



Nepenthes baramensis (Nepenthaceae) – a new species from north-western Borneo

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Key words

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Abstract *Nepenthes baramensis*, a new species from peat swamp and heath forests in north-western Borneo, is described. It is distinguished from related species on the basis of its modified pitchers, which facilitate a facultative mutualistic interaction with Hardwicke's Woolly Bat, *Kerivoula hardwickii*, which roosts in its pitchers and may provide the plant with a substantial proportion of its foliar nitrogen.

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INTRODUCTION

Pitcher plants of the genus *Nepenthes* (Nepenthaceae) are carnivorous, producing jug-shaped leaves that serve primarily as traps for arthropods and other small animals (Clarke 1997). Raffles' pitcher plant, *N. rafflesiana* Jack (Nepenthaceae), occurs in Borneo, Peninsular Malaysia and Sumatra (Clarke 1997, 2001), where it commonly grows in disturbed vegetation and ecotones over nutrient-deficient substrates up to 1200 m altitude. It is very common in northern Borneo and the Malaysian state of Johor in the Malay Peninsula, but patchy elsewhere throughout its range. The plant is a robust climber, producing vines that may exceed 15 m in length. The pitchers of the rosettes and climbing stems demonstrate pronounced dimorphism which enables this species to target crawling and flying arthropods in those parts of the habitat where these prey are most abundant (Moran 1996, Moran et al. 1999, Di Giusto et al. 2008, 2010). *Nepenthes rafflesiana* displays considerable morphological variation (Cheek & Jebb 2001, Clarke 2001, Phillipps et al. 2008) and in Borneo, a sub-specific taxon that produces, narrow, elongated pitchers has been recorded on a number of occasions (Clarke 1997, Phillipps et al. 2008). There are several consistent morphological differences between this elongate taxon and 'typical' *N. rafflesiana* (Moran 1996, Gaume & Di Giusto 2009, Bauer et al. 2011; Fig. 1, 2; Table 1, 2), however, their functional significance has not been addressed in recent taxonomic revisions of the genus (Jebb & Cheek 1997, Cheek & Jebb 2001).

Researchers have been intrigued by ecological differences between the 'typical' and elongate forms of *N. rafflesiana* for some time – these are summarised in Table 1. Notably, Grafe et al. (2011) have demonstrated that the elongate form utilises a unique, facultative nitrogen (N) acquisition strategy, in which Hardwicke's Woolly Bats (*Kerivoula hardwickii* Horsfield, (Chiroptera: Vespertilionidae)) roost and defecate in its upper pitchers. Bat faeces potentially represents an important nutri-

ent resource for the plant: on average, 34 % of foliar N may be derived from this source; in contrast, pitchers of the typical form are not used as roosting sites by bats and faecally-derived N is not present in the leaves (Grafe et al. 2011). Not all pitchers of the elongate form are host to the bats, and it is possible that the current facultative relationship represents the early stage of a nascent mutualism.

Prior to the research outlined above, the taxonomic importance of the morphological differences between these two taxa was debatable (Clarke 1997, Phillipps et al. 2008). Given that: i) similar degrees of variation exist within some other species (e.g. *N. mirabilis* (Lour.) Druce); ii) this level of intraspecific variation is not unusual in *Nepenthes*; and iii) there has been a tendency among taxonomists not to recognise subspecific taxa within the genus (Danser 1928, Jebb & Cheek 1997, Cheek & Jebb 2001, Clarke 2001), there has been some degree of uncertainty about how to treat the elongate form. Furthermore, there appears to be some disparity among ecologists regarding its identity. Moran (1996), Gaume & Di Giusto (2009) and Grafe et al. (2011) referred to it as *N. rafflesiana* var. *elongata* Hort., whereas Bauer et al. (2011) used the terms 'elongate form' and 'typical form' to distinguish between them. The name *N. rafflesiana* var. *elongata* derives from plants that were raised in cultivation at Kew (Anon. 1897) and has become popular in horticulture as a practical means of distinguishing the two taxa. However, no detailed description of *N. rafflesiana* var. *elongata* was ever published and no type is extant at Kew (Cheek & Jebb 2001). Accordingly, there is no evidence that the name *N. rafflesiana* var. *elongata* refers to the 'elongate form' of *N. rafflesiana* from Borneo. Clarke (1997) and Phillipps et al. (2008) discussed this taxon under their comments for *N. rafflesiana*, mentioning the use of the name '*N. rafflesiana* var. *elongata*' in horticulture, but did not suggest that this was the correct name for the taxon.

On the basis of the findings of Moran (1996), Gaume & Di Giusto (2009), Grafe et al. (2011) and Bauer et al. (2011), we contend that the differences between these two taxa are of sufficient importance for the elongate form to be distinguished from *N. rafflesiana* at specific rank. Although the visible morphological differences between them are comparatively slight, there are additional differences in ontogeny, physiology and chemistry (see Table 1, 2) that are consistent and appear to be

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Table 1 List of differences in pitcher characteristics and ecology of *N. rafflesiana* and *N. baramensis*. Differences are categorised on the basis of cause and effect. 'Causal' differences include characteristics that have roles in the detectable ecological differences between the taxa (i.e., the 'effects').

<i>N. rafflesiana</i>	<i>N. baramensis</i>
Names used in previous studies: 'Typical' form; var. <i>typica</i>	'Elongate' form; var. <i>elongata</i>
'Causal' differences	
Epicuticular wax zone on upper part of inner pitcher wall reduced as plant matures; absent from upper pitchers of mature plants ¹	Epicuticular wax zone retained throughout ontogeny ¹
Copious nectar secretion by extrafloral nectaries of the peristome ²	Little nectar secreted (up to seven times less) ²
Complex colour contrast pattern corresponding to insect visual sensitivity maxima in ultraviolet, blue and green wavebands ³	Simple colour contrast pattern ³
Upper pitchers produce insect-attracting fragrance ^{4,5,6}	No fragrance produced ^{4,5,6}
'Effect' differences	
High diversity of invertebrate prey ^{1,4,5}	Low diversity of invertebrate prey ^{1,4,5}
High prey capture rate ^{1,5}	Low prey capture rate ^{1,5}
Primary prey-trapping structure: peristome ² (plus viscoelastic pitcher fluid ⁴)	Primary prey-trapping structure: epicuticular wax zone ²
No facultative mutualism with bats ⁷	Facultative mutualism with bats ⁷

¹ Gaume & Di Giusto 2009; ² Bauer et al. 2011; ³ See Fig. 2, this paper; ⁴ Di Giusto et al. 2008; ⁵ Moran 1996; ⁶ Di Giusto et al. 2010; ⁷ Grafe et al. 2011.

Table 2 Diagnostic characteristics for distinguishing *N. rafflesiana* and *N. baramensis*.

Characteristic	<i>N. rafflesiana</i>	<i>N. baramensis</i>
Texture of the upper pitchers	Coriaceous	Chartaceous
Position of hip in upper pitchers	Absent, or immediately beneath the mouth	1/3–1/2 of the way between the mouth and the base of the pitcher
Structure of peristome at the front of the pitcher mouth	Prominently raised into a flat, horizontal 'ridge'	Not raised at all at the front, or occasionally with a small kink near the centre at the front
Shape of upper pitchers	Funnel-shaped throughout	Funnel-shaped in the lower 1/2–2/3, cylindrical in the upper 1/2–1/3
Lid shape of upper pitchers	Circular, strongly cordate at the base	Ovate, not (or only slightly) cordate at the base
Waxy zone on upper inner surface of upper pitchers on mature plants	Reduced or entirely absent	Always present
Strong fragrance associated with upper pitchers	Present	Absent

involved in divergent N-acquisition strategies. Accordingly, we here describe the elongate form as a new species, *Nepenthes baramensis* sp. nov.

MATERIALS AND METHODS

Spectroradiometric analysis was carried out on the reflectance characteristics of 22 upper pitchers of *N. rafflesiana* and 17 upper pitchers of *N. baramensis* in Brunei, using a model LI 1800 spectroradiometer with an 1800-06 Microscope Receptor/UV Quartz Microscope attachment (Li-Cor Inc., Lincoln, NB). For each pitcher, reflected radiation in the waveband 350–700nm (ultraviolet to red) was measured from the peristome, which is the site of highest nectar concentration, and an adjacent area of the outer pitcher body below the peristome. All determinations were carried out in indirect natural light, and both readings on a given pitcher were taken within a few minutes of each other, to counter temporal effects on incident light quality. Colour contrast was then calculated for each pitcher, following Dusenbery (1992):

$$C = (I_p - I_b) / I_b$$

where C is the degree of colour contrast (no units), and I_p and I_b are the mean reflected radiant flux values ($W\ m^{-2}\ nm^{-1}$) for peristome and pitcher body, respectively. Since the reflectance data exhibited high noise: signal ratios in the ultraviolet waveband (< 400 nm), they were therefore smoothed using the LOWESS (locally weighted regression, tension value 0.1) algorithm of the SYSTAT v5.05 package (SPSS Inc., Chicago, IL, USA; Wilkinson 1990).

Nepenthes baramensis C. Clarke, J.A. Moran & C.C. Lee, sp. nov.

Nepenthes rafflesianae similis sed ascidiis aeriis in parte superiore cylindricae et texturae chartaceae differt. — Holotypus: *Hotta M. 12419* (SAR), Brunei, Belait District, Seria, en route K. Badas to Seria along the railway of B.S.C., 7 Dec. 1963.

Etymology. The specific epithet *elongata* was used by G. Beck to describe a specimen of the natural hybrid, *Nepenthes* × *hookeriana* Lindl. (Cheek & Jebb 2001) and therefore cannot be applied to this taxon. Instead, we have chosen the specific epithet *baramensis*, which refers to the Baram River region of north-western Borneo. This region defines the centre of abundance for this species and extends north into the Belait District of Brunei and inland as far as Gunung Mulu National Park in Sarawak.

Terrestrial climber to 6 m tall. *Stems* terete, up to 8 mm diam. Internodes 0.5–1 cm on rosettes, 10–15 cm on climbing stems. *Leaves of rosettes* chartaceous to thin-coriaceous, petiolate, the petioles narrow, lacking wings and canaliculate, up to 12 cm long, sheathing the stem for up to 1/2–3/4 of its circumference, not decurrent. Leaf blades oblong, up to 30 cm long, base abruptly contracted into the petiole; apex obtuse, acuminate, tendril insertion simple. *Longitudinal nerves* 3–5 on each side of the midrib, pennate nerves spreading towards the margins, but often inconspicuous. *Tendrils* uncoiled, up to 35 cm long. *Leaves of climbing stems* similar to those of the rosettes but smaller; petioles up to 10 cm long, not winged, sheathing the stem and not decurrent; leaf blades arising gradually from the petiole, oblong, up to 18 cm long, apex acuminate, tendril insertion simple. *Lower pitchers* up to 20 cm high, up to 5 cm wide, thin-chartaceous, arising abruptly from the tendril, broadly ovoid



Fig. 1 a. Upper pitcher of *N. baramensis* C. Clarke, J.A. Moran & C.C. Lee, Brunei. Note the funnel-shaped lower portion of the pitcher, distinct hip, and cylindrical upper portion. The waxy zone of this pitcher occupies the cylindrical portion on the inner surface. In this example, the peristome is raised slightly at the front of the mouth. This feature is generally absent or greatly reduced in *N. baramensis*. – b. An upper pitcher of *N. rafflesiana* Jack from Johor, Peninsular Malaysia. The pitcher is funnel-shaped throughout, the hip is visible only at the front of the pitcher, and is located immediately beneath the peristome. There is no waxy zone inside the pitcher.

in the lower 1/3 with a pronounced hip, cylindrical above, narrowing slightly towards the mouth. Inner surfaces of the ovoid portion below the hip glandular throughout, surfaces above the hip covered in a layer of wax crystals. *Two fringed wings*, up to 3 cm wide (widest at the base), bearing multicellular fringe elements up to 12 mm long, run from the bottom of the pitcher to the mouth at the front. *Mouth* round, oblique, concave, rising at the rear into a distinct neck. *Peristome* sub-cylindrical, up to 8 mm wide at the front and sides, up to 12 mm wide near the apex. Outer surface entire, inner surface with distinct teeth up to 5 mm long; ribs up to 1 mm apart, up to 0.5 mm wide. *Lid* broadly ovate, base cordate, up to 6 cm long, up to 5 cm wide, lacking appendages on the lower surface. Large, crater-like nectar glands, up to 0.5 mm wide, scattered sparsely to densely around the outer lower surfaces. Spur simple, up to 10 mm long. *Upper pitchers* 18–25 cm high, 3–5 cm wide, thin-chartaceous, arising very gradually from the hanging end of the tendril, narrowly infundibular in the lower 1/3, becoming noticeably broader towards the hip, which is located 1/2–2/3 of the way up the pitcher; cylindrical above the hip to the peristome. *Mouth and peristome* similar to the lower pitchers, the latter sometimes with a slight kink at the front. Glandular region covers the entire inner surface below the hip; cylindrical portion above the hip covered with wax crystals. *Lid* ovate, generally not cordate at the base, up to 6 cm long by 4 cm wide, no appendages on the lower surface. Large, crater-like nectar glands, up to 0.5 mm wide, scattered sparsely around the outer lower surfaces. Spur simple, up to 10 mm long. *Male inflorescence*

a raceme, peduncle up to 12 cm, rachis up to 30 cm, partial peduncles 1-flowered, bracts usually absent, pedicels 12–15 mm long, tepals elliptic, up to 7 by 5 mm; androphore 5–6 mm long, anther head 1.2 by 2 mm. *Female inflorescence* similar in structure to the male, peduncle up to 12 cm, rachis up to 20 cm, partial peduncles 1-flowered, lacking bracts. Valves of fruits 50 by 10 mm. *Indumentum* of stem, midribs, lower surface of the leaf blade and inflorescences from base of peduncle to lower surface of the tepals white or grey arachnoid; lower surface of leaf and outer surface of pitchers with minute grey stellate hairs. Other surfaces glabrous. *Colour* of the leaves and pitchers drying to light green or straw brown, stem white, flowers dark brown. Pitchers on living plants pure light green throughout, or green with red-purple specks on the outer surfaces and lid; peristome green throughout to striped with varying degrees of red and green. Stems whitish grey, leaves dull green.

Distribution — Borneo: Sarawak and Brunei.

Habitat & Ecology — Sparsely-distributed terrestrial climber in peat swamp forest, kerangas and kerapah habitats, occasionally locally abundant in disturbed kerangas or along kerangas forest ecotones; below 200 metres above sea level.

Other specimens examined. BRUNEI, Tutong District, near Telamba Bridge, below 100 m, *Jacobs 5684* (SAR); Belait District, Sg. Topi, Operation Raleigh Path, *Thomas SA 175* (KEP). Alt range: 50–150 m. – MALAYSIA, Sarawak, 4th Division, 5 km downstream from Marudi, to the left of Batang Baram, Lobok Pasar, in the swamp area with padang vegetation, about 3 km to the west from the bank of Baram River, *Fuchs H.P. 21247* (SAR); Bintulu, Sungai Penyilam, Pengkalan Kerupok, *Joanes U, Tan HS, Malcolm D, Rantai J et al. S97192* (KEP).

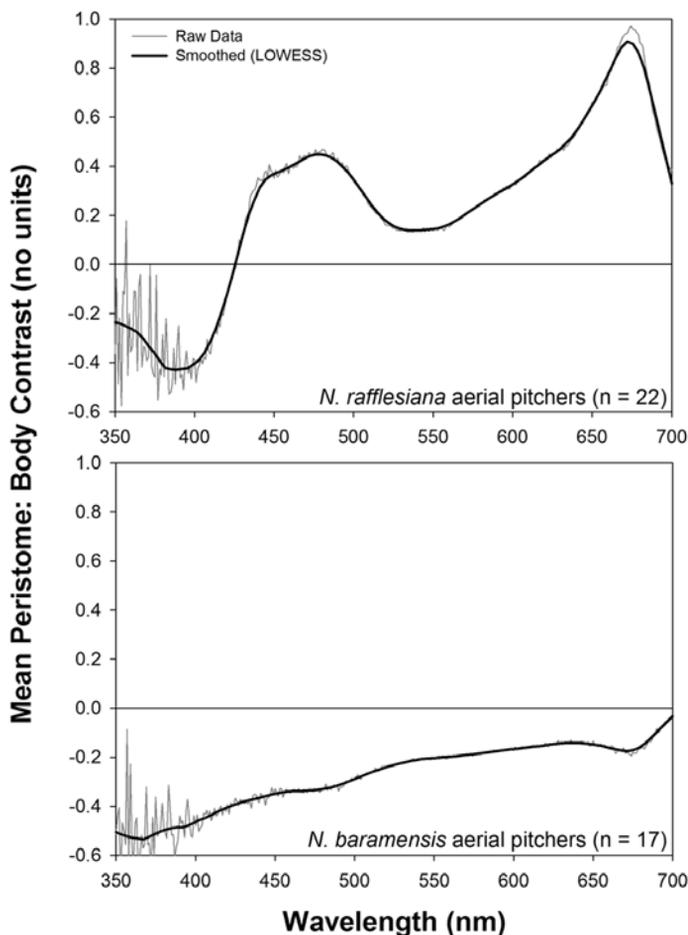


Fig. 2 Colour contrast patterns between peristome and adjacent outer surface of upper pitchers of *Nepenthes rafflesiana* Jack and *Nepenthes baramensis* C. Clarke, J.A. Moran & C.C. Lee. Note the complex contrast pattern in *N. rafflesiana* (upper panel) and the simple pattern in *N. baramensis* (lower panel).

Conservation status — Many peat swamp and kerangas habitats in the Baram River region in Sarawak have been cleared in recent years, but similar habitats are still widespread in the Belait District of Brunei and in Gunung Mulu National Park in Sarawak. As long as these areas remain largely undisturbed and protected from forest clearing, we consider this taxon to be at little risk and have classified it as low risk/conservation dependent (LR(cd)) according to the IUCN Red List categories (IUCN 2001).

Notes — It is now well established that the insect trapping capabilities of *N. rafflesiana* and *N. baramensis* are significantly different (Table 1). In addition to the production of fragrance, the complex colour contrast pattern of its pitchers (Fig. 2), that appears to be 'tuned' to the ultraviolet, blue and green visual sensitivity maxima typical of its insect prey, allows *N. rafflesiana* to attract and capture prey at higher rates than *N. baramensis*. For reasons that are yet to be determined, *N. baramensis* appears to have evolved towards an alternative supplementary nutrient acquisition strategy (i.e., capturing bat faeces). This strategy is manifested in the loss of characters that specifically attract arthropods, and thus in a syndrome of characteristics that distinguish it from *N. rafflesiana*. It has not yet been established whether *N. baramensis* pitchers possess any characteristics that specifically attract *K. hardwickii* to roost in them, but the cylindrical upper portion of the pitcher provides an ideal physical 'fit' for the bats.

The present study adds to the findings of Clarke & Moran (2011) who noted that several unique ecological relationships between highly-specialized *Nepenthes* species and various species of animals are facilitated by modifications to pitcher characters. However, these traits either went unnoticed, or were considered unimportant or insufficiently consistent, in

previous taxonomic accounts (e.g., Danser 1928, Cheek & Jebb 2001, Clarke et al. 2010). A possible explanation for this is that important ecological interactions with animals may be facilitated by minor modifications to trap characteristics (Clarke et al. 2010, Clarke & Moran 2011), and without the support of ecological data, the taxonomic importance of these traits is easily overlooked (especially when similar traits in other species vary to greater degrees, despite having no known ecological function). Our interpretation of the status of *N. baramensis* is based on both ecology and plant morphology; by linking the two, we confer taxonomic value on morphological variations that might otherwise seem unimportant.

Many aspects of the functions of the distinguishing pitcher characteristics of *N. baramensis*, and their relevance to this species' interaction with *K. hardwickii*, have yet to be investigated in detail. This also applies to other *Nepenthes* species that have highly specialised interactions with animals: the use of ecological information to address taxonomic questions and hypotheses is still in its infancy with regard to *Nepenthes*. Although the initial outcomes of this approach are encouraging, we emphasise the need for high levels of scientific rigour in designing and conducting subsequent ecological experiments for this purpose.

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