices were aligned and corrected using MAFFT v.7.017 (Katoh et al. 2002) and Geneious 9.1.4 (Kearse et al. 2012), respectively.

We used Bayesian inference (BI) and Maximum likelihood (ML) analyses to infer the phylogenetic relationships. The BI analysis was performed using MrBayes 3.2.6 (Ronquist et al. 2012) in four Markov chain Monte Carlo (MCMC) chains in parallel, with ten million generations and one tree sampled every 1000 generations. The first 25% of trees were discarded as burn-in. The ML analyses were conducted using IQ-TREE 1.6.12 (Nguyen et al. 2015) with the GTR+R6 model and 2000 ultrafast bootstrap replicates.

Results

The morphological comparison revealed that the potentially new taxon exhibited a great similarity to *D. gaoligongensis* in overall morphology. Both species have stout and creeping rhizomes, 3- to 4- large pinnate fronds, and largest and longest basal basiscopic pinnule. However, there are some distinct differences. The scales of *D. gaoligongensis* are brown, ovate-lanceolate, and entire, while the potentially new taxon has thin membranous and lanceolate scales. More importantly, most scales of the potentially new taxon are overlapping and adnate to the stipe base. The fronds of *D. gaoligongensis* are deltate-lanceolate to ovate-lanceolate, and basal pinnae with stalk up to 5 cm. In contrast, the potentially new taxon has elongated lanceolate fronds, and pinna stalks of the basal pinnae are sessile or subsessile (less than 1 cm). In addition, the potentially new taxon was found on cliffs of the valley in forests (Figs 1–3, Table 1).

The DNA amount of three samples of *Zuo5378* (*Zuo5378-1* from one population, *Zuo5378-2* & *Zuo5378-3* from another nearby population) was estimated to be 15.2 ± 0.2 pg, which is very close to that of *D. gaoligongensis* (15.1 ± 0.4 pg) and other diploid species of *D.* sect. *Diclisodon* (e.g., *D. sabaei*, 14.2 ± 0.3 pg; *D. subexaltata*, 12.5 ± 0.3 pg; Hori et al. 2021). All spore counts showed that the potentially new taxon has 64 normal spores per sporangium, and the spores could germinate to produce prothallus (Fig. 4). The results of flow cytometry and spore counting implied that the potentially new taxon is a diploid, sexually reproductive species.

Phylogenetic analyses of both the plastome data (Fig. 5A) and nuclear *AK1* data (Fig. 5B) concordantly revealed that the potentially new taxon is sister to *D. gaoligongensis*. Only one haplotype of nuclear *AK1* was found in the potentially new taxon.

Discussion

Morphological comparison and phylogenetic analyses show that the potentially new taxon is a member of *D.* sect. *Diclisodon*, and is closely related to *D. gaoligongensis*. They are not only similar in overall morphology, but also in nuclear DNA content, ploidy level, and reproductive mode. However, phylogenetic data and some significant morphological differences (Table 1) suggest that they are two distinct species that may have a common ancestor but have undergone different speciation in different environments. *Dryopteris gaoligongensis* exclusively grows on the ground of the Gaoligong Mountains at an elevation of 2200–2500 meters, while the newly discovered species grows on the cliffs inside the valley at an altitude of 1000–1100 meters. We speculate that environmental differences and isolation have resulted in a lack of gene flow between the two species, which ultimately led to their differentiation and speciation.

Taxonomic treatment

***Dryopteris jinpingensis* Z.Y.Zuo, Jin Mei Lu & D.Z.Li, sp. nov.**
urn:lsid:ipni.org:names:77338637-1
Figs 1, 2
in Chinese: 金平鳞毛蕨 (jīn píng lín máo jué)

Type. China. Yunnan: Jinping, 25°17'N, 98°46'E, alt. 1050 m, 20 April 2023, *Z.Y. Zuo 5378* (Holotype, mounted in 3 cross-referenced sheets, KUN-1585758! Isotype: KUN-1585759!).

Diagnosis. *Dryopteris jinpingensis* is similar to *D. gaoligongensis* with stout and creeping rhizome, 3- to 4-pinnate large frond, and largest and longest basal

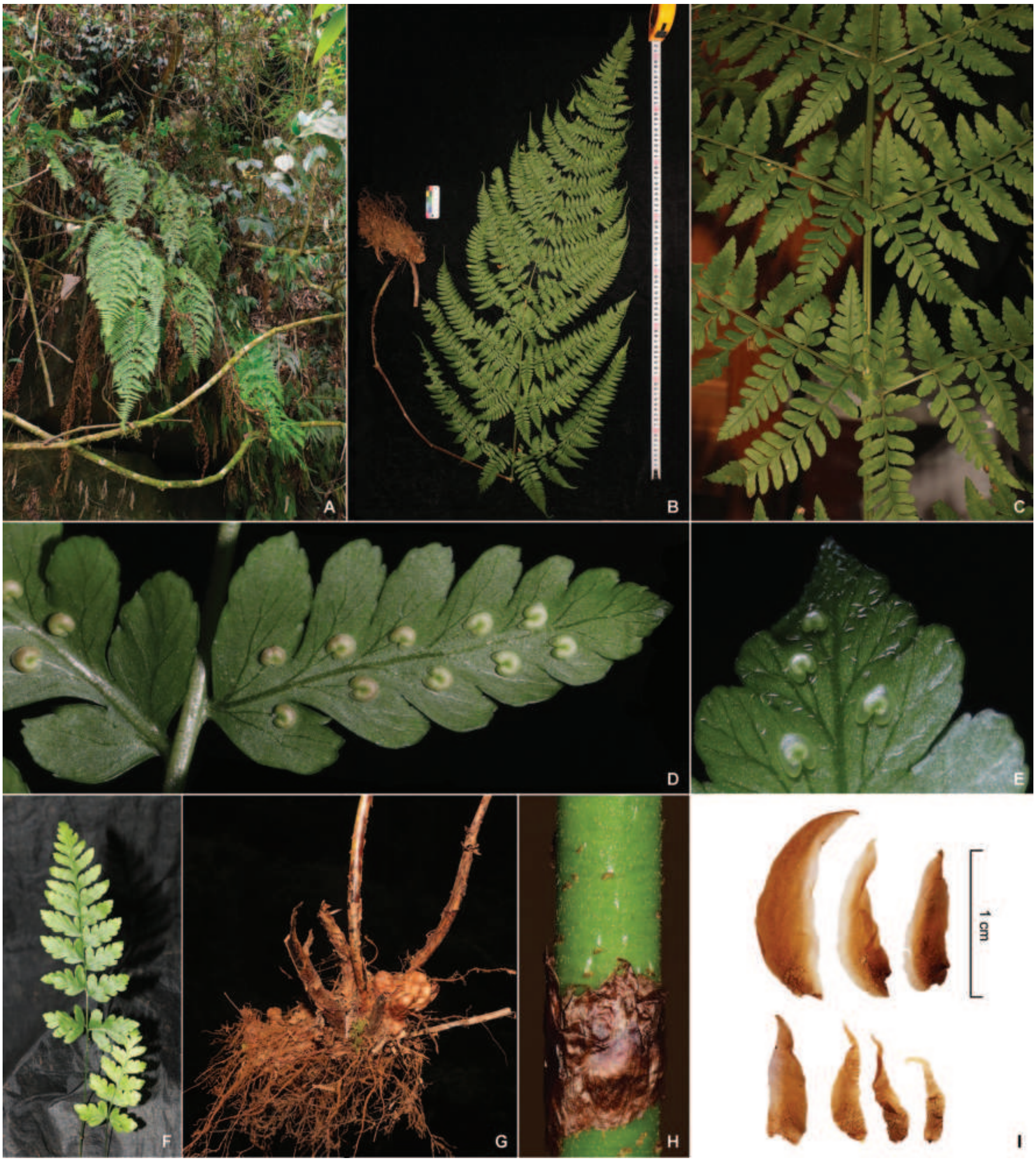

Figure 1. Photos of *Dryopteris jinpingensis* (*Z.Y. Zuo 5378*) **A** habitat **B** plant **C** proximal part of the lamina **D** sori on ultimate pinnules **E** glandular hairs on the abaxial surface of pinnules **F** young plant **G** rhizome **H** portion of stipe base, showing adnate scale **I** scales of stipe.

Table 1. Diagnostic characteristics comparison between *Dryopteris jinpingensis* and *D. gaoligongensis*.

Characters	*Dryopteris jinpingensis*	*D. gaoligongensis*
Scales on stipe base	Thin membranous, lanceolate, mostly overlapping, adnate to stipe	Thick membranous, ovate-lanceolate, mostly scattered, not adnate to stipe
Lamina	Elongated lanceolate	Deltate-lanceolate to ovate-lanceolate
Pinna stalks	Sessile or subsessile, less than 1 cm in the basal pairs of pinnae	Stalked, 2–5 cm in the basal pairs of pinnae
Habit	On the cliff of the valley in forests	On the ground in forest
Altitude	1000–1100 m	2200–2500 m

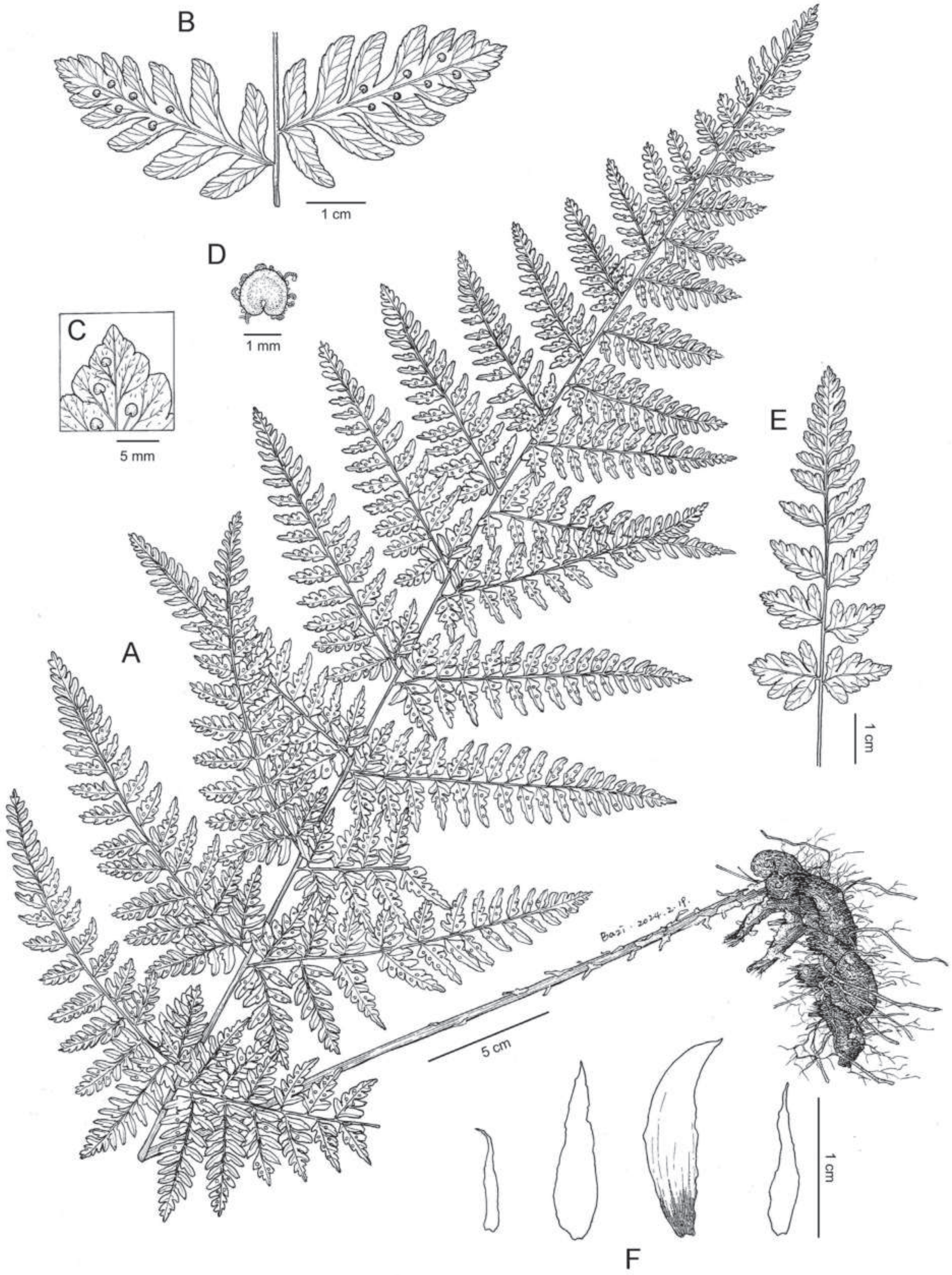

Figure 2. Illustration of *Dryopteris jinpingensis* Z.Y. Zuo, Jin Mei Lu & D.Z. Li **A** plant **B** sori on ultimate pinnules **C** glandular hairs on the abaxial surface of pinnules **D** indusia **E** young plant **F** scales of stipe (Drawn by Yi-Fan Li, based on *Z.Y. Zuo 5378*).

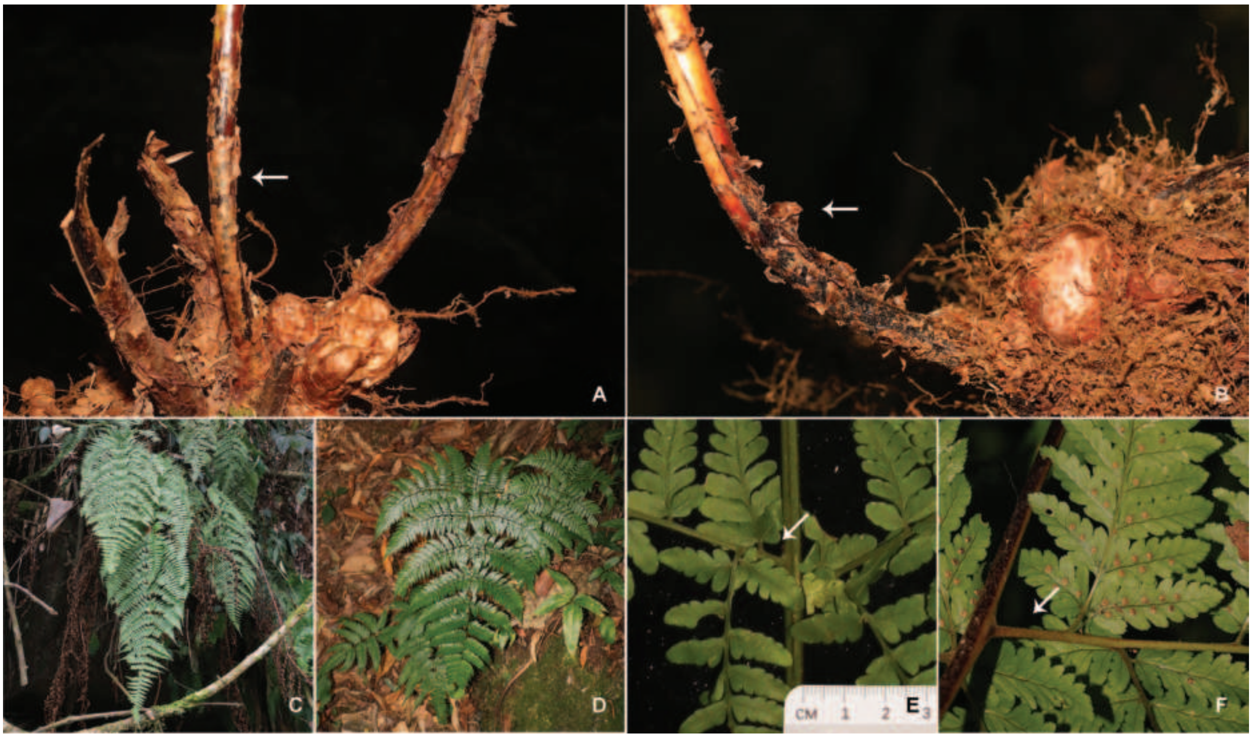

Figure 3. Morphological comparison of *Dryopteris jinpingensis* (**A, C, E**) and *D. gaoligongensis* (**B, D, F**) **A, B** rhizome and stipe base **C, D** lamina **E, F** pinna stalks of basiscopic pinnules.

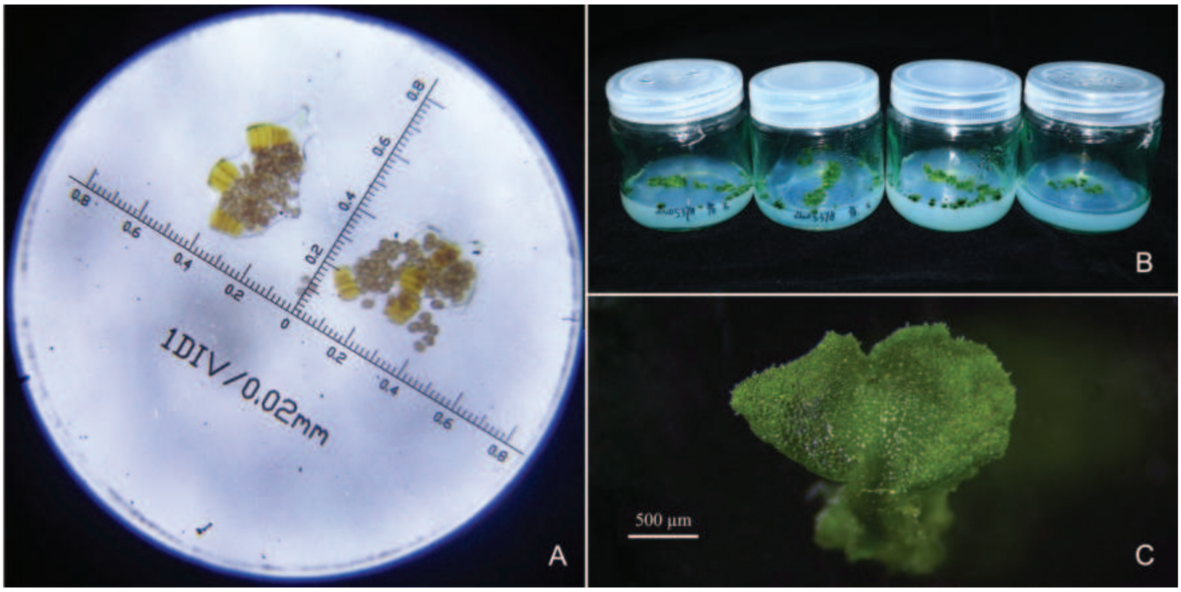

Figure 4. Spores and prothallus of *Dryopteris jinpingensis* **A** 64 spores in one sporangium **B** cultured prothallus on 1/2 Murashige and Skoog plant cell culture medium (MS) **C** prothallus.

basiscopic pinnule. However, *D. jinpingensis* differs from it in the elongated lanceolate lamina, sessile or subsessile pinna stalks (less than 1 cm), and overlapping membranous and thin scales adnate to stipe base.

Description. ***Plants*** 70–140 cm tall. ***Rhizome*** stout, creeping, up to 20 cm long and 4 cm in diameter, densely clothed with brown, lanceolate, entire scales. ***Fronds*** approximate, stipe shorter than lamina, ca. 30–60 cm, brown at base, upper stramineous, densely scaly; scales thin, lanceolate, entire, brown, overlapping and adnate to the stipe base. ***Rachis and costae*** hairy when young, glabrous when

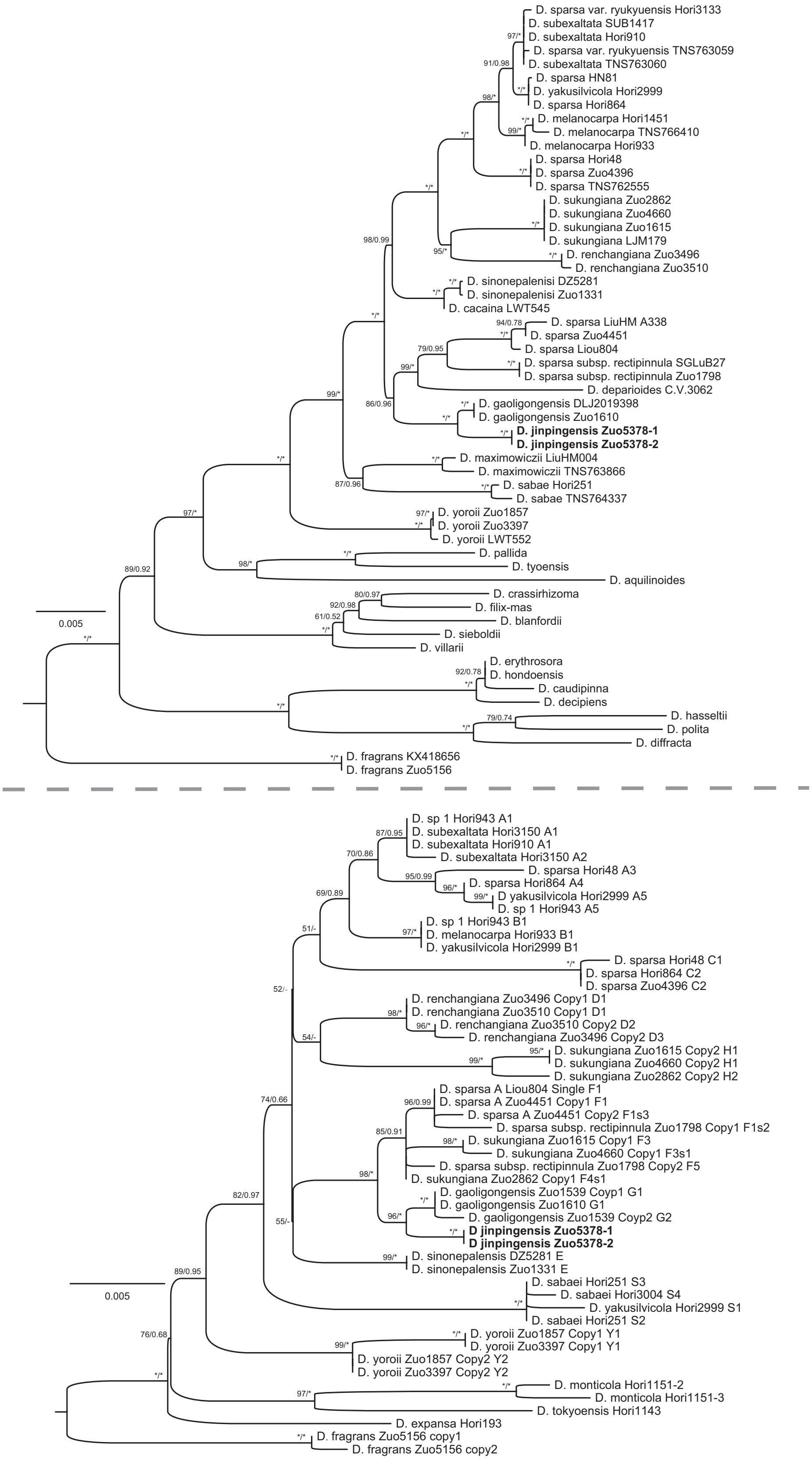

Figure 5. Maximum likelihood phylograms of *Dryopteris* sect. *Diclisodon* based on nine plastid regions (**A**) and nuclear gene *AK1* (**B**). ML ultrafast bootstrap support values (UFBS) and the posterior probabilities of Bayesian inference (BIPP) are indicated near nodes (UFBS/BIPP). The stars (*) indicate UFBS=100% or BIPP=1.00, the minus (-) indicate UFBS<50% or BIPP<0.50. The name of the new species is in bold.

mature. ***Lamina*** papery, not glossy, broadly elongated lanceolate, ca. 40–100 × 20–50 cm, 3- to 4-pinnate, base not narrowed, apex acuminate, abaxial with glandular hairs when young, glabrous when mature. ***Pinnae*** 15–30 pairs, opposite, oblique, sessile or subsessile (less than 1cm). Pinnae lanceolate, basal pinnae largest, deltoid-lanceolate, up to 40 × 18 cm, apex caudate-acuminate. ***Pinnules*** 25–35 pairs, opposite at base and alternate upward, lanceolate, base broadly cuneate, usually asymmetrical, apex long acuminate; basal basiscopic pinnule largest and longest, ca. 12 × 4 cm, base widest, 2-pinnate; Segments oblong, apices obtuse and spinulose, margin shallowly lobed to several serrate. ***Veins*** pinnate, forked, distinct on both surfaces. ***Sori*** close to costa on pinnules; indusia orbicular-reniform, entire. Reproductive mode and ploidy level: diploid sexual.

Distribution and habitat. Presently only known from Jinping County, Yunnan Province, southwestern China, with two documented small populations near each other. It grows on the cliff of the valley in subtropical evergreen broad-leaved forests, at an altitude of 1000–1100 meters.

Etymology. The specific epithet “jinpingensis” refers to its type locality, Jinping County, in the border between south Yunnan of China and Vietnam.

Conservation status. *Dryopteris jinpingensis* should be classified as critically endangered (CR) according to the IUCN guidelines (IUCN Standards and Petitions Committee 2022), due to its narrow distribution with only two small populations with fewer than 50 plants. In order to conserve and save this rare and endangered species, we have begun to propagate it using the *in vitro* culture from spores, facilitated by the Germplasm Bank of Wild Species.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

The voucher information and GenBank accession numbers of complete plastid genome used in this study

Authors: Zheng-Yu Zuo, Jin-Mei Lu, Cun-Fu Li, De-Zhu Li

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.239.118655.suppl1

Supplementary material 2

The voucher information and GenBank accession numbers of nuclear marker *AK1* used in this study

Authors: Zheng-Yu Zuo, Jin-Mei Lu, Cun-Fu Li, De-Zhu Li

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.239.118655.suppl2

Supplementary material 3

The voucher information and GenBank accession numbers of plastid regions used in this study

Authors: Zheng-Yu Zuo, Jin-Mei Lu, Cun-Fu Li, De-Zhu Li

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.239.118655.suppl3

PhytoKeys 239: 205–213 (2024)
DOI: 10.3897/phytokeys.239.119028

Research Article

Ajania flavida (Asteraceae, Anthemideae), a distinct new species from southwestern China

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Abstract

Ajania flavida, a new species from western Sichuan and eastern Xizang, China, is described and illustrated. It is readily assigned to *A.* sect. *Ajania* owing to its straw-colored, glossy involucres and marginally whitish scarious phyllaries. Within the section, it is distinct in being a shrub of 1–2 m in height, and in having creamy yellow florets. It is superficially similar to *A. ramosa* in *A.* sect. *Phaeoscyphus*, but can easily be distinguished by, among other characters, the plant height, color of the florets and margins of the phyllaries. In addition, we provide a distribution map of the new species.

Key words: Compositae, taxonomy, Yangtze River

Introduction

Ajania Poljak. (Asteraceae, Anthemideae) consists of 30–39 species mainly distributed in central Asia (Bremer and Humphries 1993; Oberprieler et al. 2007a, b, 2009; Shih et al. 2011). In China, 35 species are currently recognized, among which 23 are endemic (Shih et al. 2011). Over the past decade, taxonomic updates in this genus have been infrequent, with only a new species described from Iran (Sonboli et al. 2013).

During herbarium surveys of *Ajania* in China, seven collections, including *D. E. Boufford et al. 36429* (F, PE; Fig. 1A), *Kham Exped. 10-0662* (PE; Fig. 1B), *Y. W. Tsui 5942* (PE), and *M. Z. Wen & S. C. Xiao Xiang157* (CDBI) from Sichuan, and *HNWP Xizang Exped. 2195* (HNWP; Fig. 1C), *Kham Exped. 10-1622* (PE; Fig. 1D) and *Qinghai-Xizang Vegetat. Exped. 9655* (PE) from Xizang, all in China, caught our attention. Most of these collections have been previously identified as *A. ramosa* (C. C. Chang) C. Shih (Fig. 2), but they are quite different from that species in an array of characters. Plants of this taxon are shrubs of 1–2 m tall, with leaf blades 2-pinnatisect, involucres ca. 3 mm in diameter, and margins of the phyllaries whitish scarious, while in *A. ramosa* the plants are subshrubs of 40–60 cm tall, with leaf blades 1(–2)-pinnatisect, involucres 4–5 mm in diameter, and margins of the phyllaries brown scarious. To precisely determine the identity of these collections, we undertook a field visit to Jomda

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in eastern Xizang in September 2019. Through careful comparisons, we found that this taxon is indeed quite different from *A. ramosa* in *A.* sect. *Phaeoscyphus*, which is characterized by having larger (4–10 mm in diameter) capitula, not straw-colored, not glossy involucres and marginally dark brown or purple scarious phyllaries. It can be, however, readily referred to *A.* sect *Ajania* based on the smaller (ca. 3 mm in diameter) capitula, straw-colored, glossy involucres and marginally whitish scarious phyllaries. It is easily distinguishable from the remaining species within this section in being shrubs of 1–2 m tall and having creamy yellow florets. The taxon in question therefore represents a hitherto undescribed species, which we describe below.

Material and methods

For morphological comparisons, we examined physical or digitalized herbarium specimens (with high-resolution) of *Ajania* deposited at several major herbaria in China, including CDBI, HNWP, IBSC, KUN, NAS, PE, SZ, and WUK (acronyms follow Thiers (2024)). Specimens of *A. flavida* were collected and photographed during our field investigation to Xizang Autonomous Region in 2019. Morphological observations and measurements were based on fresh material as well as all herbarium specimens of this species. For conservation assessment, we used Geo CAT, the online geospatial conservation assessment tool (Bachman et al. 2011; http://geocat.kew.org/) to calculate the Extent of Occurrence (EOO) and Area of Occupancy (AOO) with a user-defined cell width of 2 km.

Taxonomic treatment

***Ajania flavida* Long Wang, sp. nov.**
urn:lsid:ipni.org:names:77338638-1
Figs 1, 3, 4

Diagnosis. *Ajania flavida* is distinct in *A.* sect. *Ajania* in being shrubs of 1–2 m in height and having creamy yellow florets. It is superficially similar to *A. ramosa* in *A.* sect. *Phaeoscyphus*, but can be easily distinguished by the plant habit (shrub vs. subshrub), plant height (1–2 m vs. 40–60 cm), leaf division (2-pinnatisect vs. 1(–2)-pinnatisect), size of the involucres (ca. 3 mm vs. 4–5 mm in diameter), color (creamy yellow vs. yellow) of the florets and margins (whitish scarious vs. brown scarious) of the phyllaries.

Type. China. Xizang: Jomda, Tongpu, 31°35'58.77"N, 98°22'44.19"E, rocky slopes along river, 3212 m a.s.l., 6 September 2019 (fl.), *Long Wang, Xin-qiang Guo & You-pai Zeng 3428* (holotype: IBSC; isotypes: IBSC). Fig. 4.

Description. Shrubs, 1–2 m tall. Old branches gray-black, sparsely sericeous or glabrescent, with densely leafy tips; flowering branches robust, densely grey powdery-sericeous, especially in upper parts and on peduncles. Proximal leaves of flowering branches withered during anthesis. Middle leaves of flowering branches shortly petiolate; petiole 1–2 cm long; leaf blade ovate in outline, 7–10 cm long, 6–7 cm wide, adaxially dark green, grey sericeous, abaxially greyish, densely grey sericeous, 2-pinnatisect; lobes usually 5, narrowly oblong, lateral 1 or 2 pairs 3–4 cm long, 1.0–2.5 cm wide, distal ones 4–6 cm long, 2–3 cm wide, 1-pinnatisect; segments 2–7, lanceolate to narrowly oblong, lateral 1–3

Figure 1. Specimens of *Ajania flavida* sp. nov. previously misidentified as *A. ramosa* or *A. variifolia* **A** China, Sichuan, Dêgê, *D. E. Boufford et al. 36429* (PE) **B** China, Sichuan, Baiyü, *Kham Exped. 10-0662* (PE) **C** China, Xizang, Jomda, *HNWP Xizang Exped. 2195* (HNWP) **D** China, Xizang, Jomda, *Kham Exped. 10-1622* (PE).

Figure 2. *Ajania ramosa* in the wild (China, Shaanxi, Meixian) **A** habitat **B** habit **C** basal leaves (adaxial surface) **D** synflorescence (top view) **E** synflorescence (side view) **F** phyllaries (abaxial surface) **G** marginal female florets **H** central disk florets. Photographs by Long Wang.

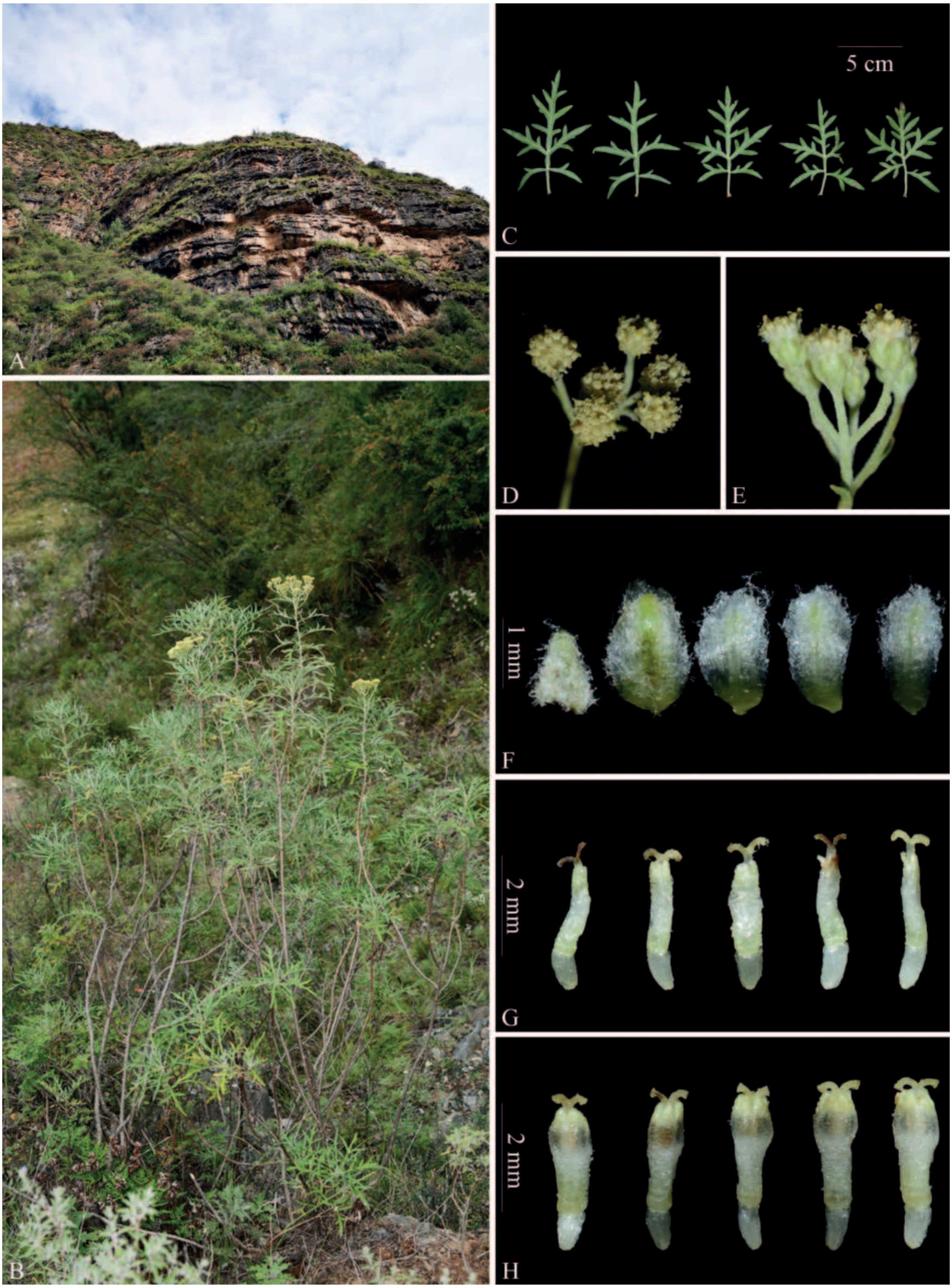

Figure 3. *Ajania flavida* sp. nov. in the wild (China, Xizang, Jomda) **A** habitat **B** habit **C** basal leaves (adaxial surface) **D** synflorescence (top view) **E** synflorescence (side view) **F** phyllaries (abaxial surface) **G** marginal female florets **H** central disk florets. Photographs by Long Wang.

中国科学院华南植物园标本采集记录

采集者：王龙 郭信强 曾佑派
采集编号：WL3428
采集日期：2019.09.06
采集地：西藏江达县日普乡附近
经纬度：N31° 35′58.77′′ E98° 22′44.19′′
海拔高度：3212m 地形：
生境：砾石山坡 分布：
习性：
根： 茎： 叶：
花： 果实/种子：
备注：
拉丁名：Ajania sp.

Holotype!

Ajania flavida **Long Wang, sp. nov.**

鉴定人 (Det.)：王龙 (Long Wang) 2023-10-01

Figure 4. Holotype sheet of *Ajania flavida* sp. nov.

pairs 4–20 mm long, 2–4 mm wide, distal ones 2–4 cm long, 2–5 mm wide. Distal leaves of flowering branches shortly petiolate to sessile; petiole, when present, 0.5–1.5 cm long; leaf blade ovate to linear in outline, progressively smaller upward, 1-pinnatisect to undivided. Synflorescence a terminal compound flat-topped panicle, 5–10 cm in diameter. Capitula many, erect. Involucres campanulate, ca. 3 mm in diameter, outside straw-colored, glossy; phyllaries in 4 rows, outer ones ovate to triangular-ovate, 1.0–1.2 mm long, 0.8–1.0 mm wide, abaxially densely whitish sericeous, apex acute, middle ones oblong to elliptic, 1.5–2.0 mm long, 1.0–1.2 mm wide, abaxially whitish sericeous, margin narrowly to broadly whitish scarious, apex rounded, inner ones narrowly oblong to oblong, 1.5–2 mm long, 0.6–1 mm wide, abaxially slightly whitish sericeous, margin broadly whitish scarious, apex rounded to obtuse. Florets creamy yellow, exterior with several sessile glands. Marginal female florets 9–11, 2–2.8 mm long; tube 0.4–0.7 mm long; corolla narrowly tubular, 0.8–1.1 mm long, apically 4–5-denticulate. Central disk florets many, 2.8–3.2 mm long; tube 0.8–1.2 mm long; corolla broadly tubular, 0.9–1.2 mm long, apically 5-denticulate, incurved; style 1.1–1.3 mm long; branches creamy yellow. Achenes (immature) 0.6–0.8 mm long, obconic. Pappus absent.

Distribution and habitat. *Ajania flavida* is currently known only from western Sichuan (Baiyü, Batang, Dêgê) and eastern Xizang (Gonjo, Jomda), China (Fig. 5). It grows on rocky slopes in gorges at elevations of 3075–3800 m above sea level.

Etymology. The specific epithet '*flavida*' refers to the creamy yellow florets of this new species.

Phenology. Flowering in September; fruiting in October.

Vernacular name. 川藏亚菊 (Chinese pinyin: chuān zàng yà jú).

Conservation status. *Ajania flavida* is currently known only from eight collections made from western Sichuan (Baiyü, Batang, Dêgê) and eastern Xizang (Gonjo, Jomda), China. It usually grows on rocky slopes along roadsides in the gorges, and its habitat is at risk through human activities, such as overgrazing and road construction (Wang, pers. obs.). The Extent of Occurrence (EOO) and the Area of Occupancy (AOO) are calculated to be 7516.23 km^2 and 32 km^2, respectively. According to the IUCN Red List Categories and Criteria (IUCN 2012, 2022), this species should be categorized as Vulnerable (VU): B1ab(iii)+2ab(iii).

Notes. Two collections of *Ajania flavida*, viz. *D. E. Boufford et al. 36429* (F, PE) and *M. Z. Wen & S. C. Xiao Xiang157* (CDBI), have been previously misidentified as *A. variifolia* C. C. Chang, a species occurring in Heilongjiang, Hubei and Shaanxi in China. *Ajania flavida* is readily distinguished from *A. variifolia* in being a shrub (vs. subshrub), 1–2 m (30–60 cm) tall and having leaf blades 2-pinnatisect (vs. 1-pinnatisect), involucres ca. 3 mm (vs. 4–5 mm) in diameter, and margins of phyllaries whitish (vs. brown) scarious.

It is noteworthy that the identity of *Ajania ramosa* needs to be further determined. According to our observations on both herbarium specimens and living plants in the wild, this species is poorly defined. It may encompass elements of multiple species in the genus.

Additional specimens examined (paratypes). China. Sichuan: Baiyü, Jinsha xiang, by the Yangtze River, among scrub in valley, 3157 m, 31°16'42.66"N, 98°49'03.32"E, 25 July 2010, *Kham Exped. 10-0662* (PE); Batang, Lieyi xiang, Yidun, on rocks along road, 3400 m, 19 September 1984, *M. Z. Wen & S. C. Xiao Xiang157* (CDBI); Dêgê, Gongya township, road (highway 317) from Dêgê to Baiyu above E

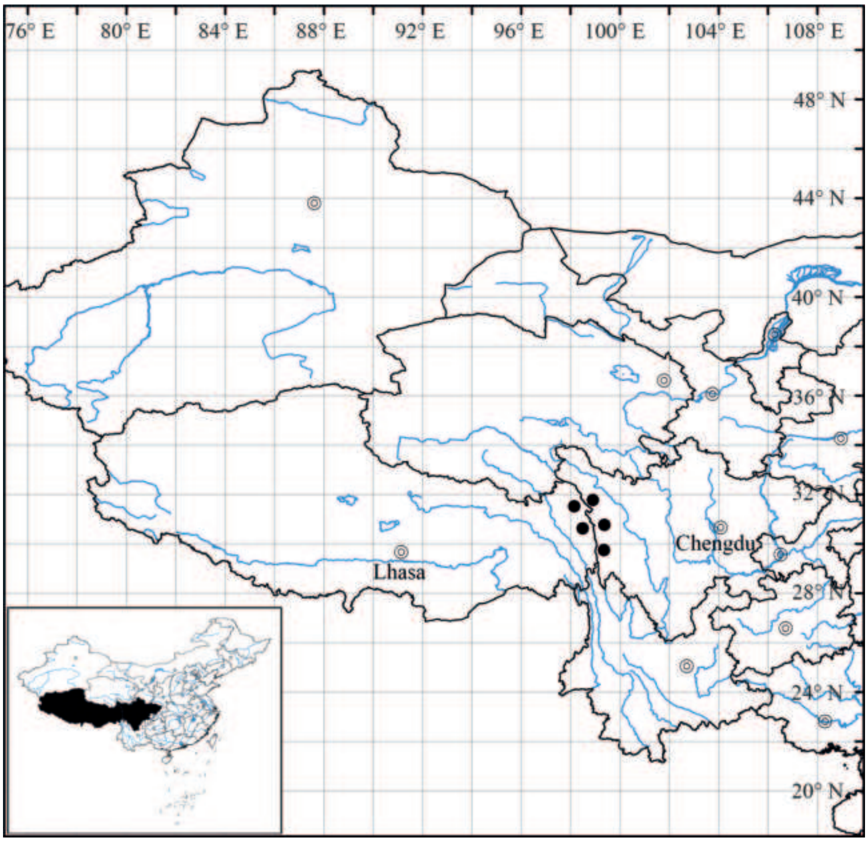

Figure 5. Distribution of *Ajania flavida* sp. nov. (Black dot).

side of bridge over Jinsha Jiang (upper Chang Jiang) connecting Sichuan and Xizang (Tibet), downstream from confluence of Serqu He (Serqu River), dry slope above Jinsha Jiang with spinescent shrubs (ca. 1 m tall) of *Sophora*, *Rosa*, and *Caragana*, 3075 m, 31°37'40"N, 98°35'28"E, 14 August 2006, *D. E. Boufford et al. 36429* (F, PE); Dêgê, Keluodong xiang, on the way from Keluodong to Damagou, 1 August 1951, *Y. W. Tsui 5942* (PE). Xizang: Gonjo, Waba [Zeba xiang], grassland on mountain slopes, 3800 m, 20 August 1976, *Qinghai-Xizang Vegetat. Exped. 9655* (PE); Jomda, near Jomda township, on cliffs in valley, 3195 m, 31°31'39.40"N, 98°14'31.03"E, 10 August 2010, *Kham Exped. 10-1622* (PE); Jomda, Tongpu xiang, terrace in valley, 3300 m, 25 August 1973, *HNWP Xizang Exped. 2195* (HNWP).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: LW. Data curation: XC. Formal analysis: XC, HW. Investigation: HW. Methodology: LW. Software: HW. Writing – original draft: XC. Writing – review and editing: LW.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Gentiana mopanshanensis (Gentianaceae), a new species from Yunnan, southwest China

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Abstract

Gentiana mopanshanensis, a new species of the family Gentianaceae is here described and illustrated. This species is presently known only from the Mopanshan Mountain, Yunnan Province, southwest China. Phylogenetic analysis based on ITS sequence data has shown that this new species is a member of the series *Fimbriatae* of the section *Chondrophyllae*. Morphologically, it mostly resembles *G. mairei* and *G. panthaica*, but differs clearly from the latter two species in the shape and size of the leaves, and the characters of the corolla throat and plicae.

Key words: Diffuse herbs, endemism, ITS sequence, Mopanshan Mountain, series *Fimbriatae*, Yunnan-Guizhou Plateau

Introduction

The genus *Gentiana* L. belongs to the family Gentianaceae and comprises more than 360 species that are distributed worldwide in the temperate and alpine regions, especially in Europe, Asia and North America (Ho and Liu 1990; Yuan et al. 1996; Yuan and Küpfer 1997). The plants of this genus are typical mountain plants, and most of the species are adapted to alpine habitats (Ho et al. 1996). The greatest diversity of *Gentiana* is found in the Tibeto-Himalayan region, where more than 250 species are native (Ho and Liu 2001). Relevant biogeographic studies have identified this region as the source area for *Gentiana* and related genera (Favre et al. 2016; Matuszak et al. 2016). The phylogenetic relationships within the genus *Gentiana* are now still incompletely clear, and its classification remains controversial (Favre et al. 2014, 2020; Sun et al. 2018; Sun and Fu 2019; Fu et al. 2021, 2022). Many *Gentiana* species have ornamental value and are also of pharmaceutical interest due to their interesting phytochemical properties (Mariana et al. 2013; Mirzaee et al. 2017; Jiang et al. 2021).

China is endowed with numerous species of *Gentiana*, including many endemics (Ho and Pringle 1995). While members of *Gentiana* can be found throughout the country, they are mostly concentrated in the Southwest Mountainous area, which includes the Qinghai-Tibet Plateau and Hengduan Mountains (Ho et al. 1988; Bai 2000). Ho and Pringle (1995) recognized 248 species

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from China in their "*Flora of China*", which accounts for more than 2/3 of the genus' total species. Nevertheless, new species have been frequently discovered in China in recent years (e.g., Hsieh et al. 2007; Yang et al. 2008; Ho and Liu 2010; Wu et al. 2012; Yu et al. 2012; Yang et al. 2020; Favre et al. 2022). These new discoveries highlighted the need for continued field exploration and taxonomic research in this area.

During recent field surveys in Mopanshan Mountain, Xinping County, Yunnan Province, southwest China, we discovered an unknown species of *Gentiana*. After a phylogenetic analysis using ITS sequences to infer its systematic position and a detailed comparison with morphologically similar species, it became clear that this plant represents a distinct new species.

Materials and methods

Morphological analyses

This study including plant collection, specimen preparation, observation, and analysis followed the normal practice of plant taxonomic survey and herbarium taxonomy (Davis and Heywood 1963). Morphology of the new species was studied based on observation of living plants and specimens housed at YUKU. Digital images of type specimens of genus *Gentiana* are available at the JSTOR Global Plants (http://plants.jstor.org/) and at the Chinese Virtual Herbarium (http://www.cvh.ac.cn/); in addition, the collections housed at GBIF, KUN and YUKU were examined and compared with the new species. The dried specimens were examined under stereomicroscopes for morphological studies, and various organs were measured using rulers and metric vernier calipers. Terminology followed Ho and Liu (2001), Beentje (2010) and Mayfield (2021).

Phylogenetic study

To determine the phylogenetic position of the putative new species, the internal transcribed spacer region (ITS) of the nuclear ribosomal DNA was used as the molecular marker. The total genomic DNA of this new species is extracted from silica-gel dried leaves using the DNA secure plant kit (Tiangen, Amsterdam, Netherlands). The PCR protocol followed by Shabir et al. (2022). The ITS primers used in this study were ITS4 and ITS5, as described by Yuan and Küpfer (1995) and He et al. (2016). The PCR products were bidirectionally sequenced with the same primers used for PCR amplifications in an ABI 3730 XL DNA Analyzer (Applied Biosystems) at the Kunming Branch of Beijing Qingke Biotechnology Co., Ltd. (Yunnan, China).

There are a total of 44 species of *Gentiana* to be used, which are representatives of most sections of *Gentiana*, including *G*. sect. *Chondrophyllae* Bunge, *G*. sect. *Frigida* Kusnezow, *G*. sect. *Monopodiae* (H. Smith) T. N. Ho, *G*. sect. *Phyllocalyx* T. N. Ho and *G*. sect. *Stenogyne* Franchet. In addition, *Swertia rosulata* (Baker) Klack, *Halenia taruga-gasso* Gilg and *Gentianella gentianoides* (Franchet) H. Smith were selected as outgroups. The dataset for phylogentic analysis consists of 60 taxa, 46 of which were obtained from the GenBank. Voucher specimen and GenBank accession information for taxon are listed in Appendix 1.

All sequences were aligned with MAFFT (Katoh and Standley 2013) using 'auto' strategy and normal alignment mode. Gap sites were removed with trimAl (Capella-Gutiérrez et al. 2009) using the "-automate" command. The best-fitting substitution models SYM+I+G model for Bayesian inference were selected using ModelFinder (Kalyaanamoorthy et al. 2017) in BIC criterion. MrBayes 3.2.6 (Ronquist et al. 2012) was used to conduct Bayesian phylogenetic analyses. Runs were performed for 5 million generations with a sampling of trees every 500 generations. The initial 25% of sampled data were discarded as burn-in.

Results and taxonomic treatment

***Gentiana mopanshanensis* Huan C. Wang & Tao Chen bis, sp. nov.**
urn:lsid:ipni.org:names77338758-1
Figs 1–3

Type. China. Yunnan Province: Xinping County, Mopanshan Mountain, near the top of mountain, alt. 2480 m, 23°56'23"N, 101°59'23"E, 3 April 2023, in flower, *H. C. Wang et al. XP19775* (Holotype: YUKU!; isotypes: YUKU!).

Diagnosis. *Gentiana mopanshanensis* is distinguishable from all other similar species of the genus by the combination of its rosulate basal leaves lanceolate to gladiate, up to 5 (6) cm long, cauline leaves lanceolate or linear-lanceolate, throat of corolla blue maculate, plicae with 5–10 fimbriations, and fimbriation irregular in length, usually 0.5–2 mm long.

Etymology. The specific epithet "*mopanshanensis*" is derived from the type locality of the new species, the Mopanshan Mountain, and the Latin suffix *-ensis*, indicating the place of origin or growth.

Description. Biennial herbs, diffuse, 5–15 cm in height. Root slightly fleshy, 4–6 cm long, with conspicuous rootstock. Stems yellow-green or purplish-red, smooth, much branched at base; branches procumbent or ascending. Basal leaves rosulate, persistent at anthesis, sessile or subsessile; blades lanceolate to gladiate, (1–) 3–5 (–6) cm long, 0.2–0.7 (–1) cm wide, both surfaces densely and minutely papillate, apex acuminate, margin transparent, densely denticulate, basal veins 1–3, distinct, midvein convex beneath. Cauline leaves opposite, semiamplexicaul, base proximally compounded, petiole tube 1–1.5 mm long; blades lanceolate or linear-lanceolate, 0.3–2 cm long, 0.1–0.6 cm wide, apex acuminate, margin transparent, densely denticulate, both surfaces densely and minutely papillate, basal veins 1–3, midvein convex beneath. Flowers solitary, terminal on branch. Pedicels yellowish green, glabrous, 3–12 mm long, purplish-red striped. Calyx 5–8 mm long, obconic, yellow-green; tube campanulate, 4–5 mm long, 2–3 mm in diameter, slightly longer than lobes; lobes 5, acicular or subulate, 1.5–3 mm long, papillate on margin; veins ridged on abaxial surface, decurrent towards calyx tube; sinus between lobes obtuse to sub-rounded. Corolla 8–14 mm long, 5–8 mm in diameter, trumpet-shaped, blue-white, outside with copper-green stripes, inside with deeply blue spots in throat; tube tubular, 5–8 mm long, 4–6 mm in diameter, golden inside; lobes ovate to broadly ovate, 2–3 mm long, 2–3 mm wide, apex acute, margin entire; plicae triangular-ovate, 2–2.5 mm long, apex irregularly laciniate, fimbriate, with 5–10 fimbriations, usually 0.5–2 mm long. Stamens 5, filaments filiform-subulate, 3–6 mm long, inflated at middle, inserted in lower middle of corolla tube; anthers rectan-

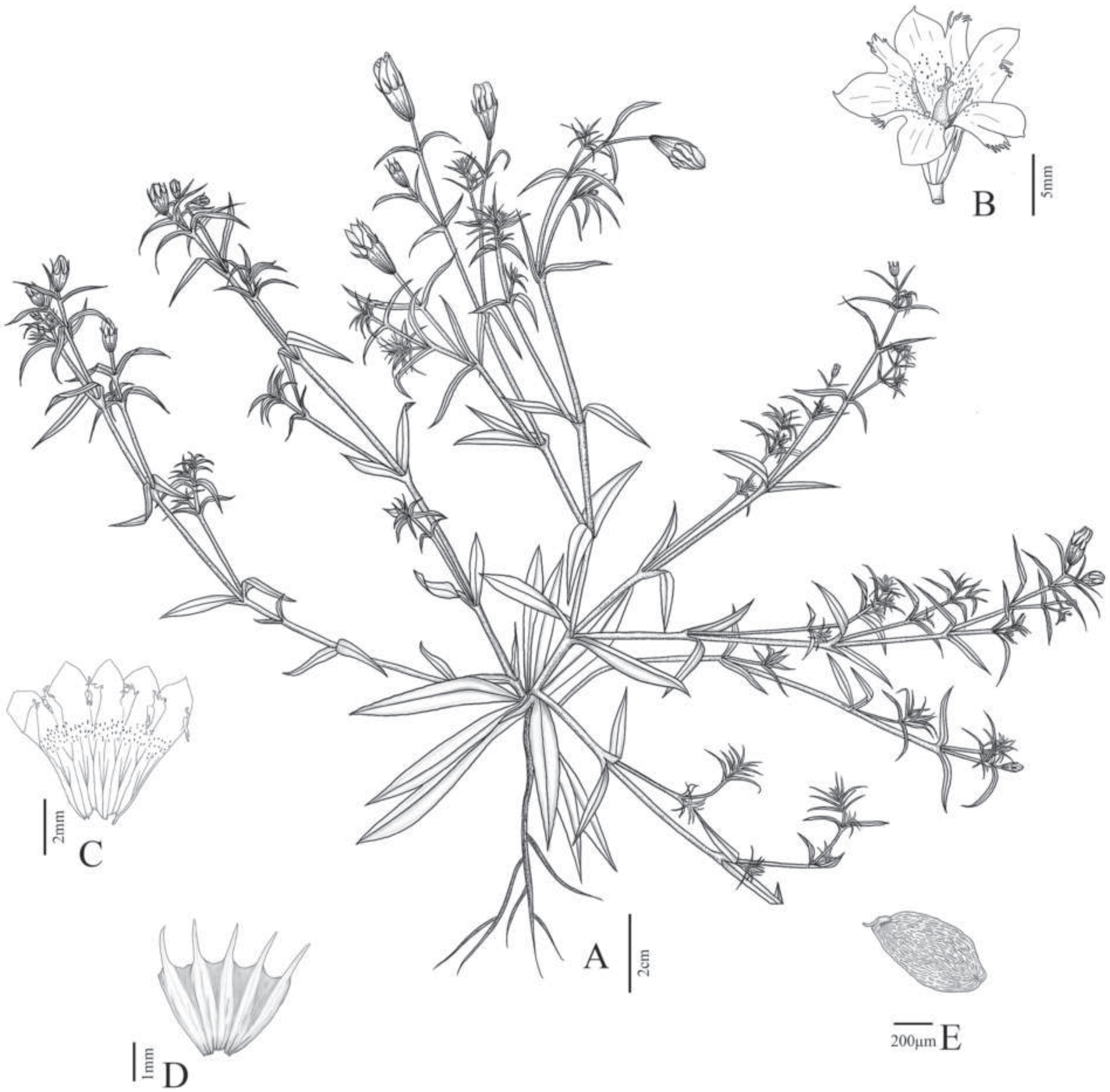

Figure 1. *Gentiana mopanshanensis* sp. nov. (Drawn by Ting T. Wang) **A** habit **B** flower (front view) **C** dissected corolla **D** dissected calyx **E** seed.

gular-rounded, 0.6–1 mm long. Ovary stipitate, ellipsoid or fusiform, 2.5–3 mm long, apex obtuse, base attenuate; style clavate, 0.5–1 mm long, stigma bifid, extrorse. Capsules obovate, exerted beyond persistent corolla, gynophore up to 15 mm long, narrowly winged on both margins. Seeds ovate-triangular, up to 1.5 mm long, yellowish-brown, densely striato-reticulate on seed coats.

Phenology. *Gentiana mopanshanensis* has a long flowering and fruiting period. It starts flowering in March and continues until August, and its fruiting period is from May to September.

Distribution and habitat. *Gentiana mopanshanensis* is currently only found in the Mopanshan Mountain (Fig. 4), which is located in the southeast of Xinping County, at the southwestern edge of the Yunnan-Guizhou Plateau. The mountain is situated east of the Yuanjiang River valley and has an elevation

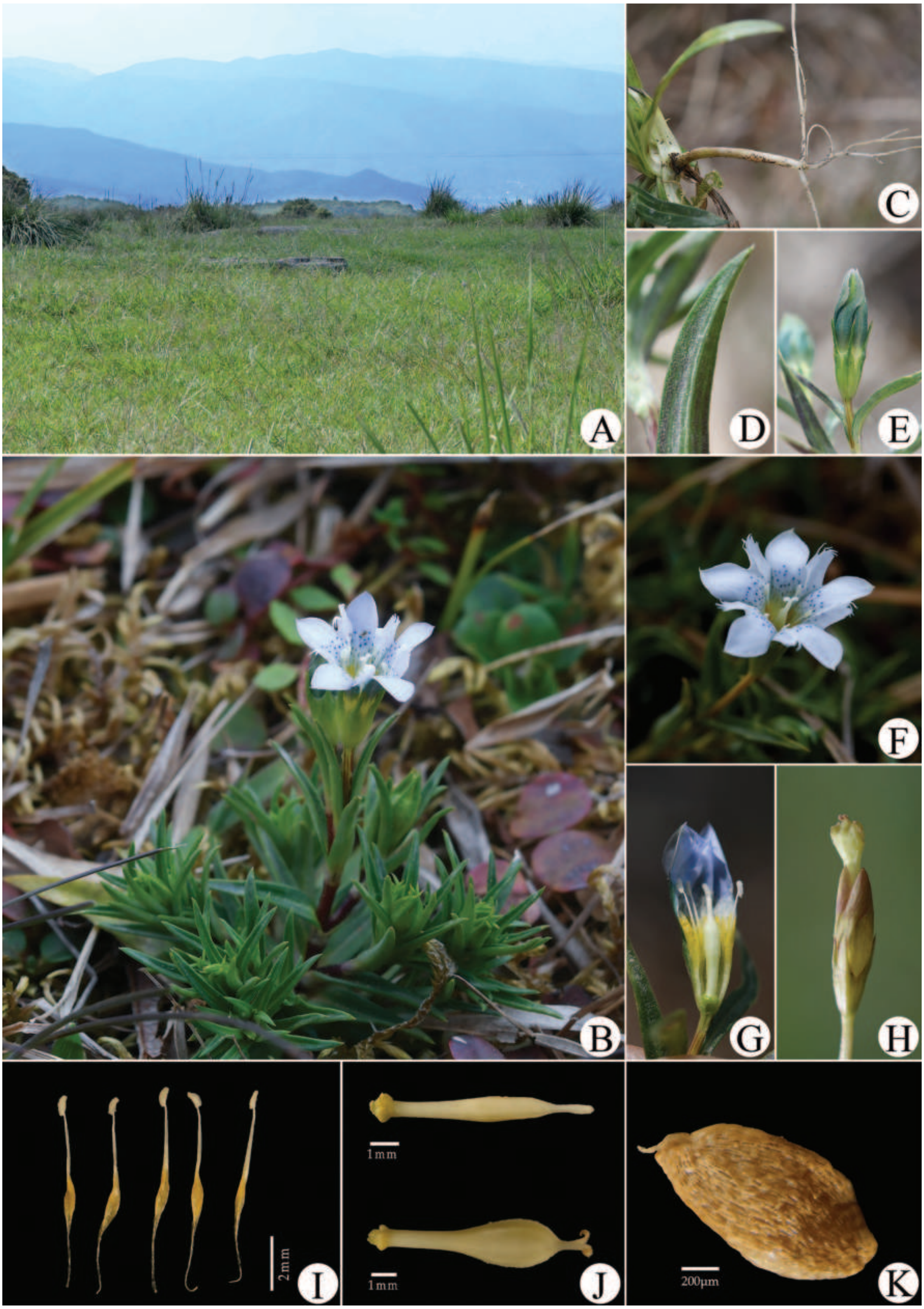

Figure 2. *Gentiana mopanshanensis* sp. nov. (Photographed by HCW and TC) **A** habitat **B** habit **C** root **D** leaf blade (side view, showing adaxially densely and minutely papillate and transparent denticulate on margin) **E** closed flower **F** flower (front view) **G** dissected flower (showing the stamens and style) **H** mature fruit protruding from persistent corolla **I** stamens **J** pistils **K** seed.

云南大学植物标本馆
Herbarium of Yunnan University

采集号：XP19775
Collection number: XP19775
采集人：王焕冲、陈涛、李世刚
Collector: Huan-Chong Wang, Tao Chen &Shi-Gang Li
采集时间：2023 年 4 月 3 日
Collection time: 3 April 2023
地点：云南省玉溪市新平县磨盘山国家森林公园
Location: Mopanshan Mountain National Forest Park, Xinping County, Yunnan Province, on the top of mountain
生境：疏生于草甸中
Habitat: sparsely grown in meadows
海拔：2480 米
Altitude: 2480 m
GPS: 101°59′23″E, 23°56′23″N
附记：5 份
Note: 5 copies
分类：龙胆属
Classification: *Gentiana*

05008414

主模式
HOLOTYPUS

YUKU

云南大学植物标本馆植物标本

采集号：XP19775　科名：龙胆科 Gentianaceae
磨盘山龙胆
Gentiana mopanshanensis **Huan C. Wang & Tao Chen**
鉴定人：王焕冲、陈涛　日期：2023.4.23

Figure 3. Holotype of *Gentiana mopanshanensis* sp. nov.(YUKU-05008414).

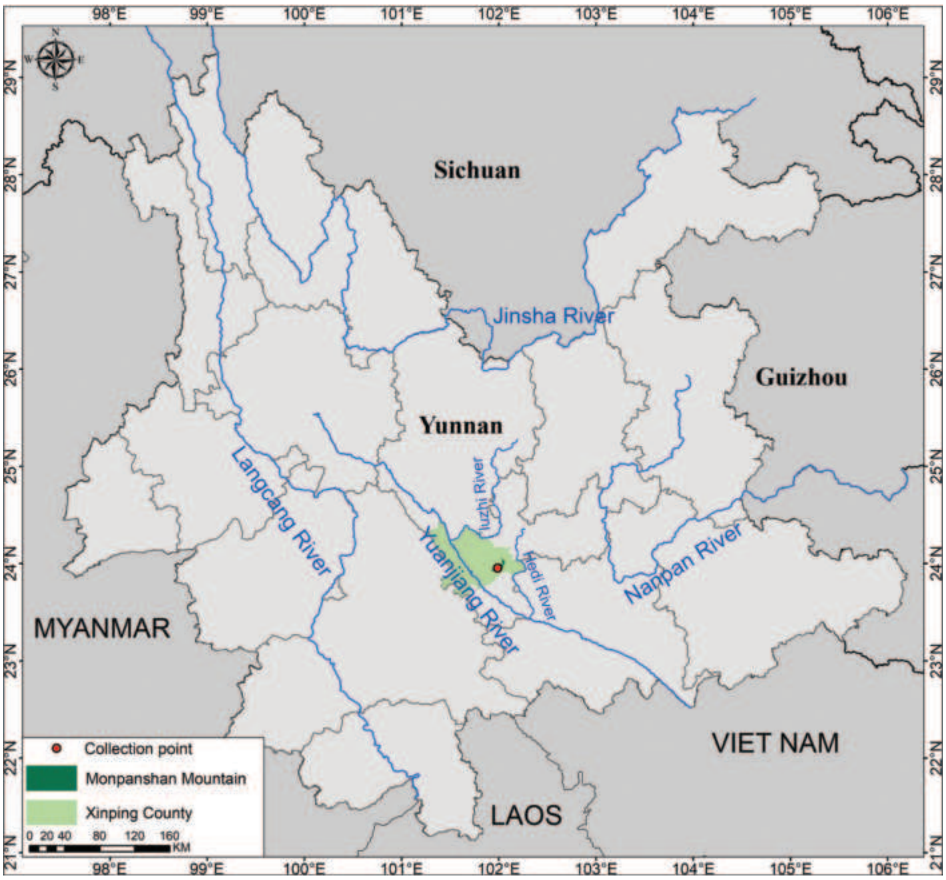

Figure 4. Geographical distribution of *Gentiana mopanshanensis* sp. nov. (red dot).

ranging from 1370 to 2611 meters. *G. mopanshanensis* usually occurs at elevations between 2400 and 2550 meters and mainly grows in wet meadows near the peak of the mountain. It can also be occasionally found under the thickets predominated by *Lithocarpus variolosus* Chun (Fagaceae) and *Quercus guyavifolia* H.Lév. (Fagaceae). In meadow habitats, this new species is commonly associated with *G. praticola* Franchet (Gentianaceae), *Polygala dunniana* H.Lév. (Polygalaceae), *Arundinella hookeri* Munro ex Keng (Gramineae), *Fragaria nilgerrensis* Schlecht. ex J. Gay (Rosaceae), *Roscoea tibetica* Batalin (Zingiberaceae) and *Bistorta paleacea* Yonek. et H.Ohashi (Polygonaceae).

Molecular phylogenetics. The ITS sequence region of *Gentiana mopanshanensis* comprises 625 base pairs with a GC content of 57.12%. The alignment of 60 ITS sequences resulted in a matrix of 662 total characters, of which 344 are constant, 93 of the variable characters are singleton sites and 225 characters are parsimony informative sites.

As shown in the phylogenetic tree (Fig. 5), phylogenetic analyses using the ITS sequence data demonstrated that the new species belongs to a clade representing the *Gentiana* section *Chondrophyllae* with maximum support. In this clade, *G. mopanshanensis* falls within the subclade corresponding to series *Fimbriata* Marq. with 0.993 posterior probabilities. It constituted a monophyletic lineage with *G. panthaica* Prain et Burkill and *G. mairei* H.Lév. with maximum support (PP = 1) and were resolved as sister to them. The phylogenetic result is also supported by the morphological characteristics.

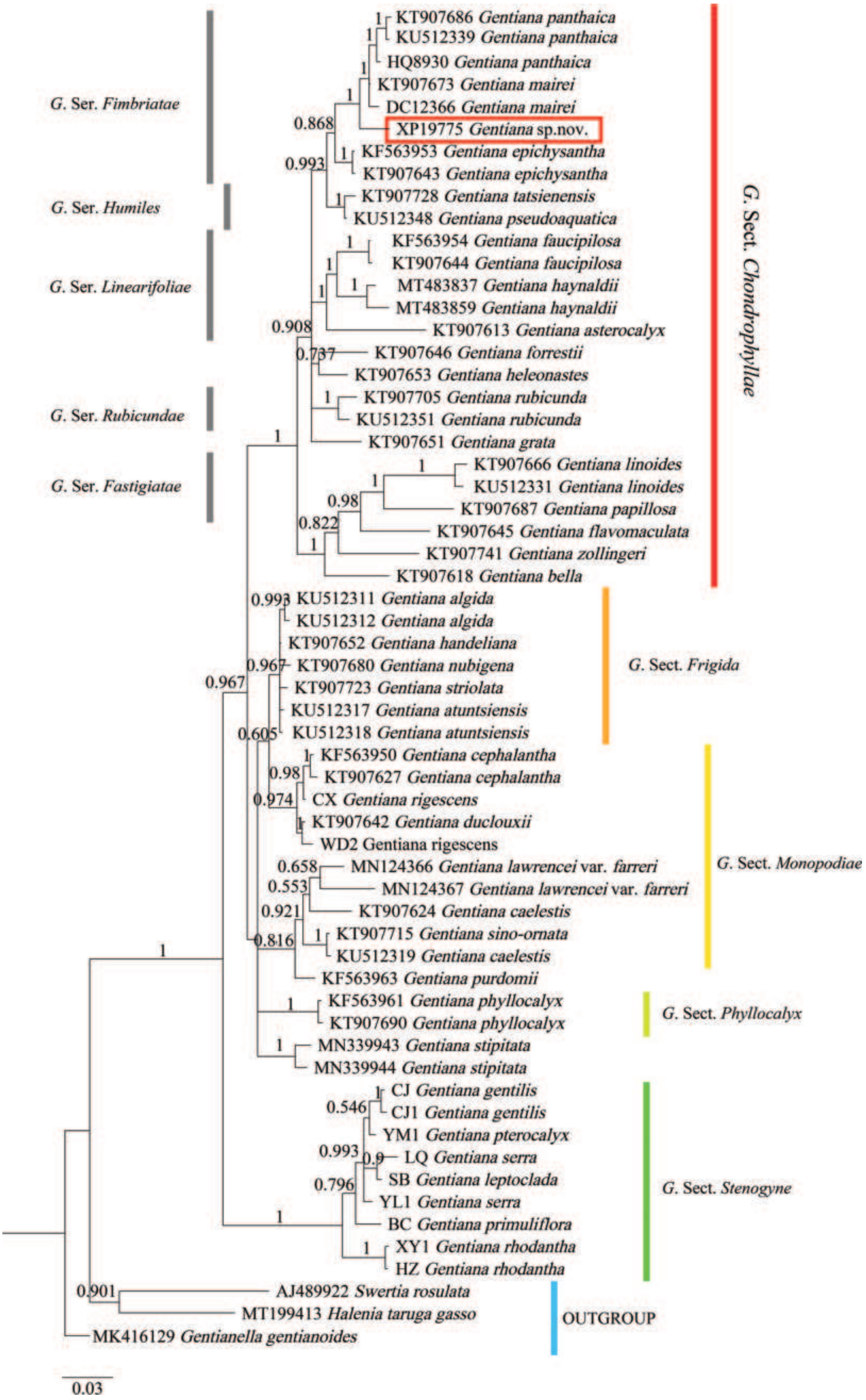

Figure 5. Mrbayes tree of *Gentiana* based on ITS sequences showing phylogenetic placement of *G. mopanshanensis*. Mrbayes posterior probabilities are shown near the nodes. *G. mopanshanensis* is marked by a red box.

Discussion. Based on phylogenetic analyses, *Gentiana mopanshanensis* should be assigned to the series *Fimbriatae* of the section *Chondrophyllae*. Its placement within this series is also supported by its particular morphological characters: stems much branched at the base, basal leaves well developed, leaf blades and calyx with densely and minutely papillate, calyx lobes acicular or subulate, plicae apex fimbriate, obovate capsule with strong and broad wings at apex.

This new species is most similar to *Gentiana mairei* and *G. panthaica* in terms of habit, and flower shape and size, especially plicae apex fimbriate. However, *G. mopanshanensis* can be distinguished from *G. mairei* by its biennial (vs. annual) habit, basal leaves lanceolate to gladiate (vs. ovate to ovate-elliptic), (1–) 3–5 (–6) cm (vs. 0.7–1.4 cm) long, 0.2–1 cm (vs. 0.3–0.7 cm) wide, cauline leaves lanceolate or linear-lanceolate (vs. ovate-triangular to ovate-lanceolate), with blue spots (vs. blackish, white or pale yellow stripes) in throat, plicae with 5–10 (vs. 8–10) fimbriations, irregular (vs. nearly equal) in length, ususally 0.5–2 mm (vs. 2–2.5 mm) long. *G. mopanshanensis* differs from *G. panthaica* in biennial (vs. annual) habit, basal leaves lanceolate to gladiate (vs. ovate-elliptic to ovate), cauline leaves lanceolate or linear-lanceolate (vs. lanceolate, narrowly elliptic or ovate-triangular), plicae with 5–10 (vs. 15–20) fimbriations, filament laciniate (vs. filiform, curly). A detailed morphological comparison between these three species is summarized in Table 1.

Additional specimens examined. *Gentiana mopanshanensis*. China. Yunnan: Xinping County, Mopan Mountain, alt. 2509 m, 13 August 2012, in flower and

Table 1. Morphological comparison of *G. mopanshanensis*, *G. maire*, *G. panthaica*.

Characters	*G. mopanshanensis*	*G. mairei*	*G. panthaica*
Habit	biennial	annual	annual
Leaf			
-Basal leaf	lanceolate to gladiate 3–5 (6) cm × 0.2–0.7 (1) cm	ovate to ovate-elliptic, 7–1.5 cm × 3–0.7 cm	ovate-elliptic to ovate, 0.9–2 cm × 0.4–1 cm
-Cauline leaf	lanceolate or linear-lanceolate, 0.3–1.5 cm × 0.1–0.4 cm	ovate-triangular to ovate-lanceolate 0.55–1.1 cm × 0.25–0.4 cm	lanceolate, narrowly elliptic or ovate-triangular, 0.6–0.8 cm × 0.25–0.3 cm
Flower			
-Calyx			
-Tube	campanulate, 4–5 mm long	obconic, 3–4 mm long	obconic, 3–4 mm long
-Lobe	acicular or subulate, 1.5–3 mm long	filiform-subulate,2–2.5 mm long	filiform to filiform-conical, 1.5–3 mm long
-Coroll	trumpet-shaped, 8–14 mm long, 5–8 mm in diam.	obconic 8.5–12 mm long, 5–8 mm in diam.	obconic 8–14 mm long, 5–10 mm in diam.
-Lobe	ovate to broadly ovate, 2–3 mm long	ovate-orbicular, 2.5–3 mm long	ovate, 2.5–3.5 mm long
-Plicae	triangular-ovate, with 5–10 fimbriae	ovate-oblong, with 8–10 fimbriae	ovate, with 15–20 fimbriae
-Stamen			
-Filament	filiform-subulate, 3–6 mm long	filiform, 3–3.5 mm long	filiform-subulate, 3–4 mm long
-Anther	rectangular-rounded	ellipsoid	ellipsoid
-Pistil			
-Ovary	ellipsoid or fusiform, 2.5–3 mm long	ellipsoid, 2.5–3 mm long	ellipsoid, 3–4 mm long
-Style	clavate, 0.5–1 mm long	linear, 0.7–1.5 mm long	clavate, 0.7–1.2 mm long
Fruit	obovoid, 4–7 mm long	obovoid, 4.5–5.5 mm long	obovoid, 4–5 mm long
Seed	ovate-triangular, 1–1.5 mm long	ellipsoid, 1.3–1.5 mm long	ellipsoid, 1.3–1.5 mm long

fruit, *Xinping County Census team 5304270757* (IMDY0019083); same location, alt. 2406 m, 18 June 2023, in flower and fruit, *T. Chen et al. XP23338* (YUKU).

Gentiana mairei. China. Yunnan: Dali City, Cangshan Mountain, alt. 3800 m, 22 July 2009, *Z.J.Yin et al. 1631* (KUN-1220364); Jingdong County, Wuliangshan Mountain, alt. 3100 m, 19 November 1956, *B.Y.Qiu 53823* (KUN-00088281).

Gentiana panthaica. China. Yunnan: Heqing County, Mae Shan, 15 August 2020, *Q.P. Wang et al. HQ 8930* (YUKU); Nanjian County, Wuliangshan Mountain, alt. 2270 m, 24 March 2012, *E.D. Liu et al. 3587* (KUN-1224606); Dali City, Cangshan Mountain, alt. 3800 m, 15 July 2009, *Z.J.Yin et al. 1362* (KUN-1220362); same location, 13 July 2009, *Z.J.Yin et al. 1111* (KUN-1220361); Luquan County, Daheiqing, alt. 3150 m, 2 July 1990, *R.F.Fang et al. 83* (KUN-551847).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Investigation: HCW,TC, SYL, TTW. Writing - original draft: TC. Writing - review and editing: HCW,TC.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Appendix 1

Table A1. Species sequence information downloaded from the GenBank.

GenBank	Species	Voucher information	Herbarium
KU512339	*G. panthaica* Prain et Burk.	GXJ2011-055	
KT907686	*G. panthaica* Prain et Burk.	Favre & Matuszak 061a	KUN
KT907673	*G. mairei* Levl.	Wang hong et al. 01-0062	KUN
KT907643	*G. epichysantha* Hand.-Mazz.	Favre & Matuszak 131a	KUN
KF563953	*G. epichysantha* Hand.-Mazz.	Favre & Matuszak 131a	KUN
KT907728	*G. tatsienensis* Franch.	Wang Lisong, et al. 07-13	KUN
KU512348	*G. pseudoaquatica* Kusnezow	GXJ2011-043	
KT907644	*G. faucipilosa* H. Smith	Favre & Matuszak 37a	KUN
KF563954	*G. faucipilosa* H. Smith	Favre and Matuszak 37a	KUN
MT483837	*G.haynaldii* Kanitz		
MT483859	*G. haynaldii* Kanitz		
KT907613	*G. asterocalyx* Diels	Favre & Matuszak 106a	KUN
KT907653	*G. heleonastes* H. Smith ex Marq.	Favre 206a	KUN
KT907646	*G. forrestii* Marq.	Penghua, Liu Ende et al. 9538	KUN
KT907705	*G. rubicunda* Franch.	Wang hong et al. 03-1098	KUN
KU512351	*G. rubicunda* Franch.	YG2011392	
KT907651	*G. grata* H. Smith	Favre & Matuszak 32a	KUN
KT907666	*G. linoides* Franch. ex Hemsl.	Chen HS, CHC 2866	TNM
KU512331	*G. linoides* Franch. ex Hemsl.	GXJ2011-068b	
KT907687	*G. papillosa* Franck.	Chen HS, CHC 2867	TNM
KT907645	*G. flavomaculata* Hayata	Chen HS, CHC 2364	TNM
KT907618	*G. bella* Franch. ex Hemsl.	H.S. Chen CHC 2850	TNM
KT907741	*G. zollingeri* Fawcett	Chen HS CHC 2372	TNM
KU512311	*G. algida* Pall.	GXJ20130174	
KU512312	*G. algida* Pall.	PG110833	
KT907652	*G. handeliana* H. Smith	Liu Ende et al. 1209080	LZ
KT907680	*G. nubigena* Edgew.	Wang Lisong, et al. 07-55	KUN
KT907723	*G. striolata* T. N. Ho	Favre 221a	KUN
KU512317	*G. atuntsiensis* W. W. Smith	GXJ2011-072	
KU512318	*G. atuntsiensis* W. W. Smith	GXJ2011-080	
KT907627	*G. cephalantha* Franch. ex Hemsl.	Favre 325	KUN
KF563950	*G. cephalantha* Franch. ex Hemsl.	Favre 325	KUN
KT907642	*G. duclouxii* Franch.	Favre & Matuszak 076	KUN
MN124367	*G. lawrencei var. farreri* (I. B. Balfour) T. N. Ho	fu2016060_2	

GenBank	Species	Voucher information	Herbarium
MN124366	*G. lawrencei var. farreri* (I. B. Balfour) T. N. Ho	fu2016176_5	
KT907624	*G. caelestis* (Marq.) H. Smith	Favre & Matuszak 193a	KUN
KT907715	*G. sino-ornata* Balf.f.	Favre & Matuszak 224a	KUN
KU512319	*G. caelestis* (Marq.) H. Smith	GXJ2011-078	
KF563963	*G. purdomii* Marq.	Favre 311	KUN
KF563961	*G. phyllocalyx* C. B. Clarke	Favre & Matuszak 33a	KUN
KT907690	*G. phyllocalyx* C. B. Clarke	Favre & Matuszak 33a	KUN
MN339943	*G. stipitata* Edgew.		
MN339944	*G. stipitata* Edgew.		
AJ489922	*Swertia rosulata* (Baker) Klack.	Piso, Wohlhauser, Zeltner M023	NEU
MT199413	*Halenia taruga-gasso* Gilg	MO05693166	
MK416129	*Gentianella gentianoides* (Franch.) H. Smith	xuechy090094	

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Research Article

Glochidion yangchunense (Phyllanthaceae), a new species with discoid flowers from Guangdong Province, China

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Abstract

Phyllanthodendron can be readily morphologically distinguished from *Glochidion*, but recent molecular evidence showed that *Phyllanthodendron* is paraphyletic due to *Glochidion* being nested within it. In this study, a new species of the former *Phyllanthodendron* is described and illustrated as *Glochidion yangchunense* Z.Q. Song & Gang Yao from the limestone areas of South China. This is a peculiar new species and morphologically distinguished by its discoid flowers, T-shaped disc segments, and glabrous flowering branches. A key to *Glochidion yangchunense* and related species in China is provided here.

Key words: Karst, Malpighiales, Phyllantheae, *Phyllanthodendron*, Taxonomy

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Introduction

Phyllanthodendron Hemsl. was previously considered as a distinct genus (Croizat 1942; Li 1987, 1994; Li and Gilbert 2008; Xia and Tong 2018), or treated as a section or a subgenus of the genus *Phyllanthus* L. (Beille 1927; Chantaranothai 2007; Webster and Carpenter 2008; Bouman et al. 2018). However, several molecular studies revealed a highly supported sister relationship between *Phyllanthodendron* and the genus *Glochidion* J.R. Forst. & G. Forst. (Kathriarachchi et al. 2006; Pruesapan et al. 2012; van Welzen et al. 2015; Luo et al. 2017; Pornpongrungrueng et al. 2017). A more comprehensive molecular phylogenetic study has recently shown that *Phyllanthodendron* is a paraphyletic group with *Glochidion* nested within (Bouman et al. 2021). In a result, *Phyllanthodendron* was formally united with *Glochidion* (Bouman et al. 2022). Currently, *Glochidion* is the largest genus of the family Phyllanthaceae and comprises 300–350 species of shrubs or trees distributed in Asia and Pacific (Yao et al. 2020; Bouman et al. 2022). In the Plants of the World Online (https://powo.science.kew.org/; POWO 2023), 328 accepted specific names are listed under the genus. Within *Glochidion*, three subgenera were elected, i.e. subg. *Glochidion*, subg. *Phyllanthodendron* (Hemsl.) R.W. Bouman and subg. *Pseudoactephila* (Croizat) R.W. Bouman. The two latter subgenera correspond to the previous *Phyllanthodendron* and consist of 19 Asian species, which can be readily distinguished from the subgenus *Glochidion* by the presence of a floral disc and apiculate anthers (Bouman et al. 2022).

During our field plant investigations in Yangchun City, Guangdong Province, South China, we found an interesting monoecious shrub in a limestone hill. The plant has five (male flowers) or six (female flowers) sepals, three stamens, connate filaments, apiculate anther connectives, 3-locular ovaries, unlobed floral disc segments, and inflated capsules (Fig. 1). These characters are consistent with those of the previous *Phyllanthodendron* and the plant may be a member of *Glochidion* subg. *Pseudoactephila* for lacking the specialized floriferous branchlets, as circumscribed in Bouman et al. (2022). After being compared with all known related species, this plant is proposed as new to science. A full description, color photographs, phenology, conservation status, morphological comparison, and a distribution map of the species are provided here.

Material and methods

All specimens of the previous *Phyllanthodendron* (now as *Glochidion* subg. *Phyllanthodendron* and *G.* subg. *Pseudoactephila*) kept in the Herbaria CANT, GXMG, GXMI, HITBC, IBK, IBSC, KUN, PE and SYS have been carefully examined by visiting these herbaria, and the images of *Phyllanthodendron* specimens deposited in the Herbaria A, BM, E, K, M, MO, P, US, WU and SZG were also studied. Acronyms for the herbaria follow the Index Herbariorum (Thiers 2023). We also observed the living status of relevant taxa through field investigations and accessing some websites such as Plant Photo Bank of China (https://ppbc.iplant.cn/), Chinese Field Herbarium (https://www.cfh.ac.cn/), and Chinese Union of Botanical Gardens (https://image.cubg.cn/). The distribution map was made by the software ArcGIS 10.2.

Result

Taxonomic treatment

Glochidion yangchunense **Z.Q. Song & Gang Yao, sp. nov.**
urn:lsid:ipni.org:names:77338772-1
Figs 1, 2
阳春珠子木

Type. CHINA. Guangdong Province, Yangchun City, Chunwan Town, Nali village, in limestone hills, 22.410809°N, 111.932152°E, alt. 200 m., 5 July 2023, *Gang Yao & Zhu-Qiu Song YGGDYC2023070501* (holotype: IBSC [IBSC1010886], Fig. 2A; isotypes: IBSC [IBSC1010887, IBSC1010888, IBSC1010889, IBSC1010890, IBSC1010891, IBSC1010892, IBSC1010893]).

Diagnosis. *Glochidion yangchunense* resembles *Glochidion anthopotamicum* (Hand.-Mazz) R.W. Bouman in general morphology, but much differs from the latter by its glabrous flowering branches (Fig. 1G, I) (*vs.* pubescent flowering branches; Fig. 3C–F), sepals with lateral veins (Fig. 1F, H) (*vs.* sepals without lateral veins; Fig. 3D–F), sepals jointly formed a discoid shape (Fig. 1F–I) (*vs.* sepals jointly formed a urceolate shape; Fig. 3D–F), T-shaped disc segments (Fig. 1F, H) (*vs.* linear disc segments; Fig. 3D), and short stipules (ca. 1 mm *vs.* 3 mm long).

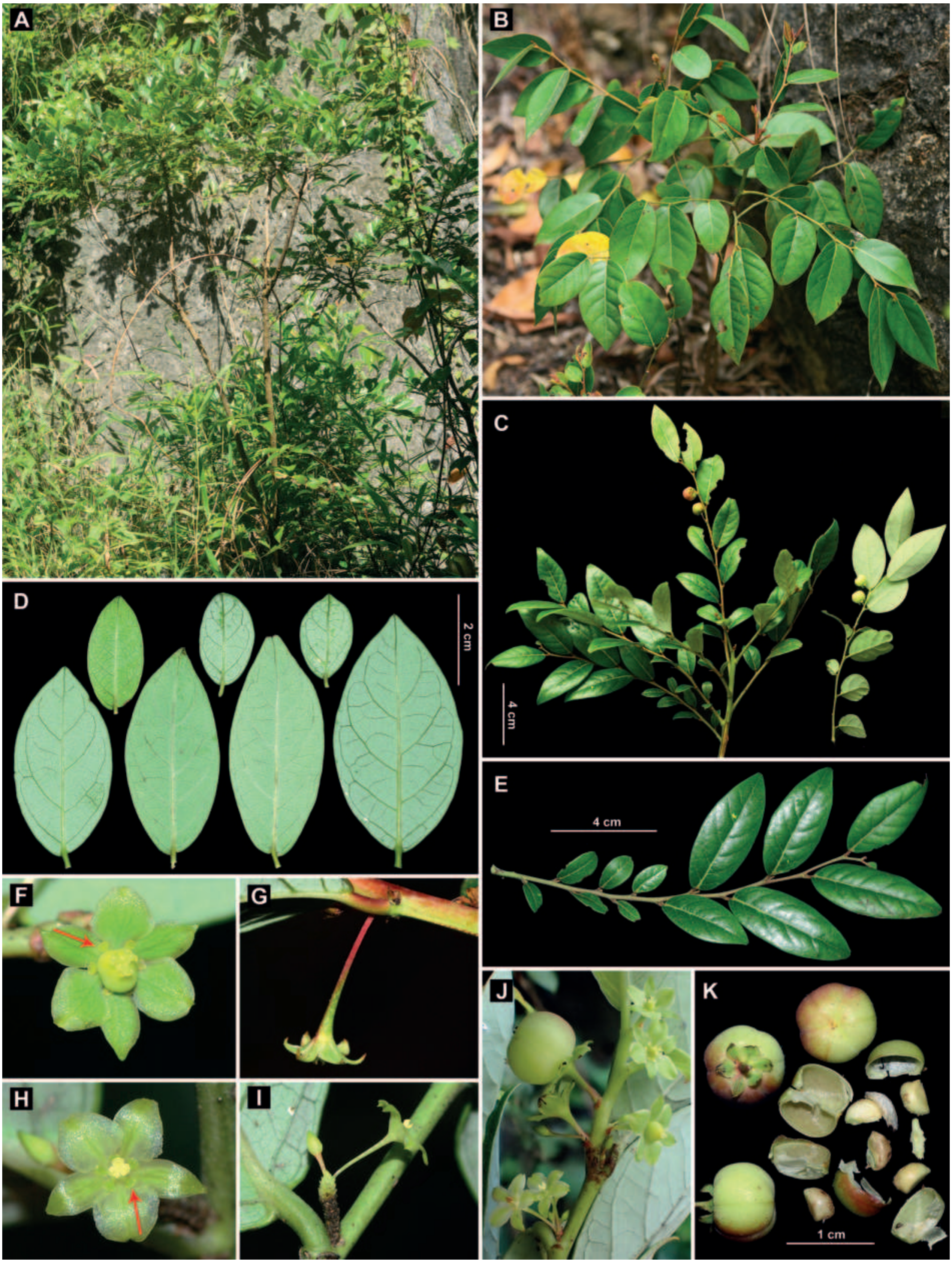

Figure 1. *Glochidion yangchunense* Z.Q. Song & Gang Yao **A** habit **B** detail of the apex of branches **C** fruiting branches **D, E** leaves, adaxial and abaxial surfaces, shapes and sizes **F, G** pistillate flower, front and lateral view **H, I** staminate flower, front and lateral view **J** branches with staminate and pistillate flowers as well as fruit **K** fruits and seeds. Arrows indicate disc segments.

Figure 2. *Glochidion yangchunense* Z.Q. Song & Gang Yao **A** holotype (IBSC1010886) **B** isotype (IBSC1010888). Used with permission.

Description. ***Shrubs***, 0.5–2.5 m tall, erect, monoecious; stem gray-brown; branches glabrous and terete, but sparsely gray puberulent and slightly angular when young. ***Stipules*** ovate-triangular, ca. 0.8 × 0.6 mm, usually caducous. ***Petiole*** 2.5–4 mm long, sparsely gray puberulent when young. ***Leaves*** simple, alternate, distichous; leaf blades papery to leathery, broad elliptic, elliptic, ovate, or narrowly ovate, length/width ratio 1.5–2.1, glabrous but puberulent on vines below when young; leaf blades at upper part of branches usually larger, 3.5–5.2 × 1.5–3 cm, lateral veins in 6–8 pairs; leaf blades at lower part of branches usually smaller, ca. 1.8–2.5 × 1.2 cm, lateral veins in 3–5 pairs; leaf blades margin entire, slightly revolute, apex acute, rarely acuminate, base sub-rounded; midrib and lateral veins flattened above, slightly elevated below, anastomosing before margins. ***Inflorescences*** axillary, 2–4-flowered; male flowers usually inserted at the lower part of branches, female flowers inserted at the upper part; flowers sometimes crowded in long-pedicelled clustered fascicles; pedicels 6–8.5 mm long, enlarged at apex. ***Staminate flower*:** sepals 5 or rarely 6, imbricate, forming a discoid shape, green yellow, midrib elevated on abaxial surface, ovate, 3.3–4.3 × 1.4–2.3 mm, outer sepals lanceolate, inner ones ovate, glabrous; petals absent; disc segments 5, rarely 6, free, T-shaped and expand at apex, slightly greenish yellow; stamens 3, or rarely 4; filaments connate into a terete column, anthers erect, dehiscing longitudinally, connectives usually apiculate. ***Pistillate***

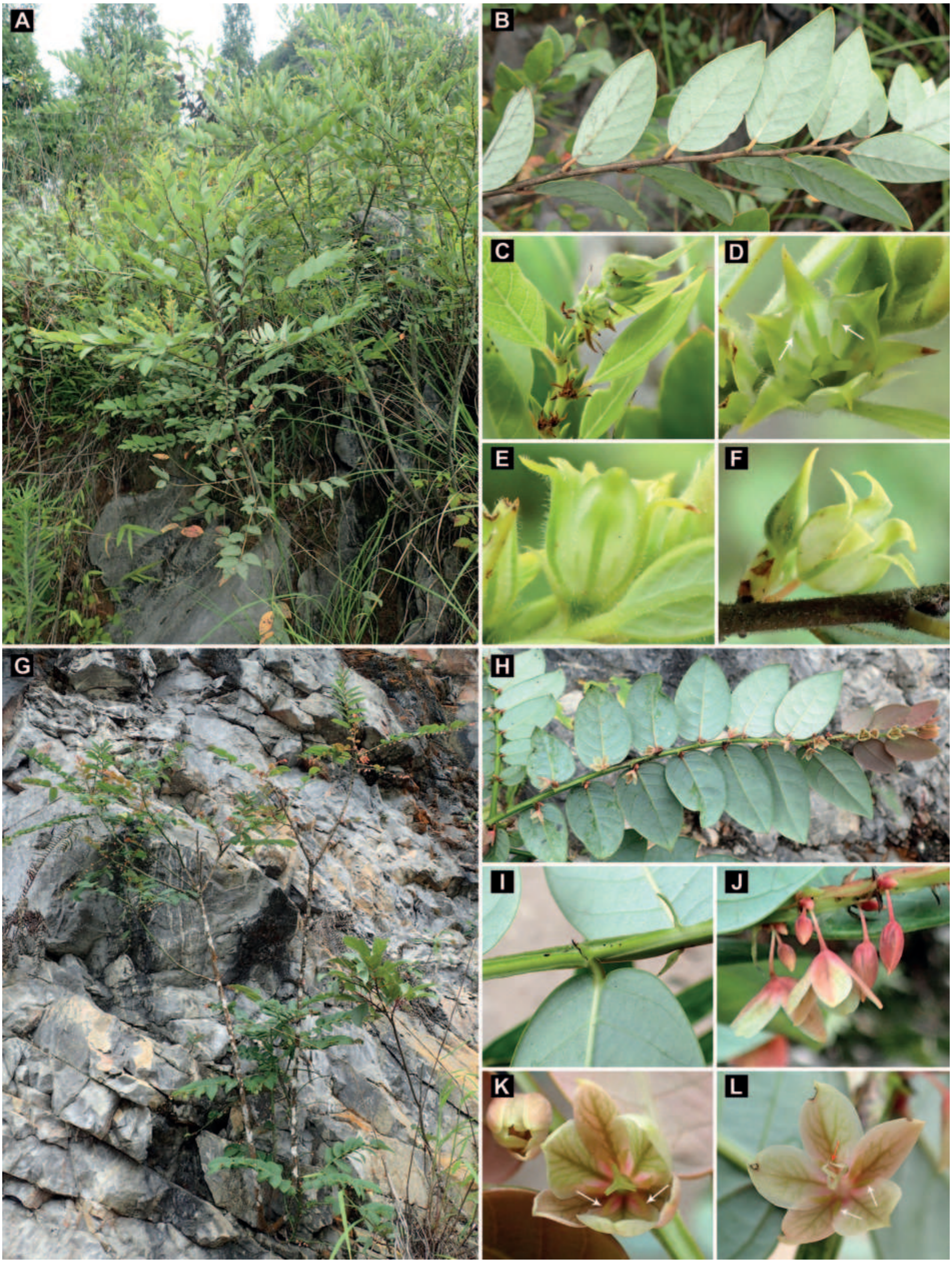

Figure 3. Related species of *Glochidion yangchunense* Z.Q. Song & Gang Yao **A–F** *Glochidion anthopotamicum* (Hand.-Mazz.) R.W. Bouman **G–L** *Glochidion dunnianus* (H. Lév.) R.W. Bouman **A, G** habit **B, H, I** branches **C–F, J–L** flowers, front and lateral view **H** part of winged branch with stipules **D, K** pistillate flowers **E, F, L** staminate flowers. White arrows indicate disc segments and red arrow indicates stamen.

flower*:** sepals 6, imbricate, forming a discoid shape, glabrous, size as in staminate flower; petals absent; disc segments 6, free, T-shaped and expand at apex, slightly greenish yellow; ovary 3-locular; styles 3; stigmas evidently bifid. ***Capsules subglobose, 8–10 mm in diam., smooth outside, brownish when mature, fruiting pedicels 6–9 mm long, enlarged at apex. ***Seeds*** obscurely 3-angled or laterally compressed, ca. 4.2–4.5 × 2.7 mm, brownish when mature.

Phenology. Flowering and fruiting from March to December.

Distribution and habitat. *Glochidion yangchunense* is currently known only from the type locality, Chunwan Town, Yangchun City, Guangdong Province, China (Fig. 4), and it grows in limestone hills usually at elevations over 200 m.

Etymology. The specific epithet refers to the type locality, Yangchun City in Guangdong Province, China, a hotspot for biodiversity research in Guangdong Province, where multiple new taxa of plant (e.g. *Ilex yangchunensis* C.J. Tseng, *Chiritopsis subulata* var. *yangchunensis* W.T. Wang, *Hedyotis yangchunensis* W.C. Ko & Zhang, *Itea yangchunensis* S.Y. Jin, *Cleyera yangchunensis* L.K. Ling, *Alpinia stachyoides* var. *yangchunensis* Z.L. Zhao & L.S. Xu, *Symplocos yangchunensis* H.G. Ye & F.W. Xing, *Lithocarpus yangchunensis* H.G. Ye & F.G. Wang, *Croton yangchunensis* H.G. Ye & N.H. Xia, *Mitreola yangchunensis* Q.X. Ma, H.G. Ye & F.W. Xing, *Helicia yangchunensis* H.S. Kiu, *Primulina yangchunensis* Y.L. Zheng & Y.F. Deng, and *Spiradiclis yangchunensis* R.J. Wang) have been described (see Song et al. 2023).

Preliminary conservation status. This new species is known from one locality, situated in the unprotected limestone area, and more than 500 individuals

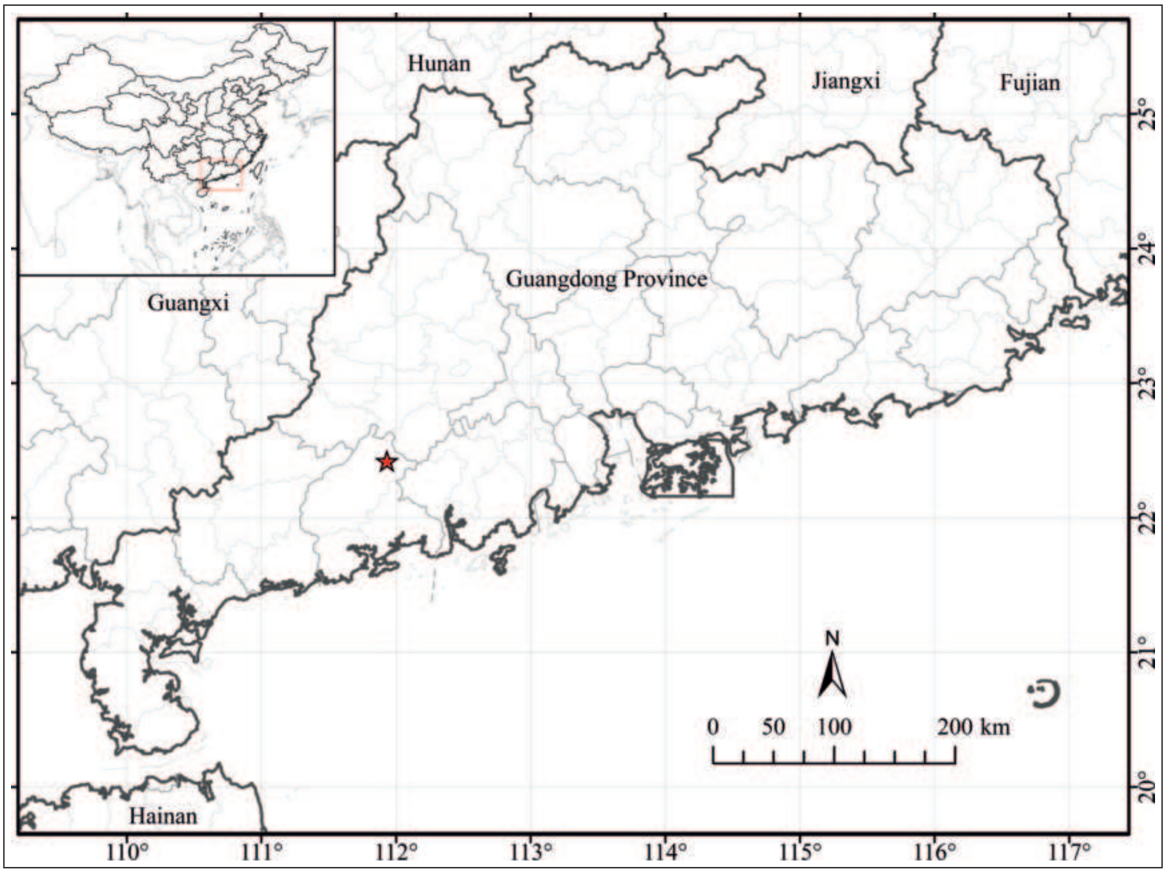

Figure 4. Distribution map of *Glochidion yangchunense* Z.Q. Song & Gang Yao in China (red star).

(including many mature and young plants) were found. It may be considered as 'Vulnerable' (VU) under the IUCN (2001) categories and criteria D1.

Additional specimens examined. CHINA. Guangdong Province, Yangchun City, Chunwan Town, Nali village, in limestone hills, 22.410809°N, 111.932152°E, alt. 200 m., 21 March 2023, *You-Sheng Chen, Zhu-Qiu Song, Bu-Yun Zhang & Zhen Wang YC20230221* (IBSC).

Discussion

In China, *Phyllanthodendron* was usually accepted as a distinct genus, and 10 species were recorded in the limestone area (Li 1987, 1994; Wei 2005; Li and Gilbert 2008; Xia and Tong 2018). Yao et al. (2021) synonymized *Phyllanthodendron orbicularifolium* P.T. Li under *P. petraeum* P.T. Li, because they found a continuous variation in the characters that have been used to distinguish them through examination of herbarium specimens and field observations. Ding et al. (2023) newly reported *Phyllanthus mirabilis* Müll. Arg. (= *Glochidion mirabile* (Müll. Arg.) R.W. Bouman) from China. Thus, 11 species (including *G. yangchunense*) of the previous *Phyllanthodendron* are distributed in China. Due to these changes, a new key for the 11 species in China is provided here.

Morphologically, in the previous *Phyllanthodendron*, the sepals of most species are concave inside and form a cup-shaped or urceolate shape, and the shape of disc segments is usually described as linear, oblong, or ligulate (Li and Gilbert 2008; Bouman et al. 2022; also see Fig. 3). But the new species described in this study, *Glochidion yangchunense*, is a peculiar species and it has the sepals jointly to a discoid shape, and T-shaped disc segments (Fig. 1F, H). The new species resembles *Glochidion anthopotamicum*, a species widely distributed from southwestern China to southeastern China (Li and Gilbert 2008). However, the new species differs greatly from the latter by a series of morphological characters that can be referenced from the above chapter "Diagnosis". Additionally, the new species usually has larger leaves at the upper part of branches and smaller leaves at the lower part of branches (Fig. 1C, E), and sepals acute to slightly acuminate at apex (Fig. 1F, H). While the species *G. anthopotamicum* usually has smaller leaves at the upper part of branches and larger leaves at the lower part of branches, and sepals caudate-acuminate at apex (Fig. 3C–F). The new species is also similar to *G. dunnianus* (H. Lév.) R.W. Bouman in having evident lateral veins in sepals (especially in female flowers; Figs 1F, H, 3K, L), but it differs from the latter by its terete branches (Fig. 1C, E), outer sepals much narrower than inner ones (Fig. 1F, H), anther connectives with an apiculate apex (Fig. 1I), T-shaped disc segments (Fig. 1F, H), and smaller fruits (ca. 8–10 mm in diameter; Fig. 1K). In contrast, *G. dunnianus* has 2-winged branches (Fig. 3H, I), equivalent or sub-equivalent sepals (Fig. 3K, L), anther connectives with a narrowly subulate apex (Fig. 3L), linear-shaped disc segments (Fig. 3K, L), and larger fruits (ca. 10–15 mm in diameter).

Key to *Glochidion yangchunense* and related species in China

1 Sepals forming discoid or broadly campanulate **2**
– Sepals forming urceolate or cup-shaped...**4**

2 Sepals forming discoid; disc segments T-shaped; stipules ovate-triangular, ca. 1 mm long .... ***G. yangchunense* Z.Q. Song & Gang Yao**
– Sepals forming broadly campanulate; disc segments linear; stipules lanceolate, 3–5 mm long **3**
3 Branchlets prominently winged; sepals with reticular lines........................ .... ***G. dunnianus* (H. Lév.) R.W. Bouman**
– Branches terete; sepals without reticular lines .... ***G. petraeum* (P.T. Li) R.W. Bouman**
4 Branches angulose or prominently winged, glabrous or pubescent **5**
– Branches terete, pubescent **8**
5 Branches pubescent; leaf blades oblong, oblique at base, obtuse at apex; fruiting pedicels less than 1 cm long..... ***G. breyniopsis* Esser & R.W. Bouman**
– Branches glabrous; leaf blades lanceolate, symmetrical at base, acuminate to caudate at apex; fruiting pedicels 3–4 cm long **6**
6 Ovaries and fruits glabrous........... ***G. caudatifolium* (P.T. Li) R.W. Bouman**
– Ovaries and fruits pubescent... **7**
7 Male sepals and disk segments 5 or 6, stamens 3 .... ***G. lativenium* (Croizat) R.W. Bouman**
– Male sepals, disk segments, and stamens 4.... ***G. moi* (P.T. Li) R.W. Bouman**
8 Leaf base obliquely cordate; fruits triangular-globose .... ***G. mirabilis* (Müll. Arg.) R.W. Bouman**
– Leaf base cuneate or rounded; fruits subglobose **9**
9 Ovaries and fruits glabrous; fruiting pedicels less than 1 cm long .... ***G. anthopotamicum* (Hand.-Mazz.) R.W. Bouman**
– Ovaries and fruits pubescent fruiting pedicels more than 3–4 cm long **10**
10 Leaf blades 6–12 cm long .... ***G. yunnanense* (Croizat) R.W. Bouman**
– Leaf blades 11.5–23.5 cm long.... ***G. roseum* (Craib & Hutch.) R.W. Bouman**

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Formal analysis: ZQS, GY. Funding acquisition: ZQS. Investigation: GY, ZQS. Methodology: GY. Writing – original draft: ZQS. Writing – review and editing: GY.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

A new combination and synonym in *Bupleurum* (Apiaceae, Apioideae), based on morphological, molecular and cytological evidence

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Abstract

Specimen examinations and field observations revealed that *Bupleurum smithii* var. *parvifolium* was distinctly different from *B. smithii* var. *smithii* in umbel, leaf, and fruit morphology, but was very similar to *B. commelynoideum* var. *flaviflorum*. Based on these morphological evidences, the present study re-examined the taxonomic status of these taxa through morphological, cytological, and phylogenetic analyses. The results showed distinguishable features in the width of middle leaves and bracteoles of *B. smithii* var. *parvifolium* compared to *B. smithii* var. *smithii*. Morphological variation between *B. smithii* var. *parvifolium* and *B. commelynoideum* var. *flaviflorum* was continuous and overlapping. Notably, the chromosome number of *B. smithii* var. *parvifolium* was 2n = 14 (x = 7), consistent with *B. commelynoideum* var. *flaviflorum*, whereas *B. smithii* var. *smithii* was 2n = 64 (x = 8). Additionally, phylogenetic analyses revealed *B. commelynoideum* var. *flaviflorum* nested within *B. smithii* var. *parvifolium*, and that both were distant from the *B. smithii* var. *smithii* and *B. commelynoideum* var. *commelynoideum*. Based on the evidence above, the differences between *B. smithii* var. *parvifolium* and *B. smithii* var. *smithii* extend beyond the level of intraspecific variation, and *B. commelynoideum* var. *flaviflorum* is considered to be identical with *B. smithii* var. *parvifolium*. Hence. A new combination and status, *B. parvifolium* (Shan & Y.Li) Q.R.Liu & L.H.Wang, **comb. et stat. nov.**, is proposed. Furthermore, *B. commelynoideum* var. *flaviflorum* should be treated as a synonym of *B. parvifolium*.

Key words: Apiaceae, chloroplast genome, chromosome counts, new combination, synonymy

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Introduction

The genus *Bupleurum* (Apiaceae, Apioideae), comprising 180–220 species (Sheh and Watson 2005; https://wfoplantlist.org/plant-list/), is widely distributed in the North Temperate Zone of Eurasia and is utilized in traditional herbal medicines in China, East Asia, and North Africa (Teng et al. 2023). Phylogenetic studies supported the *Bupleurum* as a basal clade within the subfamily Apioideae and categorized this morphologically unusual genus as the monotypic tribe Bupleureae Spreng. (Downie et al. 2000). 42 species and 16 varieties are recorded in the

“Flora of China”, widely distributed in the NE, NW, and SW of China, and approximately 22 taxa (included varieties) are endemic (Sheh and Watson 2005). Due to the high morphological variability of *Bupleurum* and the quantitative traits used for interspecific identification, species identification is challenging and the taxonomic status of some taxa is uncertain. It is necessary to conduct comprehensive studies by integrating multiple lines of evidence (e.g., cytology, phylogenetic, and biogeography) to clarify the taxonomic status of taxa in doubt.

Bupleurum smithii Wolff was classified into three varieties: *B. smithii* var. *smithii*, *B. smithii* var. *parvifolium* Shan & Y.Li, and *B. smithii* var. *auriculatum* Shan & Y.Li, based on leaf morphology (Shan and Li 1974). After reviewing the specimens and field surveys, it was found that the *B. smithii* var. *parvifolium* was dwarfed, the leaves became narrower and smaller from *B. smithii* var. *smithii*. *Bupleurum smithii* var. *smithii* is a widely distributed species in Northeast China, thriving above 1800 m. The species was initially described based on collections from Xiaowutai Mountain, situated within the Taihang Mountains. On the other hand, *B. smithii* var. *parvifolium* is prevalent in the grasslands of the Qinghai–Tibetan Plateau, with type specimens collected from Wushaoling, belonging to the Qilian Mountains (Shan and Li 1974). The distribution areas of these varieties are significantly separated, showing clear discontinuity. However, existing studies on phylogenetic analyses suggested that *B. smithii* var. *smithii* was more closely related to *B. smithii* var. *parvifolium* and more distantly related to *B. smithii* var. *auriculatum* (Wang et al. 2011). Phylogenetic analyses and morphological observations conflicted. Morphologically and geographically, *B. smithii* is more similar to *B. smithii* var. *auriculatum*, instead of *B. smithii* var. *parvifolium*. This precisely suggests that the taxonomic status of *B. smithii* var. *parvifolium* needs to be researched further.

Shan and Li (1974) formally described *B. commelynoideum* var. *flaviflorum* Shan & Y.Li based on type specimens collected from Min County, Gansu province. It can be differentiated from *B. commelynoideum* by its flower color and the shape of bracteoles: *B. commelynoideum* var. *flaviflorum* displays yellow flowers and narrowly ovate bracteoles, while *B. commelynoideum* var. *commelynoideum* exhibits purple flowers and broadly ovate bracteoles. Shan and Li (1974) also noted *B. commelynoideum* var. *flaviflorum* affinity to *B. smithii*, particularly *B. smithii* var. *parvifolium*, which features a short, slightly creeping stem, basal leaves that are not long-acuminate, and bracteoles that are occasionally reduced to five. These traits are often underdetermined and closely related to the environment. Regarding distribution patterns, *B. commelynoideum* var. *flaviflorum* was predominantly found in Southwest China (Gansu, Qinghai, and Sichuan), while *B. smithii* var. *parvifolium* was distributed in Northwest China (Gansu, Qinghai, Ningxia, Xizang, and Sichuan), with overlapping occurrences in Northwest Sichuan and South Gansu. A molecular study based on ITS, *trnH-psbA*, and *matK* by Wang et al. (2011) demonstrated *B. commelynoideum* var. *flaviflorum* nested within *B. smithii* var. *parvifolium* and *B. smithii* var. *smithii*. Consequently, they proposed reclassifying *B. commelynoideum* var. *flaviflorum* as a variety of *B. smithii*, naming it *B. smithii* var. *flaviflorum* (Shan & Y.Li) X.J.He & C.B.Wang. More recently, Ma (2015a) suggested that there is no interrupted morphological difference between *B. commelynoideum* var. *flaviflorum* and *B. smithii* var. *parvifolium*, implying that they might be the same species.

Upon a thorough examination of the type specimens, it was discovered that the isotype specimen of *B. commelynoideum* var. *flaviflorum* was identified as

B. commelynoideum var. *flaviflorum* (WUK0423353) and *B. smithii* var. *parvifolium* (WUK0033909). Such instances are common during specimen reviews, highlighting the need for meticulous morphological and phylogenetic analyses to elucidate the taxonomic placement and phylogenetic position of these taxa.

Materials and methods

Morphological studies

Our study involved the examination of collections and digital images of *B. smithii* var. *smithii*, *B. smithii* var. *parvifolium*, *B. smithii* var. *auriculatum*, *B. commelynoideum* var. *flaviflorum*, *B. commelynoideum* var. *commelynoideum* from the Chinese Virtual Herbarium (http://www.cvh.ac.cn/) and the Global Biodiversity Information Facility (https://www.gbif.org/). The images were sourced from specimens deposited at BJFC, BM, BNU, CDBI, HNWP, HSIB, KUN, NAS, P, PE, PEY, SZ, and WUK. The specimens with well-preserved leaves and flowers were selected, covering all districts of the distribution area. A total of 43 specimens of *B. smithii* var. *smithii*, 50 of *B. smithii* var. *parvifolium*, 29 of *B. commelynoideum* var. *commelynoideum*, and 39 of *B. commelynoideum* var. *flaviflorum* were examined, including 55 sheets of specimens collected by our team (Suppl. material 1). Given the substantial variation in leaf shape with the growth period, and the significant differences between basal, middle, and upper leaves, we selected 3 basal leaves, 2 middle leaves, and 2 upper leaves for each specimen. A total of 37 morphological characters were measured (Suppl. material 1), and after Principal Component Analysis (PCA), 16 traits were chosen for subsequent analyses, including the length, width, and ratio of length/width of basal leaves, as well as the number, length, and width of bracteoles (Suppl. material 2).

The examination of characters was conducted using ImageJ (Rasband 1997). PCA and Cluster analysis were performed in R, utilizing the factoextra package. Factoextra relies on ggplot2 (Wickham 2009), FactoMineR (Le et al. 2008), and cluster (Maechler et al. 2016) for visualization and analysis.

Cytology

The materials used in the cytological studies were sourced from Xiaowutai Mountain (for *B. smithii* var. *smithii*), Qilian Mountain (for *B. smithii* var. *parvifolium*), Luya Mountain (for *B. smithii* var. *auriculatum*) and Min Mountain (for *B. commelynoideum* var. *flaviflorum*). The voucher specimens are detailed in Table 1, asterisks. Chromosome counts were carried out through acid digestion and wall removal hypotonic procedures, adapted from Li et al. (2021). Each sample underwent three repetitions in the experimental protocol.

Plant material, DNA extraction, sequencing, assembly and annotation

In this study, the whole chloroplast (cp) genome of *Bupleurum* was sequenced to investigate its phylogeny and evolution. Fresh leaves from nine *Bupleurum* specimens were field-collected and rapidly desiccated using Silica Gel. Voucher specimens were deposited at Herbarium of Beijing Normal University (BNU), and listed in Table 1. Genomic DNA extraction was extracted using the HP Plant

Table 1. Voucher information and GenBank accession numbers of newly sequenced plastome sequences, asterisks for cytology.

Taxa	Location	Voucher information	Accession
B. baimaense	Deqincountry, Yunnan, China	YNNU-19-302 (KUN)	OR778864
B. commelynoideum var. *commelynoideum*	Kangding, Sichuan, China	BNU2023WLH0174 (BNU)	OR778865
B. smithii var. *smithii* *[1]	Xiaowutai Mountain, Hebei, China	BNU2020DT007 (BNU)	OR387522
B. smithii var. *smithii* [2]	Dongling Mountain, Hebei, China	DL023-3 (BNU)	OR811239
B. smithii var. *auriculatum**	Luya Mountain, Shanxi, China	BNU2021SX017 (BNU)	OR811240
B. commelynoideum var. *flaviflorum**	Min Mountain, Gansu, China	BNU2023WLH190 (BNU)	OR778866
B. smithii var. *parvifolium* [1]	Hualong County, Qinghai, China	BNU2022WLH061 (BNU)	OR778870
B. smithii var. *parvifolium* [2]	Haiyan County, Qinghai, China	ZZU2021QH004 (BNU)	OR778869
B. smithii var. *parvifolium** [3]	Tianjun county, Qinghai, China	BNU2022WLH030 (BNU)	OR778871

DNA Kit D2485-02 kit (Omega Bio-Tek), with Beijing Novogene Corporation conducting assessments of DNA quantity and quality. The Illumina HiSeq X Ten sequencing platform was employed, generating approximately 10 GB for each sample. The chloroplast genome was assembled by GetOrganelle (Jin et al. 2020). PGA was used to annotate (Qu et al. 2019), with the cp genome of *B. yinchowense* (MT075711) and *B. sikangense* (NC056803) as references. The cp genome has been submitted to the NCBI GenBank database (www.ncbi.nlm.nih.gov). Additionally, 18 genome sequences were downloaded from NCBI (Appendix 1), and 2 *Pleurospermum* were selected as outgroups.

Phylogenetic analyses

Phylogenetic analyses were conducted using the maximum likelihood (ML) and Bayesian inference (BI) methods with IQ-TREE (Minh et al. 2020) and MrBayes (Ronquist et al. 2012), respectively. A total of 27 sequences were aligned using the online version of MAFFT (https://mafft.cbrc.jp/alignment/server/index.html) (Katoh et al. 2019). The ModelFinder module (Kalyaanamoorthy et al. 2017) in PhyloSuite (Zhang et al. 2020) determined the best-fit model of nucleotide substitutions. The nucleotide substitution model for the ML tree was TVM+R2+F, and standard bootstrap (BS) replicates of 1000 were performed, with results deemed reliable at BS ≥70%. For the BI tree, the best model was GTR+F+I+G4, and the analysis parameters were set as follows: mcmcp ngen = 2000000, printfreq = 10000, nchains = 4, and burninfrac = 25%. Reliable results were considered when the Posterior probability (PP) was ≥0.95. The effective sample size (ESS) (>200) was confirmed using Tracer v1.7 (Rambaut et al. 2018).

Results and discussion

Morphological studies

The Principal Component Analysis (PCA) revealed that traits such as width of middle leaves, width of bracteoles, length of bracteoles, and the number of rays were effective for interspecific classification (Fig. 1). Firstly, the number of rays (Fig. 1D) and petal color (Fig. 2) emerged as distinguishing features for *B. commelynoideum* var. *commelynoideum* compared to other taxa. *Bupleurum commelynoideum* var. *commelynoideum* typically exhibited 3–4 rays and purplish-red petals, while the other three taxa had more than 5 rays and yellow petals. Secondly, the width of middle leaves (Fig. 1A), length and width of bracteoles (Fig. 1B and 1C) were effective in differentiating *B. smithii* var. *smithii* from *B. smithii* var. *parvifolium* and *B. commelynoideum* var. *flaviflorum*. Additionally, the fruits of *B. smithii* var. *smithii* and *B. smithii* var. *auriculatum* were longer, 3–3.5 mm, while those of *B. smithii* var. *parvifolium* and *B. commelynoideum* var. *flaviflorum* measured 2–2.5 mm (Fig. 3). Notably, all traits in Fig. 1 showed no discontinuity between *B. smithii* var. *parvifolium* and *B. commelynoideum* var. *flaviflorum*, and none could effectively differentiate between the two taxa. The Cluster plot illustrated that *B. smithii* var. *smithii* and *B. commelynoideum* var. *commelynoideum* formed distinct groups, while *B. smithii* var. *parvifolium* and *B. commelynoideum* var. *flaviflorum* clustered together comprehensively. Only individual specimens from these varieties exhibited clustering within other groups (Fig. 4). Morphology is compared and described in Table 2.

PCA and box plots showed intermittent distinctions in leaf shape, bracteoles, and fruit size between *B. smithii* var. *smithii* and *B. smithii* var. *parvifolium*, providing reliable evidence for interspecific differentiation. Cluster diagram results corroborated the cohesion of *B. smithii* var. *parvifolium* and *B. commelynoideum* var. *flaviflorum* into a single group, providing robust support for considering

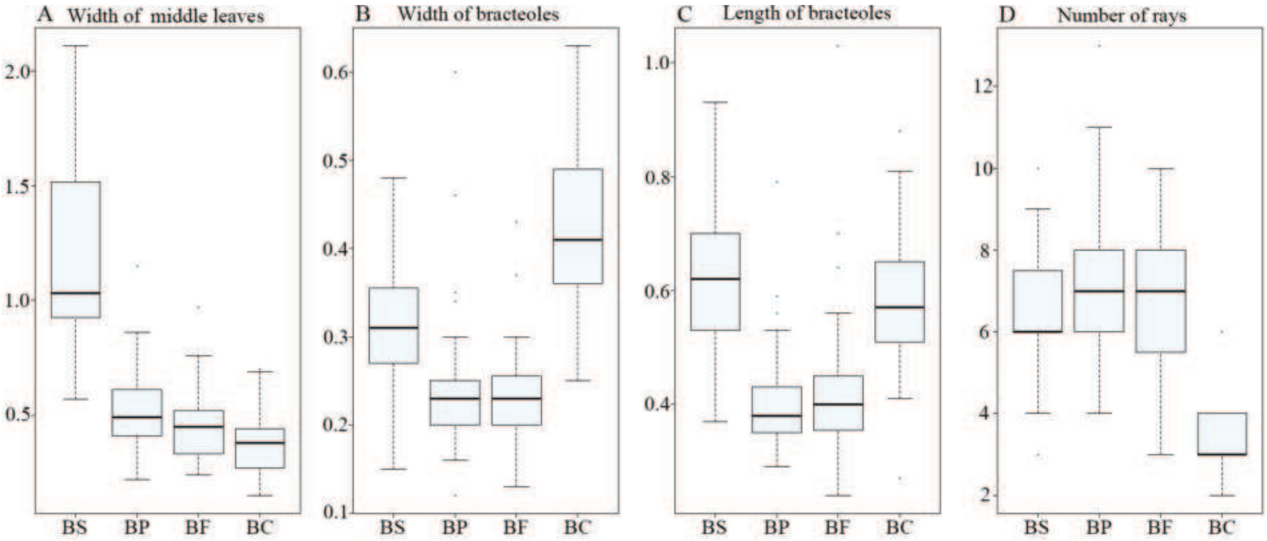

Figure 1. Comparison of the characters **A** width of middle leaves **B** width of bracteoles **C** length of bracteoles **D** number of rays. **BS** = *Bupleurum smithii* var. *smithii* **BP** = *B. smithii* var. *parvifolium* **BF** = *B. commelynoideum* var. *flaviflorum* **BC** = *B. commelynoideum* var. *commelynoideum*.

Figure 2. Umbel and bract **A** *Bupleurum smithii* var. *smithii* **B** *B. smithii* var. *parvifolium* **C** *B. commelynoideum* var. *flaviflorum* **D** *B. commelynoideum* var. *commelynoideum*.

Figure 3. Fruit morphology **A** *Bupleurum smithii* var. *smithii* **B** *B. smithii* var. *auriculatum* **C** *B. smithii* var. *parvifolium* **D** *B. commelynoideum* var. *flaviflorum*

Figure 4. Cluster plot for the morphological variations among four taxa. **C** = *Bupleurum commelynoideum* var. *commelynoideum* **F** = *B. commelynoideum* var. *flaviflorum* **P** = *B. smithii* var. *parvifolium* **S** = *B. smithii* var. *smithii*.

Table 2. Comparison of morphological characteristics and geographic distribution.

Morphology	*B. smithii* var. *smithii*	*B. smithii* var. *parvifolium*	*B. commelynoideum* var. *flaviflorum*	*B. commelynoideum* var. *commelynoideum*
Basal leaves	7–15 × 0.8–1.5 cm	6–8 × 0.3–0.7 cm	6–8 × 0.3–0.5 cm	8–15 × 0.25–0.4 cm
Middle stem leaves	7–13 × 0.8–1.5 cm	4–7 × 0.4–0.7 cm	6–9 × 0.3–0.5 cm	8–11 × 0.25–0.4 cm
Umbels	Numerous	Numerous	Numerous	Single
Rays	4–9	4–9	4–9	3–4 (6)
Bracteole	(6)7–9, 5–7 × 3–4.5 mm	(5) 6–7, 3–4.5 × 2–2.5 mm	(5) 6–7, 3–5 × 2–2.5 mm	7–9, 5–6.5 × 3–5 mm
Petal color	Yellow or abaxially purplewish-tinged	Yellow or abaxially purplewish-tinged	Yellow or abaxially purplewish-tinged	Purple or yellowish-tinged
Fruit	Rectangular, 3.0–3.6 × 1.2–1.4	Ovoid, 1.9–2.5 × 1.1–1.3	Ovoid, 2.0–2.4 × 1.1–1.3	Tapered, 2–2.5 × 1.5
Vittae in each furrow	4	6	6	4
Vittae on commissure	3	3	3	3
Distribution	Shanxi, Hebei, Beijing and N Henan	E Qinghai, Gansu, Ningxia, E Xizang, and NW Sichuan	S Gansu, S Qinghai, and W Sichuan.	W Sichuan, Xizang and NW Yunnan

them as the same taxon. Box plots visually depicted continuous and overlapping variations between these two taxa. Ma (2015a) concluded that *B. smithii* var. *parvifolium* and *B. commelynoideum* var. *flaviflorum* do not have intermittent morphological differences, and *B. commelynoideum* var. *flaviflorum* may be a synonym of *B. smithii* var. *parvifolium*, which is formally proposed herein. Morphological observations support that *B. smithii* var. *parvifolium* is a separate species and *B. commelynoideum* var. *flaviflorum* is the same entity as *B. smithii* var. *parvifolium*, and the former should be treated as a synonym of the latter.

Cytology

Cytological analysis reveals that the chromosome number of *B. smithii* var. *parvifolium* is 2n = 14 (x = 7) (Fig. 5B), consistent with *B. commelynoideum* var. *flaviflorum* (Fig. 5C). In contrast, *B. smithii* exhibited a chromosome number of 2n = 64, and that of *B. smithii* var. *auriculatum* is 2n = 32 (Fig. 5A). These findings align with previous reports, as documented by Liang et al. (2013).

Chromosome base diversity is high within the genus *Bupleurum*, including several cases with x = 4, 5, 6, 7, 8, 11, and 13 (Neves and Watson 2004; Wang et al. 2011; Liang et al. 2013). Different ploidy often occurs within a species, but the chromosome base is mostly the same. It has been found that *B. commelynoideum* exhibited complex variations in both chromosome ploidy (2x, 4x, 6x) and basic number (x = 5, x = 6) (Liang et al. 2013; Wang et al. 2011). Then, Ma et al (2015b) combined cytological and phylogenetic evidence to confirm the existence of at least three cryptic species within *B. commelynoideum*. The importance of accurate chromosome number documentation cannot be overstated, particularly given instances of misidentification. Notably, *B. smithii* was initially reported with a chromosome of 2n = 12 (Alexeeva et al. 2000). However, the voucher specimen was collected from Songpan, Sichuan Province. However, this region is not the distribution area of *B. smithii*. It is hypothesized that it may be a misidentification of other taxa, but there are no voucher specimens. To address this, we revisited the type locality, collecting specimens that

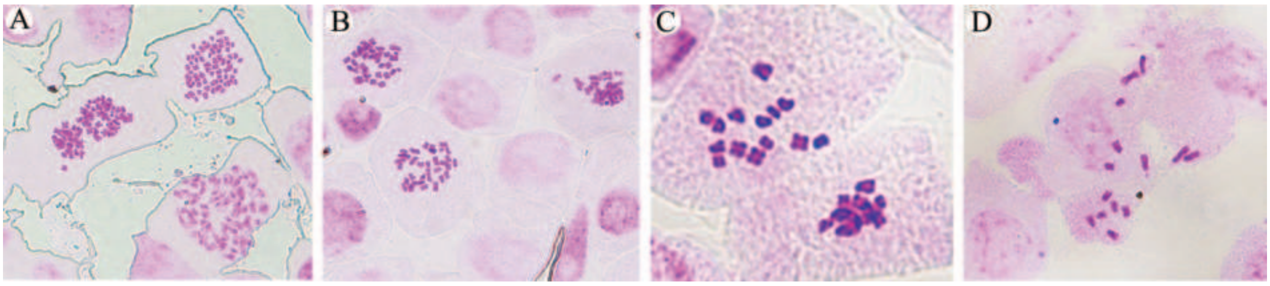

Figure 5. Metaphase chromosomes **A** *Bupleurum smithii* var. *smithii* **B** *B. smithii* var. *auriculatum* **C** *B. smithii* var. *parvifolium* **D** *B. commelynoideum* var. *flaviflorum*.

underwent meticulous comparison with the type specimen, and confirming a chromosome count of 64 for *B. smithii* var. *smithii*. This represents the highest reported chromosome number in the genus, presumed to be an octoploid with a chromosome base of 8, akin to *B. sibiricum* (Chin et al. 1989; Jiang et al. 1994). The chromosome number of *B. smithii* var. *auriculatum* is 32, presumably tetraploid. Chromosome ploidy was not the same in *B. smithii* var. *smithii* and *B. smithii* var. *auriculatum*, but the base number was the same. Therefore, *B. smithii* var. *auriculatum* will still be suitable as a variant of *B. smithii* from chromosome analysis.

In recent years, researchers have gradually emphasized the role of chromosomes in species delimitation. For example, *B. komarovianum* was once treated as a variety of *B. chinense* (Liaoning Forestry Soil Research Institute 1977). Wang et al. (2011) suggested it should still be a separate species based on chromosomal evidence and morphology, *B. komarovianum* was $2n = 2x = 8$ (*B. chinense* was $2n = 2x = 12$) and the stem of *B. komarovianum* was hollow (*B. chinense* was with pith). The chromosome information for both *B. smithii* var. *parvifolium* and *B. commelynoideum* var. *flaviflorum* are diploid with a total of 14 chromosomes. The number and base of chromosomes support that the two taxa are the same entity, and they are different from *B. commelynoideum* var. *commelynoideum* and *B. smithii* var. *smithii*.

Phylogenetic analyses

The phylogenetic analysis based on chloroplast genome sequences reveals a consistent topology between the maximum likelihood (ML) tree and the Bayesian inference (BI) tree. The genus *Bupleurum* was divided into two clades with high support (BS = 100%, PP = 1), with all Chinese *Bupleurum* species belonging to Subg. *Bupleurum*. *Bupleurum commelynoideum* var. *flaviflorum* was nested within *B. smithii* var. *parvifolium* (BS = 100%, PP = 1), forming an individual clade. This clade was further related to *B. sikangense* X.J.He & C.B.Wang (Fig. 6), and all these taxa were distantly related to *B. smithii* var. *smithii* and *B. commelynoideum* var. *commelynoideum*. *Bupleurum smithii* was closely related to *B. sibiricum* Vest ex Spreng, while *B. commelynoideum* was closely related to *B. baimaense* X.G. Ma & X.J. He (BS = 100%, PP = 1).

In this study, the reconstruction of the phylogenetic tree utilizing the chloroplast genome yielded results consistent with the topological structure presented by Wang et al. (2011). When compared to the phylogenetic tree, which employed nuclear ribosomal internal transcribed spacer, *trnH-psbA*, and *matK*, the reconstructed tree based on the chloroplast genome exhibited greater support and resulted in changes in the phylogenetic positions of several species. In his study, *B. smithii* var. *parvifolium* and *B. commelynoideum* var. *flaviflorum* were nested together, forming a sister group to *B. smithii* var. *smithii* and *B. pusillum*. However, it is noted that the material of *B. smithii* var. *smithii* was collected in Minhe, Qinghai, the primary distribution zone of *B. smithii* var. *parvifolium*, not within the range of *B. smithii* var. *smithii*. This discrepancy raises speculation that Wang might have misidentified *B. smithii* var. *parvifolium* as *B. smithii* var. *smithii*. Conversely, in his paper *B. smithii* var. *auriculatum* was collected from Wutai Mountain, which closely aligns with the type location of *B. smithii* var. *smithii*. Both studies, using different markers, indicate a close relationship between *B. commelynoideum* var. *flaviflorum* and *B. smithii* var. *parvifolium*. However, the systematic position of *B. smithii* var. *auriculatum* is uncertain, and the affinity between *B. smithii* var. *auriculatum* and *B. smithii* var. *smithii* has to be determined by more molecular markers in the follow-up.

Distribution

In terms of distribution patterns, *B. smithii* var. *parvifolium* is a widespread taxon mainly in northwest China, including Gansu, Ningxia, Qinghai, eastern Xizang, and western Sichuan. On the other hand, *B. commelynoideum* var. *flaviflorum* is distributed in SW China, including S Gansu, S Qinghai, and W Sichuan. The distribution of these two taxa overlaps in northwest Sichuan and southern Gansu, precisely where the type specimens of *B. commelynoideum* var. *flaviflorum* were collected. In contrast, *B. smithii* var. *smithii* primarily occur in the

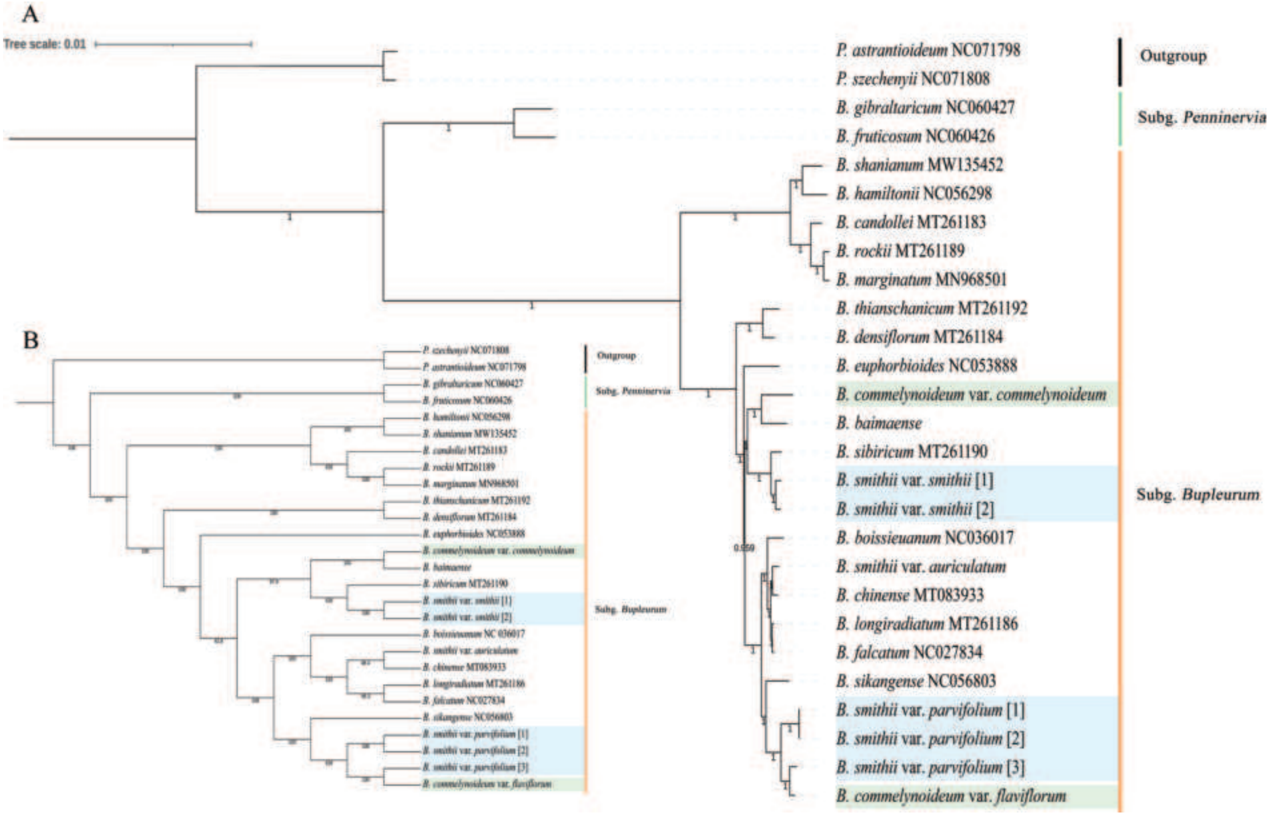

Figure 6. The phylogenetic tree was inferred from chloroplast genomes **A** BI analyses **B** ML analyses

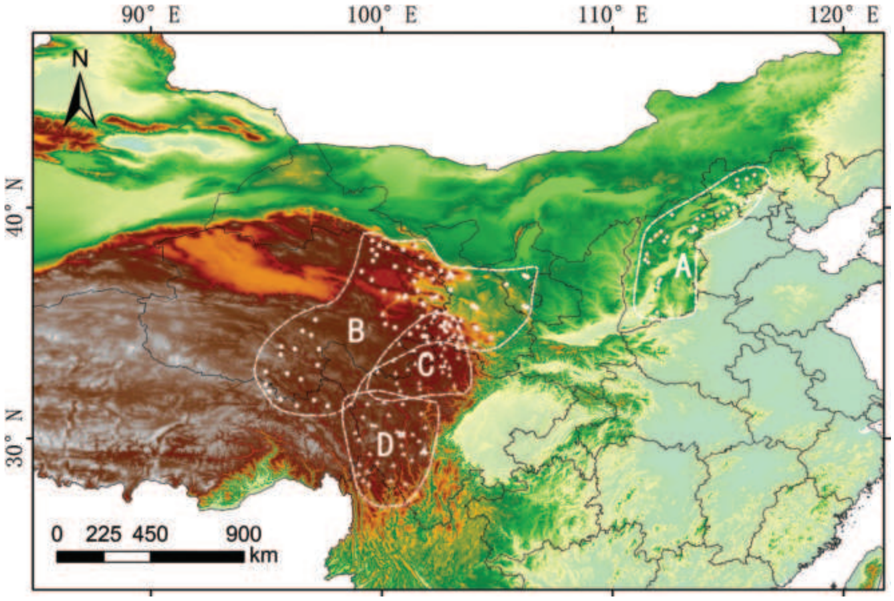

Figure 7. Distribution area based on specimen records and our field investigation **A** *Bupleurum smithii* var. *smithii* **B** *B. smithii* var. *parvifolium* **C** *B. commelynoideum* var. *flaviflorum* **D** *B. commelynoideum* var. *commelynoideum*

Taihang Mountains and Yanshan Mountains in E China. *Bupleurum commelynoideum* is a species that occurs throughout the Hengduan Mountains region. The distribution areas of *B. smithii* var. *parvifolium* and *B. smithii* var. *smithii* are separated by the Qinling Mountains and the Loess Plateau (Fig. 7).

Taxonomic treatment

Bupleurum parvifolium **(Shan & Y.Li) Q.R.Liu & L.H.Wang, comb. et stat. nov.**
urn:lsid:ipni.org:names:77338773-1

≡ *B. smithii* var. *parvifolium* Shan & Y.Li, Acta Phytotax. Sin. 12(3): 273. 1974. Type. CHINA. Gansu: Tianzhuxian, Wushao Mountain ca. 2800 m, 22. 07. 1959, *Y.Q. He 4267* (Holotype: WUK0389736!). Basionym.

= *B. commelynoideum* var. *flaviflorum* Shan & Y.Li, Acta Phytotax. Sin. 12(3): 276. 1974. syn. nov. ≡ *B. smithii* var. *flaviflorum* (Shan & Y.Li) X.J.He & C.B.Wang J. Syst. Evol. 49 (6): 586. 2011.Type. CHINA. Gansu: Min County, Min Mountain, ca. 3500 m, 10. 08. 1937, *T.P. Wang 7535* (Holotype: PE00935517! Isotypes: WUK0033909! WUK0423353!).

Diagnosis. *Bupleurum parvifolium* is morphologically similar to *B. smithii*, can be distinguished from the latter by its cauline leaves sessile, 4–9 × 0.3–0.7 cm; bracteoles 6–9, ovate or broad-ovate, 3–5 × 2–2.5 mm; fruit ovoid, brown, 2.0–2.5 × 1.1–1.3 mm; vittae 3 in each furrow, 6 on commissure.

Description. Plant 15–40 cm, perennial. Rhizome brown, usually branched. Stems many, tufted, base without fibrous remnant sheaths. Basal leaves narrowly lanceolate, 6–8 × 0.3–0.7 cm, thickly papery, base tapered into petiole, not embracing. Cauline leaves sessile, 4–9 × 0.3–0.7 cm. Apical leaf long-ovate, 1.5–7.5 × 1–1.7 cm, base rounded, sometimes auriculate, clasping, apex acuminate. Bracts 0 or 1–2, broadly ovate, 7–18 × 4–11 mm, unequal; rays 4–9, 0.5–4 cm, unequal, angled; bracteoles 6–9, ovate or broad-ovate, 3–5 × 2–2.5 mm, equal, acute, apiculate, slightly exceeding flowers; umbellules 0.8–1.1 cm across. Petals yellow, occasionally abaxially purplish-red. Stylopodium low-conic, discoid, dark yellow or purple-brown. Fruit ovoid, brown, 2.0–2.5 × 1.1–1.3 mm; ribs acute, prominent; vittae 3 in each furrow, 6 on commissure (Fig. 8). 2n = 14.

Phenology. Flowering from July to August and fruiting from August to September.

Distribution and habit. Qinghai, Gansu, Ningxia, Sichuan, Xizang. It grows on mountains at elevations of 2700–700 m.

Additional specimens examined. China. **Gansu:** Min County, 02 July 1936, *T.P. Wang 4852* (KUN), 19 August 1937, *T.P. Wang 7535* (WUK), 19 August 1937, *T.P. Wang 7535* (PE), 01 July 1936, *T.P. Wang 4742* (PE), 02 July 1936, *T.P. Wang 4852* (PE), 30 June 1936, *T.P. Wang 4699* (PE); Tianzhu County, *Y.Q. He 4267* (WUK), 12 July 1959, *Y.Q. He 4628* (WUK); Yuzhong County, 09 August 1959, *Y.Q. He 5981* (WUK), 04 August 2000, *X.G. Sun et al. 2126* (PE), 2 September 2023, *L.H. Wang & J.L. Li BNU2023-WLH242* (BNU); Xiahe County, 10 July 1937, *T.P. Wang 7171*(WUK), 29 July 1937, *K.T. Fu 1438* (PE); Minle County, 29 August 1934, *C.W. Yao 336* (NAS); Hezuo County, 09 September 2011, *X. Yin et al. LiuJQ-GN-2011-278* (KUN); Maqu County, 04 August 2011, *X. Yin et al. LiuJQ-GN-2011-280* (KUN); Shandan County, 10 July 1959, *Y.Q. He 4052* (WUK); **Qinghai:** Tianjun County, 05 August 2022, *L.H. Wang et al. BNU2022-WLH030* (BNU); Gangcha County, 30 July 2022, *L.H. Wang et al. BNU2022-WLH017* (BNU); Huzhu County, 05 August 2022, *Q.Y. Zhang ZQY2022003* (BNU); Xunhua County, 06 August 2022, *L.H. Wang et al. BNU2022-WLH039* (BNU), 06 August 2022, *L.H. Wang et al. BNU2022-WLH051* (BNU); Hulong County, 07 August 2022, *LH Wang et al. BNU2022-WLH061* (BNU); Xining City, 11 September 2022, *S.B. Zhang BNU2022-0911* (BNU); Haeyan County, 04 July 1958, *B.Q. Zhong 8410* (KUN); Angqian County, 11 August 1972, *Zangyao team 1283* (KUN); Qilian County, 27 July 1958, *Gan & Qing*, *BQ Zhong 8573*(WUK), 12 August 2013, *X.C. Chen et al. 4487* (HNWP); Xinghai County, 09 August 1919, *T.N. He 416* (WUK); Datong County, 17 August 1962, *Fan & Liang 00495* (HNWP), *B.W. Li 72-070* (HNWP); Ghindu County, 10 August 1983 *X.J. Xun 83-144* (HNWP), 15 August 1996, *T.N. Ho* et al. 1887 (PE), 15 August 1996, *T.N. Ho et al. 1887* (HNWP); Zeku County, 21 August 1967, *L.H. Zhou 1628* (HNWP); Tungrin County, 24 July 1970, *S.W. Liu et al. 1412* (HNWP), 07 August 2010, *S.L. Chen et al. ChenSL0915* (KUN); Menyuan County, 10 July 1970, *L.H. Zhou 1036* (HNWP); Zhidoi County, 10 September 1966, *L.H. Zhou 454* (HNWP); Yushu County, 30 August 1996, *T.N. Ho et al. 2698* (PE), 12 August 1964, *Qinghai Plant Team 620* (WUK); Nangqen County, 05 September 199, *T.N. Ho et al. 2913* (PE); Huangzhong County, 25 July 2014, *Y.H. Wu 050810* (HNWP), 25 July 2014, Y.H. Wu 050644 (HNWP); **Ningxia:** Jingyuan County, 14 August 1942, *T.P. Wang 13561* (KUN); Tongxin County, 12 August 1981, *Y.P. Xu et al. 1701* (WUK); Longde County, 10 July 1942, *T.P. Wang 13052* (WUK); Guyuan County, 07 August 1953, *T.P. Wang 17175* (WUK); **Sichuan:** Ruoergai, County, *X.J. He et al. SCU-20080522* (KUN), 15 July 1993, *Z.M. Tan 93-88* (PE), 06 August 1961, *S. Jiang 6833* (PE); Hongyuan County, 18 September 2012, *Y.D. Gao et al. GaoXF-12-029* (KUN); Pingwu County, *H.L. Tsising 10904* (NAS); Daofu County, 06 September 1960, *Sichuan Team 16217* (NAS); Songpan County, 3 October 1983, *F.D. Pu et al. 021* (CDBI), 02 August 1984, *J. He et al. 140* (CDBI); Daoge County, 01 August 1980, *Vegetation group 28404* (CDBI); Baxoi County, 27 August 1973, *Qinghai-Tibet Team 73-1267* (PE), 14 September 2008, *T. Zhang et al. 08CS701* (KUN), 15 August 2014, *X.C.*

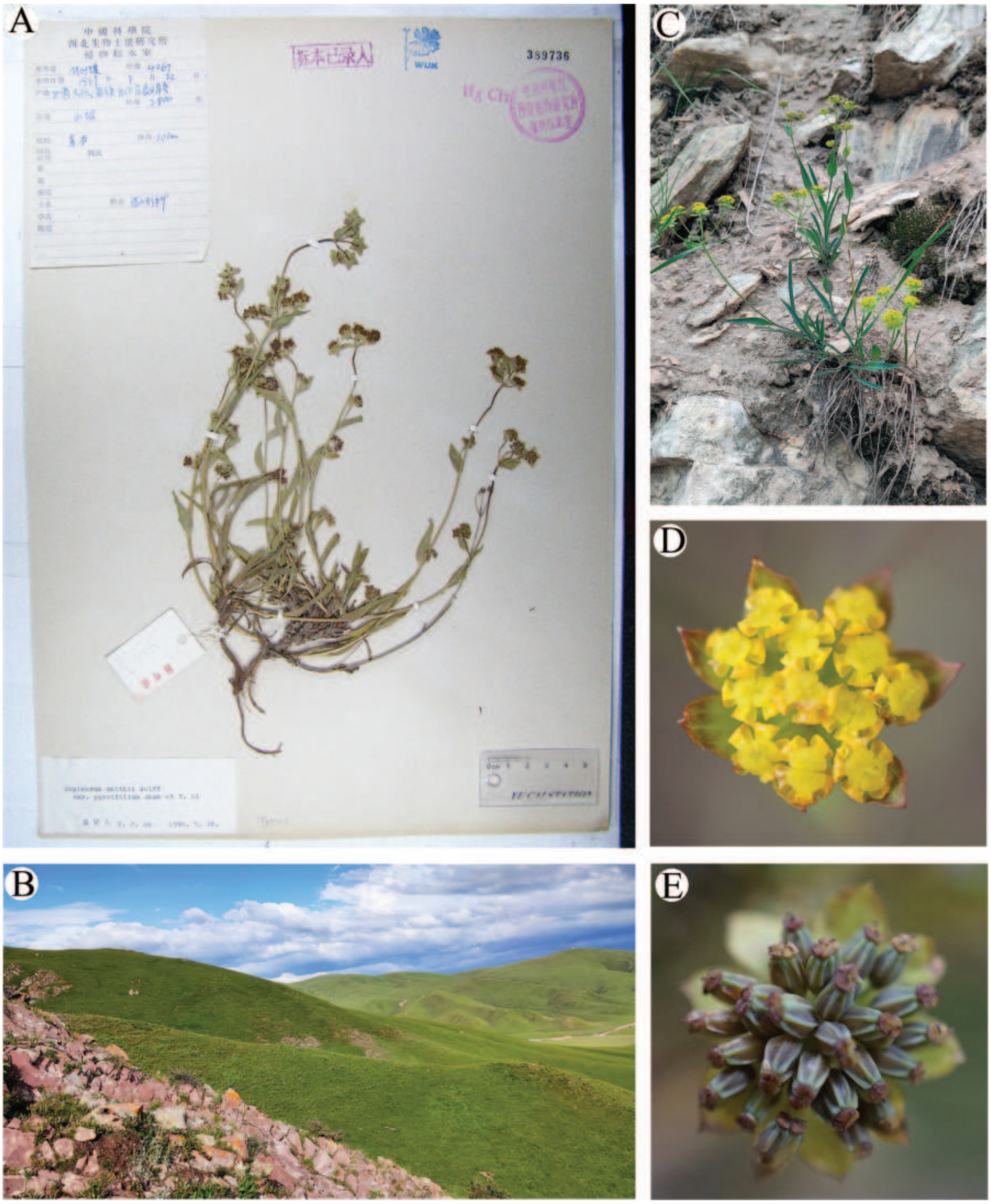

Figure 8. *Bupleurum parvifolium* **A** holotype **B** habitat **C** plant **D** flowers **E** fruits.

Chen et al. 032-2 (HNWP), 15 August 2014, *X.C. Chen et al. 032* (HNWP); Wuqi County, 27 August 1976, *Tibet Expedition Team 12951* (PE).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: LHW. Data curation: SL. Funding acquisition: QRL. Investigation: SL, DNZ, LHW. Methodology: LHW. Supervision: QRL. Writing - original draft: LHW. Writing - review and editing: LHW, QRL.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Appendix 1

Table A1. GenBank accession numbers of DNA sequences downloaded from NCBI.

Taxa	Accession number	Taxa	Accession number
B. boissieuanum	NC036017	*B. longiradiatum*	MT261186
B. candollei	MT261183	*B. marginatum*	MN968501
B. chinense	MT083933	*B. rockii*	MT261189
B. densiflorum	MT261184	*B. shanianum*	MW135452
B. euphorbioides	NC053888	*B. sibiricum*	MT261190
B. falcatum	NC027834	*B. sikangense*	NC056803
B. fruticosum	NC060426	*B. thianschanicum*	MT261192
B. gibraltaricum	NC060427	*P. astrantioideum*	NC071798
B. hamiltonii	NC056298	*P. szechenyii*	NC071808

Supplementary material 1

Specimens for measurements and initial measurements of traits data

Author: Li-Hua Wang

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.239.116877.suppl1

Supplementary material 2

Traits selected for subsequent principal component and cluster analysis after the first PGA

Author: Li-Hua Wang

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.239.116877.suppl2

PhytoKeys 239: 255–266 (2024)
DOI: 10.3897/phytokeys.239.114018

Research Article

Two new diatom species of the genus *Gomphonemopsis* (Bacillariophyceae) from the coast of China and two new combinations for the genus

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Abstract

Two new diatom species belonging to the genus *Gomphonemopsis* are described, *Gomphonemopsis nana* **sp. nov.** and *Gomphonemopsis gaoi* **sp. nov.** These two species were compared in detail with congeners. *Gomphonemopsis nana* is distinguished by its high stria density and small size. This species was found so far to be epiphytic only on the eelgrass collected from Qingdao Bay (Yellow Sea). *Gomphonemopsis gaoi* is characterized by its isopolar valves, simple proximal raphe endings and acutely rounded apices. This taxon was separated from the exoskeleton of marine copepods sampled from the Futian Mangrove Nature Reserve (South China Sea). In addition, two new combinations, *Gomphonemopsis oahuensis* (Hustedt) Lang Li, Yuhang Li & Changping Chen, **comb. nov.** and *Gomphonemopsis platypus* (Østrup) Lang Li, Yuhang Li & Junxiang Lai, **comb. nov.** are proposed. This study increases the records and knowledge of *Gomphonemopsis* along the coast of China.

Key words: Diatom, *Gomphonemopsis*, new species, South China Sea, Yellow Sea

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Introduction

Marine gomphonemoid diatoms are a complex of heteropolar biraphid taxa that are morphologically significantly different from *Gomphonema* Ehrenberg in freshwater environments. The concept was first proposed by Medlin and Round in 1986. Since then, this particular group has included several diatom genera, such as *Cuneolus* Giffen, *Gomphonemopsis* Medlin, *Gomphoseptatum* Medlin, *Pseudogomphonema* Medlin, *Tripterion* R.W.Holmes, S.Nagasawa & H.Takano, *Epiphalaina* R.W.Holmes, S.Nagasawa & H.Takano, *Tursiocola* R.W.Holmes, S.Nagasawa & H.Takano, *Chelonicola* Majewska, De Stefano & Van de Vijver and *Poulinea* Majewska, De Stefano & Van de Vijver (Medlin and Round 1986; Holmes et al. 1993a, 1993b; Denys 1997; Fernandes and Sar 2009; Majewska et al. 2015; Riaux-Gobin et al. 2017). In addition, *Medlinella* Frankovich, M.P.Ashworth & M.J.Sullivan was also considered to belong to marine gomphonemoid diatoms despite of its valvar isopolarity (Frankovich et al. 2016). It worth noting that the habitats of these genera are very special. Most of them are epizoic diatoms on marine vertebrates or epiphytic diatoms on seaweeds and seagrasses. This implies that the gomphonemoid frustules may be related by their epibiotic preference (Medlin 1991).

The genus *Gomphonemopsis* was established and separated from *Gomphonema* based on its morphological features of uniseriate striae, transapically elongated areolae occluded by hymenes, coaxial proximal raphe endings, straight internal raphe fissures, absence of septate valvocopulae and pseudoseptate valves, and lacking stigmata, terminal raphe fissures and basal pore fields (Medlin and Round 1986). Originally *Gomphonemopsis* contained only three species, i.e., *G. exigua* (Kützing) Medlin, *G. pseudexigua* (Simonsen) Medlin and *G. littoralis* (Hendey) Medlin (Medlin and Round 1986). Subsequently, four taxa were transferred to the genus, including *G. domniciae* (Guslakov) Guslakov, *G. obscura* (Krasske) Lange-Bertalot, *G. exigua* var. *platypus* (Østrup) Snoeijs and *G. novo-zelandicum* (Booth) M.A.Harper (Guslakov et al. 1992; Lange-Bertalot et al. 1996; Snoeijs and Balashova 1998; Harper et al. 2012). Recently, three new *Gomphonemopsis* species had also been described, viz., *G. lindae* Witkowski, Metzeltin & Lange-Bertalot, *G. ligowskii* Al-Handal & E.W.Thomas and *G. sieminskae* Krzywda, Gastineau, C.X.Zhou & Witkowski (Metzeltin and Witkowski 1996; Al-Handal et al. 2018; Krzywda et al. 2019). So far, all members of *Gomphonemopsis* have been found in marine or brackish waters. Most of them are distributed in temperate regions (Al-Handal et al. 2018; Krzywda et al. 2019).

Up to now, there are four species of *Gomphonemopsis* reported in China (Li et al. 2005; Cheng and Gao 2013; Sun 2013; Krzywda et al. 2019). In this paper, we report two new *Gomphonemopsis* species sampled from the coasts of the Yellow Sea and the South China Sea and make two new combinations. Detailed morphological descriptions are presented by using light microscopy (LM) and scanning electron microscopy (SEM). Also, similar taxa are compared and information on their ecology is discussed.

Materials and methods

Samples were collected at the Qingdao Bay (36°3'33.45"N, 120°18'56.26"E), Qingdao City, the Yellow Sea on 11 October 2022 and at the No. 3 fishing pond (22°31'28.11"N, 114°0'41.37"E) in the Futian Mangrove Nature Reserve, the South China Sea on 14 November 2016. Qingdao Bay is situated in the south of Qingdao City, which lies in the north temperate monsoon zone. This is an open gulf with a natural eelgrass (*Zostera marina* Linnaeus) bed. The average water depth of Qingdao Bay is about 3.50 m, and the tides here are semidiurnal with an average tidal range of about 2.78 m (Xu et al. 2022). Futian Mangrove Nature Reserve is located in the northeast of Shenzhen Bay. The mean annual air temperature of this location is 23.0 °C (Li et al. 2015). The tides in Shenzhen Bay are also semidiurnal, with an average range of 1.90 m (Gao et al. 2018). Several fishing ponds are present in the mangrove reserve, and the No. 3 fishing pond is connected to Shenzhen Bay through a sluice.

At the site of Qingdao Bay, samples of *Z. marina* were collected by hand at low tide. The eelgrasses were sealed into a Ziploc bag and brought back to the laboratory for further processing. Simultaneously, the temperature and salinity *in situ* were measured with a thermometer and a refractometer (RHS-10ATC), respectively. In the mangrove reserve, samples of marine copepods were taken with a hand net (166 μm) from the No. 3 fishing pond at high tide. Copepods were collected from the bottom of the net and preserved in 5% seawater formalin immediately. Measurements of water temperature and salinity were performed using a U-5000 multi-parameter meter (Horiba, Japan).

Upon return to the laboratory, both samples of eelgrasses and copepods were gently washed with filtered (0.45 μm) seawater for removal of detritus and free microalgae. Diatom cells were separated from host tissues by treating with ultrasound at 300 W for 25 s (Li et al. 2020a, 2020b). They were then acidized with concentrated HCl (36%–38%) at 100 °C for 20 min, followed by rinsing with distilled water to reach neutral pH. For light microscopy (LM) observation, cleaned materials were dried onto coverslips and permanently mounted in Naphrax or Mountmedia. Slides were examined with a Zeiss Imager Z2 (Carl Zeiss, Germany) equipped with differential interference contrast (DIC) and an Olympus BX51 (Olympus, Japan) fitted with phase contrast optics. For scanning electron microscopy (SEM) observation, diatom suspensions were fixed on aluminum stubs after airdrying. Ultrastructural analysis was carried out with a JSM-6390LV (JEOL, Japan) and a Hitachi S-4800 (Hitachi, Japan).

Terminology follows Medlin and Round (1986), Round et al. (1990), Al-Handal et al. (2018) and Krzywda et al. (2019). Because the LM images are not detailed enough to illustrate the morphology, we assigned a SEM image as the iconotype for each species. The term “iconotype” means an icon of the type, which is the most representative illustration of the protologue (Jahn and Kusber 2009). For comparison, SEM illustrations from the literature are cited in Table 1.

Table 1. Comparison of measurements and habitats among *Gomphonemopsis* species, modified from Krzywda et al. (2019).

Species	Length (μm)	Width (μm)	Striae (10 μm)	Habitat	References (including SEM documentation if available)
G. nana	4.0–7.4	1.1–1.5	26–30	Marine, epiphytic	This paper
G. gaoi	28.5–30.5	4.0–5.0	24–26	Brackish, epizoic	This paper
G. oahuensis	26	3–4	25	Freshwater	Hustedt 1942
G. domniciae	6–8	1.7–2.5	10–18	Marine to brackish, epiphytic and epilithic	Guslakov 1981; Guslakov et al. 1992
G. littoralis	14–22	2–3	16–19	Marine, epiphytic	Medlin and Round 1986: SEM figs 52–54
G. pseudexigua	3.5–15.0	1.5–2.5	18–22	Brackish, epiphytic	Medlin and Round 1986: SEM figs 48–51
G. exigua	9–34	2–6	16–30	Marine and brackish, epiphytic	Medlin and Round 1986: SEM figs 39–45
G. platypus	9.5–24	3–4.5	17.5–21	Marine and brackish, epiphytic	Snoeijs and Balasova 1998: SEM fig. 443
G. lindae	16.0–18.5	2.5–3.0	18–24	Marine, benthic	Metzeltin and Witkowski 1996: SEM pl. 79: fig. 3, pl. 92: figs 3, 4
G. ligowskii	11–17	1.5–2.5	11–14	Marine, epiphytic	Al-Handal et al. 2018: SEM figs 18–22
G. obscura	10–17	2–3	16	Marine to brackish, epiphytic	Lange-Bertalot et al. 1996
G. novozelandicum	12–35	2–3	20–22	Marine, epiphytic	Booth 1984: SEM fig. 4
G. sieminskae	9–18	2.0–2.5	18–22	Brackish, epiphytic	Krzywda et al. 2019: SEM fig. 2C’–G’

Results

Gomphonemopsis nana **Lang Li, Yuhang Li & Junxiang Lai, sp. nov.**
Fig. 1A–P

Type materials. ***Holotype*****.** Slide MBMCAS286906 deposited in the Marine Biological Museum, Chinese Academy of Sciences (MBMCAS), Qingdao, China.

Iconotype**.** Fig. 1K.

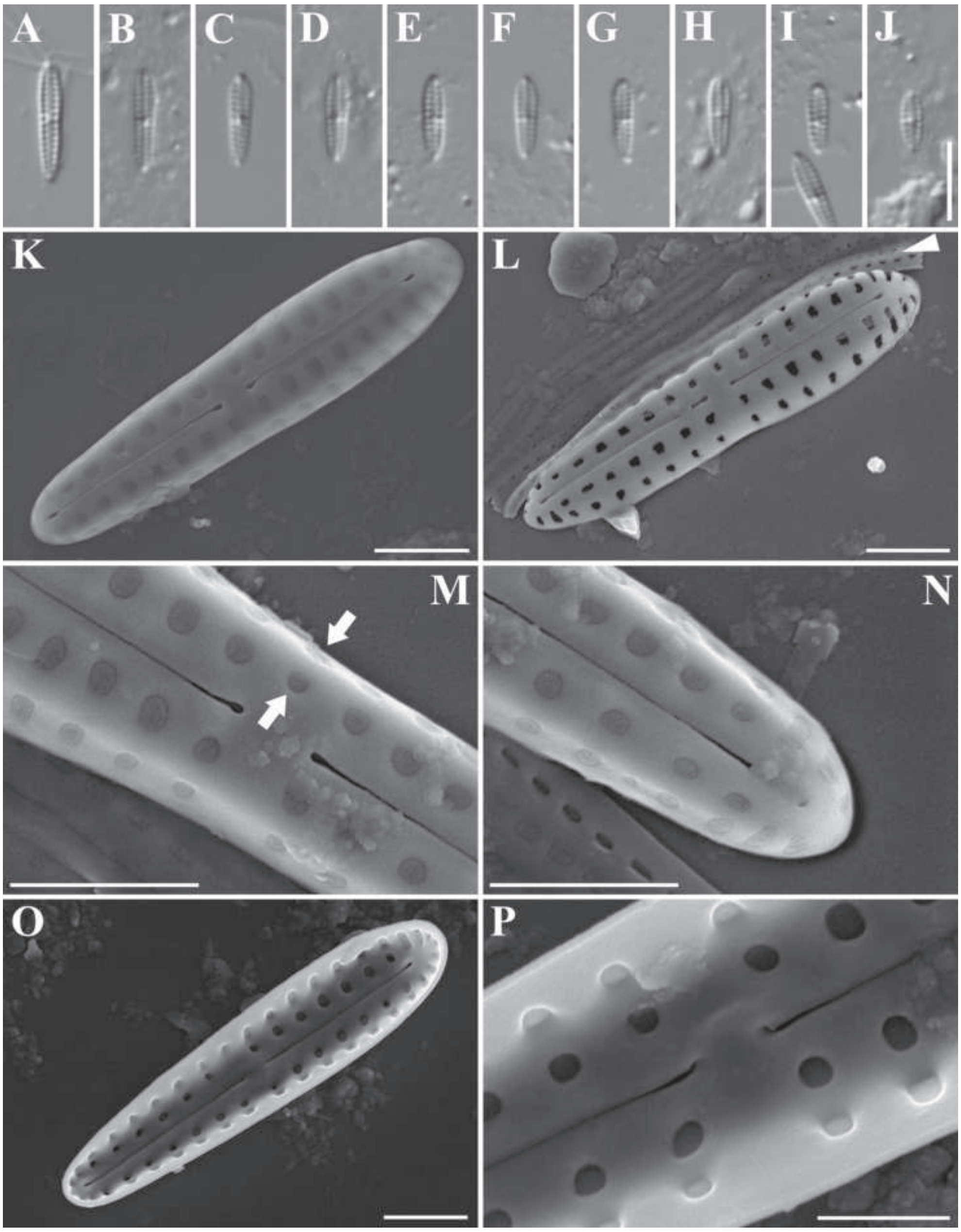

Figure 1. *Gomphonemopsis nana* **A–J** light micrographs (differential interference contrast, DIC) **K–P** scanning electron micrographs **K** external view of an entire valve with hymenes covering areolae, iconotype specimen **L** external view of an entire valve without hymenes covering areolae, note the girdle bands perforated with two rows of pores (white arrowhead) **M** external detail of the central area, note the presence of two areolae on the primary side (white arrows) **N** external detail of the foot pole **O** internal view of an entire valve **P** internal detail of the central area. Scale bars: 5 µm (**A–J**); 1 µm (**K–O**); 0.5 µm (**P**).

Type locality. Qingdao Bay, Qingdao City, the Yellow Sea (36°3'33.45"N, 120°18'56.26"E). Collected from the blades of seagrass *Zostera marina* by Lang Li, 11 October 2022.

Description. ***LM*** (Fig. 1A–J). Valves linear, heteropolar with obtusely rounded head pole and sub-acutely rounded foot pole, 4.0–7.4 μm long, 1.1–1.5 μm wide. Axial area very narrow. Raphe indistinguishable in LM. Central area hyaline, extended transapically, or occasionally asymmetrical because of the presence of a stria on primary side of the valve (Fig. 1A). Transapical striae sub-parallel throughout, except slightly radiate at apices, 26–30 in 10 μm.

SEM (Fig. 1K–P). Externally, each stria composed of two elongate to round areolae, one on the valve face, the other on the mantle. A row of areolae presented around apices (Fig. 1K). Areolae occluded by hymenes and becoming smaller towards the foot pole (Fig. 1K). Raphe central, more or less straight (Fig. 1K, L). Proximal raphe endings expanded, pore-like, and deflected in the same direction (Fig. 1K, M). Distal raphe endings slightly expanded and terminating on the valve face (Fig. 1K, L). Central area expanded transapically to the valve margin, but two areolae occasionally present on primary side (Fig. 1M, white arrow). Girdle bands perforated with a double row of pores (Fig. 1L, white arrowhead). Internally, areolae smaller and rounder than external ones (Fig. 1O). Central area slightly elevated. Proximal raphe endings bent to the same side (Fig. 1P) distal raphe endings terminate in small helictoglossae (Fig. 1O).

Etymology. The Latin adjective *nana* refers to the tiny dimensions of the new species as compared to other *Gomphonemopsis* species.

Distribution and ecology. *Gomphonemopsis nana* is an epiphytic species known only from the type locality, where it occurs mainly in the low intertidal region at a temperature of 23.3 °C. The water salinity here was about 30 psu during sampling. Other species that were observed in the same sample include *Amphora* spp., *Navicula* spp., *Nitzschia* spp., *G. exigua* (Kützing) Medlin, *Licmophora californica* Grunow, *Tabularia parva* (Kützing) D.M.Williams & Round, *T. fasciculata* (C.Agardh) D.M.Williams & Round, *Berkeleya rutilans* (Trentepohl ex Roth) Grunow, *Cocconeis scutellum* Ehrenberg and *Seminavis robusta* Danielidis & D.G.Mann.

PhycoBank registration. http://phycobank.org/104208.

Gomphonemopsis gaoi Lang Li, Changping Chen & Junxiang Lai, sp. nov.

Fig. 2A–P

- *Gomphonemopsis* aff. *G. exigua* in Lange and Tiffany 2002, p. 198, fig. 74.

Type materials. ***Holotype*.** Slide SZIII161114 deposited in Biology Department Herbarium, Xiamen University (AU), Xiamen, China.

***Iconotype*.** Fig. 2J.

Type locality. No. 3 fishing pond, Futian Mangrove Nature Reserve, the South China Sea (22°31'28.11"N, 114°0'41.37"E). Separated from the exoskeleton of marine copepods by Lang Li, 14 November 2016.

Description. ***LM*** (Fig. 2A–I). Valves narrowly lanceolate, isopolar with acutely rounded apices, 28.5–30.5 μm long, 4.0–5.0 μm wide. Primary and secondary sides can be easily distinguished because of the obvious interruptions in the stria pattern, which are termed “Voigt faults” (Fig. 2A, black arrowheads).

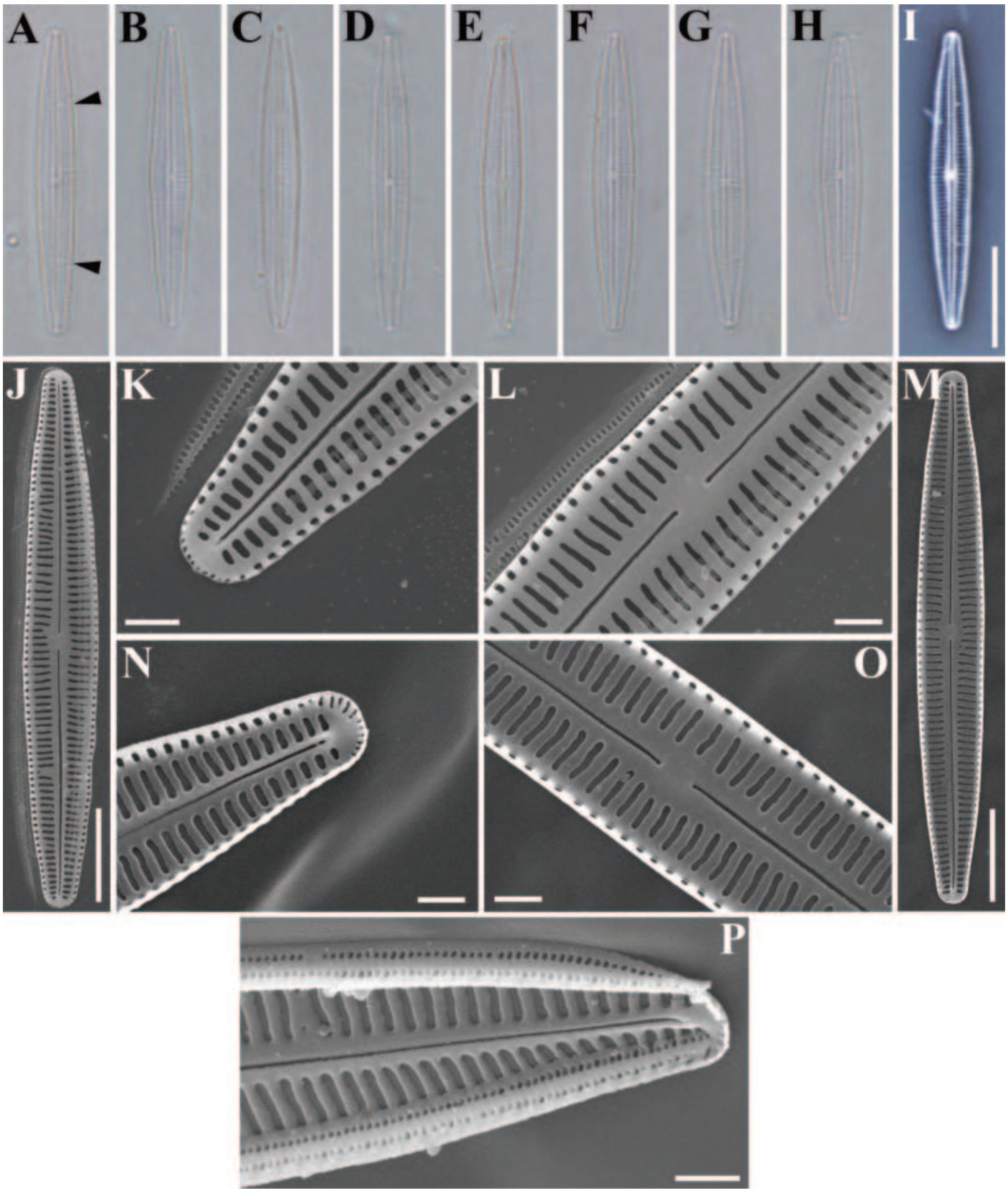

Figure 2. *Gomphonemopsis gaoi* **A–I** light micrographs (**I** phase contrast), note the Voigt faults on the secondary side (black arrowheads) **J–P** scanning electron micrographs **J** external view of an entire valve, iconotype specimen **K** external detail of the apex, showing the slit-like pores **L** external detail of the central area **M** internal view of an entire valve **N** internal detail of the apex, showing the slit-like pores **O** internal detail of the central area **P** valvocopula with two rows of subcircular poroids. Scale bars: 10 µm (**A–I**); 5 µm (**J**, **M**); 1 µm (**K, L, N–P**).

Axial area linear and very narrow, widening towards valve centre. Central area small, sometimes slightly wider on the primary side than the secondary side. Raphe straight with distant simple proximal endings. Striae uniseriate, parallel in the middle and slightly radiate near apices, 24–26 in 10 µm.

SEM (Fig. 2J–P). Valve face flat, with a clear transition to mantle (Fig. 2J). Each of striae comprised of one narrow, elongated areola on valve face and one oblong areola on the mantle (Fig. 2J–L). Valve mantle relatively shallow, with 10–14 radiated slits at apices (Fig. 2K, L). Axial area distinct, forming a narrow, lanceolate hyaline zone and becoming wider in the central area (Fig. 2J). Central area transversely expanded, surrounded by irregularly shortened striae

(Fig. 2L). Raphe filiform, composed of two coaxial branches of equal length (Fig. 2J). Both proximal and distal endings almost straight, not enlarged (Fig. 2K, L). Internally, proximal raphe endings small, slightly deflected towards the primary valve side (Fig. 2M, O), whereas distal endings terminate as weakly developed helictoglossae (Fig. 2N). Valvocopula open, possessing two parallel rows of subcircular poroids (Fig. 2P).

Etymology. The epithet honours Prof. Yahui Gao (Xiamen University, China), in recognition of his contributions to marine diatom taxonomy research in China.

Distribution and ecology. In addition to the type locality, *Gomphonemopsis gaoi* may also be distributed in the Salton Sea of the United States (Lange and Tiffany 2002: fig. 74). This taxon is an epizoic diatom on marine copepods. Water temperature of the sampling site was 27.7 °C, and salinity was 12 psu.

PhycoBank registration. http://phycobank.org/104209.

Discussion

Gomphonemopsis nana sp. nov. possesses heteropolar valves, rounded poles, straight raphe and uniseriate striae consisting of two hymenate areolae but lacks stigmata, terminal raphe fissures, basal pore fields, pseudosepta on the valves and septa on the valvocopulae. All these features justify assigning this new species to the genus *Gomphonemopsis* (Medlin and Round 1986). *G. nana* shares similar stria density with *G. exigua* (Table 1, modified from Krzywda et al. 2019). In addition, both have a row of areolae extending along the whole mantle. However, *G. nana* differs from *G. exigua* by having a wide central area expanding laterally to the valve margin, round to oblong areolae (vs. narrow elongate areolae in *G. exigua*), and a smaller cell (4.0–7.4 μm vs. 9–34 μm). As for other species within the genus, all of them display much lower stria densities than *G. nana*, and most of them have larger cell sizes (Table 1).

Gomphonemopsis gaoi sp. nov. also has all the features typical for the genus *Gomphonemopsis* except for its isopolar valves. The taxonomic value of polarity is still under debate (Sabbe et al. 2001). Moreover, in the marine gomphonemoid diatom genus *Tursiocola*, both heteropolar and isopolar species exist (Denys 1997; Frankovich et al. 2015). After assessing the questionable characters, we assigned this species to the genus *Gomphonemopsis*. Despite the difference in valve symmetry, *Gomphonemopsis gaoi* closely resembles *Gomphonemopsis exigua*. Both species have slit-like areolae, narrow axial areas, small central areas, and overlapping valve dimensions and stria densities. However, *Gomphonemopsis gaoi* can be distinguished by its simple proximal raphe endings (vs. pore-like proximal endings), distinctive Voigt faults (vs. lacking Voigt faults) and small slits at both apices (vs. only present at the foot pole). On the other hand, *Gomphonemopsis gaoi* is most similar to *Gomphosphenia oahuensis* (Hustedt) Lange-Bertalot, a freshwater diatom species with isopolar valves and slit-like areolae as well. But there are still some subtle differences between the two species: in *Gomphonemopsis gaoi*, the valve apices are acutely rounded and no T-shaped fissures can be seen at the distal raphe endings, whereas in *Gomphosphenia oahuensis* the valve apices are capitate and the distal raphe endings terminate in T-shaped depressions (Hustedt 1942; Simonsen 1987; Moser et al. 1998).

Lange-Bertalot established a subgenus *Costericardia* Lange-Bertalot under the genus *Gomphosphenia* Lange-Bertalot to accommodate the isopolar and naviculoid species, i.e., *Gomphosphenia oahuensis* (Moser et al. 1998). However, *Gomphosphenia oahuensis* lacks the diagnostic feature of the genus *Gomphosphenia*, namely anchor or T-shaped internal proximal raphe endings. In addition, as in *Gomphonemopsis gaoi*, *Gomphosphenia oahuensis* also has all the features of *Gomphonemopsis*, except for the polarity. Therefore, we propose the transfer of *Gomphosphenia oahuensis* to *Gomphonemopsis.* An alternative option would be to establish a new genus to accommodate *Gomphonemopsis gaoi* and *Gomphosphenia oahuensis*, because their valves are isopolar rather than heteropolar. However, in the absence of supporting molecular data, we refrain from doing so.

Gomphonemopsis oahuensis **(Hustedt) Lang Li, Yuhang Li & Changping Chen, comb. nov.**

Cymbella oahuensis Hustedt 1942. Internationale Revue der gesamten Hydrobiologie und Hydrographie 42 (1/3): p. 98, figs 193–195. Lectotype: designated by Simonsen (1987, p. 282). BRM 163/65, illustrated as pl. 416, figs 4–8. Basionym.
Gomphosphenia oahuensis (Hustedt) Lange-Bertalot in Moser, Lange-Bertalot and Metzeltin 1998, p. 42, pl. 5, figs 6–8, pl. 53, figs 1–9. Synonyms.
Navicula oahuensis (Hustedt) Krammer in Krammer and Lange-Bertalot 1985, p. 83.

PhycoBank registration. http://phycobank.org/104211.

Notes. *Gomphonemopsis exigua* var. *platypus* was originally described from Bornholm, Denmark as *Gomphonema platypus* Østrup. Subsequently, Krammer and Lange-Bertalot (1985) reclassified this taxon as a variety of *Gomphonema exiguum*. Snoeijs transferred it to *Gomphonemopsis* (Snoeijs and Balashova 1998). Despite sharing a similar size dimension and stria density with the nominate variety (Medlin and Round 1986; Snoeijs and Balashova 1998), it has a unique widened foot pole differing from other congeners (Snoeijs and Balashova 1998). Therefore, we suggest elevating *Gomphonemopsis exigua* var. *platypus* to the species level.

Gomphonemopsis platypus **(Østrup) Lang Li, Yuhang Li & Junxiang Lai, comb. nov.**

Gomphonema platypus Østrup 1910. Danske Diatoméer, p. 65, pl. II, fig. 49. Basionym.
Gomphonemopsis exigua var. *platypus* (Østrup) Snoeijs in Snoeijs and Balashova 1998, p. 55, fig. 443. Synonyms.
Gomphonema exiguum var. *platypus* (Østrup) Lange-Bertalot in Krammer and Lange-Bertalot 1985, p. 47.

PhycoBank registration. http://phycobank.org/104420.

Dichotomous key to distinguish the *Gomphonemopsis* species

In order to facilitate the identification of the *Gomphonemopsis* species, a dichotomous key to all known species is presented as follows:

1 Valves isopolar **2**
– Valves heteropolar.......... **3**
2 Apices capitate .... ***G. oahuensis***
– Apices acutely rounded.......... ***G. gaoi***
3 Valves clavate with widened foot pole.......... ***G. platypus***
– Valves linear to lanceolate.......... **4**
4 Central area small .... ***G. exigua***
– Central area wide or asymmetrical **5**
5 Striae 26–30 in 10 μm.......... ***G. nana***
– Striae ≤ 24 in 10 μm **6**
6 Areolae round **7**
– Areolae elongate or round near poles.......... **8**
7 Mantle areolae only extending along the wider part of valve ..... ***G. ligowskii***
– Mantle areolae extending along the whole mantle .... ***G. littoralis***
8 Striae ≤ 18 in 10 μm **9**
– Striae ≥ 18 in 10 μm **10**
9 Valves 10–17 μm long, 2–3 μm wide; striae 16 in 10 μm .... ***G. obscura***
– Valves 6–8 μm long, 1.7–2.5 μm wide; striae 10–18 in 10 μm.......... ***G. domniciae***
10 Central area extending to valve/mantle junction.......... **11**
– Central area extending to valve margin **12**
11 Transapical striae divided the into two parts .... ***G. sieminskae***
– Transapical striae not divided the into two parts.......... ***G. pseudexigua***
12 A row of small slits around the foot pole.......... ***G. lindae***
– One or two pores around the foot pole .... ***G. novozelandicum***

To date, the genus *Gomphonemopsis* contains thirteen diatom species, six of which have been reported in China seas. This genus may have a wider distribution in the marine coastal waters of subtropical to Polar regions, with the exception of *G. oahuensis*, which lives in tropical freshwater environments. According to Table 1, *Gomphonemopsis* exhibits diverse habitat preferences. Most species are epiphytic on seaweeds and seagrasses, whereas, interestingly, *G. gaoi* “chooses” copepods as its hosts in this study. This may be not the first report of epizoic *modus vivendi* in *G. gaoi*. Lange and Tiffany (2002) found that this species could attach to both green algae and the stalk of the ciliate, but they couldn’t determine whether the ciliate was its strict host. Hence, further ecological studies are needed to reveal the habitats of *G. gaoi* and other species within the genus.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Oxalis xishuiensis (Oxalidaceae), a new species from Danxia landforms in Guizhou, China

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Abstract

Oxalis xishuiensis, a new species of Oxalidaceae from Danxia landforms of Xishui County, Guizhou, China, is described and illustrated. It is morphologically similar to *O. wulingensis* by the two lateral leaflets arranged at about 180° angle and oblong pink petals with lilac veins, but clearly differs from the latter by leaflets almost as long as wide, obliquely obcordate lateral leaflets, shorter peduncles, longer capsule (1.2–1.5 cm vs. 0.5–0.7 cm) and alveolate seeds.

Key words: China, Danxia landforms, Oxalidaceae, *Oxalis*, Xishui

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Introduction

Oxalis L. contains about 500–800 species and is distributed all over the world, but South America and southern Africa are thought to be the two centres of diversity (Azkue 2000; Sidwell and Knapp 2002; Vaio et al. 2016). This genus is characterised by 3-foliolate leaves, solitary, cymose or umbellate inflorescence, five-numerous flowers, free sepals and petals (Liu and Watson 2008). Based on morphological characteristics, the genus was divided into *Oxalis* subgen. *Thamnoxys* (Endl.) Reiche, *O*. subgen. *Monoxalis* (Small) Lourt., *O*. subgen. *Oxalis* L. and *O*. Subgen. *Trifidus* Lourt. (Moura et al. 2020). In the *Flora of China*, six native species in *Oxalis* are recorded, namely *O. acetosella* L., *O. corniculata* L., *O. griffithii* Edgew. & Hook. f., *O. leucolepis* Diels, *O. obtriangulata* Maxim. and *O. stricta* L. (Liu and Watson 2008). In the past two decades, two new species were described in China (*O. wulingensis* T. Deng, D. G. Zhang & Z. L. Nie and *O. shibeishanensis* Huan C. Wang & Y. Tian) (Deng et al. 2013; Tian et al. 2020).

During field surveys to Xishui County, north Guizhou Province, China, in November 2022, a population of *Oxalis* with special morphological characteristics attracted our attention. To conduct further detailed observation, we transplanted five individuals in the greenhouse of the Guizhou Academy of Forestry and three individuals were made into herbarium specimen after flowering. After careful morphological examination and comparison with morphologically similar species in *Oxalis*, it is confirmed as an undescribed new species of *Oxalis*. Here, we formally describe this new species.

Materials and methods

Morphological characteristics were observed and measured from the living plants. The comparison with morphologically similar species was based on the digital specimens from the online database CVH (https://www.cvh.ac.cn/) and JSTOR Global Plants (https://plants.jstor.org/), as well as the descriptions from relevant literature (Liu and Watson 2008; Deng et al. 2013; Aoki et al. 2019; Tian et al. 2020).

Taxonomic treatment

***Oxalis xishuiensis* Y.B. Yang, M.T. An & H. Li, sp. nov.**
urn:lsid:ipni.org:names:77339170-1
Figs 1, 2

Type. China. Guizhou Province, Xishui County, Xishui National Nature Reserve, 28°8'25"N, 105°53'32"E, alt. 1200 m, 10 November 2022, xs2022103 (holotype: GF, isotypes: GZAC).

Diagnosis. The new species is most morphologically similar to *Oxalis wulingensis*, but differs from the latter by its leaf blade ca. as long as wide, obliquely obcordate lateral leaflets (vs. long obtriangular), shorter peduncle (ca. 3–4 cm long, shorter than leaves vs. 10–12 cm long, longer than leaves), longer capsule (1.2–1.5 cm long vs. 0.5–0.7 cm long) and alveolate seeds (vs. only with longitudinally ridge).

Description. Perennial herbs, 8–15 cm tall; rhizome creeping underground, densely covered by dark brown, scale-like remains of leaf bases, ca. 1 cm thick including scales; scales pilose. Leaves radical, 3-foliolate, the two lateral leaflets arranged at about 180° angle; petioles 4.5–8 cm long, densely covered with white, pubescent over their entire length; lateral leaflets blades obliquely obcordate, 1.4–2.1 × 1.3–2 cm; middle leaflet blades obcordate, 2–3.1 × 1.9–3 cm; leaflets blades adaxially light green to green, abaxially pale green, purple when young; both surfaces white pubescent or adaxially glabrous, apex broadly emarginate, base cuneiform, lobe apices obtuse. Flowers solitary, nodding; peduncles ca. 3–4 cm long, shorter than leaves at flowering time, peduncle much longer than petioles due to pedicel extension at maturity of capsule; bracts at middle of flowering stalk, triangular, ca. 4 mm long, apex bifid with dense trichomes along mid-vein and margins; sepal oblong, ca. 7 × 3 mm, green, surface and margins with some hairs, persistent; petals pink with lilac veins and a yellow patch at base, oblong, ca. 2 × 1 cm, apex obtuse or irregularly denticulate; stamens 10, alternately long and short, the longer ones ca. 1.8 cm, the shorter ones ca. 1.4 cm, all basally connate, filaments purple-red, glabrous, anthers white; pistil ca. 2.1 cm long; ovary glabrous, locules 5, each with a single ovule, styles 5, slender, stigma linear. Capsule erect, cleistogamous capsule with persistent calyx,

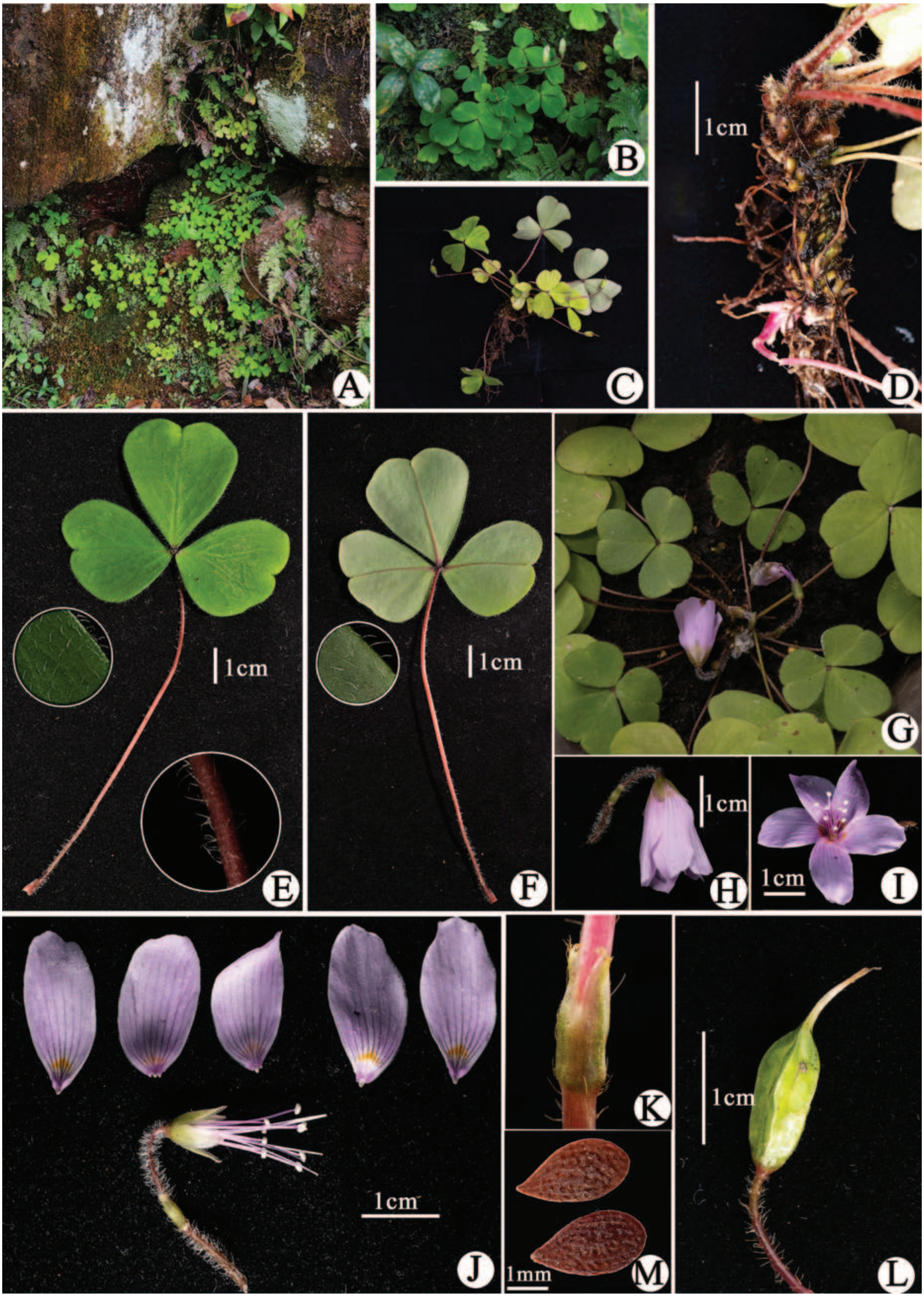

Figure 1. *Oxalis xishuiensis* Y.B. Yang, M.T. An & H. Li **A, B** habitat **C** plants **D** rhizome **E** upper surface of leaves **F** lower surface of leaves **G** flowering plant **H** lateral view of the flower **I** frontal view of the flower **J** dissected flower **K** bract **L** capsule **M** seeds.

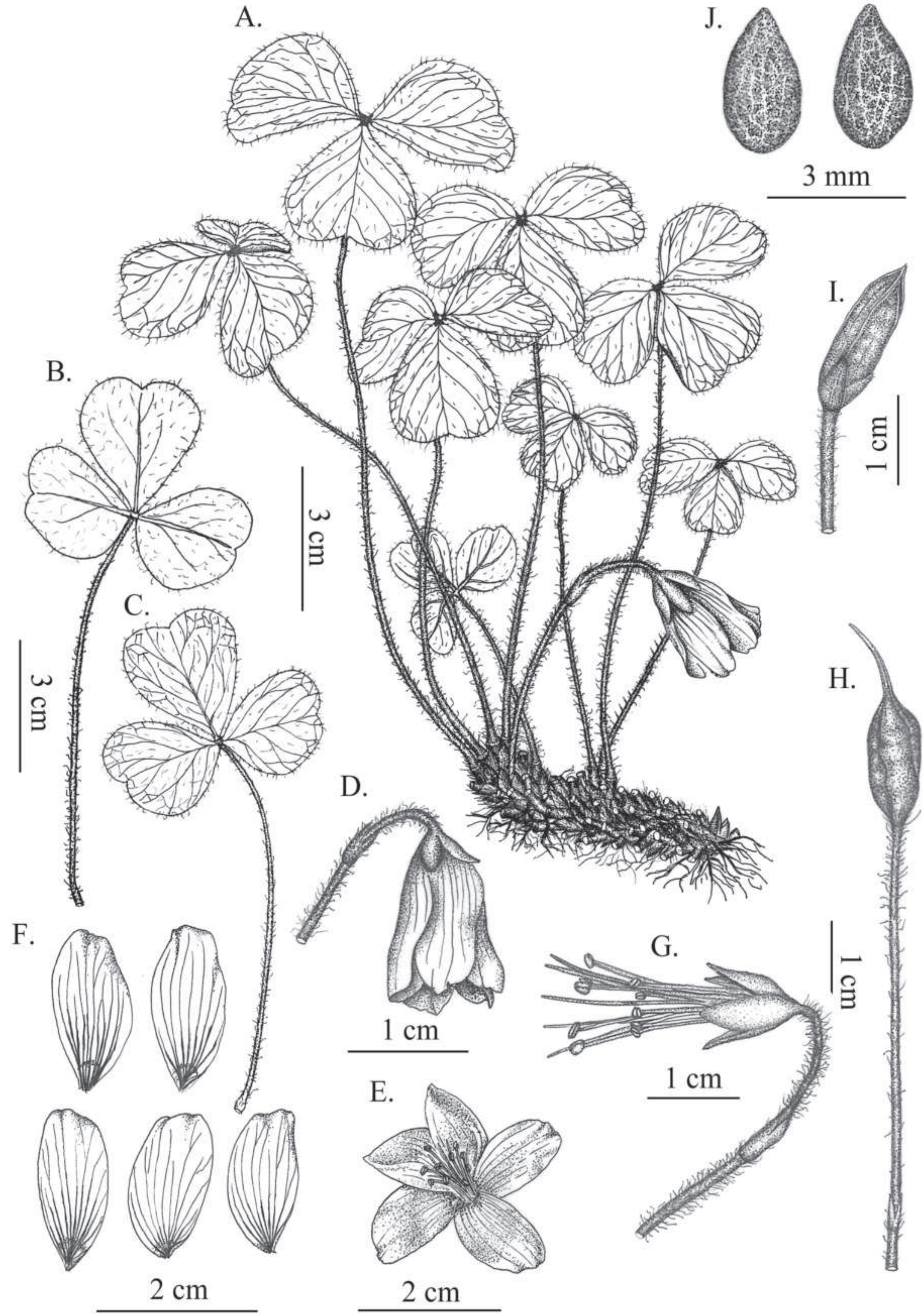

Figure 2. *Oxalis xishuiensis* Y.B. Yang, M.T. An & H. Li **A** habit **B** lower surface of leaves **C** upper surface of leaves **D** lateral view of the flower **E** frontal view of the flower **F** petals **G** stamens **H** chasmogamous capsule **I** cleistogamous capsule **J** seeds.

ovoid to oblong 1.2–1.5 × 0.4–0.5 cm, with five alar ridges; seeds ovoid, ca. 3 × 2 mm, with longitudinally ridge and alveolate on surfaces, dark brown when dry.

Distribution and habitat. *Oxalis xishuiensis* is currently only known from Danxia landforms hills in the Xishui National Nature Reserve, Xishui County, Guizhou Province, south-western China. It grows on humid slopes in purple sand shale under the evergreen broad-leaved forest, at an altitude of 1200 m, along with *Marchantia polymorpha* L., *Pteris cretica* L., *Metathelypteris laxa* (Franch. & Sav.) Ching, *Trigonotis omeiensis* Matsuda, *Saxifraga stolonifera* Curtis, *Carex baccans* Nees and *Lysimachia paridiformis* Franch.

Phenology. Chasmogamous flowers from February to March; Cleistogamous flowers from May to June. Fruiting from February to July.

Etymology. The species epithet, *xishuiensis*, refers to the type locality of the new species.

Vernacular name. 习水酢浆草 (xí shuǐ cù jiāng cǎo)

Conservation status. Currently, only one population of the new species with approximately 60 individuals has been found. Danxia landforms are widely distributed in this area, so we speculate that there may be other populations of this new species. Due to insufficient field investigations, the natural range of this species in the wild is unclear. According to the IUCN Red List Categories and Criteria (IUCN 2022), we recommend this species placement in the ‘Data Deficient’ (DD).

Discussion

In the *Oxalis*, there are eight native species in China, but only two native species in Guizhou (Liu and Watson 2008; Deng et al. 2013; Tian et al. 2020). Discovery of *Oxalis xishuiensis* adds to the native local floras.

According to the classifications by Lourteig (2000) and Aoki et al. (2019), *Oxalis xishuiensis* should be classified into *Oxalis* subgen. *Oxalis* sect. *Oxalis* subsect. *Oxalis*. *Oxalis xishuiensis* is characterised by the obliquely obcordate lateral leaflets arranged at about 180° angle, shorter peduncles and alveolate seeds. This unique combination of morphological characteristics distinguishes *O. xishuiensis* from all other species of subsect. *Oxalis* (Liu and Watson 2008; Deng et al. 2013; Aoki et al. 2019; Tian et al. 2020). We made a detailed morphological comparison between *O. xishuiensis* and its relatives (Table 1). *Oxalis xishuiensis* morphologically is most similar to *O. wulingensis* by the two lateral leaflets arranged at about 180° angle and oblong pink petals with lilac veins, whereas *O. xishuiensis* leaflets are almost equal in length and width, two lateral leaflet blade shapes are asymmetric (obliquely obcordate) and smaller in size than the leaflet blades in the middle, mature leaf blades abaxially pale green (vs. purple in *O. wulingensis*), peduncles shorter than leaves, longer capsule 1.2–1.5 cm long (vs. 0.5–0.7 cm in *O. wulingensis*) and seeds with alveolate on both surfaces. Furthermore, the new species was discovered only from Danxia landforms hills, which is completely different from *O. wulingensis* growing in limestone habitat. *Oxalis xishuiensis* resembles *O. acetosella* in the obcordate leaf blades, but differs in leaf blades ca. as long as wide, two lateral leaf blades asymmetric and arranged at about 180° angle, peduncles shorter than leaves and petals oblong, pink with lilac veins (vs. obovate, white, lilac to pinkish veined in *O. acetosella*).

Table 1. Morphological comparison of species of *Oxalis xishuiensis* and its relatives.

Characters	***O. xishuiensis***	***O. wulingensis***	***O. acetosell*a**	***O. griffithii***
Rhizomes (including scales)	Ca. 10 mm in diameter	Ca. 10 mm in diameter	Ca. 3 mm in diameter	6–12 mm in diameter
Two lateral leaflets arrangement	About 180° angle	180° angle	120° angle	120° angle
Leaflets	Two lateral leaflets obliquely obcordate, 1.4–2.1 × 1.3–2 cm; middle leaflets obcordate, 2–3.1 × 1.9–3 cm	Long obtriangular, 2.2–3.1 × 1.6–2.5 cm	Obcordate, 0.5–2 × 0.8–3 cm	Obtriangular, 1–2.5(–4.5) × 1.5–3.5(–5.5) cm
Leaflet apex	Broadly emarginate	Broadly emarginate	Deeply emarginate	Broadly emarginate to subtruncate
Leaflet indumentum	Both surfaces white pubescent or adaxially glabrous	Both surfaces villous (densely covered with long, brown hairs)	Both surfaces pubescent	Abaxially pubescent, adaxially glabrous
Leaflet adaxial surface colour	Light green to green	Green	Green	Green
Leaflet abaxial surface colour	Pale green, purple when young	Purple	Whitish-green, purple or red	Pale green or green
Peduncles in flowering	Ca. 3–4 cm long, shorter than leaves	10–12 cm long, longer than leaves	Peduncle equal to or longer than leaves	4–15 cm long, equal to or longer than leaves
Petal	Oblong ca. 2 cm, apex obtuse or irregularly denticulate	Oblong ca. 2.5 cm, apex obtuse or irregularly denticulate	Obovate, (1.2–)1.5–2.2 cm, apex retuse to deeply emarginate	Narrowly obovate, 1.2–1.6(–2) cm, apex retuse to deeply emarginate
Petal colour	Pink with lilac veins	Pink with lilac veins	White, lilac to pinkish veined	White, rarely pink (Hubei)
Capsules	Ovoid or oblong, 12–15 × 4–5 mm	Ovoid, 5–7 mm long	Ovoid, 3–4 mm	Oblong-conic, 5–13 × 5–6 mm
Seed	Ovoid, ca. 3 mm long, with longitudinally ridge and alveolate	Ovoid, ca. 2.1 mm long, with longitudinally ridge	Ovoid, with longitudinally ridged	Ovoid, 2.5–3.5 mm, with longitudinally ridged
Flowering time	Chasmogamous flowers: February to March, Cleistogamous flowers: May to June	March	July to August	March to September

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Data curation: Yan-Bing Yang, He Li, Lang Huang. Funding acquisition: Ming-Tai An, Guo-Xiong Hu. Investigation: Yan-Bing Yang, He Li, Cheng-Hua Yang, Zheng-Xian Dai. Methodology: Yan-Bing Yang, Ming-Tai An, He Li. Project administration: Guo-Xiong Hu. Supervision: Ming-Tai An. Visualisation: Lang Huang, Zheng-Xian Dai. Writing – original draft: Yan-Bing Yang. Writing – review and editing: Ming-Tai An, Guo-Xiong Hu.

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Data availability

All of the data that support the findings of this study are available in the main text.

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