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Revisions in *Nepenthes* following explorations of the Kemul Massif and the surrounding region in north-central Kalimantan, Borneo

ALASTAIR S. ROBINSON^{1*}, MICHAL R. GOLOS^{2*}, MARC BARER³, YOSUKE SANO⁴, JENNIFER J. FORGIE⁵, DIEGO GARRIDO⁶, CHANDLER N. GORMAN⁷, ADI O. LUICK⁸, NICK W. R. MCINTOSH⁹, STEWART R. MCPHERSON¹⁰, GREGORY J. PALENA¹¹, IVAN PANČO¹², BRIAN D. OUINN¹³ & JEFF SHEA¹⁴

¹ National Herbarium of Victoria, Royal Botanic Gardens, Melbourne, VIC 3004, Australia; email: alastair.robinson@rbg.vic.gov.au

² School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol, BS8 1TQ, UK; email: michal.golos@bristol.ac.uk

³ 18–34 Waverley Street, Bondi Junction, NSW 2022, Australia.

⁴ Graduate School of Human Sciences, Waseda University, 359–1192 Saitama, Japan.

⁵ Lower Tropical Nursery, Royal Botanic Gardens Kew, Richmond, Surrey, TW9 3AE, UK.

⁶ 508 Clinton Drive, Gastonia, NC 28054, USA.

⁷ University of California Davis, 1 Shields Ave, Davis, CA 95616, USA.

⁸ Obergraben 15, 01097 Dresden, Germany.

⁹ 69 Lansdowne Crescent, West Hobart, TAS 7000, Australia.

¹⁰ Redfern Natural History Productions, 61 Lake Drive, Hamworthy, Poole, Dorset, BH15 4LR, UK.

¹¹ 116 West Maple Ave 2B, Denver, CO 80223, USA.

¹² Wimbledon Park Golf Club, Home Park Road, London, SW19 7HR, UK.

¹³ 231 Morrin Road, St Johns, Auckland 1074, New Zealand.

14 2785 Goodrick Avenue, Richmond, CA 94801, USA.

* Authors for correspondence

Abstract

An expedition to the highest peak of the Kemul Massif located a number of different *Nepenthes* taxa, including the type populations of *N. fusca* and *N. mollis*, neither of which have been observed *in situ* since they were first collected in 1925. Studies of the type form of *N. fusca* show that two further species should be considered, one largely restricted to Sabah's Crocker range—here reinstated as *N. zakriana*—the second a southerly distributed species from Brunei, Sarawak and Kalimantan, named here as *N. dactylifera*. Analysis of the type population of *N. mollis* indicates that *N. hurrelliana* is a heterotypic synonym of *N. mollis*, and reveals an additional undescribed *Nepenthes* species from Sarawak and Kalimantan with a widespread but highly localised range.

Keywords: Indonesia, Malesia, Nepenthaceae, new species, non-core Caryophyllales, taxonomy

Introduction

Nepenthes Linnaeus (1753: 955) (Nepenthaceae Dumort.) comprises at least 160 species and is one of the world's largest carnivorous plant genera (Clarke *et al.* 2018). *Nepenthes* is widespread within the Malesian phytogeographic region, with centres of diversity in Borneo, the Philippines, and Sumatra (Robinson *et al.* 2009, Cheek & Jebb 2001, Clarke 2001a), although the majority of species are known from individual mountains or just a few closely-situated mountain tops. This endemism is thought to be the result of allopatric speciation caused by vicariance within the principal territories occupied by *Nepenthes* (Robinson *et al.* 2009).

Danser (1928) in his "The Nepenthaceae of the Netherlands Indies" recognised just 65 *Nepenthes* species worldwide, including 17 new species. Among the latter were *N. fusca* Danser (1928: 288) and *N. mollis* Danser (1928: 338), both described from material collected by Frederik Endert from the flanks of the Kemul Massif (1500 m a.s.l. for *N. fusca*, 1800 m a.s.l. for *N. mollis*). Endert was the lead botanist and plant collector on the 1925 Midden-Oost-Borneo Expeditie (Central East Borneo Expedition) that ran from April to December of that year (Indisch Comité voor Wetenschappelijke Onderzoekingen 1925, Indisch Comité voor Wetenschappelijke Onderzoekingen *ca.* 1926, Buijs *et al.* 1927, Endert 1927). Since Endert's time, no botanical expeditions have been made to the Kemul Massif and this fact has led to taxonomic questions for both *N. fusca* and *N. mollis*.

Although Danser's description of *Nepenthes fusca* is largely complete, a detailed description of lid characters is lacking, particularly for the upper pitcher lids which are absent from two of the four type accessions (lectotype and isotype at BO), an issue compounded by possible artefactual folding of the pressed lids in the remaining accessions (isotypes at K and L). Since lid morphology is regarded as a crucial diagnostic characteristic (see e.g., Clarke et al. 2018) of a number of Nepenthes sections, interpretations of what constitutes N. fusca have varied. For example, plants with very narrowly triangular lids from Sabah's Crocker Range, including Mt. Kinabalu, were assigned to N. fusca by Kurata (1976), an interpretation that quickly gained wide acceptance (Clarke 2006). It is this Sabah taxon that has been most commonly referred to and illustrated as N. fusca, the narrow lids of the upper pitchers being the principal diagnostic characteristic. A closely related taxon is also found across the central highlands of Sarawak, at least as far north as Gunung Mulu National Park, as well as in Brunei and Kalimantan. Substantive morphological differences between the Sabah and Sarawak taxa have long been appreciated, and the two were initially treated separately. Phillipps & Lamb (1988), who were the first to illustrate the Sarawak plant, treated it as an undescribed species, as did Clarke (1997) in his monograph on Bornean Nepenthes. Jebb & Cheek (1997) introduced a broad circumscription of N. fusca that, in addition to the Kemul and Sabah plants, also encompassed the taxon from Sarawak. This interpretation was accepted and followed in most subsequent works (Cheek & Jebb 2001, Clarke 2001b, Clarke & Lee 2004, Phillipps et al. 2008, McPherson 2009, McPherson & Robinson 2012).

Although discrepancies between the *Nepenthes fusca* type description and the taxa from Sabah and Sarawak were noted by the various authors, a definitive resolution of how to correctly circumscribe *N. fusca* could not be made without living reference material from the type locality bearing intact lids. Interestingly, the figure accompanying Danser's (1928) description of *N. fusca* shows upper pitchers with ovate, complanate lids—markedly different from the extremely narrow and revolute lids of the plants from Sabah and Sarawak—the description itself simply stating that the lids of the upper pitchers are "like those of the lower pitchers", *viz.* narrowly ovate and sub-cordate, with an applanate appendage towards the base. The abbreviated description led Jebb & Cheek (1997) to suggest a possible explanation for the discrepancy: that the lids of the upper pitchers in the plate were drawn not from real specimens but copied from preserved lower pitchers. However, they later note in Cheek & Jebb (2001) that "the isotypes at K and L have upper pitchers with the characteristic lid", which one must assume refers to those with revolute margins. Examination of the isotype at K (*Endert 3955*) does reveal a lid with folded margins, but the single fold (rather than rolled edges) of the margin does little to rule out suspicions that the material was inaccurately pressed.

Only Adam *et al.* (1992) deviated from the aforementioned broad consensus by maintaining a narrow circumscription of *Nepenthes fusca*. Adam and his colleagues considered the Sabah plants to represent *N. curtisii* Masters (1887: 681) (Adam 1998, Adam & Wilcock 1998), a problematic taxon based on cultivated material of uncertain provenance, and which is now generally regarded as a synonym of *N. maxima* Reinwardt *ex* Nees von Esenbeck (1824: 369) (Cheek & Jebb 2001). They initially described it as *Nepenthes curtisii* subsp. *zakriana* Adam & Wilcock (1998: 151), but later elevated it to species rank as *Nepenthes zakriana* (Adam & Wilcock) Adam & Hamid (2006: 434). This taxon was considered by other authors to fall within the wider interpretation of *N. fusca s.lat.*, and was treated as such by Phillipps *et al.* (2008) and McPherson (2009).

Concerning *Nepenthes mollis*, the type material (at BO) consists of one stem fragment without pitchers. As Danser (1928) reported, although "the pitchers are unknown, the other parts are so peculiar and differ from all other species in such a striking manner, that it seems allowed to me to base a new species on it." *N. mollis* is the only *Nepenthes* besides *N. ephippiata* Danser (1928: 286) and *N. villosa* Hooker (1852: tab. 888) to be described with unknown pitchers (though Danser was able to include pitcher material of the former in a last-minute addition to his monograph). *N. mollis* is characterised by its very dense and particular indumentum, and by its lanceolate to spathulate-lanceolate leaves. The identity of this taxon has been the subject of much conjecture, including suggestions that it might represent an isolated example of a hybrid between e.g. *N. fusca* and *N. hirsuta* Hooker (1873: 99) (see Cheek & Jebb 2001) or that it could be conspecific with *N. hurrelliana* Cheek & A.L.Lamb in Cheek *et al.* (2003: 118), a species described in 2003 but documented from at least as early as 1988 (Phillipps & Lamb 1988, Phillipps & Lamb 1996, Clarke 1997, Steiner 2002). The latter hypothesis was proposed following a comparison of herbarium materials of both taxa, whereupon it was recognised that most key characteristics matched, the exception being the degree of leaf base decurrency and the presence of bracts on the pedicels, the differences being postulated to be the result of natural variation across a wide geographical range (Salmon 1999).

Our recent surveys of putative *Nepenthes fusca* and *N. mollis* on the Kemul Massif showed that the plants found *in situ* match the deposited types, indicating a successful rediscovery of these two species after 93 years. Observations of type *N. fusca* showed that this taxon is distinct from the two *N. fusca s.lat.* taxa found primarily in Sabah and Sarawak (respectively), while *in situ* observations of *Nepenthes mollis* showed that this species is conspecific with *N. hurrelliana*. An updated taxonomy of these taxa is provided here.

Materials and Methods

To resolve the taxonomic uncertainties surrounding *Nepenthes fusca* and *N. mollis*, an expedition to the Kemul Massif was carried out by the authors. It was deemed critical to ascend towards the highest point of the massif, the western peak Batu Luye'u (meaning 'Tiger Rock' in the local Dayak Punan Aqut dialect), rather than the sub-peak to the east reached by Endert in 1925 (1847 m; Fig. 1). This decision was made because the type of *N. mollis* (*Endert 4282*) is pitcherless. Endert spent approximately a month on the flanks of Kemul and summited that eastern peak several times (Endert 1927). As an experienced botanist who had five days prior collected *N. fusca*, Endert would have known to collect *Nepenthes* material bearing pitchers—if present. Endert collected only pitcherless material, suggesting that pitcher-bearing plants were not observed on any of his ascents of this peak. Since the *N. fusca* materials bear numerous pitchers, we can infer that the absence of *N. mollis* pitchers was probably not due to unusually dry conditions, which, as repeated recent El Niño years have highlighted, can lead to wholesale pitcher senescence throughout a population. Instead, it is likely that the material was collected at the lower elevational range for *N. mollis*; many montane *Nepenthes* are restricted to the very tops of mountains (see e.g., Clarke 1997, Clarke 2001a, McPherson 2009, Robinson *et al.* 2009) and often fail to pitcher when isolated individuals develop at sub-optimal elevations. It was thus hoped that the highest ridges would provide the greatest odds of locating *N. mollis* in pitcher.



FIGURE 1. A map showing the location of the Kemul Massif with respect to the principal logistics access route from Wahau Baru town, the expedition starting point (Long Sule village) and Mt. Bagong. Extents of geological terranes extracted from Tate (2001). Drawn by A.S. Robinson.

In order to provide the significant food and safety equipment logistics needed to support the twelve-person expedition team, the local coordinator (YS), and nineteen supporting indigenous Dayak Punan guides, it was necessary for an advance group to transport cargo by road and river to the settlement nearest to the planned ascent route of the Kemul Massif, namely the Dayak Punan village of Long Sule (North Kalimantan). This journey took AR, DG, NM and BQ over a track that summits the geologically distinct (see Discussion) Mt. Bagong to the south, allowing for a comparison of the flora between the two mountains and additional *Nepenthes* surveys.

The logistics team departed Wahau Baru (East Kutai Regency, East Kalimantan) on 23 June 2018, surveyed the *Nepenthes* flora of Mt. Bagong from 27–28 June, and reached Long Sule on 29 June to await the arrival of the remaining expedition team by air. The expedition team departed Long Sule on 02 July and successfully reached the twin-peaked summit of Batu Luye'u (measured at *ca*. 2054 m) in the Kemul Massif on 07 July 2018 (Fig. 1).

The ascent route of the Kemul Massif from Long Sule was plotted by AR using low resolution GIS topological data exported from the United States Geological Survey EarthExplorer (earthexplorer.usgs.gov) and Google Earth Pro (2018), providing a principal (southwestern) and a contingency (western) route to the summit along safe gradients of ascent. YS generated a high resolution (1:50,000) topographical chart of the region from the NASA global digital elevation model compiled from Shuttle Radar Topography Mission data ("SRTM V3.0, 1 arcsec", NASA JPL 2014) using ArcGIS 10.4 software, with contours set at 20 m intervals; stream lines set to include watercourses down to small streams with flow accumulation values of >150 (using Arc Hydro Tools 10.3); and local place names gleaned during a 2 year residency with the Dayak Punan at Long Sule. Comparing data sets, the plotted routes were deemed sound, but the western route was designated the preferred route of ascent owing to the layout of stream lines; accessibility to water was regarded as critical owing to the anticipated high-porosity limestone bedrock of the mountain.

All *de novo* georeferencing was made using a Garmin Oregon 600 GPS unit with dual GPS and GLONASS telemetry enabled. Key measurements were made with a minimum of 5 averaged waypoint readings over the course of a 20-minute period, with an estimated accuracy of ± 2 m. An iPhone X served as a backup device, yielding almost perfectly congruent data.

Maps were drawn by AR with Adobe Illustrator CC 2018 (Mac OS) using exported GIS and geological data layers, GPS data collected during the expedition, and herbarium data as required.

The species descriptions are based on both field observations and examinations of herbarium specimens deposited at BO, K, L, and SAR (acronyms follow Thiers 2019+). A stereo-microscope with a 1 mm graticule and side illumination was used to document and measure small-scale structures such as hairs, nectar glands, and peristome ribs. In the case of specimens whose lids were excessively recurved or otherwise unfavourably pressed, controlled applications of small amounts of soapy water were made to render the lids pliable and allow for the manipulation necessary to examine their abaxial surfaces.

All known archival documents belonging to Endert and relating to the 1925 expedition were reviewed by MG at the Naturalis Biodiversity Center in Leiden, the Netherlands. This material comprises 13 large folders and includes original notebooks, written correspondence, maps (both printed and sketched), newspaper clippings, and several hundred original glass positives and negatives. Detailed inspection of all glass slides and corresponding documentation revealed that Endert did not photograph any *Nepenthes* plants during the 1925 expedition, and that, therefore, the appearance of live *N. fusca s.str.* and *N. mollis* remained completely undocumented.

Results

Nine different species of Nepenthes were observed during the expedition (Table 1, Fig. 2).

Mount Bagong Nepenthes	Elevation (m)	Notes
N. chaniana	1300–1600	Terrestrial on clay laterite and sand washes adjacent to track. Not recorded from Kalimantan
N. fusca s.lat. 'Sarawak form'	1100–1500 (–1900)	Terrestrial on clay laterite. Widespread in Sarawak
N. hirsuta	1100	Few, terrestrial along sandstone ridge
N. lowii	1960-2110	Epiphytic on trees and terrestrial adjacent to track
N. reinwardtiana	1100-2100	Terrestrial, climbing strongly in trackside trees
N. tentaculata	1480	Terrestrial in humus in shady forest
N. sp. Bagong	1850-2110	Terrestrial to epiphytic in ridge forest and adjacent to track
Kemul Massif Nepenthes		
N. fusca (type)	1400–1600	Terrestrial in humus pockets along a rocky ridge
N. lowii	2000-2054	Terrestrial and epiphytic in summit region only
N. tentaculata	1600–2054	Terrestrial and epiphytic in humus or moss pads
N. mollis (type)	1840–2054	Initially epiphytic, often terrestrial towards summit in humus or mossy banks
N. reinwardtiana	1450	Terrestrial in tuff on a rocky ridge

TABLE 1. Nepenthes taxa encountered on Mt. Bagong and the Kemul Massif, north-central Kalimantan.



FIGURE 2. *Nepenthes* documented during the expedition (all photographs taken *in situ* on Mt. Bagong and the Kemul Massif). Species recorded on both Mt. Bagong and the Kemul Massif: A—*N. lowii* (plant from Kemul); B—*N. reinwardtiana* (Bagong); C—*N. tentaculata* (Bagong); recorded on Mt. Bagong only: D—*N. chaniana*; E—*N. fusca s.lat.* 'Sarawak form' (named here as *N. dactylifera*); F—*N. hirsuta*; G—*N.* sp. Bagong; recorded on Kemul Massif only: H—*N. fusca s.str.*; I—*N. mollis.* Photograph A by S.R. McPherson; B–I by A.S. Robinson.

Nepenthes species recorded on both Mt. Bagong and the Kemul Massif

Nepenthes reinwardtiana Miquel (1852: 168) and *N. tentaculata* Hooker (1873: 101), both of which are widespread generalists over a range of elevations across Borneo (Clarke 1997, Cheek & Jebb 2001), as well as an unusual form of *N. lowii* Hooker (1859: 420), a species otherwise known from Sabah, northern Sarawak and Brunei, and noted for its mutualistic relationship with tree shrews (Clarke *et al.* 2009, Clarke *et al.* 2010). Though the latter taxon was initially contemplated to represent the closely related *N. ephippiata* (from C. Kalimantan and E. Sarawak, Lee 2004) on account of its atypical pitcher orientation, the diagnostic ephippium (after which *N. ephippiata* is named) was found to be wholly absent from the climbing stems, while the pitcher waist and vestigial peristome are closer to *N. lowii*, and the appendages within the lid cavity are not consistently reduced to tubercles in all upper pitchers as in *N. ephippiata*. These almost intermediate characteristics are not surprising given the location of these peaks between the generally accepted ranges of *N. ephippiata* and *N. lowii*, although why there should be graduation towards one form or the other based on latitude is wholly unknown.

Nepenthes species recorded only on Mt. Bagong

Nepenthes chaniana Clarke, Lee & McPherson (2006: 56), known from Sabah and Sarawak primarily from mossy forest on sandstone (Clarke *et al.* 2006, Cheek & Jebb 2001), but unusual in this case for producing pitchers 1/3 larger (to *ca.* 35 cm tall excluding lids) and suffused with orange or red, rather than entirely yellowish-green or occasionally red speckled as on Mt. Alab in Sabah and Batu Buli in Sarawak; *N. fusca s.lat.* 'Sarawak form', known mainly from Sarawak where it is especially abundant on clay laterite road embankments in the Hose Mountains and Kelabit Highlands at 1000–1300 m elevation (AR, MB, SM pers. observ.); and the widespread *N. hirsuta*, also typically found on sandstone (Clarke 1997, Cheek & Jebb 2001). Also observed along summit ridges, either in humus overlying clay and sand or in moss pads, was a *Nepenthes* taxon (*N.* sp. Bagong) that was initially considered a potential candidate for *N. mollis* on account of its densely pubescent foliage and decurrent leaves (see Discussion).

Nepenthes species recorded only on the Kemul Massif

Nepenthes fusca s.str., found growing discontinuously in forest along the top of a narrow ridge, favouring brighter situations with a more open canopy; and *N. mollis*, first sighted by Punan guides in the form of a large, fallen pitcher, revealing a high epiphyte hanging from a bough *ca*. 20 m overhead identifiable by decurrent leaves on its 3 m pendent stem, and soon after confirmed by examination of plants growing either terrestrially or on climbable trees in the summit area.

Discussion

Floral assemblages

Exploration of the Kemul Massif and Mt. Bagong found unexpected differences in the structure of their forests. Although many of the common Bornean montane tree genera were present on both mountains, including Shorea Roxb. ex C.F.Gaertn. (Dipterocarpaceae Blume), Elaeocarpus L. (Elaeocarpaceae Juss.), Ficus L. (Moraceae Gaudich.) and Lithocarpus Blume (Fagaceae Dumort.), the forests encountered along the route of ascent of the Kemul Massif were found to be comparatively very open, with less dense understorey vegetation, greatly facilitating expedition progress. At higher elevations on Kemul (1500–2054 m), there was also a greater preponderance of large Podocarpaceae Endl., including Dacrycarpus (Endl.) de Laub., Dacrydium Lamb., Phyllocladus Rich. ex Mirb., and Podocarpus L'Hér. ex Pers., as well as Agathis borneensis Warb. (Araucariaceae Henkel & W.Hochst.), Tristaniopsis whiteana (Griff.) Peter G.Wilson & J.T.Waterh. (Myrtaceae Juss.), Castanopsis (D.Don) Spach (Fagaceae) and, notably, an isolated true pine (*Pinus* L., Pinaceae Spreng. ex F.Rudolphi). Though acid-loving herbaceous plants were abundant in the high elevation moss forest, calcicolous Ardisia Sw. (Primulaceae Batsch ex Borkh.), Didymocarpus Wall. (Gesneriaceae Dumort.) and Paphiopedilum bullenianum Pfitzer (Orchidaceae Juss.) were observed on or atop vertical walls of metamorphosed limestone. This strongly contrasted with the denser understorey of Mt. Bagong and shorter trees at higher elevations, with a more pronounced transition towards the summit into elfin montane forest and scrub, including Quercus L. (Fagaceae), Leptospermum J.R.Forst. & G.Forst. (Myrtaceae), numerous Rhododendron L. (Ericaceae Juss.) species, Camellia lanceolata (Blume) Seem. (Theaceae Mirb. ex Ker Gawl.), Schefflera J.R.Forst. & G.Forst. (Araliaceae Juss.), and herbaceous plants including Gvnura Cass. (Asteraceae Bercht. & J.Presl), various terrestrial or lithophytic orchids like Coelogyne Lindl., Dendrobium Sw. and Peristylus Blume (Orchidaceae), and a lithophytic carnivorous bladderwort, Utricularia striatula Sm. (Lentibulariaceae Rich.).

The differences in general floral makeup seem to be reflected somewhat in the *Nepenthes* flora of these neighbouring peaks, particularly the terrestrial species. Though the authors note that the presence of a 4WD track across the length of Mt. Bagong opens up considerable habitat for ruderal species of genera like *Nepenthes*, four of the primarily terrestrial taxa found on Mt. Bagong were not observed in suitable habitats on the Kemul Massif despite three of them being widespread in Borneo. While the topography of each mountain and its effects on orographic rainfall undoubtedly affect local plant assemblages, striking differences in geology between the two mountains are likely to account for the rather different forest compositions observed.

Mount Kemul is the easternmost peak of a mountain massif (Rutten 1947) whose main prominence runs eastwest across the present-day borders of North Kalimantan and East Kalimantan, and approximately 37 km north of Mt. Bagong (*ca.* 2165 m), the highest peak in the locally named Pegunungan Dua-Lima range to the south (Fig. 1). The mountain complexes are thought to have formed from the mid-Neogene period onwards (10–5 million years ago), during a set of geological episodes that also resulted in the formation of Sabah's Crocker Range, including Mt. Kinabalu (Collenette 1964, Hall 2002). However, despite their relative proximity, the two prominences are geologically distinct; the uppermost part of the Kemul Massif is derived from uplifted Oligocene limestone, and Miocene alkaline granites, both of which are apparent along the expedition route at 1300–1500 m (rock thrusts and cliffs of limestone and slate) and 1700–1850 m (talus slope of igneous rock) elevation respectively; whilst the Dua-Lima range, including Mt. Bagong and much of the surrounding area, is derived from older sediments (Tate 2001) that mainly include clays and sandstones, both of which have given rise to surface laterites and washes of quartzitic sand (AR, DG, NM, BQ pers. observ.), in keeping with the known substrate preferences of *N. chaniana*, *N. fusca s.lat.* 'Sarawak form' and *N. hirsuta* found there.

Observations of Nepenthes fusca

Plants matching the *Nepenthes fusca* type materials (at BO, K, and L), as well as the description and illustration provided by Danser (1928), were first located at 1400 m a.s.l. on a steeply ascending ridge. Whilst clearly related to the taxa currently included within *N. fusca s.lat.*, it was apparent that the lids of the type *N. fusca* are flat, more or less ovate and usually with only a basal keel, and are larger than the pitcher opening, becoming longer in the upper pitchers but not showing pronounced marginal revolution. Taking into account this and other morphological and ecological differences (Table 1), *N. fusca s.lat.* clearly represents a species complex from which we can separate two well characterised taxa whose ranges are centred on Sarawak and Sabah. *N. fusca s.lat.* 'Sarawak form' is here proposed as *N. dactylifera spec. nov.*, while the name *N. zakriana* is reinstated from synonymy for the Sabah taxon with an emended description (see Taxonomy). A comparison of the upper pitchers of each species is provided (Fig. 3) and their approximate ranges in Borneo indicated (Fig. 4).



FIGURE 3. Comparison of the upper pitchers of (A) *Nepenthes fusca*, (B) *N. dactylifera* (two pitchers) and (C) *N. zakriana*. Illustrated by M. Barer.



FIGURE 4. Distribution of *Nepenthes dactylifera*, *N. fusca* and *N. zakriana* in Borneo based on accessions held at BO, K, L and SAR herbaria, supplemented by field observations. Drawn by A.S. Robinson.

Observations of Nepenthes mollis

Plants matching the *Nepenthes mollis* type material (at BO), as well as the description provided by Danser (1928), were located from 1840 m a.s.l. Identity was determined by examination of the leaves, stems, indumentum, and male inflorescences. Observations of living material bearing pitchers satisfied all authors that this taxon is conspecific with *N. hurrelliana*, as hypothesised by Salmon (1999), making the name *N. hurrelliana* a later heterotypic synonym of *N. mollis*. Additional measurements of living material at the type locality were made in order to provide an emended and more representative circumscription of this species. The discrepancies between *N. hurrelliana* and the type material of *N. mollis* raised by Salmon (1999) are addressed following the emended description of *N. mollis* (see Notes).

Observations of *Nepenthes mollis* at the type locality ruled out the initial belief that *Nepenthes* sp. Bagong might represent *N. mollis*. The pitchers and laminae of the two taxa are very similar, however requisite comparisons of the plants indicate that they represent a pair of closely related species that diverge markedly in terms of their petioles, axillary buds, lids, stems and general stature, but particularly their inflorescences (summarised in Table 2). In fact, *Nepenthes* sp. Bagong represents an undescribed taxon that has been documented across eastern Sarawak; including only records for which clear photographic evidence or collections are immediately available to the authors, this taxon has also been recorded from Batu Lawi (Jean De Witte pers. comm. 2003) and Batu Buli (Martin Dančák pers. comm. 2009), both in the Kelabit Highlands, as well as on Mt. Mulu (*ca.* 1400 m on the Melinau stream trail, AR, BQ pers. observ. 2014) and in the Hose Mountains (MB pers. observ. 2016). Its known range thus includes peaks across an area of 39,000 km², but with only a few specimens noted at each locality, it remains a poorly-documented taxon.

	Nepenthes dactylifera	Nepenthes fusca	Nepenthes zakriana
Rosette leaves	Broadly obovate to elliptic, base abruptly attenuate, apex obtuse to truncate	Obovate to sub-elliptic, base gradually attenuate, apex obtuse to emarginate	Elliptic to obovate, base gradually attenuate, apex acute to obtuse
Vining stem leaves	Oblong to elliptic, apex acute to acuminate, adaxial surface with sparsely scattered glands	Elliptic, apex obtuse, occasionally acute	Narrowly elliptic to elliptic, rarely obovate, apex acute
Leaf base decurrency	Base decurrent into two narrow wings 1–3 mm wide down entire internode (but up to <i>ca</i> . 1.3 internodes, e.g. <i>Prance</i> 30548)	Not decurrent, base amplexicaul, clasping stem by ca . 1/2 its dia.	Not decurrent to slightly so, usually by < 8 mm, base amplexicaul by <i>ca</i> . $1/2-4/5$ stem dia.
Lower pitcher shape	Ellipsoid in the lower half, cylindric and slightly narrower above, widening towards mouth, peristome oblique, somewhat uniform in width and strongly raised at rear to form a neck	Sub-cylindric, slightly narrowed at the midpoint with slight gibbosity below the mouth, peristome strongly oblique, widening from midpoint of mouth towards raised and slightly recurved neck	Cylindric to sub-ellipsoid throughout or narrowly ellipsoid in lower half and cylindric above, often narrowing slightly towards mouth, peristome oblique, typically wider towards raised neck, neck often recurved forwards over mouth
Lower pitcher lid	Narrowly ovate, usually complanate, pronounced abaxial midline rib with slight basal bulge but no keel, distal part with few, large crateriform glands, rarely with terminal protuberance	Ovate, base sub-cordate, adaxial surface typically channelled along midline rib, abaxial rib only slightly pronounced, but with large basal keel bearing rounded glands, abaxial surface with small scattered glands and fine brown hairs to 0.5 mm long	Ovate to sub-triangular, margins sinuate, occasionally revolute, abaxial midline rib pronounced with large basal keel, distal part sometimes with apical protuberance up to 3 mm long, bearing small crateriform glands
Upper pitcher shape	Generally tubulose to broadly infundibular, rarely narrowly infundibular, peristome broad and strongly oblique, pitchers often large (15–25 cm tall)	Narrowly infundibular throughout, peristome robust, often slightly raised at front between wings, slightly oblique thereafter then rising more or less vertically to form a slightly recurved neck	Generally infundibular with prominent ventral gibbosity below peristome, rarely narrowly infundibular throughout, peristome ± horizontal at front, rising sharply towards rear into neck, neck often recurved over mouth
Lid shape in upper pitchers	Very narrowly ovate to triangular, appearing sagittate to ligulate due to revolution or conduplication of margins about 2/5 from base, thereafter usually complanate	Ovate, base cordate, flattened, margins sometimes sinusoid, longer and broader than in lower pitchers	Narrowly triangular-ovate, appearing ligulate due to revolute margins
Lid length in upper pitchers	3.5–6.5(–7.5) cm long, generally >4.5 times longer than wide	4.5–6.5 cm long, generally 1.8–2 times longer than wide	1.5–3.8(–5) cm long, generally >4.5 times longer than wide
Lid appendages in upper pitchers	Pronounced abaxial midline rib, slight basal bulge or keel, rib extending into an apical protuberance 3–8 mm long	Abaxial midline rib only slightly pronounced, but with a pronounced basal keel, few to no glands, usually with marginal hairs	Abaxial midline rib with pronounced basal keel, apex with or without apical protuberance up to 3 mm long
Lower lid surface in upper pitchers	Distal 2/3 of abaxial mid line rib and protuberance with very large, scattered crateriform nectar glands, abaxial surface of lid densely scattered with smaller nectar glands	Indumentum of brown hairs on both surfaces, to 0.5 mm long, but up to 1 mm along lower edge of keel	Crateriform glands sometimes present along abaxial midline rib, small nectar glands present across abaxial surface
Indumentum of floral parts	Glabrous to sparsely pubescent	Raceme, pedicels and abaxial floral parts densely pubescent	Generally pubescent
Elevation	(300–)800–1500(–1900) m	1400–1600 m	(800–)1200–2500 m
Growth habit	Predominantly a high epiphyte at lower elevations, frequently a ruderal terrestrial in clay laterite above 1200 m	Exclusively terrestrial in humus on rocky, freely draining ridges	Predominantly epiphytic, but occasionally terrestrial above 1300 m, favouring serpentine rubble or humus banks

TABLE 2. A morphological comparison of Nepenthes dactylifera, N. fusca, and N. zakriana.

Taxonomic treatment

1. Nepenthes dactylifera A.S.Rob., Golos, S.McPherson & Barer, spec. nov. (Figs. 5-6)

Type:—Borneo, Brunei, Temburong, Amo, Bukit Belalong, 4.33°N 115.09°E, 869 m a.s.l., 24 February 1992, *Prance 30548* (holotype K!, iso-L!) [K—climbing stem with upper pitchers; L—climbing stem with upper pitchers, infructescence].

- Nepenthes sp. ["undescribed species collected from the Mulu area"] in Phillipps & Lamb (1988: 8, 1 fig.).

- Nepenthes sp. A in Clarke (1997: 141, fig. 97) and Steiner (2002: 112).

Nepenthes fusca auct. non Danser [Jebb & Cheek (1997: 41), partim; Cheek & Jebb (2001: 64), partim; Phillipps et al. (2008: 121), partim [figs. 151, 154–155]; McPherson (2009: 346), partim].

Diagnosis:—*Nepenthes dactylifera* differs from *N. fusca* in the long-decurrent leaf bases (*vs.* non-decurrent), upper pitchers tubulose to broadly infundibular (*vs.* narrowly infundibular), and upper pitcher lids very narrowly ovate, appearing sagittate to ligulate through marginal revolution (*vs.* ovate and \pm complanate).

Description:—Epiphytic or terrestrial scrambling, climbing or pendent shrub, to 4 m tall. *Stems* of rosettes terete, 0.6–0.9 cm in diameter, internodes 0.3–1.1 cm long; vining stems ca. 0.8 cm in diameter, internodes 6–12 cm long. Leaves of rosettes coriaceous, petiolate, lamina broadly obovate-oblong to elliptic, 8-12 cm long, 5.5-8.5 cm wide, apex obtuse to truncate, not peltate, base abruptly attenuate, petiole canaliculate, 3.5-5.5 cm long, sheathing and clasping stem for >3/4 of its circumference. Longitudinal veins 2–3 on either side of midrib, restricted to outer third of lamina, where they run parallel to the laminar margin, somewhat inconspicuous. Pinnate veins numerous, irregularly reticulate, indistinct. Leaves of tall stems coriaceous, petiolate, lamina oblong to elliptic, 12-18 cm long, 6.5-9.5 cm wide, adaxial surface with sparsely scattered glands, apex acute to acuminate, occasionally obtuse, base abruptly attenuate, obtuse, petiole canaliculate, 4.5-6.5 cm long, base decurrent into two narrow wings, each 1-3 mm wide, decurrent for 1–1.3 internodes. Tendrils to 35 cm long. Lower pitchers ellipsoid in the lower half, cylindric and slightly narrower above, widening towards mouth, 8–16 cm tall, 2–3.5 cm wide, with fringed wings 2–4 mm wide, fringe elements ≤ 6 mm long, 2–5 mm apart; peristome oblique, somewhat uniform in width and strongly raised at rear to form a neck, 2.5-4 mm wide at front of pitcher, ribs very fine, ca. 0.2-0.4 mm apart, teeth minute. Lid narrowly ovate, usually complanate, 2.5–3.5 cm long, 1.4–1.8 cm wide, with a pronounced abaxial midline rib and slight basal bulge but no keel, distal part with few, large crateriform glands, rarely with terminal protuberance, abaxial surface of lid with scattered crateriform glands 0.2–0.4 mm in diameter. Spur filiform, ca. 0.8–1.2 cm long. Upper pitchers tubulose to broadly infundibular, rarely narrowly infundibular, 15–25 cm tall, 4.5–6.5 cm wide, wings absent or reduced to ridges; peristome broad, 4–8 mm wide at front of pitcher, and strongly oblique, sometimes slightly raised at the front, ribs and teeth as per lower pitchers. Lid very narrowly ovate to triangular, appearing sagittate to ligulate due to revolution or conduplication of margins about 2/5 from base, thereafter usually complanate, 3.5-6.5(-7.5) cm long, generally >4.5 times longer than wide, with pronounced abaxial midline rib, slight basal bulge or keel, rib extending into an apical protuberance 3–8 mm long; distal 2/3 of abaxial rib and protuberance with nectar glands scattered, narrowly elliptic, very thickly bordered, ocellate-crateriform, ca. 1-1.5(-2) by 0.5(-1) mm, abaxial surface of lid densely scattered with smaller \pm circular, thinly bordered, crateriform nectar glands, *ca.* 0.3–0.6 mm in diameter. Spur filiform, 0.8–1.2 cm long. Male inflorescence to 40 cm long, ca. 180 flowers, peduncle 10-15 cm long, 4-5 mm in diameter at the base, rachis 15–25 cm long, partial peduncles 2-flowered, bifurcating 1–2 mm from base, bracts absent, pedicels to 0.8–1.2 cm long at base of rachis; tepals green, suffusing red once opened, broadly elliptic, 3–3.5 mm long, 2–2.5 mm wide, apex more or less obtuse; staminal column 2 mm long, anther head to 2.5 mm in diameter, consisting of eight fused anthers. Female inflorescence to 30 cm long, ca. 30-50 flowers, peduncle 15-20 cm long, ca. 5 mm in diameter at the base, rachis 8–12 cm long, partial peduncles 2-flowered, lowermost sometimes with filiform bracts to 6 mm long, tepals elliptic, ca. 3 mm long, 1.5–2 mm wide, apex acute, ovary ovoid, 4 mm tall, to 2.5 mm in diameter, fruit 1.5–2.5 cm long, seeds filiform, ca. 1.2 cm long, pale brown. Indumentum of short, fine brown hairs to ca. 0.5 mm scattered over exterior surface of pitchers, tendrils, abaxial midrib and leaf margins, as well as petioles of rosette leaves and all juvenile foliage, stem more or less glabrous, especially in tall stems. Inflorescences sparsely to densely pubescent, with simple, reddish-brown woolly hairs present on the main axis, pedicels and abaxial surface of tepals. *Colour* variable, mature stems usually reddish to black, leaves bright green, sometimes suffused with red, lower pitchers often dark, olive green blotched with deep red or black, peristome green to deep red, often suffusing to pale green on inner margin, upper pitchers from entirely pale green (almost white) to green blotched with red or, typically, green suffused with orange with a whitish peristome striped with deep red.



FIGURE 5. *Nepenthes dactylifera* A.S.Rob., Golos, S.McPherson & Barer. A—climbing stem with emerging inflorescence. B—detail of internode showing leaf base decurrency. C—lower pitcher. D—abaxial surface of lid of lower pitcher with crateriform glands. E—detail of crateriform glands along midline rib as well as adjacent scattered pitted glands. F—upper pitchers, *left* lateral view, *right* ventral view. G—lateral view of upper pitcher lid. H—detail of upper lid apical protuberance. I—inflorescence. J—seed capsules. K—male flowers. Scale bars: A, B, C, D, F, G, J = 1 cm, E, H, K = 5 mm, I = 2 cm. Based on *Prance 30548*, as well as on photographs and measurements made of *in situ* material. Illustrated by M. Barer.



FIGURE 6. Pitchers of *Nepenthes dactylifera*. A—lower pitcher (Kelabit Highlands). B—lower pitcher (Hose Mountains). C—upper pitcher (Kelabit Highlands). D—upper pitcher (Hose Mountains). E—exposed clay laterite habitat (Hose Mountains). F—thinly bordered crateriform nectar glands on abaxial lid surface. G—ocellate-crateriform glands in the apical region of an upper pitcher lid. F & G from *Prance 30548*, grids = 1 mm. Photographs A–C by A.S Robinson; D, E by M. Barer; F, G by M.R. Golos.

Etymology:—The epithet *dactylifera* is derived from the Greek δάκτυλος (*daktylos*; finger) and the Latin suffix *-fer* (bearing), a reference to the extremely long and narrow lid of this species, which fancifully resembles the arched fingers of the Grim Reaper in popular culture.

Phenology:—Flowering and fruiting have been observed in the months of February, March, July, August, September, and October.

Distribution and ecology:—*Nepenthes dactylifera* is widely distributed across the central highlands of Sarawak, its range stretching the length of the state from at least the Second Division (e.g. Bukit Bangai) in the west to the Fifth Division (e.g. Mt. Murud) in the east (Fig. 4). It has also been recorded from Brunei's eastern exclave (Temburong), from both North and East Kalimantan (Mt. Bagong), and from West Kalimantan (Mt. Keburau and Mt. Kenepai). It grows mainly as a high epiphyte in trees from about 800 m a.s.l. but widely colonises ruderal habitats such as cleared road cuttings generally above 1200 m, especially clay laterite sites in full sun. It is abundant on road embankments at *ca.* 1300 m in the Kelabit Highlands and on logging roads in the Hose Mountains, Sarawak (AR pers. observ.). It is only occasionally recorded above 1500 m elevation, such as on Mt. Bagong where isolated individuals were observed during this expedition at 1900 m. At the other extreme it may grow as low as 300 m a.s.l. in hill forest (see Phillipps *et al.* 2008: 127).

Nepenthes dactylifera is known to hybridise in nature with both *N. platychila* Lee (2002a: 257) and *N. veitchii* Hooker (1859: 421) in the Hose Mountains (see Lee 2002a, Lee 2002b) and with *N. vogelii* Schuiteman & de Vogel (2002: 537) in the Kelabit Highlands (AR pers. observ.).

Conservation status:—*Nepenthes dactylifera* is widespread in north-central Borneo above elevations of 800 m and grows within a number of protected areas, including Ulu Temburong NP in Brunei, and Batang Ai NP, Gunung Buda NP, Gunung Mulu NP and Pulong Tau NP in Sarawak. It is also likely to be present in the large Kayan Mentarang NP in North Kalimantan, which runs along the border with Sarawak and Sabah. It therefore qualifies as *Least Concern* when evaluated against the IUCN 3.1 criteria (IUCN 2012).

Notes:—The ocellate crateriform glands observed on the apical protuberance of the lid of the upper pitchers (Fig. 6G) are variable in size, but they can be exceptionally large, in some cases exceeding 2 mm in width and 1 mm in gape, rivalling those on the much larger appendages of *Nepenthes appendiculata* Chi.C.Lee, Bourke, Rembold, W.Taylor & S.T.Yeo in Lee *et al.* (2011: 24). The glands were observed to be heavily frequented by ants on some plants, but not on others, and ants were found to be a fairly common prey type on Mt. Bagong.

A taxon belonging to *Nepenthes fusca s.lat.* that closely resembles *N. dactylifera* has been recorded from Mt. Lumarku in southern Sabah. This taxon differs in having unusually narrow, yellowish lower and upper pitchers (Clarke 1997: fig. 58, Phillipps *et al.* 2008: fig. 156). In the absence of representative herbarium material and detailed field observations, it is treated as an incompletely diagnosed taxon here.

Additional specimens examined:—KALIMANTAN: Hallier 1716 (K! [4 sheets]), G. Kenepai [W. Kalimantan], no elevation data, 30 December 1893 – 5 January 1894 [separate climbing stem, leaf and upper pitcher elements]; Schmutz 7288(a) (L!), Kalimantan Barat (W. Borneo), Mt. Keburau, 1000 m, 28 May 1989 [short stem with lower pitcher, pitcherless climbing stem]. SARAWAK: Adam 2414 (ABD!), Miri, Mt. Mulu, 1000 m, 10 December 1987 [climbing stem with upper pitcher; originally identified as N. maxima, later as N. curtisii by J.H. Adam, 25/1/1991]; Collenette 838 (K! [2 sheets]), 2nd Div., Bukit Bangai, Sungai Lemanak, 3000 ft [=914 m], 22 October 1961 [rosettes with lower pitchers]; Collenette 844 (K! [2 sheets]), 2nd Division, Bukit Bangai, Sungai Lemanak, 3000 ft [=914 m], 22 October 1961 [climbing stem with upper pitcher, female inflorescence, infructescence; climbing stem with upper pitchers]; S. 19609 (Ashton) (K!, L, SAR!) Carapa Pila, Pila [Hose Mountains]/Mujong watershed, Balleh, 900 m, 7 April 1964 [K—climbing stem with upper pitchers; SAR—short stem with lower pitchers]; S. 33945 (Chai) (K!, KEP, L, MO, SAN, SAR!), 2nd Division, Lubok Antu District, Lanjak-Entimau P.F. [Protected Forest], Bukit Sengkajang, 3200 ft [=975 m], 17 March 1974 [K, SAR—climbing stem with upper pitchers, infructescence]; S. 64997 (Yii et al.) (K, L! [2 sheets], SAR!), Bintulu div., Tatau, Ulu Sg. Sangan, Bukit Kana, 700 m, 8 October 1994 [L-climbing stem with upper pitchers, female inflorescence; pitcherless climbing stem with male inflorescence; SAR-climbing stem with pitcher (largely missing), female inflorescence]; S. 65959 (Mohtar & Yii) (K, KEP, SAR!), Bintulu Division, Bukit Lumut, 800 m, 24 September 1992 [SAR—climbing stem with lidless upper pitchers, male inflorescence]; S. 66985 (Yii et al.) (K, KEP, L, MO, SAN, SAR!), Bintulu Division, Tatau, Ulu Sg. Sangan, Bukit Kana, 820 m, 11 October 1994 [SAR—climbing stem with upper pitcher bearing very broad peristome]; S. 67027 (Yii et al.) (KEP, SAR!), Bintulu Division, Tatau, Ulu Sg. Sangan, Bukit Kana, 800 m, 13 October 1994 [SAR-climbing stem with upper pitcher]; S. 77568 (Pearce et al.) (SAR!), Ulu Engkari LEWS [Lanjak Entimau Wildlife Sanctuary], Bukit Pininjau, 1150 m, 1 September 1998 [climbing stem with upper pitchers]; S. 87448 (Lee & Jong) (SAR! [2 sheets]), Limbang, Gunung Murud, side of logging road, 4°00'N 115°33'43"E, 1298 m, 24 August 2005 [climbing stem with

upper pitchers, infructescence; leaf with lower pitcher]; *S. 90479 (Lim & Lee)* (SAR!), Marudi, Sungai Silat Basin, SW ridge of Bukit Palutan, 2°48.00'N 115°01.33'E, 1100 m, 28 March 2003 [stem with short internodes and small laminae but bearing typical upper pitchers].

The following specimens from the Bukit Robertson area were examined as part of the assessment of *N. dactylifera*, but are incompletely diagnosed:—**SARAWAK:** *S. 80625 (Julaihi et al.)* (SAR!), Belaga, ulu sungai Danum, summit of hill next [to] Bukit Robertson, 02°28'42[.]82"N 114°33'9[.]62"[E], 1100 m, 7 August 1999 [climbing stem with upper pitchers]; *S. 81064 (Julaihi et al.)* (SAR!), Belaga, ulu sg[.] Danum, hill near Bukit Robertson, 02°28'7[.]10"N 114°34'2[.]98"E, 850 m, 9 August 1999 [stem with lower pitchers].

Notes on specimens examined:—The taxon from Bukit Robertson—represented by (*Julaihi et al.*) 80625 and 81064—is rather distinctive, having narrowly infundibular upper pitchers with a very narrow peristome and an extremely narrow and densely hairy lid. Lower pitchers likewise have an unusually narrow peristome and lid. While *N. dactylifera* shows considerable variability in these characters, their expression in the plants from Bukit Robertson is extreme. Field studies are needed before a more definitive determination can be made, and we therefore treat this taxon as incompletely diagnosed at present.

At the other end of the spectrum, *N. dactylifera* can be a very robust species with a very broad peristome, as exemplified by (*Yii et al.*) 66985.

2. Nepenthes fusca Danser (1928: 288, fig. 6) descr. emend. A.S.Rob. & Golos (Figs. 7-8)

Lectotype (designated by Jebb & Cheek 1997: 41):—Borneo, Kalimantan, W. Koetai, G. Kemoel, ±1500 m, 12 October 1925, Endert 3955 (BO!, isotypes BO!, K!, L) [date incorrectly listed as 12 November in Jebb & Cheek (1997) and Cheek & Jebb (2001)] [lectotype BO—climbing stem with lidless upper pitchers, male inflorescence; iso- BO—separate lidless upper pitcher and intermediate pitchers, leaf and stem elements; K—climbing stem with upper pitcher, male inflorescence].

- Nepenthes veitchii? auct. non Hook.f. [Endert (1927: 277)].

Other concepts of *Nepenthes fusca s.lat*.:—From our concept of *Nepenthes fusca* are to be excluded those of Kurata (1976: 48, pl. 13), Phillipps & Lamb (1988: 24, 3 figs.), Phillipps & Lamb (1996: 87, fig. 48), and Clarke (1997: 87, figs. 57–58), *quae pro parte = N. fusca* Danser & *N. zakriana* (J.H.Adam & Wilcock) J.H.Adam & Hafiza, as well as those of Jebb & Cheek (1997: 41), Cheek & Jebb (2001: 64), Phillipps *et al.* (2008: 121, figs. 149–156), and McPherson (2009: 346, figs. 183–185), *quae pro parte = N. dactylifera* A.S.Rob., Golos, S.McPherson & Barer, *N. fusca* Danser & *N. zakriana* (J.H.Adam & Wilcock) J.H.Adam & Wilcock) J.H.Adam & Wilcock) (J.H.Adam & Wilcock) (J.H.Adam & Mathematica) (J.H.Adam & Wilcock) (J.H.Adam

Moreover, our concept of *Nepenthes fusca* does not include: – "*Nepenthes fusca* subsp. *apoensis*" J. H.Adam & Wilcock *ex* Jebb & Cheek (1997: 41), *nomen nudum; quae* = *N. stenophylla* Mast., material at K!: *S. 35939* (*Chai*), Borneo, Sarawak, 4th Div., Baram District, Kelabit Highland[s], summit of Apo Dari, 1550 m, 17 November 1974 [climbingstem with upper pitchers, female inflorescence; annotated as *N. fusca* var. *apoensis*(*sic*) by J.H.Adam, 25/1/1991)]. – "*Nepenthes fusca* subsp. *kostermansiana*" J.H.Adam & Wilcock *ex* Jebb & Cheek (1997: 41), *nomen nudum; quae* = *N. epiphytica* A.S.Rob., Nerz & Wistuba, material at L! and K! (type material of *N. epiphytica*—see under "Additional specimens examined").

Description¹:—Terrestrial climbing or scrambling shrub, to 5 m tall. *Stems* of rosettes terete, 0.6–0.8 cm in diameter, internodes 0.4–1.5 cm long; vining stems 0.4–0.6 cm in diameter, internodes 8–15 cm long. *Leaves of rosettes* coriaceous, petiolate, obovate to sub-elliptic, 12–15 cm long, 4–5.5 cm wide, apex obtuse to emarginate, base gradually attenuate, petiole narrowly canaliculate, 2–3.5 cm long, base amplexicaul and sheathing stem for *ca*. 1/2 its circumference, rarely more. Longitudinal veins 4 on either side of midrib in outer third of lamina, where they run parallel to the laminar margin, originating at base of leaf, inconspicuous. Pinnate veins numerous, irregularly reticulate, indistinct. Tendrils more or less equal in length to lamina. *Leaves of climbing stems* scattered to sub-alternate, coriaceous, petiolate, rarely sub-petiolate, lamina elliptic, 10–16 cm long, 3.5–6 cm wide, apex obtuse, occasionally acute, base gradually attenuate, petiole 1.5–4.5 cm long, base amplexicaul and sheathing stem for *ca*. 1/2 its circumference, rarely more. Longitudinal veins 2 either side of midrib in outer third of lamina, parallel with laminar margin, indistinct. Tendrils equal or up to twice as long as lamina, typically curling once only. *Lower pitchers* sub-cylindric, narrowing slightly in the middle, with slight gibbosity below the mouth, 9–16 cm tall, 2.5–4.5 cm wide, with fringed wings 1–3 mm wide, fringe elements to 8 mm long, 3–5 mm apart; peristome strongly oblique, widening

¹This emended description is based on measurements made of *N. fusca in situ* in the Kemul Massif and on examination of the type material deposited at BO and K.



FIGURE 7. Nepenthes fusca Danser. A—climbing stem with emerging inflorescence. B—lower pitcher. C—intermediate pitcher. D base of lower/intermediate pitcher lid, showing detail of highly glandular keel. E—upper pitchers, top right ventral view, bottom left lateral view. F—base of upper pitcher lid showing distribution of indumentum. G—lower pitcher lid, top adaxial surface, bottom abaxial surface. H—peristome in cross-section. I—dehiscing seed capsules. J—male flowers. Scale bars: A, B, C, E, G = 1 cm, D, F, H, I, J = 5 mm. Based on Endert 3955 (isotype K) and supplemented with photographs and measurements made of *in situ* material. Illustrated by M. Barer.

from midpoint of mouth towards raised and slightly recurved neck, 2.5-4 mm wide at front of pitcher, sub-cylindric in section, broadening and increasingly flattened towards neck and ≤ 12 mm wide, ribs *ca.* 0.3–0.5 mm apart, teeth fine, \leq 0.4 mm long. Lid ovate, \pm complanate, base sub-cordate, 3.5–5 cm long, 1.8–2.5 cm wide, adaxial surface typically channelled along midline, with abaxial midline rib only slightly pronounced, but with pronounced semi-circular basal keel 3–5 mm tall, bearing rounded glands and appearing bumpy, abaxial surface of lid with small, densely scattered pitted circular glands and fine brown hairs to 0.5 mm long, apex slightly retuse, no apical protuberance but frequently with a patch of sub-apical ocellate-crateriform glands. Spur filiform, simple, rarely branched at base into 2(-3) parts, 6-8 mm long. Upper pitchers narrowly infundibular throughout, 12-18 cm tall, 2.5-5.5 cm wide at mouth, wings reduced to prominent ridges, with slight ventral flattening in between; peristome robust, 4–6 mm wide at front of pitcher and flattened, usually slightly raised at front between wings, slightly oblique thereafter and increasingly cylindric, rising more or less vertically to form a slightly recurved neck and widening to ≤ 15 mm wide. Lid ovate, base cordate, \pm complanate, margins sometimes sinusoid, longer and broader than in lower pitchers, 4.5–6.5 cm long, generally 1.8–2 times longer than wide, abaxial midline rib only slightly pronounced, but with a pronounced basal keel, keel semicircular, 2–4 mm tall, bearing few inconspicuous to no glands and usually with brown, woolly hairs 0.8–1 mm long along lower margin, shorter and sparser on appressed surfaces either side, distal part of midline rib sometimes with longitudinally distended crateriform glands, apex usually diminished and without apical swelling, rarely with minute apical protuberance ca. 1 mm long, indumentum of short, simple, brown hairs on abaxial and adaxial surfaces of lid, to 0.5 mm long. Spur filiform, simple or branched at base into 2 parts, 0.8–1.2 cm long. Male inflorescence to 20 cm long, ca. 60–80 flowers, peduncle ca. 6–8 cm long, 4–5 mm in diameter at the base, rachis 8–12 cm long, partial peduncles 1- to (mainly) 2-flowered, bracts absent, bifurcating 0.5–1 mm from base, pedicels ca. 9 mm long; tepals green, distal 2/3 suffused with purple-red, elliptic, 3–3.5 mm long, 2 mm wide, apex acute, adaxial surface with 40–50 conspicuous glands, typically green; staminal column to 2-3 mm long, anther head 1.8 mm in diameter, consisting of 8 fused anthers, anthers red, pollen grains yellow. Female inflorescence to 18 cm long, peduncle 8–12 cm long, rachis 6–8 cm long, partial peduncles 2-flowered, pedicels 5–7 mm long, tepals narrowly elliptic, ca. 2.5 mm long, apex acute, fruit 1.5–2.2 cm long, seeds filiform, 7–9 mm long, pale brown. *Indumentum* of rufous simple and branching hairs present on stems, petioles, leaf margins and both surfaces of midrib, especially dense on emerging foliage and rachis, laminae with simple, minute white hairs on adaxial surface, becoming somewhat caducous in mature leaves, and simple, sparse, rufous hairs on abaxial surface and on pitchers. Colour of mature stems, leaves and tendrils green, developing foliage flushed red or bronze, pitchers pale green (lowers) to yellowish green (uppers) and spotted externally and internally (within the waxy zone only) with red to purple blotches, peristome colour as per pitchers with variable amounts of red striation.

Phenology:—Male and female plants were observed in flower and fruit in July 2018, while the type materials (all male) were collected in October. The region is not strongly seasonal and it is possible that flowering occurs spontaneously throughout the year.

Distribution and ecology:—*Nepenthes fusca* was observed from 1400–1600 m a.s.l. on narrow, rocky, freedraining ridges amidst relatively open ridge forest including small-trunked *Elaeocarpus*, *Phyllocladus*, and *Tristaniopsis*, alongside various grasses, shrubs and the resam fern *Dicranopteris linearis* (Burm.f.) Underw.. All observed plants were terrestrial in rocky humus banks or pockets of humus at the bases of trees, in breezy conditions that led to significant drying of surface moisture during the day. Although these observations do not rule out an epiphytic habit for *N. fusca*, no epiphytic plants were observed in damper forest away from the drying ridge-top conditions. This is in contrast with *N. dactylifera* and *N. zakriana*, which are occasionally found growing as epiphytes in sheltered situations close to where terrestrial plants are noted. In the absence of evidence to the contrary, *N. fusca* is regarded as a terrestrial species, as per Danser (1928).

Although *Nepenthes tentaculata* occurs close to the upper elevation limits of *N. fusca*, no hybrids between the two species were observed.

Conservation status:—*Nepenthes fusca* clearly has a restricted distribution, being thus far known only from the Kemul Massif, with no equivalent material being noted by this expedition on Mt. Bagong to the south, where *N. dactylifera* was present. However, in the absence of further explorations of the massif and adjacent mountains to the north and west, the species must be listed here as *Data Deficient* (DD; IUCN 2012). The remoteness of the massif and great expense of access present good barriers to unscrupulous collection; coupled with the low value of the plant, *N. fusca* is unlikely to be meaningfully threatened by the horticultural trade.

Notes:—The overall characteristics of *Nepenthes fusca*, but especially its flattened lid, peristome and its general colouration, resemble *N. platychila* and *N. vogelii*. Taking into account its basal lid appendage and mainly 2-flowered partial peduncles, it appears close to *N. epiphytica* Robinson, Nerz & Wistuba (2011: 36), a species currently known

from only two limestone peaks in East Kalimantan (Robinson *et al.* 2011), which differs in being apparently exclusively epiphytic, producing lids bearing a greatly reduced but nonetheless glandular basal swelling, and for its very widely flaring upper pitchers. In common with *N. mollis*, the basal keels in the lids of the upper pitchers of *N. fusca* were found to be hairy, with few to no glands, contrasting with those of the *N. fusca* lower pitchers, which appear bumpy as they are covered with large, rounded glands.

Syrphid flies were observed on the male inflorescences of *Nepenthes fusca*, suggesting that they might represent a pollinator. Muscid flies were also observed feeding on the basal keels of upper pitchers, although ants were found to be the primary prey caught within the pitchers.



FIGURE 8. *Nepenthes fusca.* A—lower pitcher. B–C—upper pitchers. D—detail of male partial peduncles showing red thecae. E—aerial camera view of the western flanks of the Kemul Massif. Approximate elevations for the main habitats of *N. fusca* (1400 m) and *N. mollis* (2000 m) are indicated. Photographs A, B by A.S. Robinson; C–E by M.R. Golos.

Additional specimens examined:—*Nepenthes epiphytica:*—KALIMANTAN: *Kostermans 21495* (holotype L!, iso-K! [2 sheets]), Indon. E. Borneo [East Kalimantan], Berau, Mt. Njapa on Kelai R. limestone, 1000 m, 25 October 1963 [L—climbing stem with upper pitchers; annotated as *N. fusca* var. *kostermaniana* (*sic*) by J.H. Adam, 25/?/1991; K—climbing stem with upper pitchers, female inflorescence; climbing stem with upper pitchers, infructescence].

The following specimens were examined as part of the assessment of N. fusca s.lat., but are incompletely diagnosed: SARAWAK: Anderson 218 (K!), Gunong Rumput, no elevation data, August 1912 [stem with lower and upper pitchers]; B. 2791 (Burtt & Woods) (SAR! [2 sheets]), First Division, Poi [Pueh] Range, Gunong Berumput [=G. Rumput], 4870 ft [=1484 m], 12 August 1962 [separate pitcherless stem, leaf, infructescence and male inflorescences; climbing stem with upper pitchers]; Beccari 2386 (K!), locality given only as "Sarawak", no elevation data, November 1871 [short stem with lower pitchers]; Beccari 2387 (K!), locality given only as "Sarawak, Borneo", no elevation data, collected 1865–1868 [stems with upper pitcher]; (Clemens & Clemens) 20233 (SAR!), Mt. Poi [=G. Pueh], 4500 ft [=1372 m], September 1929 [climbing stem with upper pitcher]; Jacobs 5115 (K!, L, SAR!), 1st div., N. slopes of Mount Penrissen (S. of Kuching), approx. 1°5'N 110°15'E, 1000–1200 m, 7 August 1958 [K-climbing stem with upper pitcher, male inflorescence; SAR-short stem, separate leaf with upper pitcher]; S. 513 ("Museum Collector") (SAR! [2 sheets]), foot of Mt Penrissen, no elevation data, 24 November 1909 [stem with intermediate pitchers; climbing stem with lidless upper pitcher]; S. 12645 (Smythies) (K! [2 sheets], L, S, SAR!), Lundu District, G. Berumput [=G. Rumput], 4877 ft [=1487 m], 25 August 1960 [K—leaf with upper pitchers; climbing stem with upper pitchers; SAR—climbing stem with upper pitchers]; S. 15654 (Smythies) (K!, SAR!), Lundu District, G. Pueh Forest Reserve, S. Sebat Kechil/S. Tembaga ridge, 3700 ft [=1128 m], 5 November 1961 [K-climbing stem with upper pitcher; SAR—short stem with lower pitchers]; S. 42609 (Paie) (SAR!), 2nd Division, S'ggang Road, 85th Mile, Silantek Kiri, Ulu Sg., path to Gunong Silantek, 564 m, 27 August 1980 [climbing stem with upper pitchers]; (Vogel) 933190 (L!), near Padawan, Gunung Penrissen, 800 m, October 1993 [two upper pitchers detached from leaves].

Notes on specimens examined:—Anderson 218, Beccari 2386 and 2387, (Burtt & Woods) 2791, (Clemens & Clemens) 20233, Jacobs 5115, ("Museum Collector") 513, (Paie) 42609, (Smythies) 12645 and 15654, and (Vogel) 933190 all represent an unusually robust form of Nepenthes fusca s.lat. with somewhat flattened lids that is periodically photographed in western Borneo from the mountains (>900 m) S and W of Kuching, Sarawak, especially around the popular Borneo Highlands Resort and Mt. Rumput. Danser (1928) placed the Anderson, Beccari and "Museum Collector" specimens of this taxon within N. maxima, and Cheek's notes on the first two accessions, as well Lee's on the last, place them within N. fusca s.lat. We are unable to place this taxon within N. fusca s.str. owing to the atypical lid morphology, long-decurrent leaf bases, and particularly robust pitchers, while the form of the lid would also exclude it from N. dactylifera. In situ studies of this taxon are merited.

The isotype of *Nepenthes fusca* at L, cited by Cheek & Jebb (2001), is not found in the herbarium's database and could not be located by MG during a visit in January 2018. According to Cheek & Jebb (2001), it and the isotype at K are the only two original sheets with intact upper pitcher lids.

3. *Nepenthes zakriana* (J.H.Adam & Wilcock) J.H.Adam & Hafiza (2006: 434, figs. 3–4) *descr. emend.* A.S.Rob. & Golos ≡ *Nepenthes curtisii* subsp. *zakriana* J.H.Adam & Wilcock (1998: 151, fig. XXIIa–b) (Figs. 9–10)

Type:—Borneo, Sabah, Mt. Kinabalu, Mamut, 1100 m, 21 January 1988, *Adam, Adam & Aliosman 2431* (holotype UKMB, iso-ABD). – "*Nepenthes stenoperculum*" *ined.* [annotated on the specimen (*Clemens & Clemens*) 30980/31092, deposited at BO].

- Nepenthes fusca auct. non Danser Kurata (1976: 48), partim [pl. 13]; [Phillipps & Lamb (1988: 24), partim [3 figs.]; Phillipps & Lamb (1996: 87), partim [fig. 48]; Jebb & Cheek (1997: 41), partim; Clarke (1997: 87), partim [fig. 57]; Cheek & Jebb (2001: 64), partim; Phillipps et al. (2008: 121), partim [figs. 149–150, 152–153]; McPherson (2009: 346), partim [figs. 183–185]].
- Nepenthes maxima auct. non Reinw. ex Nees [Kondo & Kondo (1983: 110), partim [1 fig.]; Kondo & Kondo (2006: 121), partim [1 fig.]].

Description²:—Epiphytic or terrestrial climbing or scrambling shrub, to 3 m tall. *Stems* of rosettes terete, 0.4–0.6 cm in diameter, internodes 0.5–1.5 cm long; vining stems *ca*. 0.5 cm in diameter, internodes 6–15 cm long. *Leaves of rosettes* coriaceous, petiolate, elliptic to obovate, 10–12 cm long, 2.5–4.5 cm wide, apex acute to obtuse, base gradually attenuate into petiole, petiole 1.5–4 cm long, base amplexicaul and sheathing stem by 1/2 to 4/5 its circumference, not decurrent to slightly decurrent for less than 8 mm. Longitudinal veins 2–3 on either side of midrib in outer third of lamina, running parallel to the laminar margin, originating at base of leaf, inconspicuous. Pinnate veins numerous, irregularly reticulate, indistinct. Tendrils ±2 times the length of the lamina, generally 15–20 cm long. *Leaves of climbing stems* scattered, coriaceous, petiolate, lamina narrowly elliptic to elliptic, rarely obovate, 9–16 cm long, 3.5–5 cm wide, apex acute, base gradually attenuate, petiole 3.5–6 cm long, base amplexicaul, sheathing stem by 1/2 to 4/5 its circumference, not decurrent to slightly decurrent for less than 8 mm. Tendrils ±1.5–2 times the length of the lamina, generally 12–20 cm long, often curling twice. *Lower pitchers* cylindric to sub-ellipsoid throughout or narrowly ² The emended description is based on measurements made of herbarium specimens and *in situ* material, and is provided in order to supplement the incomplete description presented in Adam & Hamid (2006).

ellipsoid in lower half and cylindric above, often narrowing slightly towards mouth, 12-16(-23) cm tall, 3-5 cm wide, with fringed wings 2-3 mm wide, fringe elements to 7 mm long, 3-6 mm apart; peristome oblique, typically wider towards raised neck, neck often recurved forwards over mouth, 3-5 mm wide at front of pitcher, sub-cylindric, slightly flattened, increasingly so towards neck and broadening to 6–8 mm wide, ribs ca. 0.3–0.4 mm apart, teeth minute, ≤ 0.4 mm long. Lid ovate to sub-triangular, 3–5 cm long, 1–1.8 cm wide, margins sinuate, occasionally revolute, abaxial midline rib pronounced, with semi-circular basal keel to 3.5 mm tall, distal part sometimes with apical protuberance 2-3 mm long, bearing ocellate-crateriform glands 0.5-0.8 mm in diameter, abaxial surface of lid with small, scattered, pitted glands ca. 0.2 mm in diameter. Spur simple, 5–8 mm long. Upper pitchers generally infundibular with a prominent ventral gibbosity below peristome, rarely narrowly infundibular throughout, 10–16(–19) cm tall, 4–6 cm wide, wings reduced to prominent ridges, peristome sub-cylindric, somewhat flattened, 2-6 mm wide at front and ca. 1/3 wider at rear, ±horizontal at front, rising sharply towards rear into neck, neck often recurved over mouth. Lid narrowly triangular-ovate, appearing ligulate due to revolute margins, 1.5-3.8(-5) cm long, generally >4.5 times longer than wide, typically 0.5-1 cm wide, abaxial midline rib with pronounced semi-circular basal keel, apex with or without glandular apical protuberance up to 3 mm long bearing ocellate-crateriform glands, same glands sometimes present along abaxial midline rib, small nectar glands present across abaxial surface. Spur simple, filiform, 4–12 mm long. Male inflorescence to ca. 20 cm long, 30–80 flowers, peduncle 3–8 cm long, rachis 9–15 cm long, partial peduncles 2-flowered, pedicels ca. 0.8 mm long, tepals elliptic, 3-4 mm long, 2.5-3 mm wide, apex acute, staminal column 3-4 mm long, anther head 1.5 mm in diameter. Female inflorescence to ca. 28 cm long, 30-50 flowers, peduncle 5-12 cm long, rachis 4–13(–20) cm long, partial peduncles 2-flowered, pedicels 0.8–1.2 cm long, tepals elliptic in shape, 3.5–5 mm long, 2.5–3 mm wide, apex acute, fruit 2.5–3 cm long, seeds filiform, 1.2–1.8 cm long, pale brown. Indumentum variable, consisting of short, simple, rufous to white hairs present on stems, pitchers, leaf margins, abaxial leaf surfaces, abaxial midribs, and on developing foliage, becoming caducous in some plants such that older stems and leaves may appear sub-glabrous, generally denser and more persistent on inflorescences. Colour of stems and leaves green, new foliage sometimes suffused with red, pitcher colouration highly variable, lower pitchers green, grey-green or yellowgreen, usually mottled red, purple or black, peristome green, yellow to almost black, typically striated with bands of red or purple, but often of uniform colour, upper pitchers equally variable, externally solid vellow-green or with red to purplish-brown blotches, peristome often striated yellow and red, occasionally wholly yellow or red.

Phenology:—Herbarium specimens of *Nepenthes zakriana* in flower exist for almost every month of the year, suggesting that flowering may occur at any point in time for a given individual.

Distribution and ecology:—*Nepenthes zakriana* has been recorded with certainty only from Sabah, and chiefly the Crocker Range (Fig. 4), with Mt. Kinabalu and surrounding areas being its *locus classicus*. A single, pitcherless specimen from Sarawak's Gunung Mulu National Park (*(Jermy) 13253*) is labelled as *N. fusca* and resembles *N. zakriana* (lacking the decurrent leaf bases of *N. dactylifera*), but its laminae are broadly elliptic with obtuse apices and abruptly attenuated bases, atypical for the species; more complete material would be needed to confirm the identity of this taxon.

Nepenthes zakriana is generally found at elevations of 1200–2500 m, but occasionally down to 800 m. This species appears to be predominantly epiphytic, but is often observed growing terrestrially above 1300 m, being ruderal at sites like road cuttings and on serpentine rubble, but also occurring on natural humus and moss banks.

Like most *Nepenthes*, *N. zakriana* hybridises readily with its congeners. The literature records putative natural hybrids between *N. zakriana* (under the name *N. fusca*) and the following species: *N. burbidgeae* Hook.f *ex* Burbidge (1882: 56) on Mt. Kinabalu and adjacent areas such as Mamut copper mine (AR, MG pers. observ., Lowrie 1983); *N. lowii* on Mt. Alab (Phillipps *et al.* 2008; originally identified as *N. lowii* × *N. pilosa* Danser (1928: 355) by Clarke 1997) and Mt. Trus Madi (Fretwell 2013); *N. reinwardtiana* near Mt. Kinabalu (S. Hirosi pers. comm., McPherson 2009; *N. naquiyuddinii* Adam & Hamid (2006: 431) may represent this cross, per Phillipps *et al.* 2008); *N. stenophylla* Masters (1890: 240) on Mt. Trus Madi (Phillipps *et al.* 2008) and Mamut copper mine (AR pers. observ., Thong 2006); *N. tentaculata* on Mt. Alab (Phillipps *et al.* 2008); and *N. rajah* Hooker (1859: 421) in the Mt. Kinabalu area (Clarke 1997).

Conservation status:—*Nepenthes zakriana* occurs widely across the western highlands of Sabah and is found in a number of protected areas including the Crocker Range NP and Kinabalu NP. It qualifies as *Least Concern* when evaluated against the IUCN 3.1 criteria (IUCN 2012).



FIGURE 9. Nepenthes zakriana (J.H.Adam & Wilcock) J.H.Adam & Hafiza. A—climbing stem. B—lower pitcher. C—abaxial surface of lid of lower pitcher. D—upper pitchers, top right Mamut copper mine, bottom left, Mt. Trus Madi. E—abaxial surface of lid of upper pitcher. F—cross section of peristome. G—inflorescence. H—dehiscing seed capsules. Scale bars: A, B, D, G, H = 1 cm, C, E, F = 5 mm. Based on *Beaman 9957* and *Hobbs 17*, and supplemented with photographs and measurements made of *in situ* material. Illustrated by M. Barer.



FIGURE 10. Pitchers of *Nepenthes zakriana*. A—lower pitcher (Mamut copper mine). B—lower pitcher (Mt. Trus Madi). C—upper pitcher (Mt. Alab). E—climbing stem with pitchers, showing non-decurrent leaf bases (Mamut copper mine). Photographs A–E by A.S. Robinson.

Notes:—The name *Nepenthes zakriana* is applied to this taxon as it was validly published by Adam & Hamid (2006) to describe type material collected from a well-characterised and representative population of *N. fusca sensu* Kurata (1976) from Mamut copper mine (Mt. Kinabalu). However, the protuberant apical lid appendage cited by Adam & Hamid (2006) as a key characteristic of *N. zakriana* cannot be regarded as a reliable diagnostic feature of this species. Different plants within a single population may or may not produce apical appendages, while different pitchers on a single plant can be equally variable—an inconsistency that can be verified at the type locality (AR, MG pers. observ.), as well as on trails around the Kinabalu Park Headquarters, Mt. Alab and Mt. Trus Madi (AR pers. observ.). However, other features (listed in Table 2) including leaf base decurrency, lid morphology, pitcher shape and indumentum make it possible to distinguish readily between this taxon and the closely related *N. dactylifera*.

Additional specimens examined:—SABAH: *Beaman 8178* (K!, L!; photo), Penampang District, Crocker Range, Km 50.7 on Kota Kinabalu–Tambunan Road, 5°50'N 116°19'E, 1600 m, 2 January 1984 [K, L—climbing stem with upper pitcher]; *Beaman 8910* (K! [2 sheets]), Penampang District, Crocker Range, Km 51.8 on Kota Kinabalu–Tambunan Road, 5°50'N 116°20'E, 1500–1600 m, 16 March 1984 [separate leaves and pitchers; pitcherless climbing

stem]; Beaman 9957 (K!, L!; photo), Ranau District, Mamut Copper Mine, 6°02'N 116°39'E, 1600-1700 m, 30 May 1984 [K—climbing stem with upper pitchers, separate lower pitcher; L—leaf with lower pitcher, separate lower pitchers]; (Clemens & Clemens) 30980/31092 (BO!), single sheet combining two labels: (30980) Upper Kinabalu, Penibukan, near Table rock, left trail, north ridge, 5000 ft [=1524 m], 16 January 1933; (31092) Mt. Kinabalu, Penibukan, ridge above Kina Taki river, 4000 ft [=1219 m], 16 January 1933 [climbing stem with upper pitchers, infructescence; "N. stenoperculum MSC"—annotation by M.S. Clemens]; (Clemens & Clemens) 31570 (BO!), two conflicting labels: (1) Mt. Kinabalu, Penibukan, 4000–5000 ft [=1219–1524 m], 7 February 1933; (2) Mt. Kinabalu, Keebambang river, 4000 ft [=1219 m], 3 August 1933 [climbing stem with upper pitchers, male inflorescence]; (Clemens & Clemens) 34454 (BO! [2 sheets]). Mt. Kinabalu, Colombon basin, below Keebambang lobang, 3500 ft [=1067 m], 14 August 1933 [climbing stems with upper pitchers]; (Clemens & Clemens) 50961 (K!), Upper Kinabalu, 7000–8000 ft [=2134–2438 m], 7 December 1933 [climbing stem with upper pitchers]; Collenette 815/a] (K!), Royal Society Route [up Mt. Kinabalu], near platform 2 hrs above Base, 5275 ft [=1608 m], 16 August 1961 [separate leaf and lower pitcher elements]; Collenette 815/b] (K!), Mt. Kinabalu, eastern shoulder, 4000-5000 ft [=1219-1524 m], 16 August 1961 [short stem with lower pitchers]; Collenette 816/a] (K!), Royal Society Route [up Mt. Kinabalu], near platform 2 hrs above Base, 5275 ft [=1608 m], 16 August 1961 [leaf with upper pitcher]; Collenette 816[b] (K!), Mt. Kinabalu, eastern shoulder, 4000–5000 ft [=1219–1524 m], 16 August 1961 [climbing stem with upper pitchers]; *Comber 4031* (K!), Sapong, 3000 ft [=914 m], no date [climbing stem with upper pitchers, male inflorescences]; *de* Vogel 8078 (L!), West Coast Residency, road Kimanis-Keningau, Crocker Range, on the watershed, 5°28'N 116°03'E, 1500 m, 6 October 1986 [stem with intermediate pitchers]; Hobbs 17 (K!), Trus Madi, SE ridge, 4500 ft [=1372 m], 22 August 1977 [pitcherless climbing stem and leaf with lower pitcher]; Hobbs 18 (K!), Trus Madi, SE ridge, 4500 ft [=1372 m], 22 August 1977 [short stem with lower pitchers]; Hobbs 72 (K!), Ranau, Mt. Kinabalu, 5500 ft [=1676 m], 26 September 1977 [climbing stem with intermediate pitcher, separate lower pitcher]; Hobbs 73 (K!), Ranau, Mt. Kinabalu, 6500 ft [=1981 m], 26 September 1977 [short stem with lower pitchers]; Rickards 101 (K!), Mt. Kinabalu, 5400 ft [=1646 m], 19 June 1976 [short stem with lower pitchers]; *Rickards 156* (K!), Mt. Kinabalu, 5500 ft [=1676 m], 20 June 1976 [short stem with lower pitchers]; RSNB 4377 (Chew & Corner) (K!), Bembangan River, 5000 ft [=1524 m], 19 February 1964 [climbing stem with upper pitchers, male inflorescence]; RSNB 4415 (Chew & Corner) (K!), Bembangan River, 5000 ft [=1524 m], 20 February 1964 [stems with lower pitchers]; SAN 60818 (Amin et al.) (K!), Tambunan District, Gu. Alab Range, 600 ft [=183 m] [sic—clearly an error; the elevation of Mt. Alab is ca. 6200 ft (1900 m)], 21 July 1984 [climbing stem with upper pitcher, female inflorescence]; SAN 82759 (Lantoh) (K!, KEP, L, SAR), Ranau District, Kinabalu Sabah National Park, 6000 ft [=1829 m], 26 January 1976 [K-climbing stem with upper pitchers, male inflorescences]; SAN 91184 (Aban & Dewol) (K!, KEP, L, SAR, SING), Beluran District, Bukit Liminintong, 2800 ft [=853 m], 9 April 1980 [K—short stem with lower pitchers]; SAN 91185 (Aban & Dewol) (BO, K!, KEP, L, SAR, SING), Beluran District, Bukit Liminintong, 2800 ft [=853 m], 9 April 1980 [K-climbing stem with upper pitcher, infructescence]; SAN 121014 (Amin et al.) (K!, L!), Ranau District, Bambangan, no elevation data, 10 September 1987 [K, L-climbing stem with intermediate pitcher]; SAN 127727 (Fidilis) (K!, L!), Penampang District, Togudon/Tungol Km 48 Jalan Tambunan/Penampang, 1400 m, 14 August 1989 [K-two climbing stems: one with upper pitcher, one pitcherless with male inflorescence; L—pitcherless climbing stem with infructescence]; SAN 147507 (Suzana) (K!, L!), Ranau, Mamut Copper Mine, 6°20'N 116°40'E, 1200 m, 29 November 2005 [K-climbing stem with upper pitcher, female inflorescence; L-pitcherless climbing stem with female inflorescence]; Schwallier 60 (L!), Crocker Range, down main road [from] Alab Station, 5°49'4.09"N 116°20'23.16"E, 1836 m, 24 September 2012 [climbing stem with upper pitcher, male inflorescence]; Schwallier 61 (L!), Crocker Range, down main road [from] Alab Station, 5°48'51.2"N 116°20'23.58"E, 1778 m, 24 September 2012 [climbing stem with upper pitcher, female inflorescence (unopened flowers)]; Schwallier 62 (L!), Crocker Range, down main road [from] Alab Station, 5°48'52.38"N 116°20'23.82"E, 1764 m, 24 September 2012 [short stem with lower pitcher]; Schwallier 63 (L!), Crocker Range, down main road [from] Alab Station, 5°48'52.38"N 116°20'23.82"E, 1764 m, 24 September 2012 [climbing stem with upper pitcher, inflorescence (unopened flowers)]. SARAWAK: (Jermy) 13253 (K!), Gunung Mulu National Park, around Camp 3 [of Royal Geographical Society's Expedition to Gunong Mulu 1977–78], 1150– 1250 m, 5 October 1976 [pitcherless climbing stem—in the absence of pitchers, the specimen is of limited value].

Nepenthes stenophylla:—**SABAH:** *SAN 83146 (Cockburn)* (K!, L), Lamag District, Inarat, S. ridge of Gunung Lotung, 3000 ft [=914 m], 15 May 1976 [K—high epiphyte; climbing stem with upper pitcher, lid absent]; *SAN 83251 (Cockburn)* (K!, L), Lamag District, Inarat, S. slopes of Gunong Lotong [Maliau Basin], 4300 ft [=1311 m], 16 May 1976 [K—climbing stem with upper pitcher, infructescence]; *SAN 151747 (Pereira)* (L!), Ranau, west of Bkt. Hampuan FR [Forest Reserve], 6°01'26"N 116°39'41", 1489 m, 12 May 2010 [climbing stem with upper pitcher, infructescence].

Notes on specimens examined:—*SAN 83251 (Cockburn)* was labelled as *Nepenthes* cf. *stenophylla* but subsequently identified as *N. fusca* by Smythies (20/12/1977) and Jebb (9/11/1993) on the sheet. However, the lid, though partially folded, appears complanate and is noted to be as large as the pitcher opening, which is atypical of *N. fusca s.lat.*—based on extensive exploration of the Maliau Basin, AR, SM and BQ determine that this material represents the diminutive heath-forest form of *N. stenophylla* found throughout the Maliau Basin above elevations of *ca.* 1000 m. *SAN 83146 (Cockburn)* is conspecific with this taxon. *SAN 151747 (Pereira)*, identified as *N. fusca* by Madani (7/2010), likewise represents *N. stenophylla* (det. AR & MG), which is widespread at the stated locality.

The isotype of *Nepenthes zakriana* at the University of Aberdeen Herbarium (ABD) could not be located despite an extensive search of the collections; staff indicate that there are no records that it was ever deposited.

4. Nepenthes mollis Danser (1928: 338, fig. 14) descr. emend. A.S.Rob. & Golos (Figs. 11-12)

- Type:—Borneo, Kalimantan, W. Koetai, G. Kemoel, ±1800 m, 17 October 1925, *Endert 4282* (holotype BO!) [pitcherless climbing stem with male inflorescence; single sheet labelled "Unicum!"].
- = Nepenthes hurrelliana Cheek & A.L.Lamb in Cheek et al. (2003: 118, figs. 1–3), syn. nov.
- Type:—Borneo, Sabah, Gunung Lumarku, August 1999, Lamb & Surat 145/99 (holotype SAN, iso-K).
- Nepenthes fusca × N. veitchii in Phillipps & Lamb (1988: 26, 1 fig.).
- Nepenthes sp. in Phillipps & Lamb (1996: 150, fig. 80) and Salmon (1999: 24, fig. 1).
- Nepenthes sp. B in Clarke (1997: 142, fig. 98) and Steiner (2002: 110, figs. 172-173).

Description³:—Epiphytic or terrestrial climbing or pendent shrub, to 5(-10) m tall. Stems of rosettes terete, 7-10 mm in diameter, internodes 0.6–2.5 cm long; vining stems ±terete, 5–9 mm in diameter, internodes 9–15 cm long, axillary buds nodular, ca. 5–7 mm in diameter, 1–3 mm tall, 5–12 mm above the axil, occasionally apically filiform to 5 mm. Leaves of rosettes coriaceous, petiolate, lamina obovate, becoming narrowly obovate to oblanceolate with increasing internode length, 10–15 cm long, 3.5–5 cm wide, apex retuse, becoming acute, not peltate, base gradually attenuate, petiole canaliculate, 2-3.5 cm long, not winged, not decurrent, sheathing and clasping the stem for its entire circumference. Longitudinal veins (1-)2-3 on either side of midrib, restricted to outer third of lamina where they run parallel to the laminar margin, inconspicuous. Pinnate veins numerous, irregularly reticulate, indistinct. Tendrils ca. 1.5 times longer than the laminae, without curl. Leaves of tall stems coriaceous, initially petiolate and winged, to 5 cm long with wings 0.3-0.8 cm wide, sheathing stem for 3/5-4/5 its circumference, becoming sub-petiolate and shortly decurrent to *ca.* 2 cm, thereafter sessile and strongly decurrent with ±parallel margins towards the base, lamina oblanceolate to oblong-spathulate, (11.5-)14-20(-24) cm long, 3.5-5(-6.5) cm wide, apex acute, rarely sub-peltate, to obtuse, base almost wholly amplexical, strongly oblique and decurrent into two wings for 2-5(-6) cm, usually 1/4-1/3 of total internode length, wings ca. 0.8-1.4 cm wide either side of stem, thereafter gradually attenuate into stem, longitudinal veins 2(-3), inconspicuous in living material. Tendrils *ca*. 2 times longer than the laminae, typically with 2.5 curls. Lower pitchers sub-cylindric, 9-15(-21) cm tall, 2-5.5 cm wide, with fringed wings 2-5 mm wide throughout, fringe elements 3–7 mm long, 3–5 mm apart; peristome horizontal between wings, thereafter strongly oblique, becoming vertical in the rear half and slightly recurved over pitcher opening towards lid, sub-cylindric at the front, 3–7 mm wide, rear part flattened, ca. 5 times wider than at front, usually without marginal lobes, ribs pronounced ca. 0.8 mm apart, teeth ca. 0.8-1 mm long. Lid ovate, complanate, base cordate, apex obtuse to retuse, 2.5-5 cm long, 1.5-3 cm wide, with pronounced abaxial midline rib and a prominent keel, projecting 4-7 mm below lid and hooked towards rear, keel minutely and densely glandular, glands crateriform, ca. 0.2 mm in diameter, and pubescent, apical protuberance absent. Spur simple, filiform, 0.6–1.1 cm long. Intermediate pitchers sub-cylindric to slightly infundibuliform, gradually widening from base to apex, 12-22(-30) cm long, 3.2-8 cm wide, with fringed wings in the upper half, (0-)1-2(-5) mm wide, fringed elements 2-3(-7) mm long, 2-4 mm apart, or with wings occasionally reduced to prominent ridges; peristome broad, often slightly raised between wings, front 1/2 to 2/3 near horizontal, abruptly becoming vertical in the rear 1/2 to 1/3, forming a column 4-8(-12) cm tall, 3-15 mm wide at the front of the pitcher, sub-cylindric, the raised, rear part flattened, up to 5 times wider than front of pitcher, outer edge sinuate, shallowly 1–3–lobed, ribs strongly pronounced, 1-1.5(-2) mm apart, 0.3-1 mm high, teeth 1–1.5 mm long at the front of the pitcher, 2–3.5 mm long on the column, where they project downwards at an acute angle into the mouth. Lid triangular-ovate with a slightly cordate base, 2.5–8 cm long, 2–4 cm wide, apex rounded, lower surface with pronounced basal keel projecting 8–10 mm below lid on a base about as long, strongly hooked towards rear, nectar

³This emended description incorporates details from the description of *Nepenthes hurrelliana* in Cheek *et al.* (2003), observations of same *in situ* on Mt. Murud, the type description of *N. mollis* (Danser 1928), and measurements made of *N. mollis in situ* in the Kemul Massif.

glands extremely dense on basal appendage and immediately adjoining part of lid, orbicular, 0.15 mm in diameter with a thin, raised border, keel often slightly pubescent, abaxial surface of lid with thinly scattered smaller glands mainly in the basal half, orbicular to shortly transversely elliptic, 0.15–0.25 mm long, often fewer or absent from apical half, apical protuberance sometimes absent, otherwise umbonate-conic to filiform, to ca. 5 mm long, 1 mm in diameter. Spur simple, filiform, 1–1.5 cm long, slightly recurved. Upper pitchers infundibular throughout, 18–24 cm long, 6–9 cm wide just below the mouth, often abruptly constricted at peristome, wings reduced to prominent ridges; form of peristome similar to intermediate pitchers, but 4-6 mm wide at front of mouth, rear, flattened part only up to 3.5 times wider than front of pitcher and usually slightly more cylindric, column 5.5–9 cm tall. Lid triangular-ovate with a cordate base, 3.5–5 cm long, 2–3 cm wide, midline rib prominent with large, pubescent glandular keel and usually with a 2–3 mm apical appendage with large pitted glands. Spur filiform, up to 25 mm long. Male inflorescence 20-27 cm long, 80-150 flowers, peduncle 6-9(-12) cm long, 3-4 mm in diameter at the base, rachis 10-15 cm long, partial-peduncles 2-flowered, bifurcating 1–1.5 mm from the base, base with bract, linear, rarely bifurcated, patent to ascending, 3–4 mm long, caducous, pedicels 7–10 mm long, tepals deep burgundy to green, elliptic, 3.5–4 mm long, 2-3 mm wide, deflexed and somewhat concave, adaxial surface with 30-40 deeply pitted glands, apex rounded to acute; staminal column 2.8-3.5 mm long, anther head 1.5 mm in diameter, thecae and pollen grains yellow. Female inflorescence 22-30 cm long, 40-70 flowers, peduncle 12-15 cm long, rachis 10-12 cm long, partial-peduncles 2flowered, 5–7 mm long, without bracts, pedicels 5–10 mm long, tepals elliptic, apex acute, 4–5(–6) mm long, ovary sessile, ellipsoid, 5 mm long. Seed 10–12 mm long. Indumentum abundant, consisting of coarse, brown to rufous hairs, partly shorter, branched and spreading, partly simple and up to 1.2–1.8 mm long, especially dense on young foliage, the stem, leaf margins, the abaxial leaf surface, the abaxial midrib, basal adaxial midrib and on the tendril, as well as more sparsely on the exterior surface of the pitchers, including the adaxial surface of the lid, and the abaxial surface mainly on the basal keel. The indumentum of the adaxial leaf surface differs in being covered with short, simple, whitish hairs. The inflorescences are densely pubescent with woolly, rufous hairs in the main axis, while the partialpeduncles, pedicels, abaxial tepal surface, tepal margins and staminal column are covered with shorter, simple hairs. Colour of mature stems usually green to olive green, lower pitchers often olive green to yellowish green, sometimes blotched with deep red or purple, peristome purple to brown and striped with vellow or green, upper pitchers entirely yellowish green to green blotched with red or suffused with deep red throughout.

Phenology:—Flowering was observed in Kemul Massif plants in early July. Flowering has been observed on Mt. Murud (Sarawak) in July and October (AR pers. observ.).

Distribution and ecology:—Outside of north-central Kalimantan (Kemul Massif), *Nepenthes mollis* has been recorded (and ascribed to *N. hurrelliana*) from Brunei (Bukit Pagon), southwestern Sabah (Mt. Lumarku, Meligan Range), and northeastern Sarawak (Mt. Mulu, Mt. Murud) (Cheek *et al.* 2003, Phillipps *et al.* 2008). However, the plants from Mt. Mulu are atypical in a number of respects (AR, BQ pers. observ., Phillipps *et al.* 2008); coupled with the established presence of *N.* sp. Bagong on Mt. Mulu, it cannot be unequivocally stated here whether the plants in the cited literature describe one taxon or the other without pointed investigation.

The known elevational range is that previously reported for *N. hurrelliana*: 1300–2400 m (Phillipps *et al.* 2008). On Mt. Murud and the Kemul Massif, plants occur in high montane forest, persisting in relative shade but growing most strongly in canopy breaks and more open areas. On Mt. Murud, where the expansive sandstone escarpment that makes up the mountain emerges above 2100 m, plants also occur in exposed sites, occupying humus pockets within a rocky, elfin forest habitat where its congeners *N. lowii* and *N. murudensis* Culham *ex* Jebb & Cheek (1997: 66) predominate.

Nepenthes mollis has been documented (as *N. hurrelliana*) to form natural hybrids with *N. chaniana* and *N. lowii* on Batu Buli (Phillipps *et al.* 2008, Scharmann 2010a, Scharmann 2010b) and also with *N. veitchii* (McPherson 2009).

Conservation status:—Though *Nepenthes mollis* is known from a relatively small number of mountains, these span a wide area in north-central Borneo. Its range is therefore large and encompasses dozens of peaks of suitable elevation that have not been explored or at least well botanised, making a wider distribution likely. Large populations are afforded protection in Pulong Tau NP (Sarawak), with additional populations protected in Ulu Temburong NP (Brunei). The remaining sites occur at high elevations on steep terrain unlikely to be subject to logging. The species therefore qualifies as *Least Concern* when evaluated against the IUCN 3.1 criteria (IUCN 2012).

Notes:—Salmon (1999) recognised that the taxon that would be described as *N. hurrelliana* (Cheek *et al.* 2003) matched the type material of *N. mollis* closely, noting two exceptions: that the leaf bases of the *N. mollis* type are decurrent for 4–6 cm, while those of *N. hurrelliana* are decurrent for 1–2 cm; and that the pedicels of *N. mollis* (a male inflorescence) lack bracts, while those of *N. hurrelliana* bear 3–4 mm long bracts at the base of the pedicels.



FIGURE 11. Nepenthes mollis Danser. A—rosette with right lower and left intermediate pitchers. B—climbing stem bearing upper pitchers and male inflorescence, note increasing leaf decurrency. C—adaxial detail of a climbing stem leaf showing leaf attachment. D—detail of leaf margin and adaxial surface. E—detail of upper pitcher lid, left adaxial surface, middle abaxial surface, right lateral view showing keel. F—cross section of peristome. G—male flowers. H—dehiscing seed capsules. Scale bars: A, B, C, E, F = 1 cm, D, H = 5 mm, G = 2 mm. Based on *Endert 4282* and supplemented with photographs and measurements made of *in situ* material. Illustrated by M. Barer.



FIGURE 12. Pitchers and leaves of *Nepenthes mollis. Top row* Kemul Massif, *middle row* Mt. Murud. A & D—lower pitchers. B & E—intermediate pitchers. C & F—upper pitchers. G—petiolate bases of rosette leaves (Kemul Massif). H—decurrent bases of climbing stem leaves, abaxial perspective, and I—lateral perspective (both Kemul Massif). Photographs A, B, D, E, F, H by A.S. Robinson; C, I by M.R. Golos; G by S.R. McPherson.

In addressing these inconsistencies, it is first necessary to better characterise *Nepenthes hurrelliana*. When the species was described, it was relatively poorly known, the protologue (Cheek *et al.* 2003) notably describing the "Rosette and short stems [as] unknown". Since then, numerous excursions have been made to Mt. Murud to study *N. hurrelliana in situ* (for example, 6 separate ascents of Murud have been made between AR and SM alone). Observations have found that the leaves of plants in the rosette stage are strongly petiolate, lack wings and exhibit no apparent decurrency; with increasing internode length, however, there is a shift towards the production of oblanceolate leaves with winged petioles that are slightly decurrent, while in tall climbing stems the leaves become sub-petiolate to wholly spathulate-lanceolate and decurrent for *ca.* 3–5 cm, that is, decurrent for approximately 1/3 of any given climbing internode. This same progression was noted in *N. mollis* in the Kemul Massif and is documented in Fig. 12. This trait, which is uncommon in *Nepenthes*, presents a particular problem of material consistency in terms of the specimens collected for common reference, whereby the vertical position along the stem of the collected material affects not only pitcher morphology but also the morphology of the leaf bases! Explorations of Mt. Murud have shown that there is considerable variation in leaf decurrency according to the length of the stem, but moreover that there is overlap in the degree of decurrency between *N. hurrelliana in situ*, the type material of *N. mollis*, and living specimens of *N. mollis* observed in the Kemul Massif.

With regard to the floral inconsistencies, while measuring living male inflorescences of *N. mollis in situ*, it was noted that bracts were present on the pedicels of many of the flowers, but not on all. Additionally, examination of dead male inflorescences on the same plants found scant evidence of floral bracts. This suggests either that bracts are produced inconsistently or, more likely, that the bracts might be caducous, which could explain the stated absence of bracts from the type material. Surprisingly, examination of the *N. mollis* type material (*Endert 4282*) held at BO found what appear to be several bracts towards the distal part of the damaged inflorescence, which suggests that these might have been overlooked by Danser. Field observations show that bracts do appear to be more consistently produced in the Mt. Murud population, but inconsistency in bract production has been noted between wild populations of other species of *Nepenthes*, most notably *N. robcantleyi* Cheek (2011: 678) and *Nepenthes graciliflora* Elmer (1912: 1494) (AR pers. observ.). The presence of floral bracts is therefore perhaps best regarded as a secondary diagnostic in *Nepenthes* except where extensive field observations support the inferences made from pressed materials.

The Nepenthes mollis on Mt. Murud represent the most visited and most extensive populations of this species currently known, and occur along much of the >6.5 km (2000–2400 m elevation) ridge used as the main approach to the mountain summit, also a site of biannual religious pilgrimage. The greatest range of diversity in form and colour is recorded here, no doubt partly because of the number of visits made to the habitat, but also because the plants occur in a range of situations from dense forest to exposed expanses of rock. This diversity is especially apparent in the neck of the peristome, which in some plants can become extremely exaggerated, more so than at other known sites. Whether or not the species evolved here is a matter of conjecture, but the mountain is certainly one of its major strongholds.

Additional specimens examined:—BRUNEI: *Cantley s.n.* (K! [3 sheets]), Gunong Pagon Priok, 5700 ft [=1737 m], 20 October 1984 [separate lower pitchers; lower pitcher with leaf, rosette with lower pitcher; lower pitcher with leaf fragment]. SABAH: *Hurrell s.n.* (K!), S. Sabah, Gunung Luma[r]ku, 1700 m, 8 June 1995 [stem with intermediate pitcher; annotated *Nepenthes "hurrellii"*; labelled as paratype of *N. hurrelliana* but not cited in protologue].

Notes on specimens examined:—The isotype of *N. hurrelliana* at K was not located by MG during a visit in July 2018 and may have been misplaced.

	Nepenthes mollis	Nepenthes sp. Bagong
Stem characteristics	Stems stiff, 5–9 mm dia., straight between nodes	Stems slender, somewhat lax, 3–5 mm dia., fractiflex between nodes
Axillary buds	Nodular or slightly filiform	Usually activated, forming obvious bract-like prophylls 0.8–3.5 cm long
Leaf base decurrency	Decurrent 2–5 cm (<i>ca</i> . 1/3 to 1/4 of internode, proportion decreasing with increasing internode length)	Decurrent for entire internode
Inflorescences	Emergent from axils, opposed to leaves	Emergent from middle of internode, appearing adnate to stem
Laminae	Longitudinal veins inconspicuous, indumentum dense on both surfaces, persistent	Paired longitudinal veins conspicuous along outer edges of laminae, indumentum dense, caducous on adaxial surface

FABLE 3. A table listing the key difference	es between Nepenthes mollis	and N. sp. Bagong
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TABLE 3. (Continued)

	Nepenthes mollis	Nepenthes sp. Bagong
Lower pitchers	Ventral wings well developed	Wings reduced to ridges, otherwise vestigial towards peristome
Upper pitchers	Dense exterior indumentum of scattered short brown hairs throughout	Indumentum sparser, particularly in upper half
Upper pitcher lid	Triangular-ovate with a cordate base, midline rib prominent with large glandular keel and a 2–3 mm apical appendage with large pitted glands	Narrowly elliptic and revolute, midline rib prominent but basal appendage reduced to a slight swelling
Peristome	Broad, generally 3.5 (upper pitchers) to 5 (lower pitchers) times wider at column than at front of pitcher; teeth large, 2–3 mm long	2 (upper pitchers) to 3.5 (lower pitchers) times wider at column than at front of pitcher; teeth fine, to 1 mm long

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