

NEPENTHES BERBULU (Nepenthaceae), A PITCHER PLANT FROM
PENINSULAR MALAYSIA WITH REMARKABLY LONG LID BRISTLES

HONG L. TAN* • Monash University Malaysia • Jalan Lagoon Selatan • Bandar Sunway • 47500
Subang Jaya • Selangor • Malaysia • nicholas.hl.tan@gmail.com

GIDEON LIM* • B-07-03, Tower B, Epic Residence • Jalan BP 7/12 Bandar Bukit Puchong 2 • 47120
Puchong • Selangor • Malaysia • malaysiacarnivorouplants@gmail.com

FRANÇOIS SOCKHOM MEY* • 2 bis rue de l'église • 27110 Le Tremblay-Omonville • France
• meyfr@yahoo.fr

MICHAL R. GOLOS* • School of Biological Sciences • University of Bristol • 24 Tyndall Avenue
• Bristol, BS8 1TQ • UK • michal.golos@bristol.ac.uk

ANDREAS WISTUBA • Friedhofweg 4 • 88437 Maselheim • Germany • andreas@wistuba.com

STEWART R. MCPHERSON • Redfern Natural History Productions • 61 Lake Drive • Hamworthy
• Poole, Dorset, BH15 4LR • UK • stewart@mcpherson.net

ALASTAIR S. ROBINSON* • National Herbarium of Victoria • Royal Botanic Gardens Victoria
• Melbourne, VIC 3004 • Australia • alastair.robinson@rbg.vic.gov.au

* Authors for correspondence

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Abstract: A species of *Nepenthes* endemic to Peninsular Malaysia and distinctive for its extremely developed lid hairs is described and illustrated. *Nepenthes berbulu* is a highland species known only from a handful of peaks in the Titiwangsa Range. It is classified here within the recently defined *N. macfarlanei* group, for which a dichotomous key is provided. The description of this taxon brings the total number of *Nepenthes* species recognised from Peninsular Malaysia to eighteen.

Introduction

Nepenthaceae Dumort. is a monotypic family comprising the genus *Nepenthes* L., a group of carnivorous plants commonly known as tropical pitcher plants, or *periuk kera* ('monkey pots') in Malay. This genus of at least 160 accepted species is primarily distributed across the Malesian and Papuan biogeographic regions, with centres of diversity in Sumatra, Borneo, and the Philippines (Danser 1928; Jebb & Cheek 1997; Clarke *et al.* 2018). In the last 20 years, the genus has received significant attention from botanists and enthusiasts alike, resulting in a series of significant discoveries that have led to the description of many taxa at species rank, as well as emended circumscriptions of existing species concepts (Akhriadi *et al.* 2004; Clarke *et al.* 2006; Mey *et al.* 2011; Cheek & Jebb 2013; Robinson *et al.* 2019; Bianchi *et al.* 2020; Golos *et al.* 2020).

Despite being situated between the exceptionally speciose islands of Sumatra and Borneo, Peninsular Malaysia has, until very recently, been considered comparatively poor with respect to *Nepenthes* with only 11 recognised species (Clarke 1999, 2001; McPherson 2009; Clarke & Lee 2012; McPherson & Robinson 2012).

Recently, novel explorations of poorly botanised peaks coupled with systematic reviews of living and pressed *Nepenthes* from more frequently visited peaks across the Malay peninsula have led to the definition of several hitherto undescribed species. Since 2020, five species have been named: *N. domei* M.N.Faizal, A.Amin & Latiff; *N. latiffiana* M.N.Faizal, A.Amin & Dome; *N. malayensis* A.Amin, M.N.Faizal & Dome; *N. sericea* Golos, Wistuba, G.Lim, Mey, S.McPherson & A.S.Rob.; and *N. ulukaliana* Wistuba, Mey, Golos, G.Lim, S.McPherson & A.S.Rob. (Ghazalli *et al.* 2020; Tamizi *et al.* 2020a; Lim *et al.* in prep. 2023). One nothospecies — *N. × setiuensis* A.Amin, M.N.Faizal & Dome — has also been described during this time (Tamizi *et al.* 2020b). Though considered a natural hybrid between *N. macfarlanei sensu lato* and *N. gracilis* by its describing authors, it is here found indistinguishable from *N. gracillima*, of which *N. setiuensis* is thus considered a later synonym.

Building on the works of Hemsley and Ridley in the region (Hemsley 1905; Ridley 1908, 1909, 1924), an outcome of these recent studies has been a revised delimitation of the *Nepenthes macfarlanei* concept — resolving some taxonomic uncertainty surrounding this species — and the circumscription of a group of taxa closely allied with it. These comprise *N. macfarlanei sensu stricto*, *N. alba*, *N. gracillima*, and the as yet undescribed *N. sericea* and *N. ulukaliana* (Lim *et al.* in prep. 2023). To this group is here added *Nepenthes berbulu* H.L.Tan, G.Lim, Mey, Golos, Wistuba, S.McPherson & A.S.Rob., thus far observed from five peaks in the Titiwangsa Range, all in the Pahang–Perak and Pahang–Selangor border regions. This brings the total number of species recognised from Peninsular Malaysia to eighteen (Table 1).

Materials and methods

Field observations of *Nepenthes berbulu* were made in February 2020 and August 2022. Allied taxa were studied across peaks of the Bintang Range (Gunung Bubu), Timur Range (Gunung Tahan), and Titiwangsa Range (Cameron Highlands, Genting Highlands, Fraser’s Hill, and others). Voucher specimens were examined at K, KEP, L, and SING herbaria (acronyms follow Thiers 2022+).

Herbarium material was collected by Gideon Lim under permit ref. JH/100 Jld. 33(35) issued by the Forest Department of Peninsular Malaysia, and subsequently deposited at KEP and KLU. Fine measurements of live material were made using Vernier callipers and a tape measure. Measurements on herbarium material of small-scale structures such as hairs were made using a stereomicroscope. Close-ups of voucher specimens were taken using a Canon EOS 80D with Canon EF 100mm f/2.8L Macro IS USM.

Locality data for the distribution map was taken from herbarium records and information gathered from field observations and plotted using SimpleMapp (Shorthouse 2010).

Species description

The following description of *Nepenthes berbulu* is based on the type material, and observations and measurements made *in situ* at the type locality, chiefly of the summit population; plants growing at slightly lower elevations in montane forest generally produce larger foliage and longer tendrils.

Nepenthes berbulu H.L.Tan, G.Lim, Mey, Golos, Wistuba, S.McPherson & A.S.Rob., *spec. nov.* (Figs. 1–10)

Table 1. A summary of the known *Nepenthes* of Peninsular Malaysia.

Species	Elevational range (m)	Distribution
<i>N. alba</i>	1400–2187	Peninsular Malaysia
<i>N. albomarginata</i>	0–1100	Borneo, Peninsular Malaysia, and Sumatra
<i>N. ampullaria</i>	0–2100	Borneo, Maluku Islands, New Guinea, Peninsular Malaysia, Riau Islands, Singapore, Sumatra, and Thailand
<i>N. benstonei</i>	150–1350	Peninsular Malaysia
<i>N. berbulu</i>	1400–2100	Peninsular Malaysia
<i>N. domei</i>	850–1000	Peninsular Malaysia
<i>N. gracilis</i>	0–1100	Borneo, Cambodia, Peninsular Malaysia, Riau Islands, Singapore, Sulawesi, Sumatra, and Thailand
<i>N. gracillima</i>	900–2000	Peninsular Malaysia
<i>N. kerrii</i> *	150–700	Peninsular Malaysia (Langkawi) and Thailand
<i>N. latiffiana</i>	1000–1100	Peninsular Malaysia
<i>N. macfarlanei</i>	1500–1657	Peninsular Malaysia
<i>N. malayensis</i>	800–1000	Peninsular Malaysia
<i>N. mirabilis</i>	0–1500	Malay Archipelago, Indochina, southern China, northern Australia, and western Micronesia
<i>N. rafflesiana</i>	0–1200	Borneo, Peninsular Malaysia, Riau Islands, Singapore, and Sumatra
<i>N. ramispina</i>	900–2000	Peninsular Malaysia
<i>N. sanguinea</i>	300–1800	Peninsular Malaysia and Thailand
<i>N. sericea</i>	900–2150	Peninsular Malaysia
<i>N. ulukaliana</i>	900–1800	Peninsular Malaysia

*The presence of this species in Peninsular Malaysia is based on a population occurring on Langkawi Island, in the Malaysian state of Kedah. This island taxon, clearly a member of the Indochinese *Nepenthes thorelii* aggregate, is tentatively identified as *N. kerrii* following Clarke (2018).

Type: — MALAYSIA. **Perak:** Titiwangsa Range, above 1900 m (exact location withheld for conservation reasons), 23 August 2022, *Lim 4* (holotype KEP!, isotypes KEP! [7 sheets] & KLU! [2 sheets]) [holotype: stem with three upper pitchers, female inflorescence, and infructescence; iso-KEP: stem with two lower pitchers (sheet 1), stem with two upper pitchers (sheets 2 & 3), stem with two lower to intermediate pitchers (sheet 4), stem with intermediate pitcher (sheet 5), stem with two infructescences (sheet 6), stem with male inflorescence (sheet 7); iso- KLU: stem with upper pitcher and infructescence (sheet 1), stem with two lower pitchers (sheet 2)].

Diagnosis: — *Nepenthes berbulu* differs from *N. macfarlanei* in having laminae of short and climbing stems that are oblong-elliptic with rounded-obtuse apices (vs. lanceolate with acute apices); lower pitchers that are broadly infundibular in lower half and cylindrical above a pronounced hip (vs. ovate in lower half and cylindrical above a faint hip); upper pitchers that are infundibular at the base and broadly cylindrical above a basally situated hip, with a flattened ventral surface between

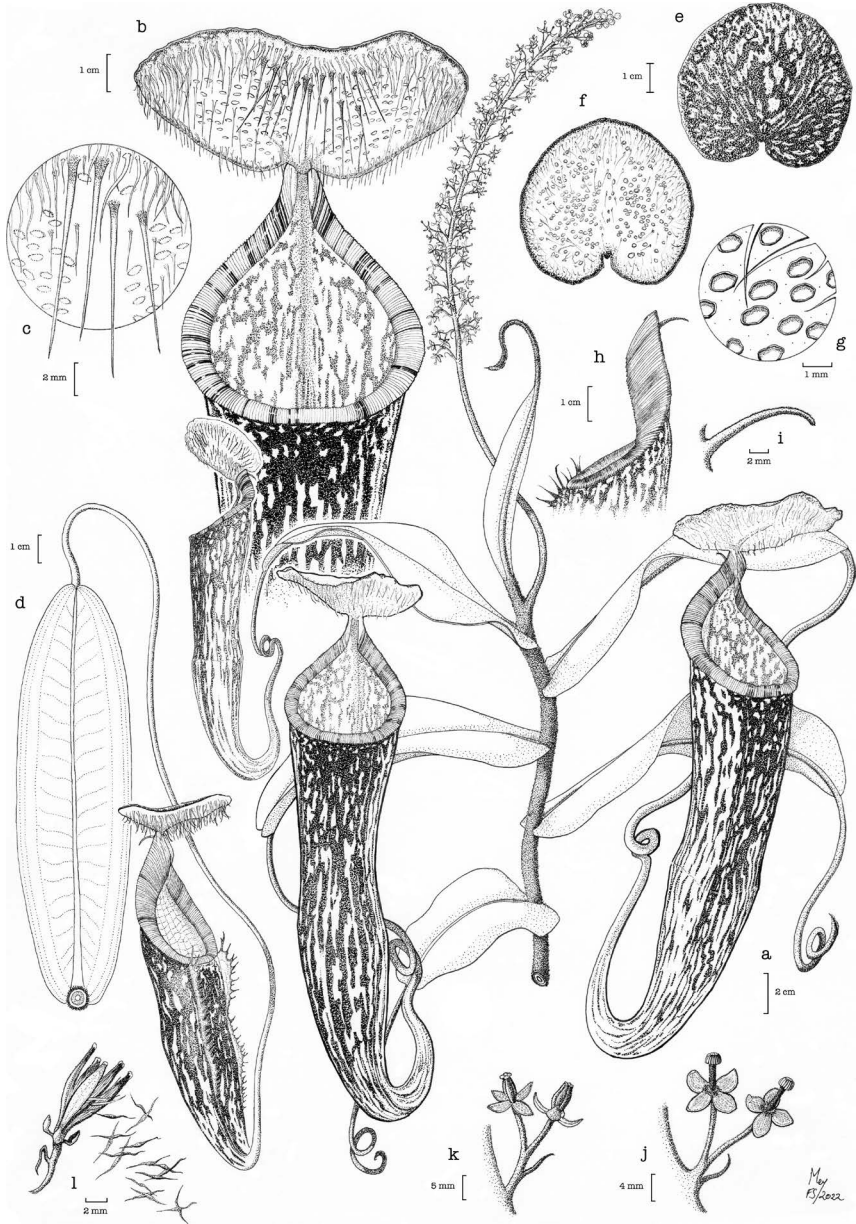


Figure 1: *Nepenthes berbulu* H.L.Tan, G.Lim, Mey, Golos, Wistuba, S.McPherson & A.S.Rob. (a) Habit with upper pitchers and male inflorescence. (b) Close-up of upper pitcher showing lid underside and mouth. (c) Detail of thickened bristles near lid apex. (d) Rosette leaf with lower pitcher. (e) Upper surface of lower pitcher lid. (f) Lower surface of lower pitcher lid. (g) Detail of lower pitcher lid glands. (h) Peristome of lower pitcher in lateral aspect, showing pronounced column. (i) Spur. (j) Male flowers. (k) Female flowers. (l) Seedpod with dispersing seeds. Based on the type material (*Lim 4*) and photographs and measurements made *in situ* at the type locality. Illustration by F.S. Mey.



Figure 2: *Nepenthes berbulu*. Robust female flowering plant with upper pitchers growing among summit scrub at the type locality; note the dried infructescence to the left. Photograph by F.S. Mey.

the wing vestiges (vs. wholly infundibular with a hip just below peristome or absent, and often slightly constricted below the mouth causing ventral gibbosity); and bristles on lower surface of lid aggregated towards lid apex (vs. evenly distributed).

Description: — Terrestrial, erect, subscentent or climbing shrub. *Stems* branched, to ca. 3–5 m long, generally terete, occasionally slightly angular in basal part of mature vine, 5–10 mm in diameter, basal part ligneous, woody, becoming brittle with age, herbaceous and ductile above. Internodal length 1.5–5.5 cm in rosettes, 1.7–9 cm in climbing stems. *Leaves* sessile, ± spirally

arranged, sometimes intermittently distichous. Laminae coriaceous, thick, brittle when mature, suboblanceolate to oblong in seedlings and young rosettes, oblong-elliptic to slightly obovate in short and climbing stems, 9.5–19 cm long, 3.5–6.5 cm wide, margins entire, apex rounded-obtuse, sometimes emarginate and/or slightly asymmetrical at tendril attachment, base cuneate, clasping stem for $\geq 3/4$ of its circumference, not decurrent, sometimes very slightly auriculate with indistinct lobes in rosette stage. Longitudinal veins 3 on either side of midrib in outer 1/2 of lamina, barely discernible in living specimens, conspicuous in herbarium material, pinnate veins distinct near midrib. Tendrils of rosette pitchers uncoiled, 10–26 cm long, tendril length to pitcher height ratio 3:1 to 4:1; of lower to intermediate pitchers uncoiled, 23–41 cm long, 3–5 mm wide, generally of ratio 1.7:1 to 2.5:1; of upper pitchers coiling once or twice, 9–22(–50) cm long, 2–5 mm wide, often shorter than pitcher height, generally of ratio 1:1 to 1:1.7. *Rosette pitchers* infundibular to narrowly obovate in lower half, slightly constricted at midpoint to form a hip, \pm cylindrical above, widening slightly



Figure 3: *Nepenthes berbulu*. Lower pitchers borne on long tendrils among summit scrub at the type locality. Photograph by F.S. Mey.

towards mouth, to *ca.* 7 cm tall, *ca.* 2 cm wide, tendril ventrally attached, wings ≤ 3 mm wide with fringe elements ≤ 3 mm long and ≤ 2.5 mm apart, mouth ovate, oblique, raised towards rear to form a recurved neck ≤ 3 cm tall, peristome sub-cylindric in section, 1.6–2 mm wide at front, broadening and flattening towards rear of pitcher, reaching 3.2–4 mm at column, ribs fine but pronounced, teeth triangular-acuminate, minute. Lid sub-elliptical to orbicular or reniform, apex rounded to obtuse, occasionally retuse, base sometimes cordate, lower surface densely covered with bristles ≤ 4 mm long, inclined towards lid base and interspersed with large nectar glands. Spur simple, filiform, apex acute. *Lower to intermediate pitchers* often with free-hanging tendrils, broadly infundibular in lower half, delimited by \pm pronounced hip, cylindrical above, 12–25 cm tall, 4–6 cm wide at peristome, 4–5.5 cm wide at hip, tendril ventrally or laterally attached. Wings 2–5 mm wide with fringe elements ≤ 8 mm long, widely spaced. Mouth ovate to rounded-triangular, oblique. Peristome 10–17 mm wide at column, 4–7 mm wide at front, with fine but pronounced ribs, teeth minute but clearly



Figure 4: *Nepenthes berbulu*. Lower to intermediate pitchers at the type locality. Photograph by A. Wistuba.

discernible in rear portion. Lid orbicular to reniform, usually slightly broader than long, 5–6.5 cm long by 5–7 cm wide, orientated horizontally to *ca.* +30° from horizontal, apex rounded to obtuse, rarely broadly retuse, base cordate, lower lid surface with rigid aciculate bristles, fleshy at base where 0.5 mm wide, 7–10 mm long, ± orientated towards centre of lid, often with particularly dense aggregations near lid apex and largely absent from central portion, interspersed with large glands, lid glands elliptical, crateriform, conspicuously rimmed, *ca.* 0.5–1.5 mm in diameter, concentrated in two groups on either side of midline or ± evenly distributed throughout. Inner pitcher surface glandular in basal half, remainder waxy. Spur inserted near base of lid, simple, filiform, 8–14 mm long, apex acute, often slightly curved downwards. *Upper pitchers* broadly infundibular in basal 2/5 to 1/2, narrowing slightly just above the pronounced hip, ± cylindrical above with flattened ventral surface between wing vestiges, often widening markedly just below peristome, chartaceous in upper portion, becoming woody below hip, 15–27 cm tall, 4–8 cm wide at peristome, 3.5–5 cm wide at hip, tendril dorsally attached. Wings reduced to prominent ridges, sometimes with fringed remnants immediately below peristome. Mouth ovate to rounded-triangular, oblique, ascending laterally at an angle of 50–60° towards pitcher rear, gradually becoming vertical at column, column ≤5.5 cm tall and recurved towards pitcher opening at angle of 10–20°. Peristome sub-cylindric in section, 3–8 mm wide at front, broadening and flattening towards rear of pitcher, reaching 9–18 mm at column, ribs *ca.* 0.5 mm apart, conspicuous teeth present only in rear portion of peristome, serrulate, fine, triangular-acuminate. Lid orbicular to reniform, often slightly wider than long, 5–7.5 cm long by 5–7 cm wide, otherwise as in lower to intermediate pitchers. Lower lid surface with numerous rigid bristles ≤10 mm long, form and distribution as in lower to intermediate pitchers. Basal half to two-thirds of inner pitcher surface densely glandular, upper third waxy. Spur as in lower to intermediate pitchers, 3–10 mm long. *Male inflorescence* mostly two-flowered throughout, *ca.* 100 flowers in total, peduncle *ca.* 16 cm long, rachis *ca.* 19 cm long, bracts prominent, simple, filiform, inconsistently produced. Tepals ovate to broadly elliptic, *ca.* 4 mm long, 2 mm wide, apex obtuse to rounded, adaxially concave with numerous nectar glands. *Female inflorescence* basally two-flowered, one-flowered above, *ca.* 35 flowers in total, peduncle 16–20 cm long, rachis 8.5–10 cm long, bracts as in male flowers, tepals elliptic, *ca.* 5 mm long, 2 mm wide, apex acute. Seeds fusiform, *ca.* 5 mm long, centrally rugose, with well-developed wings. *Odour* vanilla-like. *Indumentum* of orange-brown to rufous hairs, variable in development and extent; that of stem ≤1 mm long in leaf axils, apical portion with dense layer of fine brown hairs, otherwise much shorter, patchy to glabrescent; inconspicuous on abaxial leaf surface except on midribs where similar to that of leaf axils, adaxial surface mostly glabrous, but sparsely covered in short, fine brown hairs, mainly concentrated on and around midrib; emergent tendrils covered in short, soft, velvety brown caducous hairs; mature pitchers appearing glabrous; inflorescences with brown pubescence throughout, particularly on partial peduncles, pedicels, tepal bases and abaxial surfaces, fruit bases, and androphore.

Colour of mature stems dark orange, dark brown or nearly black. Leaves bright green. Lower pitchers yellow, yellowish green, olive green or dark pink, mottled with dark red, dark brown to purple speckles. Peristome yellowish green with reddish stripes so numerous that it appears entirely red, dark red, or dark purple. Lower pitcher lid as per the pitcher body on the upper surface, yellowish green slightly suffused with red in the margins on the lower surface. Upper pitchers pale green at the base becoming progressively creamy to bright white above, with red, dark red, or maroon speckling, or occasionally coloured entirely red or black with white, yellow, or green speckles. Peristome predominantly bright to pure white with some red stripes. Lid mostly white on both surfaces, sometimes suffused with red in the margins. Bristles white, pale green, orange, dark orange to dark brown or almost black.

Additional specimens examined

Nepenthes berbulu — MALAYSIA. **Pahang:** Titiwangsa Range, summit, ca. 2040 m [“6700 ft”] (exact location withheld for conservation reasons), no date, *Wray 339* (SING!) [stem with upper pitchers; identified as possibly *N. gracillima* × *N. macfarlanei* by B.H. Danser, August 1927]; Titiwangsa Range, ca. 1400 m [“ca. 4600 ft”] (exact location withheld for conservation reasons), June 1933, *Banfield s.n.* (SING! [2 sheets]) [stems with lower pitchers (both sheets)]; Titiwangsa Range, near summit, ca. 1460 m [“4800 ft”] (exact location withheld for conservation reasons), 30 December 1939, *Holtum S.36511* (SING! [2 sheets]) [rosette with pitchers and stem with lower pitcher



Figure 5: *Nepenthes berbulu*. Intermediate pitcher at the type locality. Photograph by F.S. Mey.



Figure 6: *Nepenthes berbulu*. Intermediate pitcher at the type locality; note the exceptionally dense, whitish, thickened bristles of the lid. Photograph by A. Wistuba.

(sheet 1); separate lower pitcher and lamina (sheet 2)]; Titiwangsa Range, ca. 1460 m [“4800 ft”] (exact location withheld for conservation reasons), 30 December 1939, *Holttum 36512* (SING!) [stem with upper pitcher]; Titiwangsa Range, summit, ca. 1370 m [“ca. 4500 ft”] (exact location



Figure 7: *Nepenthes berbulu*. Upper pitchers from the type locality at ca. 1900 m (A–C) and from a different peak at ca. 1400 m (D). Photographs by A. Wistuba (A) & F.S. Mey (B–D).

withheld for conservation reasons), 23 September 1940, *Addison S.37379* (SING!) [stem with upper pitchers and infructescence]; Titiwangsa Range, heath forest at summit plateau, ca. 2020 m [“6600 ft”] (exact location withheld for conservation reasons), 22 September 1994, *Chua et al. FRI 39045* (KEP!) [stem with upper pitchers and infructescence]; Titiwangsa Range, heath forest at summit plateau, ca. 1430 m [“4700 ft”] (exact location withheld for conservation reasons), 23 September



Figure 8: *Nepenthes berbulu*. A robust plant with particularly colourful upper pitchers growing among summit scrub at the type locality. Photograph by F.S. Mey.

1994, *Chua et al. FRI 39048* (KEP! [4 sheets], L!, SING!) [stems with upper pitchers and female floral material (all sheets)].

Nepenthes macfarlanei — MALAYSIA. **Perak:** G. Bubu, ca. 1460–1620 m [“4800–5300 ft”], March 1885, *Dr. King’s Collector 7395* (SING!) [stem with upper pitcher and male inflorescence]; G. Bubu, ca. 1460–1620 m [“4800–5300 ft”], March 1885, *Dr. King’s Collector 7421* (**lectotype** K! [designated by Jebb & Cheek 1997:57], isolecto- K! [3 sheets]) [separate lower, intermediate, and upper pitchers (lecto-); stem with upper pitcher and male inflorescences (isolecto- sheet 1); stem with upper pitchers (isolecto- sheet 2); separate lower and intermediate pitchers (isolecto- sheet 3)]; G. Bubu, summit, no elevation data, 8 April 1933, *Symington FMS 30848* (KEP!) [stem with upper pitchers]; G. Bubu, summit, 1656 m [“5434 ft”], 31 January 1938, *Lindow FMS 45159* (KEP!) [stems with upper pitchers and female inflorescences]; summit of G. Bubu via Manong, ca. 1650 m [“5400 ft”], 10 June 1978, *Shah & Mahmud MS 3986* (KEP!, SING!) [stem with upper pitcher (KEP); stem with upper pitchers and infructescence (SING)]; G. Bubu Besar, summit trail to G. Bubu Kecil, 1600 m, 20 April 1995, *Chua*



Figure 9: *Nepenthes berbulu*. Lid underside showing thickened bristles; note that they are concentrated towards the apex and margins of the lid. Photograph by A. Wistuba.

FRI 39091 (KEP!, L!) [stem with upper pitcher and infructescence (KEP); stem with upper pitchers and male inflorescence (L)]; G. Bubu summit, exposed montane forest, 1657 m, 20 December 2006, *Lim FRI 52833* (KEP!) [stem with upper pitcher]; G. Bubu summit, mossy shaded montane forest, 1653 m, 20 December 2006, *Lim FRI 52835* (KEP!) [stem with lower pitchers]; G. Bubu, 1615 m, 17 August 2022, *Lim 2* (KEP! [3 sheets]) [stem with upper pitchers and infructescence (sheet 1); stem with lower pitchers (sheet 2); stem with upper pitchers and male inflorescence (sheet 3)].

Only type material is enumerated for the following species. For an exhaustive list of examined specimens refer to Lim *et al.* (in prep. 2023).

Nepenthes alba — MALAYSIA. **Pahang:** G. Tahan, ca. 1520 m [“5000 ft”], 3 June 1905, *Wray & Robinson 5411* (**lectotype** SING! [designated by Jebb & Cheek 1997:44], isolecto- BO n.v.) [stem with upper pitchers and male inflorescence (SING)].

Nepenthes gracillima — MALAYSIA. **Pahang:** G. Tahan, ca. 1010 m [“3300 ft”], 29 May 1905, *Wray & Robinson 5309* (**lectotype** SING! [designated by Jebb & Cheek 1997:43], isolecto- BO n.v.) [stem with upper pitchers].

Nepenthes sericea — MALAYSIA. **Kelantan:** G. Warpu, 1745 m, 19 August 2022, *Lim 3* (**holotype** KEP!, isotypes KEP! [3 sheets]) [stem with upper pitchers and male inflorescences (holo-); stem with lower pitcher (iso- sheet 1); stem with upper pitchers and infructescences (iso- sheet 2); stem with upper pitchers (iso- sheet 3)].

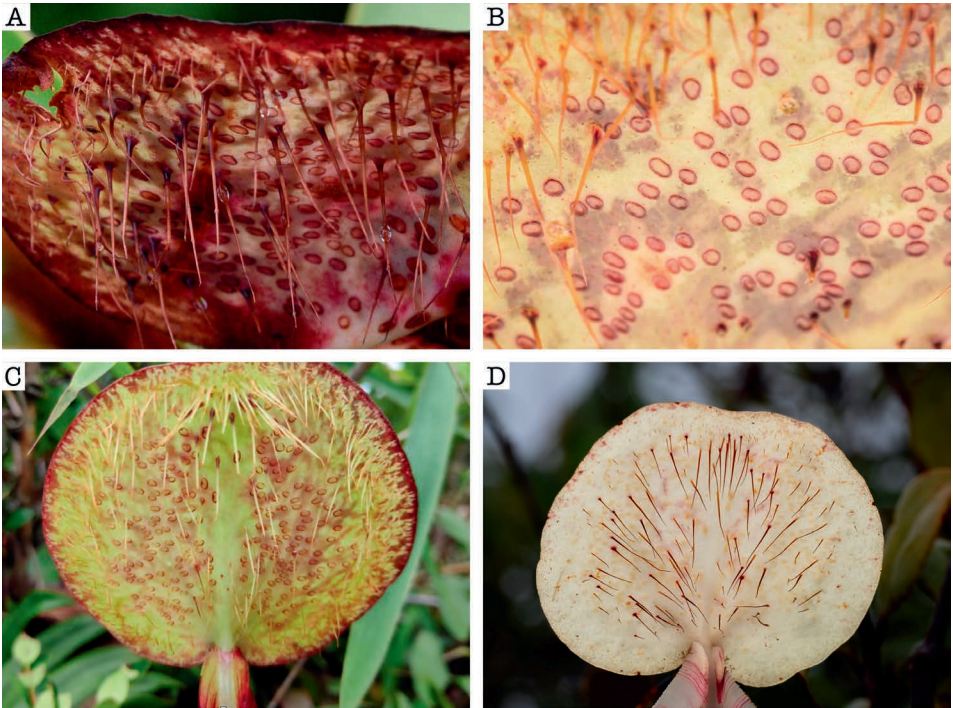


Figure 10: *Nepenthes berbulu*. Details of lower lid surface: (A) close-up of the thickened bristles of an aged lower pitcher; note droplets of condensed water; (B) conspicuously rimmed, crateriform nectar glands of a preserved pitcher; (C) a typical arrangement of bristles with two 'bald patches', one either side of the midline; note dense apical aggregation; (D) an upper pitcher lid unusually lacking both the lateral 'bald patches' and bristles near the lid margins. Photographs by M.R. Golos (A), H.L. Tan (B), G. Lim (C) & A. Wistuba (D).

Nepenthes ulukaliana — MALAYSIA. Pahang: G. Ulu Kali, 3°26.21'N 101°47.11'E, 1707 m, 16 February 2007, *Julius FRI 54894* (holotype KEP!) [stem with upper pitchers and male inflorescences].

Etymology: — The epithet *berbulu* is derived from the Malay prefix *ber-* (having) and the noun *bulu* (hair, bristle), in reference to the basally fleshy bristles found on the lower surface of the pitcher lid.

Botanical history: — In 2019, photographs taken by hikers in the southern Titiwangsa Range (Peninsular Malaysia) were noticed online by author GL showing a highland *Nepenthes* with long, needle-like bristles beneath its lid. An expedition by HLT, GL, Bryan Chong Yik Khuan, Khairisyahmie Bin Khairisham, and two guides was successfully made in February 2020 to survey the plants *in situ*. Inspection of the plant's coarse morphological characteristics suggested that the plants represent an undescribed species.

However, author ASR noted that the lid hairs of this undetermined taxon closely resemble those present in the type material of *Nepenthes macfarlanei* at Kew herbarium (*King's Collector 7421*; lecto- K, isolecto- K) collected on Gunung Bubu, though the pitchers were otherwise divergent in

shape. The original description of *N. macfarlanei* by Hemsley (1905) refers specifically to the “stiff bristles” present beneath the lid; however, Macfarlane (1914) describes the taxon as “bearing few to many long rigid unicellular hairs”, a different prospect to thickened, multicellular bristles. The possibility was thus raised that the newly documented plants might be congruent with type *N. macfarlanei* from its *locus classicus* on Gunung Bubu, leading to concerns about the appropriateness of the prevailing concept of *N. macfarlanei sensu lato* as a widely distributed and highly variable species that produces hairs beneath its lid that are simply highly variable in terms of length, firmness, and micromorphology (Danser 1928; McPherson 2009; Cheek & Jebb 2012; Clarke & Lee 2012; McPherson & Robinson 2012). Herbarium specimens of *N. macfarlanei* from Gunung Bubu held at Kepong Herbarium (KEP) were examined by HLT, who noted that, though they possessed the stiff, thickened bristles described, they exhibited a different distribution of bristles beneath the lid to the taxon described here as *N. berbulu*, in addition to different upper pitcher shape.

Subsequent expeditions were organised in order to visit the *locus classicus* of *Nepenthes macfarlanei*, Gunung Bubu, to generate an up to date and accurate circumscription of the species, as well as to visit several parts of the Titiwangsa Range to photograph, collect, and study both the potentially undescribed taxon and other populations of *N. macfarlanei sensu lato* so as to support a comprehensive comparison with the type. These expeditions were halted when the SARS-CoV-2 (Covid-19) pandemic made non-essential travel impossible for 2 years.

In August 2022, the study resumed when FSM, SRM, AW, and MRG set up an expedition to Peninsular Malaysia to join the Malaysian authors HLT and GL. The team was able to locate *Nepenthes macfarlanei* on Gunung Bubu that perfectly matched the Kew type specimens.

The field study led to an emended description of the hitherto poorly understood *Nepenthes macfarlanei*, and descriptions of two taxa previously lumped within “*N. macfarlanei*” *s.lat.*, namely *N. sericea* and *N. ulukaliana* from the Cameron Highlands and Genting Highlands, respectively (Lim *et al.* in prep. 2023). It also became clear that the plants found in the southern Titiwangsa Range that prompted this comprehensive study do indeed differ consistently from *N. macfarlanei s.str.*

During the course of the second expedition series, mountain guides showed the authors a photograph of a half-dried pitcher with long bristles resembling those of *Nepenthes berbulu* and *N. macfarlanei* taken on a low (*ca.* 1400 m asl) peak 15 km to the south of the type locality. This specimen matched herbarium records of a species with long bristles collected from the same location. That peak was climbed by GL, FSM, MRG, and AW, who were able to locate three plants and confirm that they also represent *N. berbulu*. These three individuals represent the currently known southernmost occurrence of this species, as well as the lowest elevation from which it has been recorded. Most other known records of *N. berbulu* are from above 1900 m asl.

Phenology: — Male inflorescences of *Nepenthes berbulu* were observed during the first expedition in late February 2020. Some developing female inflorescences and seedpods were found as well but in smaller numbers. Infructescences and both male and female inflorescences were observed in August 2022 (Fig. 2).

Distribution and ecology: — *Nepenthes berbulu* has been recorded from five peaks in the south-central Titiwangsa Range, between 1400 and 2100 metres above sea level (Fig. 11). At the type locality, *N. berbulu* is common within a relatively narrow elevational band from *ca.* 1900 m to the summit, where it is the only *Nepenthes* present. The upper reaches of the mountain are frequently covered in dense cloud even at midday during the dry season, supporting the development of an extensive mossy forest (Fig. 12). On one other peak, at *ca.* 1400 m, *N. berbulu* grows sympatrically

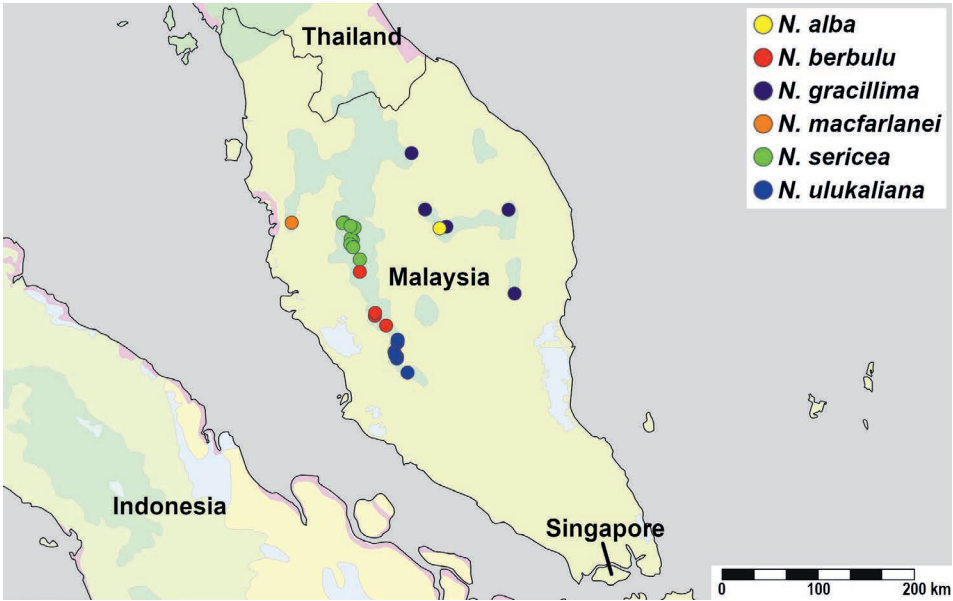


Figure 11: Known distribution of *Nepenthes berbulu* and closely related species of the *N. macfarlanei* group, based on field observations and voucher specimens. Several of the *N. gracillima* localities are based on tentative identifications and require field work to confirm. The coloured areas show ecoregions defined by the World Wide Fund for Nature (WWF); note that all known species of this group are confined to the 'Peninsular Malaysian montane rain forests' ecoregion, which roughly corresponds to areas above 1000 m in elevation. Drawn by M.R. Golos & G. Lim.



Figure 12: Mossy upper montane forest just below the summit at the type locality of *Nepenthes berbulu*. Photograph by M.R. Golos.



Figure 13: *Nepenthes berbulu* plant with lower pitchers growing in mossy forest just below the summit. Note the larger foliage and longer internodal length as compared to summit plants. Photograph by M.R. Golos.

with an undescribed taxon, and a handful of putative natural hybrids between the two have been recorded. Here, the summit habitat was observed to be considerably drier than at the type locality.

Nepenthes berbulu is known only from a *ca.* 60 km stretch of the Titiwangsa Range. Herbarium specimens, supported by photographs shared by hikers on social media, show that it occurs on at least two peaks up to 50 km north of the type locality; however, further north of that the species is replaced by *N. sericea*. South of the type locality, *N. berbulu* ranges for a further 15 km before it is likewise replaced in its habitat niche by *N. ulukaliana*. At present, there are no known locations where the three species co-occur, and no natural hybrids have been recorded.

At the type locality, *Nepenthes berbulu* grows terrestrially in stunted ericaceous forest at the summit, and in mossy forest below the summit. In the mossy forest, *N. berbulu* grows terrestrially



Figure 14: *Nepenthes berbulu* climbing stem with upper pitchers (centre) and rosette with lower pitcher (top left) growing epiphytically in mossy forest at the type locality. Photograph by M.R. Golos.



Figure 15: Flowering plants of *Nepenthes berbulu* emerging above the surrounding summit vegetation at the type locality. Photograph by G. Lim.



Figure 16: Putative natural hybrid between *Nepenthes berbulu* and *N. sanguinea*; note the lack of bristles under the lid. Photograph by M.R. Golos.

ally or an as an epiphyte on moss-covered trees (Fig. 13), or on *Sphagnum* moss-covered earth banks. Plants growing in the mossy forest tend to be comparatively longer and vine up the trees. Pitchers may be seen hanging down from the trees as the plant scrambles up the canopy (Fig. 14). Conversely, plants at the summit are usually shorter and grow upright, intertwined among bamboos and stunted shrubs. On the summit, the upper pitchers of *N. berbulu* can be easily spotted thanks to their brightness as they protrude out of surrounding vegetation in a manner similar to the Bornean species *N. muluensis* (Fig. 15); the lower pitchers are often hidden within the shrubs. A single putative hybrid with *N. sanguinea*, recorded at a lower elevation of *ca.* 1700 m, was observed (Fig. 16).

Infauna and prey: — During the August 2022 field trip, some *Nepenthes berbulu* upper pitchers were found to contain groups of very small dipterans just above the water line, perhaps in the pro-



Figure 17: Arthropods found in association with the pitchers of *Nepenthes berbulu*, as visitors, infauna, and prey, at the type locality at ca. 1900 m (A–E) and on a second peak at ca. 1400 m (F): (A) live dipterans resting just above the fluid level in an upper pitcher; (B) live infaunal larva from an upper pitcher – note the dark colour of the fluid; (C) beetle and ant prey from a lower pitcher; (D) spider prey from a lower pitcher; (E) long-legged centipede and dipteran prey from an upper pitcher; (F) ants massing at the lid nectaries of a lower pitcher. Photographs by F.S. Mey (A) & M.R. Golos (B–F).

cess of emerging, and resting on the inner walls (Fig. 17A). One pitcher contained a living larva that resided in very dark, orange-brown pitcher fluid (Fig. 17B).

Larger prey items included a beetle (Fig. 17C), a spider (Fig. 17D), a long-legged centipede of the order Scutigera (Fig. 17E), and several dead Tenebrionidae larvae, the latter all found in a single pitcher. These were often accompanied by a number of small dipteran and hymenopteran prey, including ants. Ants have been observed gathering under some pitcher lids, presumably feeding on the nectar therein (Fig. 17F).

The pitcher fluid of *Nepenthes berbulu* is notably viscous, both in open and late-stage unopened pitchers. Litmus paper was used to measure the acidity of fluid in unopened pitchers at pH 4 and that of opened pitchers at pH \pm 3.

Conservation status: — *Nepenthes berbulu* has been observed by botanists on a few peaks and according to citizen science (in the form of photographs taken by tourist hikers) it is likely to occur on several others. The species is afforded a certain level of protection since the peaks where it is confirmed to occur are part of a protected area, and the species' range encompasses other suitable mountains with steep terrain unlikely to be subject to development or logging. However, all these peaks are quite accessible for experienced hikers and the species is therefore subject to unscrupulous collection. During the preparation of this paper, images of *N. berbulu* briefly appeared on certain social media groups advertising wild plants for sale; these plants were apparently soon sold. The potential value of this species in the horticultural trade means that it is at significant risk of over-collection.

Observations of *Nepenthes berbulu* made *in situ*, together with information gleaned from voucher specimens, satisfy the IUCN 3.1 Red List EN (Endangered) criteria B1ab(ii,iii,v)+2ab(ii,iii,v) (IUCN 2012), i.e. the species has an extent of occurrence (EOO) of <5000 km², an area of occupancy (AOO) of <500 km², and is known from no more than five locations, with projected declines in area of occupancy, quality of habitat, and number of mature individuals. Though all known populations of *N. berbulu* occur in areas that are unlikely to be impacted by land development in the foreseeable future, habitat degradation and population decline are anticipated as a result of poaching for the horticultural trade, which has already significantly impacted a number of *Nepenthes* and is estimated to threaten almost a third of known species (Cross *et al.* 2020).

Discussion

The *Nepenthes macfarlanei* group is being circumscribed in Lim *et al.* (in prep. 2023). The most remarkable character shared by all these taxa is the presence of hairs under the lid that are developed to varying degrees. This group of species includes *N. macfarlanei*; the as yet undescribed *N. sericea* and *N. ulukaliana* (two taxa long included within a broad concept of *N. macfarlanei*); *N. alba*; *N. gracillima*; and now *N. berbulu*. A key to the currently recognised members of the group is provided below. The *N. macfarlanei* group appears closely related to the other highland species from Peninsular Malaysia, namely *N. sanguinea* and its close relatives *N. latiffiana* and *N. malayensis*, as well as to *N. ramispina*. The clade of Peninsular Malaysian species itself seems to be closely related to the Indochinese ones, i.e., the species of the *N. thorelii* aggregate (Murphy *et al.* 2020). The divergence between the two groups might originate from the geographical division between the strongly seasonal Indochina, with its group of pyrophytic species (Mey *et al.* 2010), and the perhumid conditions of Peninsular Malaysia.

The *Nepenthes macfarlanei* group comprises species that are all endemic to Peninsular Malaysia. The monophyly of this informal unit is yet to be established and its relationship with the other species endemic to the Malay peninsula (*N. ramispina*, *N. sanguinea*, and the aggregate of *N. benstonei*, *N. domei*, and *N. thai*, three taxa which might turn out to be conspecific) investigated.

Within the *Nepenthes macfarlanei* group, *N. berbulu* appears closest to *N. macfarlanei*, as documented in the differential diagnosis, though it also shows close affinities to *N. alba*, *N. gracillima*, *N. sericea*, and *N. ulukaliana* (Fig. 18).

Key to the species of the *Nepenthes macfarlanei* group

- 1a. Pitchers with thickened lid hairs ≥ 5 mm long 2
- 1b. Pitchers with filamentous lid hairs ≤ 2 mm long 3

- 2a Upper pitchers wholly infundibular, typically white, base green *N. macfarlanei*
- 2b Upper pitchers broadly cylindrical, white with dark speckling, base green *N. berbulu*

- 3a Lower pitchers wholly ovate, amphora-shaped *N. ulukaliana*
- 3b Lower pitchers infundibular to ovate in the lower part, cylindrical or slightly infundibular above the hip 4

- 4a. Small upper pitchers, <13 cm tall, usually conspicuously white and often with red speckling, hip at or above the midsection *N. alba*
- 4b. Large upper pitchers, often >20 cm tall 5

- 5a. Upper pitchers slender, cylindrical, predominantly mottled with black or red speckling, hip at or typically below the midsection *N. gracillima*
- 5b. Upper pitchers broadly infundibular or broadly cylindrical, white, base green, hip at midsection to immediately below the peristome *N. sericea*

Nepenthes berbulu is easily distinguished from *N. alba* and *N. gracillima* by the large bristles present beneath the lid. However, the upper pitchers of all three species are superficially similar in being basally infundibular but cylindrical above the hip. These similarities aside, *N. berbulu* is easily distinguished from *N. alba* by its larger stems, foliage, and pitchers, the latter also differing in terms of their proportions; the diminutive upper pitchers of *N. alba* are strongly hipped, and the hip is normally present above or at the mid-point of the pitcher, whereas in *N. berbulu* the hip is not strongly pronounced and is typically present one third of the way up the pitcher from its base. While *N. gracillima* is larger and more robust than *N. alba*, being of comparable overall size to *N. berbulu*, it is a more slender plant with linear-lanceolate leaves (versus oblong-elliptic in *N. berbulu*) and narrower upper pitchers. Though dispreferred, the secondary determinants of colour and geography can be used to further distinguish these species (see Table 2).

Nepenthes berbulu also shares some characteristics in common with *N. sericea* and *N. ulukaliana*, the two remaining species of the *N. macfarlanei* group. While the former species does occasionally produce upper pitchers that are cylindrical above the hip (Fig. 18N), *N. berbulu* is easily distinguished from both based on its bristly lid hairs alone.

The function of the hairs under the lid in all species of the *Nepenthes macfarlanei* group is open to conjecture but is generally assumed to be related to prey specialisation. Their presence, especially when they are as developed as in *N. berbulu* and *N. macfarlanei*, might be an adaptation to retain insects visiting in search of nectar for longer and with more precarious footholds above the pitcher fluid, potentially increasing the likelihood of prey capture. The interaction of the long bristles of these species with heavy cloud, leading to dew formation, is a possible avenue for investigation, as one of the authors (GL) observed bristles covered with morning dew drops (Fig. 10A) that easily fall into the pitcher below at the slightest disturbance, potentially taking prey with them.

GL also noticed a species of ant (possibly of the genus *Crematogaster*) foraging on the undersides of the lid, apparently unphased by the long bristles. The ants were observed to walk safely between the bristles in search of the exudate produced by the prominent nectar glands (Fig. 10B), positioning

themselves to feed at the bases of the bristles without ever climbing on the bristles themselves. A similar observation was made by Hemsley, who noted that the bristles of *N. macfarlanei s.str.* seemed to keep away flying insects whilst allowing ants to crawl among the bristles to drink the nectar (Hemsley 1905). Also noteworthy is the fact that the bristle arrangement in *N. berbulu* is distinct from that of *N. macfarlanei*. In *N. berbulu*, the bristles are typically situated at the apex and along the margins of the lid, often leaving a bristle-free region of variable extent centred on the midline of the lid (Fig. 10C). These ‘bald’ patches vary in prominence across individuals of the population and are absent in a minority of plants which exhibit no such bald patches (Fig. 10D). The bald patches are not to be confused with a lack of bristles resulting from breakage by age or mechanical force, which seems to be quite common in older pitchers, since bristle attachment remains absent from the bald areas (Fig. 10B).

The authors hope that future studies can be conducted to better understand the complex relationships between *Nepenthes berbulu* and its associated organisms, such as the cf. *Crematogaster* ants, and to gain insight into how the different lid hair structures and arrangements produced by the respective species in the *N. macfarlanei* group optimise prey capture or enhance mutualistic relationships with organisms.

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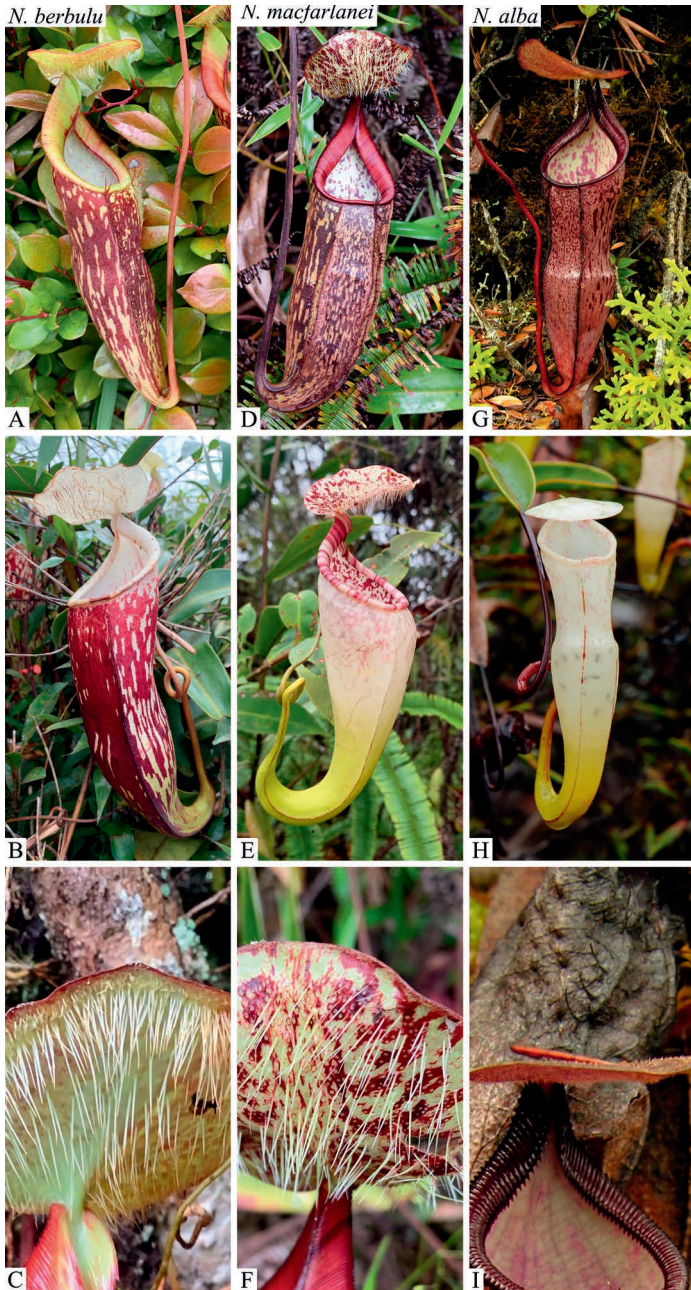


Figure 18: Comparison grid of the six species of the *Nepenthes macfarlanei* group, showing lower pitchers, upper pitchers, and hairs under the lid: (A–C) *N. berbulu*, (D–F) *N. macfarlanei*, (G–I) *N. alba*, (J–L) *N. gracillima*, (M–O) *N. sericea*, (P–R) *N. ulukaliana*. Photographs by F.S. Mey (A–C, E–F, M–N, left, O–Q), M.R. Golos (D, R), S.R. McPherson (G, I, K), Chien C. Lee (H, J, L) & the late Christophe Maerten (N, right).

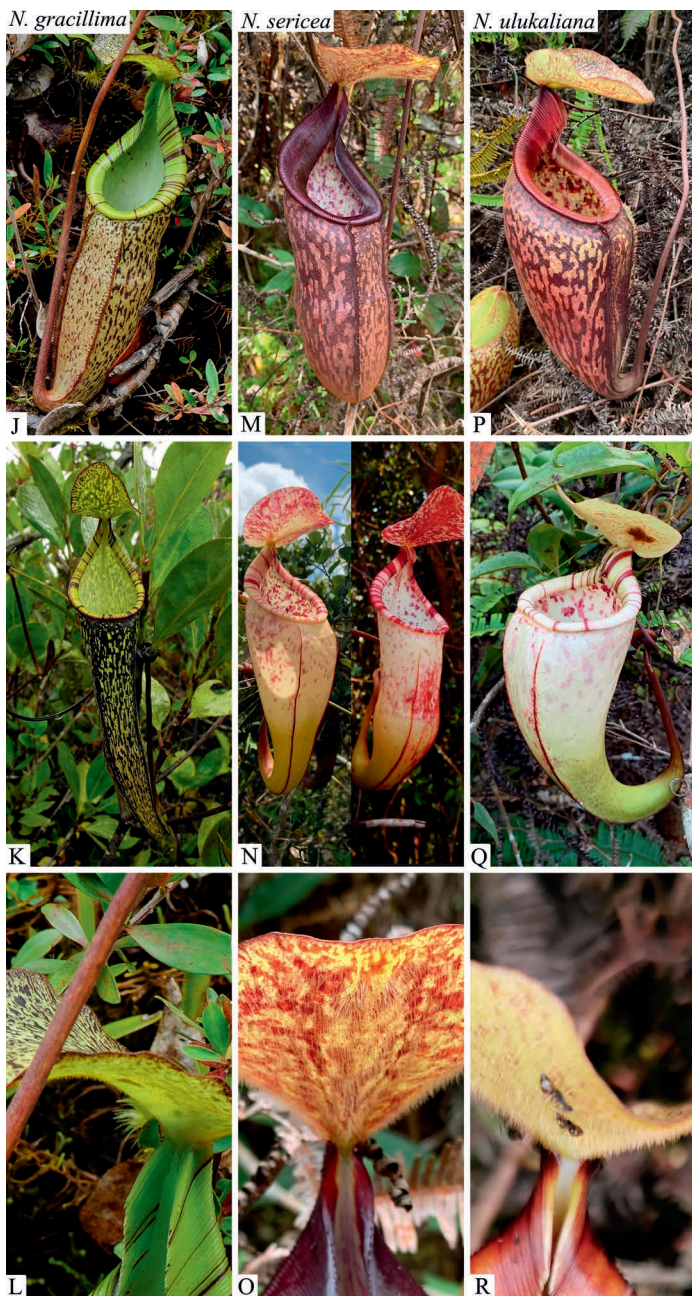


Figure 18: Continued.

combined expertise, rich mountaineering knowledge and professional services contributed greatly to the success and fulfillment of our expedition. Finally, we wish to acknowledge Malaysia Carnivorous Plants (MyCP) for initiating this venture of expeditions to develop a better understanding of the *Nepenthes* of Peninsular Malaysia.

Table 2. A comparison of the species of the *Nepenthes macfarlanei* group. Morphological characters of all taxa are based on observations made in the Bintang Range (Gunung Bubu), Timur Range (G. Tahan), and Titiwangsa Range (G. Ulu Kali, Cameron Highlands, Fraser's Hill, and others), supplemented by information from Clarke & Lee (2012).

	<i>N. berbulu</i>	<i>N. macfarlanei</i>	<i>N. alba</i>	<i>N. gracillima</i>	<i>N. sericea</i>	<i>N. ulukaliana</i>
Geographical range	Titiwangsa Range (south-central)	Bintang Range (G. Bubu)	Timur Range (G. Tahan)	Timur Range, Tapis Range, possibly northeastern Titiwangsa Range	Titiwangsa Range (north-central, mainly Cameron Highlands)	Titiwangsa Range (southern, mainly Genting Highlands)
Elevational range (m)	1400–2100	1500–1657	1400–2187	900–2000	900–2150	900–1800
Habitat	Terrestrial in ericaceous summit forest and epiphytic or terrestrial in mossy forest	Terrestrial or epiphytic in mossy forest	Terrestrial in ericaceous summit forest or in mossy forest	Terrestrial or epiphytic in montane forest	Terrestrial or epiphytic in mossy forest	Terrestrial or epiphytic in mossy forest
Leaves	Oblong-elliptic, apex rounded-obtuse	Lanceolate, apex acute	Linear to lanceolate, apex acute	Linear to lanceolate, apex acute	Lanceolate or spatulate, apex acute	Oblong to broadly lanceolate, apex rounded
Lid hairs	Thick, coarse bristles, to 10 mm long, unevenly distributed, densely aggregated near lid apex	Thick, coarse bristles 5–12 mm long, evenly distributed	Very fine, to 1 mm long	Fine, to 2 mm long	Fine, to 2 mm long	Fine, to 1 mm long
Lower pitchers	Broadly infundibular in lower half, with a pronounced hip, cylindrical above	Ovate in the lower half with a faint hip, cylindrical above	Infundibular to ovate in lower third, narrowing above a distinct hip and cylindrical to slightly infundibular toward pitcher opening	Ovate in lower half, narrowing slightly above and cylindrical toward pitcher opening	Ovate in lower half with a distinct hip, cylindrical above	Amphora-shaped to urceolate
Size of lower pitchers	To 25 cm tall and 6 cm wide	To 22 cm tall and 7 cm wide	To 12 cm tall and 4.5 cm wide, usually much smaller	To 22 cm tall and 7 cm wide	To 26 cm tall and 9 cm wide	To 25 cm tall and 8.5 cm wide

Table 2. Continued.

	<i>N. berbulu</i>	<i>N. macfarlanei</i>	<i>N. alba</i>	<i>N. gracillima</i>	<i>N. sericea</i>	<i>N. ulukaliana</i>
Colour of lower pitchers	Yellowish green, olive green or dark pink, mottled with dark red, dark brown or purple. Peristome yellowish green with reddish stripes, sometimes entirely red, dark red, or dark purple	Yellowish green, speckled dark red or purple. Inner wall of pitcher light yellowish-green. Peristome red or dark purple	Purplish brown, with a paler interior and dark purple or black peristome. Colouration very consistent	Yellowish green, speckled dark red or purple, interior pale yellowish green. Peristome green or reddish, often striped with bands of dark red or purple	Yellow, green, purple or red, mottled with dark red or purple	Yellowish green, sometimes with a reddish hue, mottled with brown, dark red or purple
Lid of lower pitchers	Orbicular to reniform	Sub-orbicular	Orbicular or elliptic	Elliptic or ovate	Sub-orbicular to ovate	Orbicular to sub-orbicular
Upper pitchers	Broadly infundibular below, slightly narrowing just above the hip, cylindrical above, ventral surface flattened between wing vestiges, often widening markedly just below peristome	Wholly infundibular, hip located just below peristome or absent, often narrowing below mouth to appear ventrally gibbous	Infundibular in the lower 1/2–2/3, sharply contracted at the hip, cylindrical to narrowly infundibular above	Narrowly infundibular in the lower 1/3, gradually contracted above the hip, cylindrical above	Wholly infundibular with hip located just below peristome or with hip located at mid-point and cylindrical to slightly infundibular above	Wholly infundibular with hip absent or located just below peristome
Size of upper pitcher	To 27 cm tall and 8 cm wide	To 24 cm tall and 7 cm wide	To 13 cm tall and 4 cm wide	To 26 cm tall and 5 cm wide	To 24 cm tall and 7 cm wide	To 18 cm tall and 7 cm wide
Colour of upper pitchers	Pale green basally, creamy white in the tubulose part to bright white near the mouth, with red, dark red or maroon speckling	White throughout with red speckling, to green with dark purple speckles and peristome banding	Predominantly white often with red speckling	Bright green, but often so strongly speckled with black as to appear almost uniformly black with green speckling	Green to yellowish green basally, white above	Green basally, yellow to creamy white above, sometimes with sparse reddish speckling
Lid of upper pitchers	Orbicular to reniform	Sub-orbicular	Orbicular or elliptic	Elliptic or ovate	Sub-orbicular	Sub-orbicular

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Front Cover: Larry Mellichamp tending to *Sarracenia* at the McMillan Greenhouses of the University of North Carolina at Charlotte. Undated photo. Article on page 4.

Back Cover: Authors Tan Hong Liang (left) and Gideon Lim holding upper pitchers of *Nepenthes berbulu* at its type locality in Peninsular Malaysia, February 2020. Composite of photos by G. Lim and H.L. Tan. Article on page 15.

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International Carnivorous Plant Society, Inc.
2121 N. California Blvd., Suite 290
Walnut Creek, CA 94596-7351, USA
icps@carnivorousplants.org

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John Brittnacher, john@carnivorousplants.org
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Daniela Ribbecke, daniela@carnivorousplants.org
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Brent Jones, brent@carnivorousplants.org
Jan Schlauer, Cultivar Registrar, jan@carnivorousplants.org
Carson Trexler, Conservation Director, carson@carnivorousplants.org
Bob Ziemer, bob@carnivorousplants.org

Cindy Slezak, cindy@carnivorousplants.org
John Brittnacher, john@carnivorousplants.org
Mark Anderson, mark@carnivorousplants.org
Marcel van den Broek, marcel@carnivorousplants.org

Science Editor Andreas Fleischmann
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