A revision of *Nepenthes* (Nepenthaceae) from Gunung Tahan, Peninsular Malaysia

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ABSTRACT. The Nepenthes from Gunung Tahan in Peninsular Malaysia are revised. We recognise four species from this mountain; N. alba, N. benstonei, N. gracillima and N. sanguinea. The reinstatement of N. alba is based on a consistent difference in upper pitcher colouration between it (typically evenly pale yellowish to ivory white) and N. gracillima (dark green with purple-brown speckles). Material from Gunung Tahan that was identified in previous treatments as N. macfarlanei belongs to N. gracillima and the former species is absent from Gunung Tahan. Nepenthes alba and N. gracillima are very similar to N. macfarlanei and further examinations of the relationships among these taxa are warranted.

Keywords. Nepenthes alba, N. benstonei, N. gracillima, N. macfarlanei, Gunung Tahan, Malaysia

Introduction

Eleven species of Nepenthes (Nepenthaceae) have been recorded from Peninsular Malaysia, including five montane species, which are generally found in habitats above 1000 m altitude (Cheek & Jebb 2001; Clarke 2001; McPherson 2009). All of the montane species have been recorded from Gunung Tahan which, at 2187 m above sea level (asl), is the highest mountain on the Malay Peninsula. Situated in the Timur Range, Gunung Tahan is isolated from the main Titiwangsa Range of Peninsular Malaysia by at least 100 km. To date, eight Nepenthes taxa have been recorded from the mountain, including N. alata Blanco, N. bongso Korth., N. singalana Becc., N. macfarlanei Hemsl., N. alba Ridl., N. gracillima Ridl., N. sanguinea Lindl. and N. benstonei C. Clarke. The Nepenthes of Gunung Tahan have been reviewed on a number of occasions (Ridley 1924; Danser 1928; Kiew 1990; Jebb & Cheek 1997; Clarke 2001; McPherson 2009), but uncertainty about the correct identity and status of several taxa persists. Most confusion relates to N. gracillima and its relationships to N. macfarlanei and N. alba. In this paper, we demonstrate that the source of much of this confusion arises from a failure by previous researchers to properly delineate N. gracillima. As a consequence, many collections of this species have been misidentified as N. macfarlanei. We argue that N. macfarlanei is absent from Gunung Tahan, where

it is replaced by *N. gracillima*, but that these taxa are very closely related, exhibiting few significant morphological differences. We conclude that only four *Nepenthes* species are extant on Gunung Tahan. These are *N. alba* (also a very close relative of *N. gracillima* and *N. macfarlanei*), *N. benstonei*, *N. gracillima* and *N. sanguinea*. Our interpretations are based on both detailed field observations and examinations of herbarium material. As all previous descriptions of *N. gracillima* have included material that we consider to belong to other taxa, and a detailed description of *N. alba* has never been published, we present revised descriptions of these taxa and a key to the *Nepenthes* of Gunung Tahan.

Discovery and description of Nepenthes from Gunung Tahan

The first botanist to describe Nepenthes from Gunung Tahan was H.N. Ridley, who was Director of the Singapore Botanic Gardens from 1888-1911. He based his initial identifications and descriptions (Ridley 1908) upon specimens collected by H.C. Robinson and L. Wray on an expedition to Gunung Tahan made in 1905. The first species he recorded was identified as N. bongso, a species that was previously known only from Sumatra. This identification was made on Wray & Robinson 5411 (SING), which comprises a fragment of a climbing stem of a diminutive plant that bears four upper pitchers and a male inflorescence (Note: Nepenthes are generally dimorphic, producing two types of pitchers that are usually referred to as "lower" and "upper". For a review of plant architecture, see Clarke (2001)). Ridley (1908) also described a new species, N. gracillima, based upon Wray & Robinson 5309 (SING). This specimen consists of a fragment of a climbing stem bearing three upper pitchers and an infructescence, which is badly damaged. The lower pitchers of N. gracillima were not described by Ridley (1908), nor were any specimens bearing lower pitchers equated with N. gracillima by him. The descriptions for both taxa are very brief and lack sufficient detail to make objective comparisons. The pitchers, leaves and stems of the two specimens are very similar in structure – the primary difference between them appears to be the colour of the pitchers. Those of Wray & Robinson 5411 were said to be white, tinted pale green at base and spotted with pink, whereas those of Wray & Robinson 5309 were stated to be "pale green, tinted in places with dull crimson and mottled with dull purple". Ridley (1908) also noted that the "neck and lamina" of the pitcher lid of N. gracillima was pubescent.

In the same year, Macfarlane (1908) identified *Wray & Robinson 5411* as *N. singalana* (another Sumatran species), but did not explain his interpretation. Macfarlane (1908) also provided a more detailed description of *N. gracillima* and stated that the pitchers were monomorphic (i.e., only one type is produced; thereby implying that lower pitchers had not been collected because they are not produced). Of the indumentum of the pitcher lids, he wrote, *extus et intus sparse pubescens...* (= "sparsely pubescent inside and out"). At the time of Macfarlane's revision, the only other species from Peninsular Malaysia that was known to have hairs on the lower surface of the pitcher lid (referred to hereafter as "lid hairs") was *N. macfarlanei*,

which had been recorded from a number of mountains in the Titiwangsa range, in addition to the type locality on Gunung Bubu in Perak. Neither Ridley (1908) nor Macfarlane (1908) discussed this distinctive, shared characteristic further, nor was any mention made regarding the presence of lid hairs on *Wray & Robinson 5411*.

In 1909, Ridley described *N. ramispina* Ridl., a species that bears strong similarities to *N. gracillima*, but which occurs in the main Titiwangsa Range, to the west of Gunung Tahan (Ridley 1909). This species lacks lid hairs, but in most other respects, its pitchers are very similar to those of *N. gracillima*. Ridley (1909) distinguished this species from *N. gracillima* on the basis of the large, branched spurs at the apices of the pitchers (the spurs of *N. gracillima* are simple).

In 1911, Ridley climbed Gunung Tahan and made several further collections, one of which (*Ridley 16097* (SING (1 sheet), K (2 sheets))) he identified as *N. singalana*. The sheet at SING consists of a fragment of a climbing stem bearing two upper pitchers and two female inflorescences. The leaf structure differs from that of *N. gracillima* in two important ways: (a) the leaf blades are subpetiolate instead of sessile, and (b) the margins of the leaf blades are decurrent along the internodes for up to 1.5 cm. The sheet at K that is barcoded *K000651565* contains a fragment of a climbing stem with an immature female inflorescence, but no pitchers. The leaf structure of this specimen is the same as that of the sheet at SING and these clearly belong to the same taxon. However, the sheet at K barcoded *K000651564* contains a fragment of a climbing stem that bears sessile, non-decurrent leaves and small, squat aerial pitchers that resemble those of *Wray & Robinson 5411*. Clearly, this is a mixed collection involving two different taxa, neither of which were equated with *N. gracillima* by Ridley.

Ridley (1924) eventually corrected his mis-identification of *Wray & Robinson* 5411, noting that it was not the same as *N. bongso* (or *N. singalana*) and instead described it as a new species, *N. alba*. Once more, the description was very brief, but Ridley clearly mentioned the distinctive colour of living plants of *N. alba*, as follows: "pitcher...ivory white, sometimes spotted with rose pink in the mouth and lid, rarely canary yellow.

Danser (1928) revised the genus for the Netherland's Indies (now Indonesia), along with a few outliers from adjacent regions, including the Malay Peninsula. With regard to the *Nepenthes* of Gunung Tahan, Danser re-determined *Ridley 16097* (SING) as *N. alata*. Prior to Danser's revision, *N. alata* was known only from the Philippines, but Danser also reduced *Nepenthes eustachya* Miq. from Sumatra to a synonym of *N. alata*, thereby extending its geographical range substantially. This interpretation also broadened the degree of morphological variation encompassed by *N. alata* and as Peninsular Malaysia lies between Sumatra and the Philippines, it is perhaps not surprising that Danser felt that *Ridley 16097* also represented this species. However, no other collections that can be equated with *N. alata* have ever been made in Peninsular Malaysia, casting doubt over the validity of his interpretation of this specimen (Kiew 1990; Clarke 2001; see below).

Danser (1928) also reduced *N. ramispina* and *N. alba* to synonyms of *N. gracillima*, stating that the differences among them were "of very little importance". He noted that herbarium material of *N. gracillima* was not always easily distinguished

from N. macfarlanei and N. sanguinea. Furthermore, he tentatively identified two specimens (Wray 339 (BO) and Ridley 16174 (SING)) as belonging to a natural hybrid, N. gracillima \times N. macfarlanei. Ridley 16174 was collected from Gunung Tahan, near Wray's Camp (the type locality for N. gracillima) and of these specimens, Danser (1928) wrote,

The pitchers are too wide for *N. gracillima* and the underside of the lid in the number *Wray 339* bears the bristles typical of *N. macfarlanei*. I should prefer to mention this specimen under the latter species, the pitchers of which vary extraordinarily, when the inner margin of the peristome were not entire. The other number, *Ridley 16174*, bears much more dense and delicate hairs on the underside of the lid, a character that is also often found in *N. sanguinea* and *N. macfarlanei*.

Below, we demonstrate that *Ridley 16174* belongs to *N. gracillima*, and that Danser was the first to confuse material of *N. gracillima* with *N. macfarlanei*, due to the presence of lid hairs. It has since been demonstrated that *N. sanguinea* lacks lid hairs, but that a few hairs may be present on lids of *N. macfarlanei* \times *N. sanguinea* pitchers (Jebb & Cheek 1997; Clarke 2001). Danser's (1928) revised description of *N. gracillima* included material of *N. ramispina* and *N. alba*, and made no mention of lid hairs in this taxon, indicating that he was of the opinion that lid hairs were found only in *N. macfarlanei*.

Kiew (1990) was the first since Ridley to combine examinations of herbarium material from Gunung Tahan with field observations (Macfarlane and Danser never visited the mountain). She re-determined *Ridley 16097* as *N. gracillima* and explained that Danser's (1928) determination was a simple misidentification (Clarke 2001). It is however intriguing that neither Ridley nor Danser equated this specimen with *N. gracillima*; suggesting that the reasons for their misidentifications were not necessarily straightforward. Kiew (1990) noted that the first *Nepenthes* to be encountered on the southern route to Gunung Tahan (from Kuala Tahan) is *N. macfarlanei*, near Wray's Camp at approximately 900 m asl (where *Ridley 16174* was collected). She distinguished it from the other species on the basis of the underside of the pitcher lid, which is covered in coarse hairs, and by the inner edge of the peristome, which is toothed. She then discussed *N. gracillima*, referring to it as the most conspicuous pitcher plant of the padang, festooning

...every bush with its small, ivory-white pitchers, which from afar look like candles. Plants begin life producing deep purple leaves and pitchers that are almost black in colour. Once a climbing stem develops the leaves produced are green and the pitchers ivory-white with rosy spots in the upper part. It is still possible to find on the same plant purplish pitchers, which are usually hidden within the crown of the supporting shrub.

Kiew (1990) indicated that Ridley (1915) was of the opinion that the white-pitchered plants belonged to *N. alba* (although the latter name was not published until 1924), whereas the purple/black-pitchered plants belonged to *N. gracillima*. However, she argued that since both pitcher types can be found on the same plant, this was not the case and all plants belonged to *N. gracillima*. This concept of *N. gracillima* is contingent on how the type specimen (*Wray & Robinson 5309*) is interpreted: if the gracile, dark-coloured pitchers of this specimen are considered to be the same as the lower pitchers of *N. alba*, then Danser's (1928) decision to reduce *N. alba* to a

synonym of *N. gracillima* is justified. However, *Wray & Robinson 5309* bears upper pitchers on a climbing stem—their shape and colouration are not consistent with the corresponding pitcher type in *N. alba*.

Kiew's (1990) observations of *N. gracillima* on Gunung Tahan also showed that clear morphological differences exist between this taxon and Ridley's *N. ramispina*, which seems to be confined to the Titiwangsa Range. As a consequence, Jebb & Cheek (1997) reinstated *N. ramispina*, thereby ending some of the confusion surrounding *N. gracillima* and limiting any persistent uncertainty to populations from the Timur Range. Jebb & Cheek (1997) retained Danser's (1928) concept of *N. gracillima*, with *N. alba* as its synonym and, like Kiew (1990), treated *Ridley 16097* as belonging to *N. gracillima* (they also reinstated *N. eustachya*, thereby removing much of the confusion about the status, morphological variation and geographical distribution of *N. alata*, which is now known to be endemic to the Philippines (Jebb & Cheek 1997)).

Clarke (2001) adopted Jebb & Cheek's (1997) interpretations of *N. gracillima* and *N. ramispina*, but rejected Kiew's (1990) interpretation of *Ridley 16097*, considering this specimen to be *N. benstonei*, a recently-described species from Bukit Bakar in Kelantan, approximately 120 km to the north of Gunung Tahan (Clarke 1999, 2001). Clarke (2001) provided a detailed explanation of the differences between *N. benstonei* and *N. gracillima*, noting that the leaf blade structure (in particular, the sub-petiolate leaf bases and decurrent leaf margins), indumentum and pitcher characteristics of *Ridley 16097* correspond with those of *N. benstonei*. Clarke's (2001) treatment of *N. gracillima*, *N. alba* and *N. ramispina* was limited to herbarium material and followed that of Jebb & Cheek (1997).

Cheek & Jebb (2001) provided a revised description and illustration of *N. gracillima*, based almost entirely on specimens at SING and K that are representative of Ridley's concept of this species (e.g., *Ridley 16174* (SING, K), *Haniff 7890* (SING), *Pannell 1132* (K) and *Ridley 16090* (K), rather than *N. alba*. For the first time, specimens bearing lower pitchers (*Pannell 1132*) were included. In terms of size and colour, the lower pitchers of *Pannell 1132* are similar to those of the upper pitchers on the type (*Wray & Robinson 5309*). Both the description and illustration of *N. gracillima* (Fig. 8) indicate that the pitcher lids have hairs on the lower surface, yet this feature was not discussed further.

McPherson (2009) climbed Gunung Tahan via the western route from Sungai Relau in 2008. He considered *N. alba* to be distinct from *N. gracillima*, stating that the taxa he observed were consistent with Ridley's original descriptions of them. Several differences in morphology were used to distinguish these taxa; these are summarised in Table 1.

McPherson (2009) placed considerable emphasis on variations in pitcher size and colour (especially the colour of the upper pitchers of *N. alba*). Although these characteristics may differ substantially between these taxa, it is worth noting that the types of both *N. gracillima* (*Wray & Robinson 5309*) and *N. alba* (*Wray & Robinson 5411*) bear upper pitchers of roughly equivalent structure and dimensions and are not atypical for their respective taxa, indicating that the types cannot be reliably or consistently distinguished on the basis of size or gross morphology: the only apparent

Table 1. Morphological characteristics that distinguish N. alba, N. gracillima and N. macfarlanei.

Characteristic	N. alba	N. gracillima	N. macfarlanei
Geographical range	Timur Range	Timur Range, Gunung Tapis	Titiwangsa Range, Gunung Bubu
Altitudinal range	1400–2150 m	900–1700 m	900–2100 m
Habitat	Terrestrial in highly stunted, open padang vegetation	Terrestrial or epiphytic in closed upper montane forest	Terrestrial or epiphytic in mossy forest
Lid hairs	Very fine, up to 1 mm long	Very fine, up to 2 mm long	Fine, up to 3 mm long, except on Gunung Bubu, where they are coarse, up to 5 mm long
Tendrils of rosette leaves	0.8–1.5 times the length of pitcher height and leaf length	2–5 times longer than pitcher height	2–5 times longer than pitcher height
Tendrils of leaves on climbing stems	Equal to or shorter than pitcher height and leaf blade length	Longer than both leaf blade length and pitcher height	Longer than both leaf blade length and pitcher height
Size of lower pitchers	Up to 12 cm tall and 4.5 cm wide, but usually much smaller	Up to 22 cm tall and 7 cm wide, often reaching these dimensions	Up to 22 cm tall and 7 cm wide, often reaching these dimensions
Colour of lower pitchers [on rosettes of mature plants]	Predominantly purplish brown, with a lighter interior and dark purple or black peristome. Colouration very consistent.	Predominantly yellow- green, with dark red or purple blotches. Interior light yellowish-green. Peristome green or reddish, often striped with bands of dark red or purple.	Predominantly yellow- green, with dark red or purple blotches. Interior light yellowish-green. Peristome red.
Lid of lower pitchers	Orbiculate or elliptic	Elliptic or ovate	Sub-orbiculate
Production of intermediate pitchers	Rare	Dominant form of pitcher on climbing stems	Occasional on climbing stems in dense forest
Intermediate pitchers	Broadly infundibular in the lower half, hip distinct, cylindrical above	Narrowly infundibular in the lower half, hip present but not pronounced, narrowly infundibular above	Narrowly infundibular in the lower half, hip present, infundibular above
Upper pitchers	Infundibular in the lower 1/2–2/3, sharply contracted at the hip, cylindrical to narrowly infundibular above	Very narrow throughout, infundibular in the lower 1/3, gradually contracted above the hip, cylindrical above	Infundibular from base to hip, hip located anywhere from immediately beneath peristome to 1/3 of the way up from the base; cylindrical to slightly infundibular above the hip

Characteristic	N. alba	N. gracillima	N. macfarlanei
Colour of upper pitchers	Conspicuous white colouration often with red blotches and flecks	Uniformly black, strongly speckled bright green.	White with red flecks and bands ont he peristome, to green, with dark purple speckles and peristome bands.
Lid of upper pitchers*	Orbiculate or elliptic	Elliptic or ovate	Sub-orbiculate
Size of intermediate pitchers on mature plants	Up to 9 cm tall by 2 cm wide	Up to 22 cm tall by 4 cm wide	Up to 18 cm tall by 5 cm wide
Size of upper pitchers on mature plants	Up to 12 cm tall by 3 cm wide	Up to 10 cm tall by 1.5 cm wide	Up to 20 cm tall by 6 cm wide
Colour of lower pitchers on seedling rosettes	Reddish-purple throughout, overlain with dark purple flecks; peristome dark pink- purple	Dull green, heavily overlain with dull red- brown flecks; peristome dull brown throughout	Variable: greenish white, heavily overlain with brown, pink or red flecks; peristome dark red or pink throughout
Colour of lower pitchers	As in the seedling rosettes	Dark to light green, moderately to heavily overlain with dark red- brown flecks throughout; peristome green with red-brown stripes or dark red-brown throughout	As in the seedling rosettes
Colour of the intermediate pitchers	Whitish-green, heavily overlain with thin, dark red-brown flecks throughout	As in the rosette pitchers	As in the rosette pitchers
Colour of the upper pitchers	Ivory white throughout, sometimes overlain with rose to red specks, to varying degrees of intensity	As in the rosette pitchers	As in the rosette pitchers, or ivory white throughout, usually with some rose pink flecks

^{*} This characteristic is informative, but we found the lids of *N. alba* pitchers to be orbiculate and cordate at the base, whereas those of *N. gracillima* are ovate and not cordate.

differences between them relate to colour (which the collectors' label annotations on the type specimens and the species descriptions (Ridley 1908, 1924) clearly record). Furthermore, there are specimens of *N. alba* from 2100 m asl on the padang (e.g., *Strugnell & Sow 42878* (KEP)) that bear heavily speckled pitchers that strongly resemble *N. gracillima*. Variation in pitcher size and colour in most *Nepenthes* species is considerable and Danser (1928) commented on its lack of taxonomic value (although

Clarke (2001) demonstrated that in some taxa, pitcher colour can be both a stable and informative characteristic).

Several characteristics of N. gracillima that were used by McPherson (2009) to distinguish it from N. alba are not consistent with Ridley's (1908) or Jebb & Cheek's (2001) descriptions of this species: these describe a small, slender plant that is very similar in most respects to N. alba, not the robust, large one discussed by McPherson (2009). In fact, the plant that McPherson treats as N. gracillima bears a very strong resemblance to N. macfarlanei. McPherson (2009) provided two photographs of N. gracillima. His Fig. 316 is a photograph of a lower pitcher that is broadly ovoid, with a peristome that is flattened and expanded towards the rear, and which bears distinct teeth. The ovate lid is densely covered with simple white hairs – these cause the central part of the lid to appear out of focus in this photograph, even though both the front and rear margins are in focus. His Fig. 317 is a photograph of an upper pitcher. Again, the ovate lid is covered with hairs on the underside, while the peristome is narrower and mostly cylindrical throughout, but small teeth are still apparent towards the apex of the orifice at the rear. The pitcher has a distinct hip approximately 1/3 of the way up from the base and appears in most respects to represent an intermediate pitcher of N. macfarlanei.

Thus, there is a distinct disparity between the published descriptions of *N. gracillima* and McPherson's (2009) interpretation of it. There are two possible explanations for this: (a) he confused plants of *N. macfarlanei* with *N. gracillima*; or (b) he correctly identified *N. gracillima*, but this species is more similar to *N. macfarlanei* than anyone has previously realised, possessing some morphological traits that have generally been considered diagnostic of that species. McPherson (2009) noted that "significant populations [of *N. macfarlanei*] occur in.... Taman Negara", indicating that he identified some plants that he saw on the mountain as this species. As a consequence, McPherson's (2009) arguments for reinstating *N. alba* have merit, but *N. gracillima* is yet to be clearly defined and delimited with regard to its putative close relatives. Against this background, we visited Gunung Tahan to study its *Nepenthes* flora and attempt to resolve some of the uncertainties about *N. benstonei*, *N. gracillima*, *N. macfarlanei* and *N. alba*.

Materials and methods

We conducted detailed examinations of herbarium material at the following herbaria: Singapore (SING), Forest Research Institute Malaysia (KEP) and Bogor (BO). Although relevant material at K and L has been seen by one of us (CC), the detailed examinations required to make a contribution in this paper have not been made, although digital images of some specimens that are available online were consulted. We conducted field observations on Gunung Tahan from March 29 to April 1, 2011, ascending the mountain by the western route, from Sungai Relau. Waypoints and locations were recorded using a Garmin Dakota 20 GPS receiver (Garmin Corporation, Kansas), using the WGS84 geodetic system.

Results

The first *Nepenthes* we encountered on the western route to Gunung Tahan was *N. benstonei*, which is common on steep ridge tops between approximately 800 and 1200 m altitude. This species is clearly abundant and widespread on Gunung Tahan, even though no other researchers have recorded it there.

From about 1350–1700 m asl, in dense vegetation up to 6–10 m tall along ridge tops, we encountered a second species, growing as both an epiphyte or terrestrially in mossy embankments. This taxon resembles N. macfarlanei in virtually all respects, with the lower surfaces of the pitcher lids being covered with short, simple white hairs. The lower pitchers of these plants frequently resemble those of Ridley 16174, which Danser (1928) thought could have been a natural hybrid between N. macfarlanei and N. gracillima. At about 1500 m asl (N 4.6354°, E 102.2051°), we encountered a Nepenthes that climbs into the forest canopy (up to 5 m) and produces very slender, small upper pitchers that match those of the type of N. gracillima. We traced the stems of this taxon to the ground and found they belong to the same plants that we had previously thought were N. macfarlanei. We repeated this exercise on many occasions throughout the range of the plants that resemble N. gracillima and N. macfarlanei that we saw on Gunung Tahan and determined that they all belonged to the same taxon. These plants also correspond well with the photographs and description of N. gracillima provided by McPherson (2009). Several plants at the location produce pitchers that closely match the large, robust "upper" pitcher of N. gracillima illustrated in Fig. 317 of McPherson (2009). These are exclusively borne on climbing stems that are 1-3 m in length. Longer stems produce the smaller, more gracile type of upper pitchers seen on the type. We observed this growth pattern (and production of two types of pitchers on climbing stems) to be common to virtually all mature plants of N. gracillima that we observed on Gunung Tahan.

On the basis of our findings, we concluded that McPherson (2009) did correctly identify *N. gracillima*, but that he mis-identified some plants of this species as *N. macfarlanei*, and that the origin of this error can be traced back to the early years of the 20th century. As a consequence, McPherson's (2009) concept of *N. gracillima* overlooks some important characteristics of this species, particularly the presence of lid hairs and the production of two types of pitchers on the climbing stems. In distinguishing *N. alba* and *N. gracillima*, he compared the upper pitchers of the former to the intermediate pitchers of the latter. In most instances, this oversight would be of little consequence, but in the case of *N. alba* and *N. gracillima*, it is the principle reason for the lack of clarity surrounding *N. gracillima*.

We tentatively support McPherson's (2009) decision to reinstate *N. alba*. However, McPherson (2009, p.567) is incorrect in stating that:

...with its white upper pitchers, *N. alba* could be confused with populations of *N. macfarlanei* that exhibit similar colouration, such as those from Mount Berincang (or Brinchang) in the Cameron Highlands. *Nepenthes alba* can be distinguished from that species by the lack of simple white hairs on the lower surface of its lid, which are a consistent feature of *N. macfarlanei*.

Lid hairs are present and prominent on both the lower and upper pitchers of *N. alba*, emphasising its close relationship with *N. gracillima* and *N. macfarlanei*. For some reason, these have not been detected or emphasised previously, even though they are easily seen, both in the field and on herbarium specimens. Table 1 presents the morphological and ecological characteristics that we consider to be stable and informative for distinguishing *N. alba*, *N. gracillima* and *N. macfarlanei*, but we contend that these three species are very closely related and exceptions to these character combinations are likely to occur. Further comments on the features of individual specimens that assist in delineating the species are provided below.

The montane Nepenthes species of Gunung Tahan

The four montane *Nepenthes* species from Gunung Tahan that we recognise are presented below. Revised, comprehensive descriptions for *N. alba* and *N. gracillima* are provided, for the first time in the case of *N. alba*. Our description of *N. gracillima* is the first since Macfarlane (1908) that does not include material of other taxa.

Key to montane Nepenthes of Gunung Tahan

Nepenthes alba Ridl.

Nepenthes alba Ridl., Fl. Mal. Pen. 3 (1924) 22; McPherson, Pitcher Plants of the Old World 1 (2009) 557–567, f. 300–306. TYPE: Wray & Robinson 5411 (lecto SING, isolecto BO), Peninsular Malaysia, Pahang, G. Tahan, 1500 m, 3 June 1905.

Nepenthes singalana auct. non Becc.: Macfarl. in Engl., Pflanzenr. 4, 3 (1908) 47, partim; Macfarl., J. As. Soc. Beng. 75, 3 (1914) 282. — Nepenthes bongso auct. non Korth.: Ridl., J. Linn. Soc., Bot. 38 (1908) 320. — Nepenthes gracillima auct. non Ridl.: Danser, Bull. Jard. Bot. Buitenz. III, 9 (1928) 296; Shivas, Pitcher Plants of Peninsular Malaysia and Singapore (1984) 31; Kiew, J. Wildlife and National Parks 10 (1990) 36; Jebb & Cheek, Blumea 42 (1997) 43; Cheek & Jebb, Fl. Malesiana 15 (2001) 69; Clarke, Nepenthes of Sumatra and Peninsular Malaysia (2001) 131, partim.

Terrestrial climber to 5 m tall. Stems cylindrical, 3-6 mm diameter. Rosette leaves coriaceous, sessile, blade narrowly oblong-elliptic, up to 6 cm long x 1.5 cm wide, apex acute, base cuneate, margins sometimes decurrent for 2-3 mm; tendrils up to 6 cm long, without a curl. Leaves of the short shoots coriaceous, sessile, blade oblongelliptic, up to 8 cm long × 2 cm wide, apex acute, base cuneate, clasping the stem for 3/4 of its circumference, margins not decurrent; tendrils up to 10 cm long, without a curl. Leaves of the climbing stems coriaceous, sessile, blade oblong to lanceolate, up to 9 cm long, up to 2 cm wide, apex generally acute, base cuneate, clasping the stem for 1/2–1/3 its circumference, margins not decurrent; tendrils up to 9 cm long, usually curled or with a kink in the middle. Longitudinal nerves of all leaf types obscure, three on each side of the midrib; pennate nerves numerous, reticulate, often indistinct; tendril insertion simple. *Pitchers of seedling rosettes* arising gradually from the tendril, ovate in cross section, infundibular in the lower 1/3–1/2, abruptly contracted at the hip, which is pronounced; upper parts cylindrical to slightly infundibular throughout; up to 5 cm tall × 1 cm wide; two wings, up to 2 mm wide, bearing multicellular fringe elements up to 4 mm long, run from the top to the bottom of the pitcher at the front; mouth ovate, acute near the lid, oblique, concave; peristome loosely cylindrical at the front and sides, flattened and slightly expanded towards the rear, 2-3 mm wide, ribs distinct, 0.2 mm apart, outer edge entire, inner edge with distinct, but minute teeth up to 0.1 mm long; lid circular, base cordate, no appendages, lower surfaces covered with simple, white or red hairs, up to 2 mm long, nectar glands large, numerous, round to elliptic, crater-like, 0.5–0.7 mm diameter; spur simple, or simple with two short, thick bristles as the apex, up to 3 mm long. Lower pitchers arising abruptly from the tendril, infundibular in the lower 1/3–1/2, abruptly contracted at the hip, which is pronounced, slightly infundibular above; up to 9 cm high × 2 cm wide; mouth round, up to 2 cm long × 2 cm wide, oblique, concave; peristome broadly cylindrical at the front and sides, expanded towards the rear, up to 5 mm wide; teeth distinct but very short, up to 0.2 mm long near the apex; lid circular, slightly larger than the mouth up to 2.5 cm long × 2.5 cm wide, strongly cordate at the base; spur simple, up to 6 mm long, usually bent downwards; other parts as for the rosette pitchers. Upper pitchers arising abruptly or gradually from the tendril, narrowly infundibular in the lower 1/4-1/3, with a pronounced hip; upper parts slightly infundibular; up to 12 cm tall × 3 cm wide; mouth ovate, oblique, not extended into a pronounced neck at the rear; peristome loosely cylindrical, up to 5 mm wide, slightly wider towards the apex, teeth distinct but short, up to 1 mm long; lid circular, strongly cordate at the base, lower surface covered with short, simple hairs; spur simple, bent downwards, up to 5 mm long; other parts

as for the rosette pitchers. *Male inflorescence* a raceme, peduncle up to 10 cm long, rachis up to 15 cm long; partial peduncles 2 flowered at the base, 1–2 flowered above, 3–4 mm long, with a filiform bract, up to 5 mm long; tepals elliptic, 3.5 × 2 mm; androphore 2.5 mm long; anther head 1.5 × 1.5 mm. *Female inflorescence* a raceme, peduncle up to 10 cm long, rachis up to 8 cm long; fruit valves 18 × 3 mm approx. *Indumentum* of very simple, short hairs, up to 0.05 mm long, in the axils, around the exterior apex of the pitchers, and inflorescence; simple red or white hairs, up to 1 mm long, on the lower surface of the lid. *Colour of living rosette pitchers dark purple throughout, overlain with darker purple flecks; intermediate pitchers light greenish-white, overlain with dark brown-purple flecks; upper pitchers ivory white throughout, sometimes with variable amounts of rose coloured flecks, sometimes heavily suffused with red pigment on the outer surfaces.*

Observations on Gunung Tahan. Along the western trail to the summit of Gunung Tahan, March 30–31, 2011. An isolated population occurs at N 4.6355°, E 102.2050°, 1520 m asl. Substantial populations were observed between N 4.6304°, E 102.2142°, 1656 m asl (near Bonsai Camp) and N 4.6288°, E 102.2268°, 1930 m asl (Bukit Botak Camp).

Comments. This is the only Nepenthes that is abundant in the short padang vegetation on the uppermost parts of Gunung Tahan. The white upper pitchers are distinctive among the taxa from Gunung Tahan and on the basis of the characteristics in Table 2, this species can be reliably distinguished from N. gracillima. However, the differences between the taxa are slight, and there is merit to the argument that both N. gracillima and N. alba are derived from N. macfarlanei and have diverged due to their isolation and exploitation of different habitats on Gunung Tahan.

Kiew's (1990) statement that pitchers on rosettes of N. alba are purple, then switch to white as the plant climbs into the canopy, is correct. However, when it switches from producing lower to upper pitchers, the first few upper pitchers are effectively an intermediate form that is richly coloured with dark and light pigments, like the upper pitchers of N. gracillima. These "intermediate" N. alba pitchers are well preserved in Strugnell & Sow 42878 (KEP), but are not readily observed on Gunung Tahan as few plants produce them at any given time. They are difficult to distinguish from the upper pitchers of N. gracillima, but they are produced at a different stage in the plants' growth cycle -N. gracillima produces these pitchers for extended periods at the tops of the longest climbing stems, whereas in N. alba they are an intermediate form that is only produced for a very short time; the plant soon switches to producing the distinctive, ivory white upper pitchers that it is noted for.

Like McPherson (2009), we saw no obvious examples of natural hybrids between *N. alba* and *N. gracillima*. Although natural hybrids of *Nepenthes* have received considerable attention from researchers (see Clarke 1997, 2001), they are generally rare in undisturbed vegetation such as occurs on Gunung Tahan, even in open areas. The two species appear to be reproductively isolated (possibly by flowering times, as there are several sites where they grow together, indicating a lack of spatial

isolation). *Nepenthes* hybrids are generally common in sites that have been recently disturbed, such as landslips or sites of human activities. In such places, plants often flower at unusual times, causing the breakdown of temporal isolation mechanisms.

Collections from Gunung Tahan examined: Chua 41539 (KEP), Haniff 7890 (SING), 7891 (BO), Holttum 20666 (BO, SING), 20644, fragment bearing smaller pitchers (SING); Kiew 2450 (KEP, SING), 4064 (KEP), Kloss 12227, 12134 (BO), Lim 56340, 56344 (KEP), Ng 020915 (KEP), Ng 1478 (KEP, SING), Ng 020954 (KEP), Noramly Muslim s.n., 4603 second sheet, s.n. (KEP), Ridley 16097 (K, sheet barcoded K000651564), Wray & Robinson 5411 (SING), Strugnell & Sow 42878 (KEP), Wong & Wyatt-Smith W58 (KEP).

Nepenthes benstonei C.Clarke

Nepenthes benstonei C. Clarke, Sandakania 13 (1999) 79, f. 1–3; Cheek & Jebb, Fl. Malesiana 15 (2001) 40; Clarke, Nepenthes of Sumatra & Peninsular Malaysia (2001) 108, f. 105–107; McPherson, Pitcher Plants of the Old World I (2009) 568, f. 307–311. TYPE: Clarke s.n., (holo KEP, iso BO, K, L, SAN, SING), Peninsular Malaysia, Kelantan, Bukit Bakar, 450–550 m, 24 July 1998.

Nepenthes alata auct. non Blanco: Danser, Bull. Jard. Bot. Buitenz. III, 9 (1928) 258, partim. — Nepenthes gracillima auct. non Ridl.: Kiew, J. Wildlife and National Parks 10 (1990) 36; Jebb & Cheek, Blumea 42 (1997) 43; Cheek & Jebb, Fl. Malesiana 15 (2001) 69, partim. — Nepenthes sanguinea auct. non Lindl.; Jebb & Cheek, Blumea 42 (1997) 79, quae = N. benstonei C. Clarke et N. sanguinea Lindl.

Description. See Clarke (1999, 2001); Cheek & Jebb (2001).

Observations on Gunung Tahan. N 4.6524°, E 102.1875°, 895 m asl, and surrounding areas, March 30, 2011.

Comments. N. benstonei is abundant in dense vegetation on steep ridges, at 800–1350 m asl. On the western route to Gunung Tahan, it grows at the edges of open, disturbed sites, such as landslips, and along the trail itself. Some plants also grow in dense forest; these are generally inconspicuous and produce few pitchers.

Collections from Gunung Tahan examined: Holttum 20643 (SING), Ridley 16097 (SING, K (sheet barcoded K000651565 only).

Nepenthes gracillima Ridl.

Nepenthes gracillima Ridl., J. Linn. Soc., Bot 38 (1908) 320; Macfarl. in Engl. Pflanzenr. 4, 3 (1908) 38; J. As. Soc. Beng. 75, 3 (1914) 282; McPherson, Pitcher Plants of the Old World 1 (2009) 581–586, f. 316–317. TYPE: Wray & Robinson 5309

(lecto SING, isolecto BO), Peninsular Malaysia, Pahang, Gunung Tahan, 990 m, 29 May 1905.

Nepenthes gracillima auct. non Ridl., Danser, Bull. Jard. Bot. Buitenz. III, 9 (1928) 296; Shivas, Pitcher Plants of Peninsular Malaysia and Singapore (1984) 31, quae pro parte = N. ramispina Ridl., N. gracillima Ridl., N. alba Ridl. et N. macfarlanei Hemsl. — Nepenthes gracillima auct. non Ridl., Kiew, J. Wildlife and National Parks 10 (1990) 36; Jebb & Cheek, Blumea 42 (1997) 43; Cheek & Jebb, Fl. Malesiana 15 (2001) 69, quae pro parte = N. gracillima Ridl., N. alba Ridl. et N. benstonei C. Clarke.

Terrestrial or epiphytic climber to 6 m tall. *Stems* cylindrical, 3–6 mm diameter. *Rosette* leaves thin-coriaceous, sessile, blade narrowly oblong-elliptic, up to 6 cm long \times 1.5 cm wide, apex acute, base cuneate, margins sometimes decurrent for 3-4 mm; tendrils up to 10 cm long, without a curl. Leaves of the short shoots coriaceous, sessile, blade elliptic to sub-spathulate, up to 18 cm long × 5 cm wide, apex acute, base cuneate, clasping the stem for 3/4 of its circumference, margins not decurrent; tendrils up to 35 cm long, without a curl. Leaves of the climbing stems coriaceous, sessile, blade oblong or narrowly elliptic-oblanceolate, apex generally acute, base cuneate, clasping the stem for 1/2-1/3 its circumference, margins not decurrent; tendrils up to 30 cm long, usually curled or with a kink in the middle. Longitudinal nerves of all leaf types obscure, three on each side of the midrib; pennate nerves numerous, reticulate, often indistinct; tendril insertion simple. *Pitchers of seedling rosettes* arising abruptly from the tendril, ovate in cross section, infundibular in the lower 1/6, ovoid for the next 1-2/6, with a pronounced hip; upper parts cylindrical throughout; up to 8 cm tall \times 1.5 cm wide; two wings, up to 3 mm wide, bearing multicellular fringe elements up to 8 mm long, run from the top to the bottom of the pitcher at the front; mouth ovate, acute near the lid, oblique, concave; peristome loosely cylindrical at the front and sides, flattened and slightly expanded towards the rear, 2–3 mm wide, ribs distinct, 0.3 mm apart, outer edge entire, inner edge with distinct, but minute teeth up to 0.2 mm long; lid broadly ovate, slightly peaked towards the apex, base simple or sometimes slightly cordate, no appendages, lower surfaces sparsely to densely covered with simple, white or red hairs, up to 3 mm long, particularly towards the margins, nectar glands large, numerous, round to elliptic, crater-like, 0.5-0.7 mm diameter; spur flattened, simple or sometimes with two short, thick bristles at the apex, or divided into two or three branches, up to 5 mm long. Lower pitchers ovoid or broadly cylindrical with a pronounced hip 1/3-1/2 way up from the bottom, up to 18 cm high \times 7 cm wide, mouth ovate up to 5 cm long × 4 cm wide, oblique; peristome flattened, expanded towards the rear, up to 25 mm wide; teeth distinct, up to 5 mm long near the apex; lid ovate, up to 5 cm long × 3.5 cm wide, barely or not cordate at the base; spur simple, up to 12 mm long, straight; other parts as for the rosette pitchers. Intermediate pitchers arising abruptly from the tendril, narrowly infundibular in the lower half, with a pronounced hip; upper parts cylindrical or slightly infundibular; up to 22 cm tall \times 4 cm wide; mouth ovate, oblique, not extended into a pronounced neck at the rear; peristome

loosely cylindrical, up to 8 mm wide, slightly wider towards the apex, teeth distinct but short, up to 3 mm long; lid ovate, not cordate at the base, lower surface covered with short, simple hairs, particularly towards the margins, spur simple, straight, up to 12 mm long; other parts as for the rosette pitchers. Upper pitchers similar to the intermediate ones but much smaller and narrower, up to 10 cm long × 1.5 cm wide. Male inflorescence a raceme, peduncle up to 10 cm long, rachis up to 20 cm long; partial peduncles 2 flowered at the base, 1–2 flowered above, 3–4 mm long, with a filiform bract, up to 5 mm long; tepals elliptic, 3.5 × 2 mm; androphore 2.5 mm long; anther head 1.5 × 1.5 mm. Female inflorescence a raceme, peduncle up to 10 cm long, rachis up to 8 cm long; fruit valves 18 × 3 mm approx. Indumentum of simple, very short hairs, up to 0.05 mm long, in the axils, around the exterior apex of the pitchers, and inflorescence; simple red or white hairs, up to 1 mm long, on the lower surface of the lid, particularly towards the margins. Colour of living pitchers dark green, heavily marked with dark purple-brown speckles, occasionally suffused with dark pink colouring throughout.

Observations on Gunung Tahan. Between N 4.6456°, E 102.1926°, 1276 m asl, below Belumut Camp, and N 4.6287°, E 102.2183°, 1694 m asl, above Bonsai Camp, on the western route to Gunung Tahan, March 30–31, 2011.

Comments. Nepenthes gracillima is one of a small number of species that is consistently trimorphic with regard to pitcher structure. Nearly all Nepenthes are dimorphic and plants of many species occasionally produce one or two "intermediate" pitchers as they switch from producing lower to upper pitchers (Clarke 1997, 2001), but it is very unusual for intermediate pitchers to be the predominant form on climbing stems, as in this species. Prior to Cheek & Jebb's (2001) revised description of N. gracillima, all previous treatments were based on either upper pitchers alone, or specimens of both N. alba and N. gracillima. Good collections of lower and intermediate pitchers of N. gracillima were made, but due to the presence of lid hairs, all of these were identified as N. macfarlanei. For instance, Cheek & Jebb (2001, Fig. 8a, e & f) used Ridley 16174 (K) in their illustration of N. gracillima. The components of the drawing derived from this specimen include a fragment of a climbing stem bearing an upper pitcher, and show detail of the pitcher lid. However, the duplicate of this collection at SING is a basal rosette bearing a lower pitcher of N. gracillima, but Danser (1928) identified it as N. gracillima \times N. macfarlanei, whereas Jebb & Cheek (1997) identified it as N. macfarlanei. As a consequence, taxonomists based their concepts of N. gracillima on the least common pitcher type that this species produces, and which bears a strong resemblance to the upper pitchers of N. alba. It is therefore unsurprising that confusion about these taxa arose, particularly among researchers who only examined herbarium specimens, as these are comprised of stem fragments that bear only one type of pitcher, making it impossible to associate the lower, intermediate and upper pitchers of any given taxon with confidence (particularly when collections comprising several sheets with the same number are split among different herbaria).

Regardless of any shortcomings in the herbarium material, it is perplexing that no researchers who visited Gunung Tahan prior to us traced the climbing stems of *N. gracillima* to the ground. Had this been done, it is possible that much of the recent confusion surrounding *N. alba*, *N. gracillima* and *N. macfarlanei* could have been avoided. Clarke & Moran (2011) stress the importance of making complete collections of *Nepenthes* for herbaria, and our findings in this study emphasise the need for detailed and accurate field observations in interpreting closely related taxa.

Collections from Gunung Tahan examined: Chua 26664 (KEP), Haniff 7890, 8306 (SING), Holttum 20644 (BO, SING, fragment bearing larger pitchers), Kloss 12211, 12212 (BO), 12259 (SING), 12297 (BO), Lim 56363 (KEP), Ng 1448, 020961 (KEP), Noramly Muslim 4603 first sheet (KEP), Ridley 16096 (SING), 16098 (SING), 16174 (K, SING), Wong & Wyatt-Smith 60 (KEP).

Nepenthes sanguinea Lindl.

Nepenthes sanguinea Lindl., Gard. Chron. (1849) 580; Danser, Bull. Jard. Bot. Buitenz. III, 9 (1928) 366, f. 20; Shivas, Pitcher Plants of Peninsular Malaysia and Singapore (1984) 43, f. 4–5, 27–28; Kiew, J. Wildlife and National Parks 10 (1990) 36; Cheek & Jebb, Flora Malesiana 15 (2001) 40; Clarke, Nepenthes of Sumatra & Peninsular Malaysia (2001) 108; McPherson, Pitcher Plants of the Old World I (2009) 568. TYPE: Griffith 4411 (K) Malaysia, Johor, Gunung Ledang.

Nepenthes pumila Griff., Post. Papers 4 (1854) 349; Jebb & Cheek, Blumea 42 (1997) 79, quae pro parte = N. benstonei C. Clarke et N. sanguinea Lindl.

Descriptions. See Lindley (1849), Jebb & Cheek (2001), Clarke (2001).

Observations on Gunung Tahan. Near Belumut Camp on the western route to Gunung Tahan, N 04.6401°; E 102.1964°, 1450 m asl, on Gunung Tahan on April 1, 2011.

Comments. This is probably the only Nepenthes species from Gunung Tahan that has not been the subject of some taxonomic confusion. Kiew (1990) states that this species is not particularly common on Gunung Tahan, but several collections have been made and conform with Lindley's description of this species. We observed only one plant of N. sanguinea on the western route to Gunung Tahan (see above), but were in no doubt that it belonged to this species. We suspect that it may not be that rare on Gunung Tahan, but as neither the southern or western trails pass through suitable habitats for N. sanguinea and most plants appear to be epiphytic, there are few specimens or visual records.

Collections from Gunung Tahan examined: Wong & Wyatt-Smith 59 (KEP), Holttum 20643 (SING).

Summary and conclusions

The montane *Nepenthes* of Peninsular Malaysia are among the most difficult to interpret, due to their collective similarities, but also minor differences that appear to reflect recent reproductive isolation of populations on different mountains. More than any other group within the genus, accurate identifications depend on both detailed field observations and careful examinations of herbarium material. The present study, along with those of Kiew (1990), Jebb & Cheek (1997), Cheek & Jebb (2001) and McPherson (2009), represents an important step towards a resolution of the confusion surrounding the montane *Nepenthes* of Peninsular Malaysia. This will facilitate a better understanding of the ecology, biogeography and conservation of these species, most of which are found nowhere else.

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