Two new species of tropical blueberry (*Vaccinium* L., Ericaceae) from central Sabah, Malaysian Borneo

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Summary. Two new species of tropical blueberry from central Sabah, Malaysian Borneo, are described and illustrated. *Vaccinium madanii* resembles *V. clementis* but is distinct by the presence of glands along the leaf blade margin, a longer inflorescence, longer pedicels, a pubescent hypanthium, and anther spurs longer than the tubules. *Vaccinium maliauense* resembles *V. phillyreoides* but is distinct by the absence of glands on the leaf blade base, a cuneate leaf blade base, non-dimorphic filaments, presence of anther spurs, and longer tubules. Photos, illustrations, and a distribution map of the new species are provided. Notes on their closest congeners are discussed, and their preliminary conservation status are assessed.

Borneo is the third largest island in the world (Wooster et al., 2011) and is shared by three Southeast Asian countries: Brunei Darussalam, Indonesia, and Malaysia. It is part of Sundaland (Breitfeld et al., 2017; Khan, 2018), a biogeographical region in Southeast Asia, composed of Indochina, Java, Sumatra, Thai-Malay Peninsula, Palawan, and other smaller islands that were once connected during the Pleistocene (Hall & Morley, 2004; Yumul, 2007; Hertwig et al., 2013). The location of Borneo in tropical Asia allowed it to become a major evolutionary hotspot for Southeast Asian fauna and flora (van Welzen et al., 2005; de Bruyn et al., 2014).

The genus *Vaccinium* L. (Ericaceae – heather family) in Borneo is characterised as shrubs, trees, or epiphytes, predominantly inhabiting montane forests, open disturbed sites, exposed mountain ridges, sandy soils, ultramafic regions, heathland zones on rocky mountain summits, and rarely at sea level (Argent, 2019). All species of *Vaccinium* in Borneo are endemic, except *V. bancanum* Miquel which can be found in Java, Malay Peninsula, Sumatra, Thailand (POWO, 2023), and possibly in the Philippines (Sleumer,

1961, 1966–1967; Pelser et al., 2011 onwards). The most recent taxonomic work on the *Vaccinium* of Borneo was the revision by Argent (2019). Argent recognized 19 species and reinstated *Rigiolepis* Hook.f. (formerly a section of *Vaccinium*) to genus status. Although this work is comprehensive, it mainly focused on collections from Sarawak and west Sabah (especially in Mt. Kinabalu and Crocker Range), with central, east and south Sabah including Kalimantan (Indonesian Borneo) being under-represented.

As part of herbarium work aimed at revisiting and rediscovering the diversity of Bornean Ericaceae, two interesting specimens of *Vaccinium* were examined at the Sandakan Herbarium (SAN), Sabah, Malaysia. The two species belong to *V.* section *Bracteata* Nakai (Nakai & Koidzumi, 1927) sensu Sleumer (1966–1967) by the combination of racemose multiflowered inflorescences, a hypanthium markedly larger than the calyx lobes, the absence of a membranaceous wing at the corolla sinuses, and anthers opening by terminal pores. These species can alternatively be treated as members of *V*. section *Euepigynium* Schlechter sensu Vander Kloet & Dickinson (2009) by their evergreen habit, single monomorphic perennating buds on leaf axils, plinerved leaf venation, the peduncle longer than pedicels, a calyx tube (hypanthium) that is wholly fused to the ovary, and a pseudo-10-locular ovary. Both species are restricted to central Sabah and are here described under a morphological species concept (Cronquist, 1978).

These discoveries increase the number of known *Vaccinium* in Borneo to 21 and underscore the extraordinary diversity of ericaceous plants in this island, especially in the state of Sabah. Previous botanical excursions aimed at documenting Ericaceae diversity in Borneo have mainly focused on the Crocker Range, Mt. Kinabalu, and sporadically on Mt. Trus Madi and adjacent areas in western Sabah. As such, botanical excursions focused on documenting Ericaceae from other areas in central, east, and south Sabah, especially within montane and ultramafic forests, can be expected to yield more discoveries of novel Ericaceous species.

MATERIALS AND METHOD

Descriptions were based on dried herbarium vouchers and in situ photographs. The flowers and fruits were dissected and examined, and their parts measured with a stereo microscope (Olympus SZ51) up to 50× magnification. Herbarium specimens were examined from BRIT, CAS, NY, and SAN, including digitized specimens at BM, G, L, MICH, and SING [herbarium acronyms follow Thiers (2023), continuously updated] available online at JSTOR Global Plants (https://plants.jstor.org). Characters in descriptions were defined as in Beentje (2016), and relevant taxonomic literature on Bornean and Malesian *Vaccinium* was consulted (i.e., Sleumer, 1961, 1966–1967; Vander Kloet, 2005; Argent, 2019). The area of occupancy (AOO) and extent of occurrence (EOO) were obtained with the use of GeoCAT (Bachman et al., 2011). Species conservation status was assessed with the use of IUCN guidelines (IUCN Standards and Petitions Committee, 2022).

TAXONOMIC TREATMENT

1. ***Vaccinium madanii*** Argent ex M.N.Tamayo, **sp. nov.**
Vaccinium madanii resembles *V. clementis* Merrill but differs by the presence of glands along the leaf blade margin (vs. absence), a longer inflorescence (4–8 cm vs. 2–5 cm), longer pedicels (10–15 mm vs. 5–8 mm), a pubescent hypanthium (vs. glabrous), and anther spurs longer than the tubules (vs. shorter than the tubules) **(Figs. 1, 2)**. TYPE: *Damit et al*. *SAN 156569*, Borneo, Sabah, Tongod, Sungai Imbak, Virgin Jungle Reserve, Block 11D, montane ultramafic forest, 1230 m, 2 Apr 2014, (holotype SAN!; isotypes K, KEP, SING).

Shrub or tree, terrestrial, evergreen, 2–10 m tall, diameter at breast height c. 6 cm, densely branched. **Young branchlets** reddish green *in vivo*, light to dark brown *in sicco*, puberulent, with simple erect trichomes, 0.10–0.15 mm long; mature branchlets dark brown *in vivo*, non-ridged, glabrous, lenticellate, 2–5 mm wide; perennating buds broadly triangular, 0.5–0.7 mm long, with several obscurely overlapping scales, apex acute, margin entire with occasional simple erect trichomes c. 0.1 mm long. **Leaves** persistent on older branchlets, densely crowded, spirally and evenly arranged; petiole reddish green *in vivo*, reddish brown *in sicco*, pubescent, with trichomes same as branchlets, in cross section abaxially rounded, adaxially nearly flat, 1–2 × 0.8–1 mm;

Fig. 1. Habit and flowering branchlets of *Vaccinium madanii* in situ. Photo of the holotype by Alviana Damit.

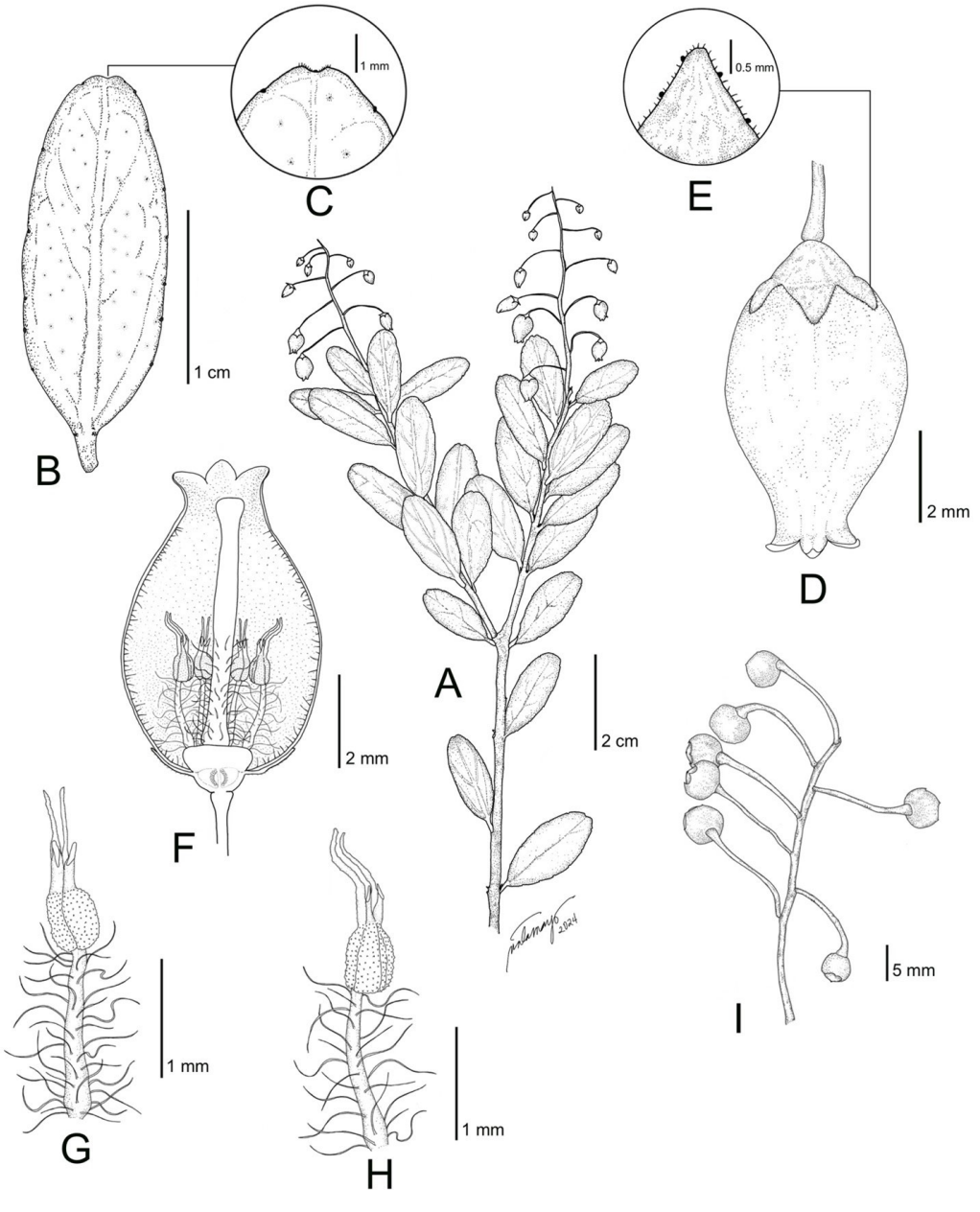

Fig. 2. *Vaccinium madanii*. **A.** Flowering branchlet. **B.** Leaf (abaxial view). **C.** Leaf apex. **D.** Flower. **E.** Details of a calyx lobe. **F.** Dissected flower showing stamens, style, ovary, and hypanthium. **G.** Stamen (ventral view). **H.** Stamen (lateral view). **I.** Infructescence. Illustrated by Maverick N. Tamayo, from the holotype.

leaf blade oblong-elliptic, coriaceous, larger leaves on each branchlet 2–2.4 × 0.8–1 cm, abaxial surface with punctae, pale green, adaxial surface leathery green, base obtuse, margin entire, shallowly crenate, revolute, with 5 to 8(–9) pairs of impressed ± evenly distributed glands per side, first pair of glands c. 3 mm from leaf blade base, 0.2–0.3 mm diameter, leaf blade apex acute, rounded, or shallowly emarginate, the very apex ± gland-tipped with minute simple hairs c. 0.1 mm long, midvein strongly raised abaxially, slightly sunken adaxially, secondary veins 3 to 5 on each side of midvein with first pair arising from base and remainder along midvein, arc-ascending, raised abaxially, obscure or non-evident adaxially, tertiary veins faintly evident or obscure. **Inflorescences** pseudo-terminal or terminal, racemose, developing beyond confines of perennating bud, 1 per leaf axil, subdensely 8- to 13-flowered, 4–5 cm long; peduncle and rachis pale green *in vivo*, brown *in sicco*, slightly ridged, puberulent; peduncle 1–1.5 cm long, rachis 4–4.5 cm long; bracts early caducous. **Flowers** with articulation between pedicel apex and hypanthium, 1–1.8 cm long; pedicel pale green *in vivo*, nodding, puberulent, 10–15 × 0.5–0.6 mm at anthesis; bracteoles 2, borne at base of pedicel, puberulent, narrowly triangular or subulate, caducous, margin entire, minutely ciliolate, 0.4–0.5 mm long; hypanthium pale green *in vivo*, reddish brown *in sicco*, broadly obconical, 0.5–1 × 0.5–0.8 mm; calyx limb 0.3–0.5 mm long; calyx lobes 5, broadly triangular, abaxially glabrous, adaxially puberulent, 1–1.3 × 0.5–0.7 mm, margin entire, puberulent, with occasional sessile glands 0.1–0.15 mm long, calyx lobe apex acute, with a few simple hairs, sessile terminal gland ± present; corolla white to pale pink, broadly urceolate, glabrous outside, pubescent on the lower ¾ inside, 4–6 × 3–4 mm, trichomes simple, 0.2–0.3 mm long; lobes 5, triangular, 0.5–0.8 × 0.5–0.6 mm, apex acute, obtuse, or occasionally rounded; stamens 10, monomorphic, distinct, 2–2.5 mm long; filaments straight or slightly curved, 1.5–2.0 mm long, white-lanate, trichomes 0.25–0.3 mm long; anthers 1.0–1.3 mm long, opening by introrse slits or terminal pores, shorter than filaments, cells ovoid to oblong, minutely echinulate, 0.4–0.5 mm long, tubules parallel, erect, cylindric, 0.3–0.4(–0.5) mm long, narrower than cells, opening by oblique ventrally oriented apical pores, pore apex oblong, spurs present, longer than tubules, arc-ascending or sigmoidal, 0.5–0.6 mm long; ovary 5- to 6-locular but appearing pseudo-10- to 12-locular with incomplete partitions extending 0.1–0.2 mm from inner wall; ovules in two columns per locule; disk non-bulky, slightly annular with obscure ridges on margin, glabrous, 1–1.5 mm diameter, 0.2–0.3 mm depth; style ± exserted from corolla, pubescent on lower ½, 4–5 mm long, stigma truncate or rounded. **Fruit** pinkish green (immature), cupuliform, subglobose, 3–4.5 × 3–4 mm.

ETYMOLOGY. The epithet honours Mr. Leopold Madani, former Senior Research Assistant of Sandakan Herbarium and collector of the first specimen of this species from Gunung Tawai.

PHENOLOGY. Flowering in April; fruiting from May to August.

DISTRIBUTION. Endemic to Borneo and found only in the montane ultramafic forest of Sungai Imbak, Gunung Tawai, and summit of Mt. Meliau at Ulu Tungud Forest Reserve **(Fig. 3)**.

PROVISIONAL IUCN CONSERVATION ASSESSMENT. *Vaccinium madanii* occupies a small area in central Sabah with less than five populations currently known. The extent of occurrence (EOO = 962.605 km^2) and area of occupancy (AOO = 16 km^2) of *V. madanii* satisfies IUCN Standards and Petitions Committee (2022) category as endangered [EN: B1ab(i, ii, iv) + B2ab (i, ii, iv)].

OTHER SPECIMENS EXAMINED–BORNEO. SABAH: Telupid, Tawai Forest Reserve, Gunung Tawai, montane forest, 914–1219 m, 20 Jun 1975 (SAN!), *L. Madani SAN 81721*; ibid. 26 Jun 1975, *L. Madani SAN 81778* (L-image! [L.2618800], SAN!, SING-image! [0196352]); Beluran, Ulu Tungud Forest Reserve, summit of Mt. Meliau, 1310 m, 8 Dec 2004*, J. Sugau SAN 145602* (SAN!); Sandakan, Mt. Meliau second summit near Kiabau Labuk, 1066 m, 14 May 1965, *W. Meijer SAN 51570* (SAN!); ibid. 14 May 1965, *W. Meijer SAN 51585* (SAN!).

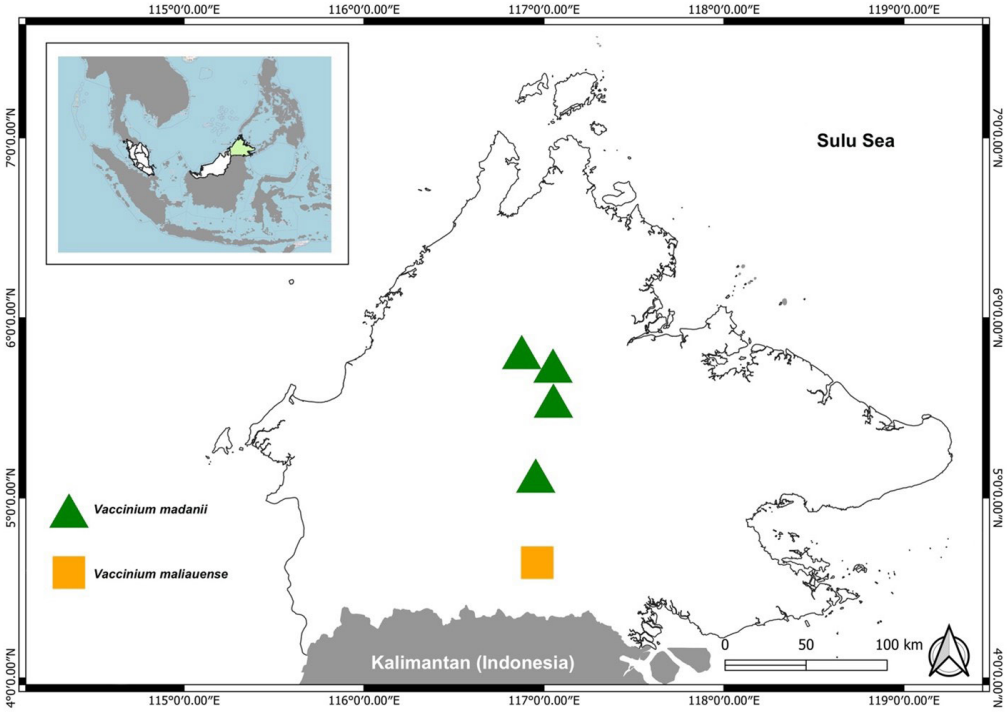

Fig. 3. Distribution map of *Vaccinium madanii* (green triangle) and *V. maliauense* (orange square) in the State of Sabah, Malaysia.

NOTES. A specimen at SING was annotated by Dr. George Argent as *Vaccinium madanii*. However, he did not publish this name, probably because all materials previously available to him were either sterile or in fruit. The paratypes at SAN were annotated by him as *V. coriaceum* Hook.f. but were not mentioned in his revision of *Rigiolepis* and *Vaccinium* of Borneo. *Vaccinium coriaceum* has four infraspecific varieties: *V. coriaceum* var. *coriaceum* Hook.f., *V. coriaceum* var. *hirsuticalyx* Argent, *V. coriaceum* var. *minus* (Sleumer) Argent, and *V. coriaceum* var. *stapfianum* (Sleumer) Argent. Among these, *V. coriaceum* var. *hirsuticalyx* most closely resembles *V. madanii*, as exhibited by its pubescent hypanthium. *Vaccinium madanii* can be distinguished from *V. coriaceum* var. *hirsuticalyx* by its larger leaf blades (2–2.4 × 0.8–1 cm vs. 0.6–1.3 × 0.3–0.5 cm), longer pedicels (10–15 mm vs. 2–4 mm), and longer anther spurs (0.5–0.6 mm vs. 0.1–0.2 mm). Moreover, *V. coriaceum* var. *hirsuticalyx* is found in Mt. Kinabalu and Sarawak (the East Kalimantan record is doubtful as the specimen is fruiting; Argent, 2019), whereas *V. madanii* is restricted only to central Sabah.

In the key to the Malesian species of *Vaccinium* (Sleumer, 1966–1967), *V. madanii* keys to *V. habbemae* var. *pluriglandulosum* J.J.Sm., endemic to New Guinea. However, *V. madanii* can be distinguished from *V. habbemae* var. *pluriglandulosum* by having a leaf blade with acute, rounded, or shallowly emarginate apex (vs. subcaudate or acuminate), more flowers per inflorescence (8- to 13-flowered vs. 4- to 6-flowered), puberulent rachis (vs. glabrous), puberulent pedicels (vs. glabrous), white to pale pink corolla (vs. purple or red), and the presence of anther spurs (vs. absence). In the key to the Bornean species of *Vaccinium* (Argent, 2019), *V. madanii* keys to *V. clementis*. Aside from the characters mentioned as divergent in the diagnosis, *V. madanii* can be further distinguished by its shorter corolla (4–6 mm vs. 7–8 mm), shorter stamens (2–2.5 mm vs. 3–4 mm), filaments pubescent throughout (vs. only in proximal 2/3), and absence of glandular hairs on tubules (vs. presence).

ADDITIONAL SPECIMENS EXAMINED. ***Vaccinium clementis*.** BRUNEI: Temburong District, north ridge of Bukit Retak, between LZ 238 and summit, 17 Sep 1988, *K.M. Wong 427* (SAN!); MALAYSIA: Sarawak, Baram District, 4th Division, Bukit Dulit, Ulu Sungai, Tinjar, 16 Aug 1974, *S. Tong* (SAN!); ibid. Hose Mountains, Bukit Salong, Ulu Sungai, Melinau, 7th Division, 25 Apr 1976, *P. Chai et al*. (SAN!). ***Vaccinium coriaceum* var. *coriaceum*.** MALAYSIA: Sabah, Mt. Kinabalu, 12 Jan 1932, *J. & M.S. Clemens 27852* (NY!); ibid. Ranau District, Pig Hill on east side of Mt. Kinabalu, 6.05º N, 116.6º E, 2000–3000 m, 25 May 1984, *J.H. Beaman et al. 9850* (NY!); ibid. Ranau District, Mt. Kinabalu National Park, along the summit trail between Layang-Layang station and Paka shelter, 6.05571º N, 116.56500º E, 2976 m, 5 Jul 2009, *P.W. Fritsch et al. 1859* (CAS! [487160]); ibid. trail between Layang-Layang station and Laban Rata guesthouse, at and around the Helipad, 6.05336º N, 116.56533º E, 3060 m, 14 Jun 2017, *D.S. Penneys et al. 2528* (BRIT! [BRIT402409]). ***Vaccinium coriaceum* var. *hirsuticalyx*.** MALAYSIA: Sabah, Sipitang District, Long Miau, Meligan, heath forest on podzol soil, 1238 m, 24 Mar 1999, *D. Sundaling SAN 141808* (SAN!); ibid.

Kuala Maga, Long Pasia, heath forest on podzol soil, 1300 m, 13 Apr 1999, *Diwol & Nilus SAN 141845* (SAN!). ***Vaccinium coriaceum* var. *minus*.** MALAYSIA: Sabah, Mt. Kinabalu, Panatara river, c. 2286 m, 14 Jun 1933, *J. & M.S. Clemens 32508* (NY!); ibid. Columbon river, 2500–2700 m, 12 Jul 1933, *J. & M.S. Clemens 33913* (NY!); ibid. c. 3657 m, 26 Jul 1981, *T. Sato 730* (SAN!). ***Vaccinium coriaceum* var. *stapfianum*.** MALAYSIA: Sabah, Ranau District, Mt. Kinabalu National Park, summit trail, Laban Rata guesthouse, 6.05863º N, 116.56586º E, 3266 m, 15 Jun 2017, *D.S. Penneys et al. 2533* (BRIT! [BRIT401237]); ibid. Ranau, Kamborongoh, below Mt. Kinabalu National Park, c. 2100 m, Aug 1964, *G. Mikil 46573* (SAN!). ***Vaccinium habbemae* var. *pluriglandulosum*.** INDONESIA: Indonesian New Guinea, Wichmann Mountains, 3000 m, 2 Feb 1913, *A.A. Pulle 1002* (L-image! [L.0008038]).

2. *Vaccinium maliauense* M.N.Tamayo, **sp. nov.**

Vaccinium maliauense resembles *V. phillyreoides* Sleumer but can be distinguished by the absence of glands on the leaf blade base (vs. presence), a cuneate leaf blade base (vs. acute or rounded), non-dimorphic filaments (vs. dimorphic), presence of anther spurs (vs. absence), and longer tubules (0.4–0.5 mm vs. 0.2–0.3 mm) **(Figs. 4, 5A, 5C, 5E)**. TYPE: *Jeprin & Sidkan MB78,* Borneo, Sabah, Maliau Basin Conservation Area, Camel Trophy Camp, heath forest, 1010 m, 9 Apr 2000 (holotype SAN 114310!; isotypes A, BORH, K, KEP, L).

Shrubs to small tree, 3–13 m tall, densely branched. **Young branchlets** reddish brown *in sicco*, puberulent, with simple erect trichomes 0.05–0.10 mm long; mature branchlets dark brown *in sicco*, non-ridged, glabrous, lenticellate, 2–5 mm wide; perennating buds broadly triangular, 0.5–1.0 mm long, scales overlapping, the first two outer scales ± longer than the rest of the scales, apex acute or acuminate, margin entire with occasional simple erect trichomes, 0.10–0.15 mm long. **Leaves** persistent on older branchlets, densely crowded, spirally and evenly arranged; petiole reddish brown *in sicco*, puberulent, with trichomes same as branchlets, in cross section abaxially rounded, adaxially nearly flat, 1.5–2 × 0.6–0.7 mm; leaf blade lanceolate, larger leaves on each branchlet 3.5–4.2 × 2–3 cm, coriaceous, abaxial surface light brown *in sicco*, with punctae and clavate trichomes c. 0.2 mm long, adaxial surface leathery green, dark brown *in sicco*, glabrous, base cuneate, margin entire, ± thinly revolute, marginal glands absent or non-evident, leaf blade apex acuminate, acumen 5–10 mm long, midvein raised abaxially, flattened or slightly sunken adaxially, secondary veins 3 or 4 on each side of midvein with first pair arising from base and remainder along midvein, arc-ascending, raised abaxially, obscure or non-evident adaxially, tertiary veins faintly evident or obscure. **Inflorescences** pseudo-terminal or terminal, racemose, developing beyond confines of perennating bud, 1 per leaf axil, subdensely 6- to 12-flowered, 3–4 cm long; peduncle and rachis reddish brown *in sicco*, slightly ridged, puberulent; peduncle 5–12 mm long, rachis 3–4 long cm; bracts early caducous. **Flowers** with articulation between pedicel apex and

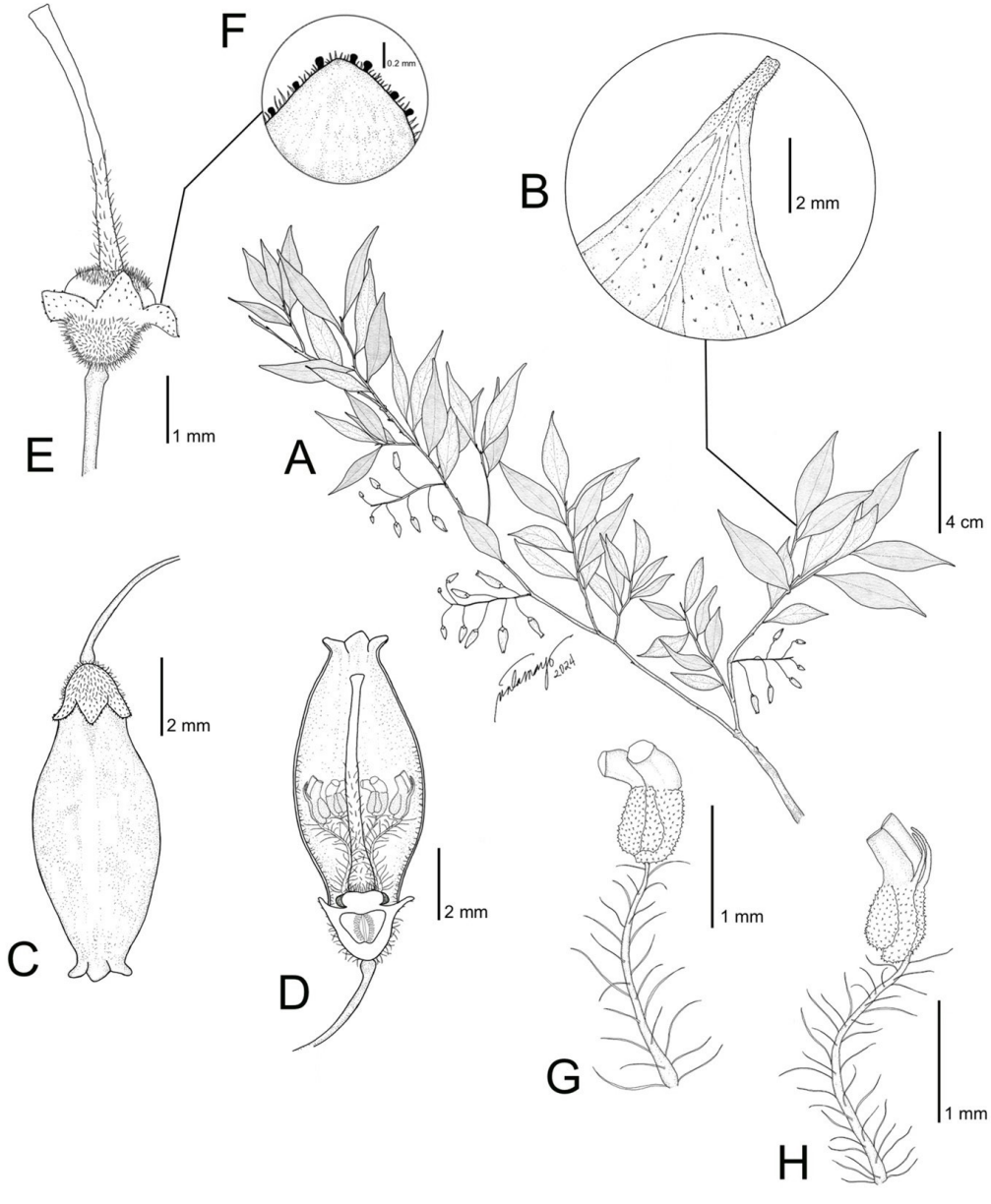

Fig. 4. *Vaccinium maliauense*. **A.** Flowering branchlet. **B.** Leaf base. **C.** Flower. **D.** Dissected flower showing stamens, style, and disk. **E.** Flower (corolla removed) exposing style and disk. **F.** Details of a calyx lobe. **G.** Stamen (ventral view). **H.** Stamen (lateral view). Illustrated by Maverick N. Tamayo, from the holotype.

Fig. 5. Comparison of characters in *Vaccinium maliauense* and *V. phillyreoides*. **A.** Leaf blade base of *V. maliauense* devoid of glands. **B.** Leaf blade base of *V. phillyreoides* showing pair of thick glands (indicated by red arrows). **C.** Flower of *V. maliauense* (corolla removed) showing hypanthium, calyx lobes, disk, and portion of style. **D.** Flower of *V. phillyreoides* showing hypanthium and calyx lobes. **E.** Stamens of *V. maliauense*, with anther spur (indicated by a red arrow). **F.** Stamens of *V. phillyreoides* showing dimorphic filaments and anthers devoid of spurs. All photos by Maverick N. Tamayo.

hypanthium, 1.5–2 cm long; pedicel reddish brown *in sicco*, slightly nodding, glabrous, 8–10 × 0.5–0.7 mm at anthesis; bracteoles early caducous; hypanthium reddish brown *in sicco*, narrowly or broadly obconical, 1–1.3 × 1–1.2 mm, densely pubescent, with simple erect trichomes 0.1–0.2 mm long and occasional clavate trichomes 0.10–0.15 mm long; calyx limb 0.3–0.4 mm long, puberulent; calyx lobes 5, broadly triangular, abaxially glabrous, adaxially puberulent, 1–1.3 × 0.5–0.8 mm, margin entire, puberulent, with occasional sessile glands 0.8– 0.10 mm long, calyx lobe apex acute, with a few simple hairs, sessile terminal gland ± present; corolla white, tubular-urceolate, glabrous outside, pubescent on lower ½ inside, 5–7 × 2–3.5 mm, trichomes simple, 0.2–0.3 mm long; lobes 5, triangular, 0.5–0.7 × 0.5–0.6 mm, apex acute or obtuse; stamens 10, monomorphic, distinct, 2.3–2.7 mm long; filaments straight or slightly curved, 1.5–1.8 mm long, white-lanate, trichomes 0.2–0.4 mm long; anthers 1.0–1.3 mm long, opening by terminal pores, shorter than filaments, cells oblong, minutely echinulate, 0.5–0.8 mm long, tubules parallel, slightly ventrally angled, broadly cylindric, 0.3–0.5 mm long, slightly narrower than cells, opening by oblique ventrally oriented apical pores, pore apex rounded, spurs present, shorter than tubules, oriented parallel to the tubules, 0.2–0.3 mm long; ovary 5- or 6-locular but appearing pseudo-10- to 12-locular with incomplete partitions extending 0.1–0.2 mm from inner wall; ovules in two columns per locule; disk semi-bulky, annular with obscure ridges on margin, 1–1.5 mm diameter, 0.3–0.5 mm depth, pubescent around base of style, hair simple, erect, 0.1–0.2 mm long; style not exserted from corolla, pubescent on lower ½ especially towards the base, 4–5 mm long, stigma truncate or rounded. **Fruit** not seen.

ETYMOLOGY. The epithet refers to the type locality at Maliau Basin, Tongod District, Sabah, Malaysia.

PHENOLOGY. Flowering in April.

DISTRIBUTION. Endemic to Borneo in the vicinity of Maliau Basin Conservation Area **(Fig. 3)**.

PROVISIONAL IUCN CONSERVATION ASSESSMENT. Only one plant in one location has been discovered. With the unavailability of data to assess this species with IUCN guidelines, we provisionally propose a conservation status of Data Deficient (DD).

NOTES. The holotype of this new species was mistakenly identified as *Vaccinium phillyreoides*. The gross morphology of the two species is similar by their multi-branching stems, lanceolate leaves with acuminate apex, and tubular-urceolate corollas. However, *Vaccinium maliauense* can be easily distinguished from *V. phillyreoides* by the absence of glands on the leaf blade base (vs. presence), broadly triangular calyx lobes (vs. ovate), and the non-dimorphic filaments (vs. dimorphic) **(Fig. 5)**. In the sterile state, the two species can be easily distinguished by the glands on the leaf blade base

(absent in *V. maliauense* vs. present in *V. phillyreoides*) **(Fig. 5A, 5B)**. The leaf blade glands may serve as extrafloral nectaries, especially in young leaves (Argent, 2019). Moreover, the distribution of the two species is non-overlapping, with *V. maliauense* found at Maliau Basin and *V. phillyreoides* restricted to west Sabah (Crocker Range, Keningau, and Sipitang).

The absence of glands on the leaf blade base of Malesian *Vaccinium* species is unusual, but it has been documented in the two Sumatran species, *V. bartlettii* Merrill and *V. nagamasu* Argent (Sleumer, 1966–1967; Argent, 2011). *Vaccinium maliauense* can be distinguished from *V. bartlettii* by having larger leaf blades (3.5–4.2 × 2–3 cm vs. 0.7–1.2 × 0.4–0.6 cm), an acuminate leaf blade apex (vs. obtuse to rounded), a longer inflorescence (3–4 cm vs. 0.5–1 cm), longer tubules (0.3–0.5 mm vs. ca. 0.1 mm), and presence of anther spurs (vs. absence), and from *V. nagamasu* by having lanceolate leaf blades (vs. obovate, broadly elliptic to subcircular), more flowers per inflorescence (6- to 12-flowered vs. 1- to 3-flowered), longer pedicels (8–10 mm vs. 3–5 mm), absence of vertical ribs on hypanthium (vs. presence), and pubescent style (vs. glabrous).

In the key to Malesian species of *Vaccinium* (Sleumer, 1966–1967), *V. maliauense* keys to *V. roseiflorum* J.J.Sm., endemic to New Guinea. *Vaccinium maliauense* can be distinguished from *V. roseiflorum* by the absence of glands at the leaf blade base (vs. presence), a long-tubular corolla (vs. suburceolate-cylindric), a pubescent corolla interior (vs. glabrous), presence of anther spurs (vs. absence), and a pubescent disk (vs. glabrous). In the key to the Bornean species of *Vaccinium* (Argent, 2019), *V. maliauense* keys to *V. elliptifolium* Merrill. *Vaccinium maliauense* can be distinguished from *V. elliptifolium* by the absence of glands at the leaf blade base (vs. presence), a cuneate leaf blade base (vs. broadly attenuate to rounded), glabrous pedicels (vs. densely pubescent), a tubular-urceolate corolla (vs. urceolate), and the presence of anther spurs (vs. absence).

ADDITIONAL SPECIMENS EXAMINED. ***Vaccinium bartlettii*.** INDONESIA: Sumatra, Summit of Dolok Soeroengan, Habinsaran, 18 May 1927, *Bartlett 8005* (G-image! [G00352256], MICH-image! [1111144]). ***Vaccinium elliptifolium*.** MALAYSIA: Sabah, Kinabalu National Park, road to power station, 13 Sep 1971, *Aban & Saikeh SAN 71862* (SAN!); ibid. Tuaran, Mt. Alab, 5º 50’ N, 116º 20’ E, slope area along Mt. Alab road on sandstone substrate, 20 Oct 2005, *Joel et al. SAN 147305* (SAN!). ***Vaccinium phillyreoides***. MALAYSIA: Sarawak, Nanga Entemu, Sungai Mengiong, Balleh, Kapit, 7th Division, mixed dipterocarp forest, 22 Oct 1988, *Othman et al. SAN 61781* (SAN!); ibid. Ulu Sungai Buong, Btg. Balui, Kapit, mixed dipterocarp forest, c. 680 m, 4 Mar 1992, *Runi et al. SAN 63618* (SAN!); BRUNEI: Belait District, Batu Patam, exposed summit, 8 Jun 1989, *K.M. Wong 1045* (SAN!). ***Vaccinium roseiflorum*.** INDONESIA: Indonesian New Guinea, Arfak Mountains, Angi lakes, edge of forest patch, December 1913, *L.S. Gibbs 5586* (BM-image! [BM000996490]).

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REFERENCES

Argent, G. (2011). *Vaccinium nagamasu* (Ericaceae), a new species (sect. *Bracteata*) from Sumatra, Indonesia. *Edinb. J. Bot*. 68: 419–422.

Argent, G. (2019). *Rigiolepis* and *Vaccinium* (Ericaceae) in Borneo. *Edinb. J. Bot*. 76: 55–172.

Bachman, S., Moat, J., Hill, A.W., dela Torre, J. & Scott, B. (2011). Supporting Red List threat assessments with GeoCAT: Geospatial conservation assessment tool. *ZooKeys* 150: 117–126.

Beentje, H. (2016). *The Kew plant glossary, Second Edition*. Kew Publishing. pp. 1–200.

Breitfeld, H.T., Hall, R., Galin, T., Forster, M.A. & BouDagher-Fadel, M.K. (2017). A Triassic to Cretaceous Sundaland-Pacific subduction margin in West Sarawak, Borneo. *Tectonophysics* 694: 35–56.

Cronquist, A. (1978). Once again, what is a species? In: Knutson, L.V. (ed.) *Biosystematics in agriculture*. Allenheld Osmin, Montclair, New Jersey. pp. 3–20.

de Bruyn, M., Stelbrink, B., Morley, R.J., Hall, R., Carvalho, G.R., Cannon, C.H., van den Bergh, G., Meijaard, E., Metcalfe, I., Boitani, L., Maiorano, L., Shoup, R. & von Rintelen, T. (2014). Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. *Syst. Biol*. 63: 879–901.

Hall, R. & Morley, C.K. (2004). Sundaland Basins. In: Clift, P., Wang, P., Kuhnt, W., Hayes, D.E. (eds.), Continent-ocean interactions within the East Asian marginal seas. *Geophysical Monogr. Ser*. 149: 55–85.

Hertwig, S.F., Schweizer, M., Das, I. & Haas, A. (2013). Diversification in a biodiversity hotspot −The evolution of Southeast Asian rhacophorid tree frogs in Borneo (Amphibia: Anura: Rhacophoridae). *Mol*. *Phylogenet. Evol*. 68: 567–581.

IUCN Standards and Petitions Committee (2022). *Guidelines for using the IUCN Red List Categories and Criteria*. *Version 15*. Prepared by the Standards and Petitions Committee. Available from: http://www.iucnredlist.org/documents/RedListGuidelines.pdf. Accessed: 2 Dec 2022.

Khan, A.A. (2018). An appraisal of the tectonic evolution of SW Borneo constraints from petrotectonic assemblage and gravity anomaly. *Bull*. *Geol*. *Soc*. *Malaysia* 66: 47–56.

Nakai, T. & Koidzumi, G. (1927). *Trees and shrubs indigenous in Japan proper* (revised ed.), Vol. 1, Seibido Shoten, Tokyo, 714 pp.

Pelser, P.B., Barcelona, J.F. & Nickrent, D.L. (ed.) (2011 onwards). *Co's Digital Flora of the Philippines*. https://philippineplants.org. Accessed: 15 Jan 2024.

POWO (2024). Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. http://plantsoftheworldonline.org/. Accessed: 21 Dec 2023.

Sleumer, H. (1961). Florae Malesianae precursores XXVVIII. The genus *Vaccinium* in Malaysia. *Blumea* 11: 9–112.

Sleumer, H. (1966–1967). Ericaceae: In: C.G.G.J. van Steenis (Ed.) *Flora Malesiana*, ser. 1, vol. 6, Parts 4, 5, Groningen, Netherlands: Wolters-Noordhoff.

Thiers, B. (2023, continuously updated). Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/. Accessed: 27 Dec 2023.

van Welzen, P.C., Slik, J.W.F. & Alahuhta, J. (2005). Plant distribution patterns and plate tectonics in Malesia. *Biologiske Skrifter* 55: 199–217.

Vander Kloet, S.P. (2005). The taxonomy of *Vaccinium* section *Rigiolepis* (Vaccinieae, Ericaceae). *Blumea* 50: 477–497.

Vander Kloet, S.P. & Dickinson, T.A. (2009). A subgeneric classification of the genus *Vaccinium* and the metamorphosis of *V.* section *Bracteata* Nakai: more terrestrial and less epiphytic in habit, more continental and less insular in distribution. *J*. *Plant Res*. 122: 253–268.

Wooster, M.J., Perry, G.L.W. & Zoumas, A. (2011). Fire, drought and El Niño relationships on Borneo during the pre-MODIS era (1980–2000). *Biogeosci*. *Discuss*. 8: 975–1013.

Yumul, G.P., Jr. (2007). Westward younging disposition of Philippine ophiolites and its implication for arc evolution. *Isl*. *Arc* 16: 306–317.