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RESEARCH ARTICLE

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Nepenthes (*Nepenthaceae*) of Halmahera, Indonesia

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Key words

character state
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Abstract Two new paniculate species of *Nepenthes*, *N. halmahera* and *N. weda*, both allied to *N. danseri* Jebb & Cheek, are described respectively from lowland and lower montane forest on ultramafic substrate. *Nepenthes weda* appears to be unique in the genus due to the adaxial tepal surfaces which in the distal portion are hairy and lack nectar glands. This species is also unique among paniculate members of the genus in its forward-facing, concave subapical lid appendage. Both species are currently only known from the Weda Bay Nickel Project concession area in Halmahera, Indonesia, and are assessed as Critically Endangered using the 2012 IUCN standard. Two character states are formally described and named for the first time in *Nepenthes*: nanophyll rosettes and multiseriate fringed pitcher wings. Stage-related heteromorphy in lid appendages is documented for the first time in the genus. Keys to the species of *Nepenthes* of Halmahera, and to the paniculate species of SE Asia are presented.

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INTRODUCTION

Halmahera, is the largest island in Indonesia's Maluku Province (formerly Moluccas) after Seram. The islands of Maluku are situated between Sulawesi (formerly Celebes) to the west, and New Guinea to the east, occupying an area of about 4 800 km^2. Biogeographically Maluku including Halmahera forms part of Wallacea, the transitional zone between the Sunda continental shelf, with its Asian taxa, and the Sahul continental shelf, with its Australasian taxa.

This paper is part of a series leading to a World Monograph of Nepenthaceae, building on Jebb & Cheek (1997) and Cheek & Jebb (2001). Over 95 % of the c. 140 known species of *Nepenthes* L. occur in SE Asia and adjoining Indo-China and N Australia. New species to science continue to be discovered frequently, e.g. 12 species being published from the Philippines alone in 2013 and more continue to be published (Cheek & Jebb 2013a–h, 2014). The most species-diverse areas for *Nepenthes* are Sumatra, Borneo and the Philippines, each of which has over 30 taxa, placed in 1–3 terminal groups that appear to be rapidly diversifying, although there are no dated phylogenies that corroborate this.

The majority of *Nepenthes* inhabit submontane forest in perhumid areas. They occur on varied substrates, including those derived from sandstones, shales, volcanic rocks and occasionally also on limestone (some Bornean and one Thai species) and ultramafic substrates (some in Borneo, many in the Philippines, one in Sulawesi and another in Waigeo).

To the west of Maluku, Sulawesi has moderate diversity with 12 species, most of which are in the *Nepenthes tentaculata* Hook.f. and *Nepenthes Regiae* Danser species groups, both of which also occur in Borneo. New Guinea, to the east also has 12 species, most of which have obscure affinities, although two belong to the *Regiae* species group. Three of the New Guinea species and one in Sulawesi have 'paniculate' inflorescences (partial-peduncles with more than two flowers), a plesiomorphic character shared with the four Indian Ocean species that form the basal grade of the genus, in the west (Jebb & Cheek 1997, Mullins & Jebb 2009).

Until 1997, just two species were known from Maluku, *Nepenthes mirabilis* (Lour.) Druce the most globally widespread species (from Indo-China to N Australia), and *N. maxima* Nees of the *Regiae* species group that extends from Sulawesi to New Guinea (Danser 1928). Jebb & Cheek (1997) described a paniculate species, *Nepenthes danseri* Jebb & Cheek, from Waigeo island, in the Raja Ampat group situated to the west of the Indonesian part of New Guinea. These authors included within *Nepenthes danseri* a single, geographically and morphologically discordant specimen from 350 km to the west, *De Haan 1718* from Weda District, Halmahera. A subsequent combined molecular and morphological phylogenetic analysis (Mullins & Jebb 2009) placed *N. danseri* in a clade with and as sister to, the two Madagascan species, with this clade itself sister to the SE Asian clade containing almost all other species of *Nepenthes*. However, bootstrap support was low.

Until late 2012 specimen sampling of *Nepenthes* on Halmahera had been mainly confined to the west coast of the western volcanic part. An exception was the anomalous *De Haan 1718* from Weda, in the eastern, partly ultramafic part of the island (Van der Ent et al. 2013).

This changed when, in September 2012, Weda Bay Nickel in collaboration with Missouri Botanical Garden and Herbarium Bogoriense began conducting an intensive specimen-based botanical survey (identifications mainly by Naturalis Biodiversity Center, Leiden) that resulted by June 2013, in 4 759 specimen numbers, thereby more than tripling the Missouri holdings for Indonesia to over 6 000 (www.tropicos.org, acc. Dec. 2014).

Among the 4 759 specimens from the Weda Bay survey, 20 numbers (< 0.5 %) are databased as *Nepenthes.* This is possibly the first study allowing quantification of relative frequency of *Nepenthes* individuals in natural habitat since most of the lead collectors of the survey were unbiased, being new to collecting in SE Asia. This admirable study approximately trebled the global number of *Nepenthes* specimens previously recorded from Halmahera (on the basis of ongoing monographic studies of *Nepenthes* specimens at over 20 herbaria around the world by Jebb and Cheek). The aforementioned survey appears to

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have been confined to an area of about 23 km N to S and 14 km E to W (analysis of Weda Bay Nickel Project data on Tropicos website, Dec. 2014). The aforementioned survey area appears to correlate with the intended infrastructure and pit footprint (ERM 2010) of the planned nickel and cobalt mine of the Weda Bay Nickel Project, majority owned by ERAMET (http://www.wedabaynickel.com/en/a-world-class-project/shareholders/).

The 2012 intensive Flora Inventory Programme was initiated by WBNP to address i) the incomplete identifications that had resulted from the first survey as reported by ERM (2010); ii) the decision to meet the exacting Environmental Performance Standard 6 of the International Finance Corporation (IFC 2012); and iii) in recognition that Halmahera is a biodiverse yet biologically poorly known area (G. Lee pers. comm. to M. Cheek, June 2015). The Flora Inventory Programme provides a focal point for species classification and evaluation, in order that management actions can be prioritised based on global threat status, local importance and impacts by the project.

To date the two species described in this paper are among about ten new species that have resulted from the studies at WBNP (G. Lee pers. comm. to M. Cheek, June 2012).

METHODOLOGY AND RESULTS

Specimens of *Nepenthes* from Halmahera at MO were sent on loan to K for study, supplementing those already present at K for ongoing monographic study of the genus. Specimens were sorted into putative species by gross morphology. Those species that matched no other and appeared to be undescribed were characterised using a Leica MZ6 dissecting microscope fitted with an eyepiece micrometre graticule measuring to units of 0.02 mm.

In order to expose critical parts of the specimens for examination, especially the lower surface of the lid, the mounting glue was moistened in order to reposition the specimen, or portions of the specimens were rehydrated to give flexibility. Drawings were made with assistance from a camera lucida. Interpretation of the herbarium specimens was greatly facilitated by access to photographs taken of the material in the wild, before preservation as specimens. These can be consulted on www.tropicos.org.

The description format follows those standard for *Nepenthes* e.g. Cheek & Jebb (2013a–h). Specimens marked n.v. have not been seen. Herbarium codes follow Index Herbariorum (Thiers et al. continuously updated)

Among the MO specimens from the Weda Bay area of Halmahera studied at K, the following three taxa were distinguished:

1. *Nepenthes mirabilis* represented by *Merrello et al. 3295*;
2. a putative undescribed paniculate species concordant with *De Haan 1718* (similar to *N. danseri*, described below as *N. halmahera*) represented by 11 specimens, supplemented by 13 photographs available on the Tropicos website. See Table 1 for characters distinguishing *N. halmahera* from *N. danseri*;
3. a putative undescribed paniculate species with numerous points of difference from any other known paniculate species of *Nepenthes*, here described as *N. weda*, represented by 6 specimens, supplemented by 51 photographs available on the Tropicos website. See Table 2 for characters distinguishing *N. weda* from *N. halmahera.*

Table 1 The more significant characters separating *N. danseri* and *N. halmahera*.

	Nepenthes danseri	*Nepenthes halmahera*
Range	Waigeo, Indonesian New Guinea	Halmahera, Maluku, Indonesia
Habitat	Lowland scrub on ultramafic substrate, rarely in forest	Lowland forest on ultramafic substrate
Length : breadth leaf blade	3 : 1	4 : 1
Indumentum of upper pitchers	Hairs almost absent except near spur	Hairs present over entire pitcher, 5–10 % cover
Frequency of upper pitchers	Rare, at most 1 per stem	Common, numerous (3–6) on each stem
Teeth on inner edge of peristome (upper pitchers)	Conspicuous	Not visible (due to involution of peristome)
Ratio of diameter of aperture : overall length of nectar gland (lower surface of lid of upper pitchers)	7 to 8 : 10	3 to 4 : 10
Inflorescence bracts	Absent	Present on 90 % of partial-peduncles
Male peduncle length	10 cm	(1.7–)3–4.7(–5.5) cm
Female inflorescence length / and length of proximal partial-peduncle	18–29 / 1.4–1.5 cm	12–16 / 0.4–0.55 cm
Seed length	11.5 mm	5 mm

Table 2 Characters separating *Nepenthes weda* from *Nepenthes halmahera*.

	Nepenthes weda	*Nepenthes halmahera*
Leaf blades of climbing stems, dimensions	20–23.5 by 4–4.5 cm	8–15(–17) by 1.5–3.5(–4.8) cm
Leaf blades of climbing stems. Marginal indumentum	Margins conspicuously covered with dense dark brown hairs 0.5–1 mm long	Margins glabrous or with very sparse brown hairs 0.5 mm long
Leaf blades of climbing stems, petiole length	5–7 cm	1.5–3.4 cm
Leaf blades of climbing stems, petiole base	Decurrent as patent wings 1–2 mm wide for 1.8–2.7(–4) cm	Not decurrent as wings, or decurrent for up to 0.5 cm
Nectar glands of lower surface of lid	Absent from midline	Present on midline
Lid appendages on lower surface of upper pichers	Subapical appendage present	Lid appendages absent
Tepals, adaxial surface	Glabrous	Distal half densely hairy
Androphore	Densely hairy	Glabrous or with 1–3 hairs
Hair density on wings of lower pitchers	Dense, 15–20 hairs per mm^2	Glabrous to sparse 0–4 hairs per mm^2
Altitudinal range	415–1014 m	10–500(–760) m

Since the survey at the Weda Bay Nickel Project preserved plants at different stages, both mature and fertile, and immature, both new species are already more completely known than most other species of the genus. Many other species of the genus are only known from the climbing phase, when inflorescences are generally produced, and as a result their immature and non-fertile stages remain unknown.

Key to the species of Nepenthes of Halmahera

1. Lower surface of the lid of upper pitchers with both an upper appendage and a lower appendage . . . . . *N. maxima*
1. Lower surface of the lid of upper pitchers lacking any appendages, or (*N. weda*) with only an apical appendage . 2
2. Blade margins of rosette and short stem leaves fimbriate (attenuated extensions of the leaf), glabrous; stems with dense fine white stellate or arachnoid indumentum; inflorescence racemose (partial-peduncles 1-flowered) . . . . *N. mirabilis*
2. Blade margins of all leaves more or less densely brown pubescent (not fimbriate); golden-brown simple hairs, at least on buds; inflorescence paniculate (partial-peduncles 3–5-flowered) in basal part of inflorescence 3
3. Upper pitchers 8–10.5 by 2.8–3.5 cm; petioles of climbing stems 1.5–2.8(–3.4) cm long; wings of lower pitchers glabrous or soon glabrescent; lower surface of pitcher lids without an appendage; lid nectar glands present in midline . . . . . *N. halmahera*
3. Upper pitchers 24–25 by 6 cm; petioles of climbing stems 5–7 cm long; wings of lower pitchers conspicuously long golden-brown hairy; lower surface of pitcher lids with a terminal appendage; lid nectar glands absent from midline . . . . . *N. weda*

Key to the paniculate species of SE Asian Nepenthes

1. Lower pitchers subglobose; ratio of width of peristome outer : inner edges 1 : 10 2
1. Lower pitchers ovoid or ovoid-cylindric; ratio of width of peristome outer : inner edges < 1 : 5 3
2. Lower pitchers orange, with a pair of spur-like teeth descending from the apex of the lid column; ratio of lid length : breadth c. 1 : 1. — N Borneo . . . . . *N. bicalcarata*
2. Lower pitchers green and/or red, without spur-like teeth, lid column absent, ratio of lid length : breadth > 5 : 1. — Borneo, Sumatra, Peninsular Malaysia, New Guinea . . . . . *N. ampullaria*
3. Longitudinal nerves confined to the outer 1/3 of leaf blade. — Mainland of New Guinea 4
3. Longitudinal nerves present throughout the blade. — Islands in Wallacea, Isle of Waigeo 5
4. Upper pitchers widest at mouth; partial-peduncles racemose . . . . . *N. paniculata*
4. Upper pitchers narrowing to mouth; partial-peduncles corymbose . . . . . *N. neoguineensis*
5. Indumentum of bushy, branched hairs; lid nectar glands > 100, tiny, 0.1–0.2 mm diam. — Sulawesi . . . . . *N. tomoriana*
5. Indumentum of simple hairs; lid nectar glands few 2–30, large, 0.3–1.2 mm diam. — Halmahera, Waigeo 6
6. Lower surface of lid with subapical appendage in rosette and upper pitchers; nectar glands absent from midline. — Bukit Limber, Halmahera . . . . . *N. weda*
6. Lower surface of lid lacking appendages; nectar glands present on midline 7
7. Partial-peduncles ebracteate; aperture of each lid nectar glands > 50 % covered by borders; teeth conspicuous on inner edge of peristome (upper pitchers); upper pitchers rarely present (c. 1 per stem). — Waigeo island . *N. danseri*
7. Partial-peduncles bracteate; aperture of each lid nectar gland < 10 % covered by borders; teeth not visible on inner edge of peristome (upper pitchers); upper pitchers frequent (3–6 per stem). — Weda Bay, Halmahera . . . . . *N. halmahera*

Nepenthes halmahera Cheek, *sp. nov.* — Fig. 1

Similar to *N. danseri* Jebb & Cheek of Waigeo Island, Raja Ampat Islands, Indonesian New Guinea, differing in the bracteate inflorescences, male peduncles 1.7–5.5 cm long (not ebracteate, male peduncles 10 cm long); upper pitchers without visible peristome teeth (unless distorted) and with hairs scattered over the whole surface (not with short teeth visible and lacking hairs except in the area of the spur). — Type: *De Haan 1718* (holotype K; isotypes A n.v, BISH n.v, BO n.v, CAL n.v, L, LAE n.v, NSW n.v, P n.v, PNH n.v, SING n.v), Indonesia, N Maluku Province, Halmahera, Weda, Nucifera, male infl., 25 Aug. 1949.

Etymology. Named for the island of Halmahera on which it occurs, as a noun in apposition.

Terrestrial climber, 2–5 m tall. *Stems* terete. *Rosette shoots* not seen. *Short shoots* (*Mahroji & Gushilman 211*) 6–7 mm diam, internodes c. 1.5 cm long, densely covered in red depressed-globose glands 0.05 mm diam, c. 5–10 per mm^2, hairs absent. *Climbing stems* 3–4(–6) mm diam, internodes 1–5.5(–9) cm long, axillary buds not conspicuous, indumentum of sessile depressed-globose glands c. 0.03 mm diam mixed with very sparse simple golden-brown hairs 0.5 mm long, or hairs absent. *Leaves of short shoots* elliptic to lanceolate, 16.5–22.5 by 4.3–6.2 cm, apex acute, base decurrent. Longitudinal nerves 6–7 pairs, evenly scattered, inconspicuous, most visible on adaxial surface. Pennate nerves inconspicuous; margin glabrous or with sparse brown simple hairs 0.3–0.4 mm long, upper and lower surfaces entirely glabrous; or with appressed sparse hairs 0.5–0.75 mm long near the midrib of lower surface. Petiole canaliculate-winged, 2.7–3.5 cm long, 0.5 cm deep, shortly sheathing the stem and clasping the stem its entire circumference. *Leaves of climbing stems* elliptic, 8–15(–17) by 1.5–3.5(–4.8) cm, apex acute, base decurrent. Longitudinal nerves 5–8 pairs, conspicuous only on younger leaves. Pennate nerves numerous, patent. Indumentum absent from upper and lower surfaces, except for sessile depressed-globose glands and for the distal midrib with a few short simple hairs, sometimes the lower midrib also with simple golden-brown hairs; margin glabrous or with sparse simple patent hairs c. 0.5 mm long. Petiole canaliculate-winged, 1.5–3.4 by 0.3 cm, base clasping the stem for the 2/3s to the entire circumference, dilating abruptly as patent wings 2 mm wide around the stem, not or shortly decurrent by 0–5 mm, the margin with sparse patent simple hairs. Tendril 9–10 cm long. *Lower pitcher* (short shoots) ellipsoid-cylindric, c. 11 by 3.6 cm, the ellipsoid base gradually constricting into the more slender cylindric upper portion, 2.2 cm wide at the mouth; fringed wings c. 1.2 cm apart, 0.7 cm wide at the pitcher base, fringed elements 1.5–2 mm long, 0.2–1.1 mm apart; outer surface of pitcher 10–20 % covered in inconspicuous simple pale brown hairs 0.5 mm long, mixed with dense depressed-globose red glands 0.05 mm diam, 15–20 per mm^2; mouth narrowly ovate, concave, strongly oblique, inner surface waxy, greenish white; peristome subcylindric, 1.5–2 mm wide, ribs 0.8 mm apart, weakly developed and differentiated, outer edge entire, inner edge with teeth inconspicuous, mainly concealed, 0.5 mm long, curved; column area not visible (due to specimen mounting); lid obovate-elliptic, c. 3 by 2.4 cm, apex rounded, base abruptly and inconspicuously cordate, upper surface with indumentum as outer pitcher, hairs short overall, but dense, longer, white and matted near the base; lower surface not visible (due to specimen

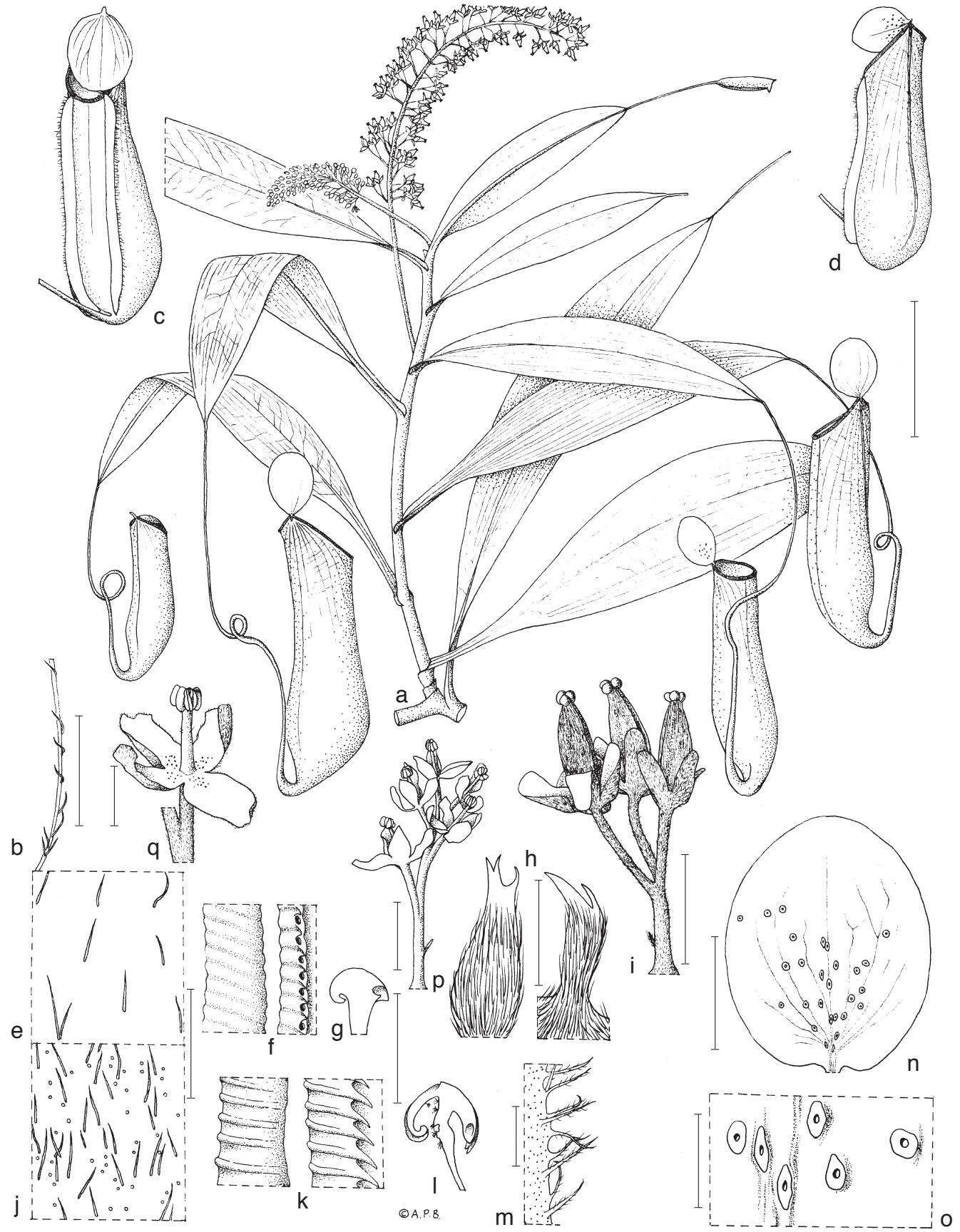

Fig. 1 *Nepenthes halmahera* Cheek. a. Habit, climbing stem with upper pitchers and female inflorescences; b. leaf margin from a, showing sparse hairs; c, d. lower pitchers; e. indumentum of upper pitcher, mid-lateral area; f. peristome, upper pitcher, from above (left), and from inside (right); g. peristome, upper pitcher, transverse section, inside to right; h. spurs from upper pitchers showing the forked and glabrous distal positions; j. partial-inflorescence, female (detail from a); j. indumentum from lower pitcher, mid-lateral area; k. peristome from lower pitcher, viewed from above (left) and from inside (right); l. peristome, lower pitcher, transverse section, inside to right; m. fringed wing of lower pitcher; n. lower surface of lid, lower pitcher; o. nectar glands from n, proximal area at midline; p. partial-inflorescence, male; q. male flower showing minute sparse nectar glands in proximal third of tepal areas (a, b, e–i, p, q from *Bangun et al. 332*; c, d, j–o from *Mahroji et al. 211*). — Scale bars: a, c, d = 5 cm; b, e–g, j–l = 1 mm; h, m, o, q = 2 mm; i, p = 5 mm; n = 1 cm. — Drawn by Andrew Brown.

mounting); spur bifurcate, stout, 1.5 mm wide at base, 2 mm long, branches 1 mm long, apices acute, indumentum as on lid base. *Upper pitchers* (climbing stems), green, ovoid-cylindric (5.8–)8.2–10.5(–11) by (2.2–)2.4–3.3(–3.9) cm, the basal ovoid portion extending (2.3–)3.2–4.7(–5) cm from the pitcher base, the 'hip' weakly developed, the upper cylindrical portion gradually contracting to the narrowest part 1.4–2.2(–2.7) cm wide, just above the midpoint of the pitcher, then slightly dilating to (1.3–)1.4–2.7(–3) cm wide just below the peristome; wings reduced to ridges < 1 mm wide, 0.8–1 cm apart; indumentum of outer surface 5–10 % covered with golden-brown appressed acute simple hairs, 0.25(–0.5) mm long, mixed with sessile red depressed-globose glands 0.03 mm diam; mouth ovate, concave, oblique, inner surface pale glaucous waxy greenish white, with red spots; column not developed; peristome cylindrical-flattened in transverse section (1–)1.5–2.5(–3.0) mm wide; ridges 0.3–0.35 mm apart, developed as low, blade-like wings 0.25 mm deep on the outer surface, ribs not prominent on the inner surface; the outer edge lacking lobes or with one ill-defined lobe, inner edge usually with teeth inconspicuous, occasionally (e.g. when distorted by pressing) with 0.1–0.15 mm long curved teeth visible; lid ovate-elliptic (1.2–)1.8–2.6(–2.7) by 1.4–2(–2.4) cm, apex rounded, base rounded and abruptly and shallowly cordate, upper surface with indumentum as outer pitcher, lower surface without appendages; nectar glands 25–30, scattered in the centre, especially along the base of the midline where linear-elliptic, otherwise elliptic or orbicular, 0.75 by 0.5 mm, thickly bordered, the borders glossy yellow, slightly raised, central aperture orbicular, 0.25–0.3 mm diam, dark brown; marginal 1–2 mm of lid lacking nectar glands, but with dense sessile red depressed-globose glands (10–15 per mm^2), becoming rapidly less dense away from the margin, and almost absent in the centre of the lid; marginal 0.5 mm with dense minute, bushy, branched hairs 0.07–0.08 mm long. Spur oblong, 1–1.2 by 1 mm, strongly dorsiventrally flattened and often recurved, apex rounded. Inflorescences terminal on main axis or (*Bangun et al. 267*, *637*, *812*, *Phillipson et al. 6450*, all MO) on short axillary spur shoots. *Male inflorescences* at least 2–3 on each flowering stem, separated from each other by 2–6 nodes, 9.8–19 by (1.8–)2–2.5(–3) cm, peduncle (1.7–)3–4.7(–5.5) cm long, (0.1–)0.15 cm diam at base; partial-peduncles 30–74, 3–4(–5)-flowered in the proximal 1/2 to 2/3s, the distal part 2-flowered; bract filiform, patent (0.5–)1–2 mm long, rarely absent, inserted variably between base and apex; partial-peduncles 1–5 mm long; partial-rhachis 0–2 mm long; pedicels 2.5–5(–6) mm long; indumentum of appressed simple, golden-brown hairs 0.15–0.25(–1) mm long, mixed with sessile depressed-globose red glands 0.03 mm diam, covering c. 80 % of the peduncle when young, but at length glabrescent, rhachis and partial-peduncles 50–60 %, covered in hairs up to 0.5 mm long. *Perianth* tepals 4, green, drying brown, proximal 1/10th connate, elliptic-oblong, c. 2 by 1.75 mm, upper surface with 10–15 nectar glands, confined to the proximal 1/3 to 1/2, orbicular to elliptic, minute, 0.02–0.03 mm long, sparse, separated by c. 0.25 mm, in dried material situated at apex of irregular convexities; distal part of tepal glabrous; margin with a fringe of patent hairs, lower surface 90 % covered by appressed simple golden hairs 0.1–0.2 mm long; androphore 5 winged, drying black, 2 mm long, glabrous or with 1–2 hairs; anther head subglobose, c. 1 by 1.1 mm, white; anthers 6, one apical, the remainder uniseriate. *Female inflorescence* as the male 12–16 by 2.8–4.5 cm, peduncle 4–6 by 0.15–0.2 cm, partial-peduncles (3–)4–5.5 mm long, 30–58, proximal half 2–3-flowered, distal half 1–2-flowered; pedicels 3–5 mm long; tepals oblong 3 by 1.5 mm; ovary narrowly ovoid 4–5 by 1.5 mm, stigmas 3–4, bilobed, apices rounded. *Infructescence* 16–26 by 5 cm, peduncle 8–11 by 0.25 cm; fruits fusiform 1.5 by 0.3–0.4 cm. Seeds filiform, 0.5 by 0.025 mm, pale yellow, central body dentate.

Distribution & Ecology — Only known currently from the area of the Weda Bay Nickel Project in Halmahera, North Maluku, Indonesia. Open areas in lowland (rarely lower montane) forest on ultramafic substrate; 10–500(–760) m altitude.

Vernacular name — Woégò (Sawai language, fide *De Haan 1718*).

Additional specimens examined. Indonesia, North Maluku Province, Central Halmahera, Weda Bay, sterile, lower pitcher, 27 Jan. 2013, *Mahroji & Gushilman 211* (BO n.v., MO); Bukit Limber, fr., 2 Oct. 2012, *Phillipson et al. 6450* (BO n.v., MO); ibid., Kao Rahai, female infl., 6 Dec. 2012, *Bangun et al. 267* (BO n.v., MO); ibid., Kao Rahai, male infl., 8 Dec. 2012, *Bangun et al. 332* (BO n.v., MO); ibid., Kao Rahai, female infl., 10 Mar. 2012, *Bangun et al. 637* (BO n.v., MO 2 sheets); ibid., Casuarina, male infl., 24 Mar. 2013, *Bidault et al. 1154* (BO n.v., MO 2 sheets); ibid., Sake West, buds, 18 June 2013, *Bangun et al. 812* (BO, MO); ibid., Kao Rahai, seedling, 27 Apr. 2013, *Hidayat et al. 5086* (BO n.v., MO).

Conservation — Although it is possible, even probable, that *N. halmahera* occurs outside the footprint of the Weda Bay Nickel Project in Halmahera, there is as yet no evidence of this. Many species of ultramafic habitats are point endemics (Ashton 2014). Therefore, using the precautionary principle, this species is here assessed as Critically Endangered B2ab(iii) according to the Categories and Criterion of IUCN (2012). This is because although seven sites and at least that number of mature individuals are known for *N. halmahera*, resulting in an 'area of occupancy' (as defined in IUCN 2012) of 32 km^2 using the preferred IUCN standard of 4 km^2 grid cells, they all appear to be within a single 'threat-based' location in the sense of IUCN (2012). That is to say that all currently known individuals of this species, since they are on the WBNP concession, are considered likely be at risk of extinction within the next 10–20 years due to the ground clearance that will be needed to put in place the infrastructure (roads, processing areas, port, accommodation, storage areas, waste areas) and open-cast mining pits planned imminently by the Weda Bay Nickel Project as expounded in ERM (2010). However, while the concession area is in the order of 50 000 ha, only c. 10 % is expected to be cleared due to the direct impact (the 'footprint') of the intended mine. The project intends to adopt the Mitigation Hierarchy (BBOP 2015), seeking options both to avoid and/or minimise, and if necessary to implement restoration trials, and offsetting residual losses, for species that have been assessed as of conservation significance (G. Lee pers. comm. to M. Cheek, June 2012). Given the facts expressed above, and the relatively widespread distribution of *N. halmahera* within the survey area, there is every chance that this species might survive in the wild if the project commitment to conservation continues at its current level.

Notes — The label data for almost all of the specimens of this species refer to it being found specifically in the more open areas of its lowland forest on ultramafic substrate habitat. This is not a spectacular species in comparison to *N. weda*. The pitchers are relatively small and green. This is reflected on the Tropicos website, since, while all of the six specimens known of *N. weda* have accompanying photographs taken in the field, for *N. halmahera*, this is true for only two of the eleven specimens.

The type was considered an aberrant specimen of *N. danseri* by Jebb & Cheek (1997).

The earliest known locality in Weda District, 'Nucifera', has not been traced, it probably refers to a coconut plantation.

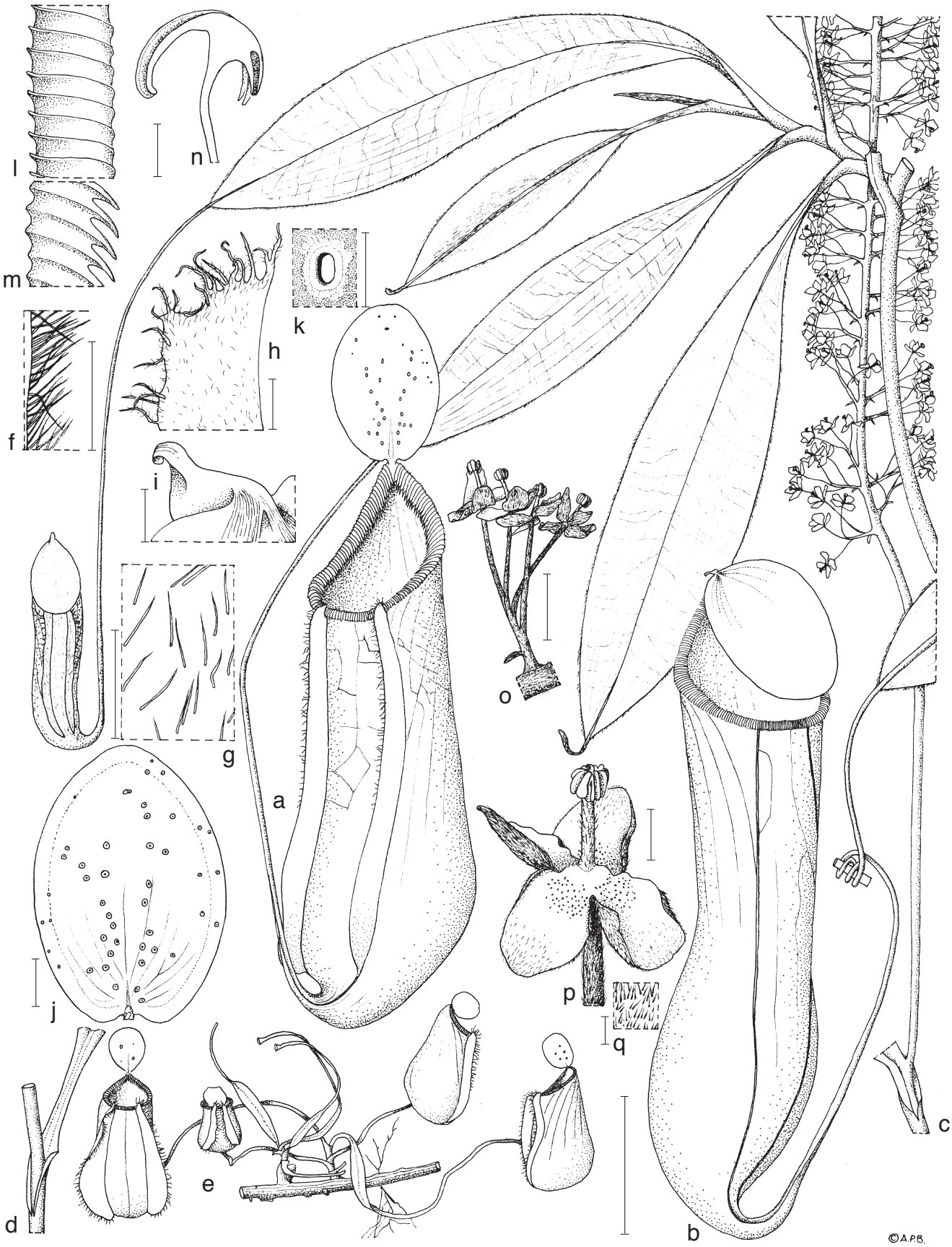

Fig. 2 *Nepenthes weda* Cheek. a. Short shoot; with lower pitcher; b. upper pitcher (from climbing stem); c. male inflorescence (lower part); d. perfoliate-decurrent leaf base from climbing stem; e. nanophyll rosette stems from horizontal, rooting main axes, note the reduced leaf-blades and compact pitchers; f. leaf-blade marginal hairs; g. hairs from mid-lateral area, lower pitcher; h. fringed wing of lower pitcher – near peristome; i. spur-lower pitcher; j. lower surface of pitcher lid, lower pitcher (submarginal line of dots indicates extent of marginal branched hairs); k. nectar gland detail from lower pitcher; l. peristome, upper pitcher, viewed from above; m. peristome, upper pitcher, viewed from inside pitcher; n. peristome transverse section, inside to right, upper pitcher; o. partial-inflorescence, male flowers; p. details of male flower; q. details of indumentum from lower surface of tepals (a, d, f–k from *Bangun et al. 218*; b, c, l–q from *Phillipson et al. 6417*; e from *Phillipson et al. 6430*). — Scale bars: a–e = 5 cm; f, g = 1 mm; h, i, k–n, p = 2 mm; j, o = 1 cm; q = 0.25 mm. — Drawn by Andrew Brown.

Nepenthes weda Cheek, *sp. nov.* — Fig. 2, 3

Distinguished from *N. halmahera* in the tepals hairy on the distal part of the adaxial surface (not glabrous); the lower surface of the lid of upper pitchers with a subapical appendage and with the midline free of nectar glands (not without any appendages and with midline with nectar glands). — Type: *Bangun et al. 218* sheet 2 of 2 (holotype MO No. 6576095; isotypes BO n.v., MO, photo K), Indonesia, Maluku Islands, N Maluku Province, Central Halmahera, Weda Bay, Bukit Limber, N00°32'41" E127°58'28", alt. 847 m, male infl., 1 Dec. 2012.

Etymology. Named as a noun in apposition, for Weda Bay in Halmahera, Indonesia, the base of the Weda Bay Nickel Project surveys for which led to the discovery of this species.

Terrestrial climber 2–4 m tall. *Stems* terete. *Short shoots* 4–6 mm diam, internodes 1.3–2 cm long, glabrous. *Climbing stems* 6–9 mm diam, internodes 10.5–14 cm long, axillary buds conical, 2–7 mm long, inserted 8–13 mm above the axil, hairs golden-brown, multicellular, simple, sparse, appressed, 0.5 mm long, mixed with sessile depressed-globose red glands 0.05–0.1 mm diam. *Horizontal stems*, subterranean, bearing vertical rosette shoots along their length, 4–6 mm diam, internodes 1.2–4.5 cm long, surface irregularly ridged, corky, glabrous. *Leaves* petiolate, coriaceous; *leaves of nanophyll rosette shoots* 3–6, with blades slender linear-oblong, 20–22 by 2.4–6 mm, apex acute, tendril 65–85 mm long, base attenuate, petiole canaliculate 6–10 by 2 mm, base shortly sheathing and clasping the stem by its whole circumference; nerves not conspicuous; both surfaces with scattered glossy pale brown, mainly straight, simple hairs 0.2–0.5 mm long, dense along the adaxial midrib groove, mixed with a few sessile depressed-globose red glands 0.05 mm diam. *Leaves of short shoots* with blades elliptic-oblong (10.5–)15.2–25.5 by (2.8–)4.1–5.8(–7) cm, apex slightly acuminate, base acute, longitudinal nerves 10–11 pairs, more or less evenly spread through the lamina, most conspicuous on the lower surface. Pennate nerves numerous, conspicuous above, almost patent, reaching the marginal nerve; margin densely dark brown hairy, hairs simple 0.3–0.6 mm long; upper surface of blade glabrous apart from the densely pubescent midrib, hairs appressed, yellow-brown, 0.5(–0.7) mm long, acute; lower surface with similar hairs covering 20–100 % of midrib, hairs 0.75–1 mm long, red-black or yellow mixed with sessile red glands 0.05 mm diam; inner 1/3 of lamina sparsely hairy, hairs 0.5–1.25 mm long, mixed with sessile red glands, outer 2/3 glabrous or very sparsely hairy. Petiole canaliculate, (1.8–)3.5–6 cm long, (0.2–)0.4–0.5 cm wide, the wings of the basal 1–1.5 cm more or less abruptly dilated by c. 5 mm, perfoliate and decurrent for c. 5 mm down the stem, indumentum as in blade in herbarium specimens the dilated wing appearing as a sheath around the stem (artefact of pressing). *Leaves of climbing stems* with blade very narrowly elliptic, 20–23.5 by 4–4.5 cm, apex rounded-obtuse, base acute-cuneate. Longitudinal and pennate nerves as in the leaves of the short stems; leaf margin indumentum dense, brown, hairs simple, 0.5–1 mm long. Upper surface of blade glossy, glabrescent, initially 10 % covered with simple appressed hairs 0.25–0.6 mm long, mixed with sessile depressed-globose red glands 0.05 mm diam. Lower surface 5–10 % covered in persistent patent pale brown hairs (0.5–)0.75(–1) mm long, and glands as upper surface. Petiole canaliculate, 5–7, 0.4–0.5 cm, base perfoliate-decurrent, clasping the stem for 3/4 its diameter, then decurrent as wings 1–2 mm wide for 1.8–2.7(–4) cm, finally the wings uniting; indumentum as blade. *Pitchers of nanophylll rosette shoots* placed on ground in leaf litter, matt dark red to red-brown, broadly subcylindric, 4.2–6.5 cm long, 2.5–3.5 cm wide at base, tapering gradually to 1.6–3 cm wide below peristome; fringed wings 1.2–1.5 cm apart, (2–)7–11 mm broad, fringed elements (1–)1.8–2.8 mm long, densely clustered, arranged in 3–4 radiating planes, 0.15 mm apart towards peristome, or more evenly spread, 0.8 mm apart in dissection of the wings; indumentum of moderately dense patent simple pale brown hairs, 0.5 mm long, c. 15–20 per mm^2, mixed with red sessile depressed-globose glands 0.03 mm diam at the same density. Mouth orbicular-ovate, slightly broader than long, oblique, slightly concave, column ill-defined, peristome brown-green, rounded in transverse section, 1–1.6 mm wide, ribs more or less conspicuous, 0.4–0.55 mm apart, raised either slightly and inconspicuously or as a short slender wing 0.1 mm high, ribs separated by 12–15 faint striae; outer edge entire, more or less revolute, inner edge extended into conspicuous narrowly triangular, papery teeth 2–2.4 mm long; lid orbicular, 1.2–1.9 cm diam, apex rounded-emarginate, base rounded and minutely cordate apex of upper surface with a circular indentation 1–2 mm diam base with 1–3 submarginal tentacles 1–2 mm long; lower surface matt pale yellow, with a corresponding raised, cup-shaped structure, 2 by 1 mm, inset 0.5 mm from apex, the interior densely hairy, otherwise appendages absent, nectar glands absent from midline and margin, 1–3 on each side of the midline, longitudinally elliptic, thickly bordered, domed, glossy yellow, 0.8–1.1 by 0.3–0.8 mm, the central aperture dark glossy brown, elliptic 0.25–0.5 by 0.25 mm, sometimes reduced to a minute pore at slit. Depressed-globose sessile red glands 0.05 mm diam and simple pale brown hairs 0.2 mm long, scattered thinly in the marginal 2–3 mm of the lid, the central portion lacking indumentum completely; marginal 0.6 mm of lid densely hairy, hairs bushy, erect, 0.1 mm long, with 1–3 basal branches; spur entire or trifid, conical, 0.5–1.5 mm long, densely appressed hairy. *Lower pitchers* (of short stems) brownish maroon, narrowly ovoid-cylindric, 11.3–20.2 cm tall, 4.7–6 cm wide a the basal, ovoid portion, gradually constricting from a point ('the hip') 6–7 cm from the base, narrowest below the peristome, 3.6–4.6 cm wide; fringed wings 1.5–2.2 cm apart, 0.9–1.4(–2.8) cm broad, involute, fringed elements 1–2(–3.5) mm long, dense, 0.3 mm apart near the peristome, more widely spaced, c. 1–2 mm apart towards the pitcher base; indumentum of appressed, simple, multicellular, glossy pale brown or red hairs, 0.3–0.6 mm long, covering 10–25 % of the surface; mouth ovate, strongly oblique, straight or very slightly concave, inner surface waxy white with purple blotches, column ill-defined; peristome flattened to rounded green or red, 4–7 mm wide, ribs conspicuous, 0.8–1.1 mm apart, abruptly raised as wings 0.5 mm high, ribs separated by striae; outer edge more or less entire, revolute, inner edge extended into conspicuous, narrowly triangular, papery teeth 2–3 mm long; lid elliptic 3.4–5.9 by 3–4.1 cm, apex rounded, base rounded and minutely cordate; upper surface with indumentum as outer pitcher, sometimes with 3–4 multicellular tentacles 2 mm long, hairy, inserted near the spur (*Mahroji 70*), purple brown; lower surface with 25–30 thickly bordered, flattened nectar glands (0.6–)0.75–1.5 mm long, borders glossy, pale yellow, central aperture purple brown 0.2–0.5 mm diam, spur 2–3 mm long, dorsiventrally flat, stout, entire, apex rounded, or (*Mahroji 70*) fasciculate, with 3 basal, equal branches 1 mm long, densely hairy, hairs 0.25–0.5 mm. *Upper pitchers* of climbing stems dark red or yellow-green, more or less tinged and mottled red-brown (*Phillipson et al. 6417*) ovoid-cylindric, 24–25 cm tall, the basal ovoid portion 10 by 6 cm, constricted to c. 4 cm wide above, dilating gradually to c. 5 cm wide below the peristome; wings reduced to two ridges, c. 2 cm apart; indumentum of appressed simple acute hairs as lower pitchers but less dense, and glabrescent in the mature pitcher; mouth ovate, oblique, straight or slightly concave, inner surface waxy white, mottled red, column ill-defined, peristome rounded-flattened in transverse section, 3.5–5.5 mm wide, ribs conspicuous, 1–1.5 mm apart, abruptly raised as wings 0.2–0.3 mm high, ribs separated by striae; outer edge entire, revolute; inner edge extended into concealed, inconspicuous curved

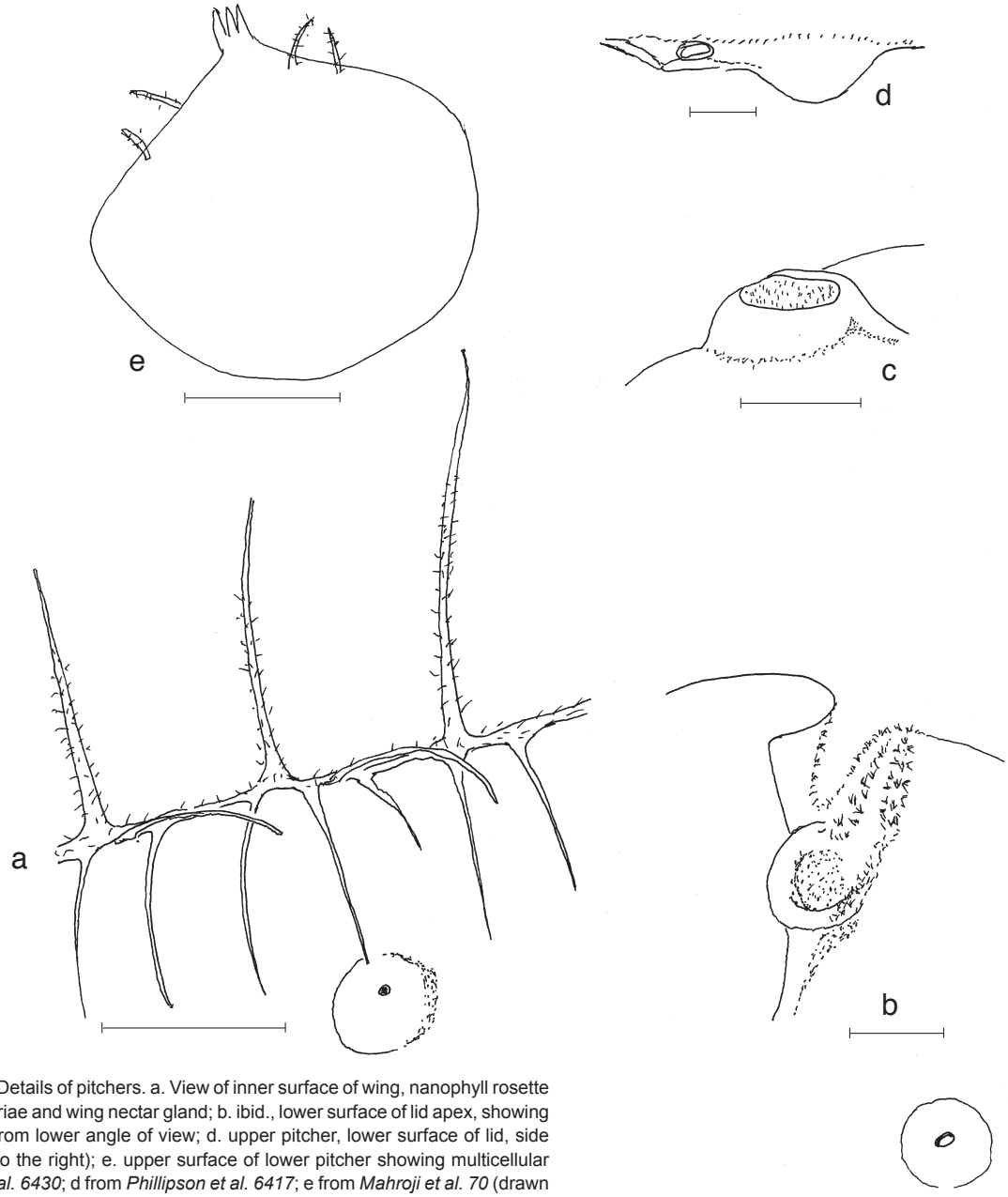

Fig. 3 *Nepenthes weda* Cheek. Details of pitchers. a. View of inner surface of wing, nanophyll rosette pitcher, showing multiseriate fimbriae and wing nectar gland; b. ibid., lower surface of lid apex, showing 'U' shaped appendage; c. ibid., from lower angle of view; d. upper pitcher, lower surface of lid, side view of lid appendage (lid apex to the right); e. upper surface of lower pitcher showing multicellular tentacles (a–c from *Phillipson et al. 6430*; d from *Phillipson et al. 6417*; e from *Mahroji et al. 70* (drawn from photo on Tropicos). — Scale bars: a–d = 1 mm; e = 1 cm. — Drawn by Martin Cheek.

teeth 1.5 mm long; lid leathery, elliptic, 6.2 by 4 cm, apex and base rounded, upper surface with indumentum as outer pitcher, lower surface without basal appendage, but with a small subapical appendage 4–5 mm long, aligned along the midline, set back 4 mm from the apex, proximal part of appendage bilaterally flattened, convex, semi-circular, 2 by 2 mm, distal part apically flattened, raised 1 mm above the surface, with a central bordered flattened longitudinally elliptic nectar gland c. 1 by 0.5 mm; nectar glands resembling that of the appendage, otherwise scattered on surface except for a midline band c. 5 mm wide at base of lid, widening to 8 mm wide at the subapical appendage; 10–15 nectar glands on each side, orbicular or longitudinally elliptic, orbicular glands 0.5–1.25 mm diam with a central glossy brown centre exposed by an aperture up to 0.5 mm diam in the glossy pale yellow border, elliptic glands 0.75 by 0.5–0.6 mm, larger glands flanking the midline band, smaller glands scattered towards margin, mixed with sparse sessile depressed-globose red glands 0.1 mm diam, marginal 1–2 mm with scattered bushy hairs 0.1 mm diam, surface white, with streaks of red radiating from the basal attachment, nectar glands pale brown in life (*Phillipson 6417*); spur dorsiventrally flattened, 2–3 by 1 mm, recurved from above half its length, apex rounded, surface minutely densely papillate, papillae translucent, 0.01 mm long. *Male inflorescence* 44.5–48 by 4.5–5 cm; peduncle 14–18.5 by 0.3–0.4 cm at base; partial-peduncles 65–70, 4-flowered in proximal half, the distal 4/5ths 3-flowered, the distal most 1/5th 2-flowered; bract filiform, reflexed, 1–4 mm long, inserted c. 2 mm above base; partial-peduncle (3–)5(–7) mm long; partial-rhachis 3–5 mm long; pedicels 8–10(–12) mm long 90 % covered in pale brown appressed simples hairs 0.25 mm long, extending to partial-peduncles, rhachis and peduncle, where covering only c. 20 % of surface. Tepals 4, divided by 9/10, lobes ovate-elliptic, 4–4.2(–4.5) by 3–3.5 mm, apex rounded, upper surface coloured green, distal half and marginal 0.5 mm with dense appressed simple brown hairs 0.1–0.2 mm long; proximal part glabrous, with minute elliptic-bordered nectar glands 0.05 mm long, c. 0.15 mm apart, at an apex of irregular raised tubercles, black (dried material). Lower surface with dense appressed golden-brown hairs 0.1–0.125 mm long, 90 % cover, androphore terete 2.5–3.5 mm long, 0.5–0.6 mm wide, with scattered simple golden-brown hairs 0.2 mm long; anther head white, subglobose, 1.5–1.6 mm diam, anthers 8 in a single whorl. *Female inflorescence*, *fruit* and *seed* unknown.

Distribution & Ecology — Lower montane forest on ultramafic substrate; 415–1014 m altitude. Only known from Bukit Limber of Weda Bay, Central Halmahera, Indonesia.

Additional specimens. Indonesia, Maluku Islands, N Maluku Province, Central Halmahera, Weda Bay, km 6 to Bukit Limber, 451 m alt., sterile, 29 Oct. 2012, *Mahroji et al. 70* (BO n.v., MO); ibid., Bukit Limber, alt. 1014 m, sterile, 1 Oct. 2012, *Phillipson et al. 6430* (BO n.v., MO 2 sheets); male infl., 25 Sept. 2012, *Phillipson et al. 6417* (BO n.v., MO 2 sheets); ibid., Bukit Limber, sterile, 20 Apr. 2013, *Bidault et al. 1129* (BO n.v., MO); ibid., 4 Dec. 2012, *Gushilman 189* (BO n.v., MO, field image viewed on Tropicos).

Conservation — Known only from six specimens collected in the course of a botanical survey (Weda Bay Nickel Project), in 2012–2013. Described as either common (*Phillipson et al. 6417*) or uncommon (*Phillipson et al. 6430*). The evidence available suggests that *N. weda* is strictly confined to Bukit Limber within the wider project area. This is because while 20 specimens of *Nepenthes* were collected from seven sites within the c. 23 by 14 km survey area, *N. weda* only occurred at one of these, Bukit Limber. The nickel and cobalt ore deposits here are among the deepest and richest known in the zone of the project, and it is planned to remove all vegetation to facilitate open-cast mining in the first phase of the project (ERM 2010). Given the current evidential basis, this will almost certainly render the species extinct in the wild, unless it can be shown to occur elsewhere, at a safe site. Implementation of the Mitigation Hierarchy in this case appears to be problematic based on current data since *N. weda* appears to sit on the main orebody (Bukit Limber). Further studies are needed to validate this. Given the higher risk to this species, collection of seed for seedbanking should be considered as a priority.

Therefore, since on current evidence a single location is known with an area of occupancy estimated as 12 km^2 (using the 4 km^2 cells currently favoured by IUCN (2012), and with a similar extent of occurrence, *N. weda* is here assessed as CR B1+B2a,b(iii), that is Critically Endangered.

The population of *N. weda* has already almost certainly been reduced by the activities of the Weda Bay Nickel Project, due to their extension of previously existing logging roads in order to access Bukit Limber itself (ERM 2010).

Population reduction has also been caused by the clearance of vegetation in 2007 for a 12 ha test pit at Bukit Limber, following a vegetation survey (ERM 2010): "Vegetation was surveyed over 15 ha in the test pit area, slightly larger than the test pit area of 11.3 ha. The survey recorded 31 species of flora, including two protected species of pitcher plants (*Nepenthes* sp. and *Nepenthes maxima* Nees). The larger surveys of lower montane forest indicate these species are distributed widely within the Contract of Work Area, and elsewhere in Halmahera and Indonesia .... Impacts on the forest are reversible and full recovery is expected in about 20 years." (ERM 2010).

It is almost certain that the two *Nepenthes* taxa referred to in the foregoing passage from ERM (2010) are misidentifications. This is because, subsequent to the initial fieldwork that resulted in ERM (2010), a second survey began in 2012 (and is ongoing) by Weda Bay Nickel, with Missouri Botanical Gardens and Herbarium Bogoriense, that resulted in the specimens identified in this paper as two new species which on the evidence currently available are unique to the Weda Bay Nickel Project area. The high intensity of specimen sampling by the second survey, using *Nepenthes* as an index, is unprecedented in Halmahera. It can be concluded that the 15 specimen records seen by us from the project footprint, probably represent all the *Nepenthes* species present within the area surveyed. At Bukit Limber the seven specimens seen belong to *N. weda* (6 specimens comprising all specimens known globally) and *N. halmahera* (1 specimen). Contrary to the suggestion in ERM (2010) as quoted above, there is no evidence seen by us to indicate that these species definitely occur elsewhere outside the survey area. While it is credible that *N. halmahera* which occurs at six out of the seven sites where *Nepenthes* occur within the survey area, might well occur outside; it is much less likely that *N. weda*, on current evidence restricted to a single location (Bukit Limber), occurs outside the survey area, although it cannot be entirely ruled out.

This may be one of many examples of a point endemic species occurring on ultramafic substrates in SE Asia forests (Ashton 2014). On current data, another point endemic in the area, which is also assessed as Critically Endangered is *Jailoloa halmaherensis* (Heatubun) Heatubun & W.J. Baker, a species representing a monotypic palm genus restricted to Gunung Batu, several kilometres to the NE of Bukit Limber, outside of the Weda Bay Nickel Project, in the neighbouring Nickel Mining concession area of Pt Buena Persada (Solway International) (Heatubun et al. 2014).

Many species of *Nepenthes* are known in the wild from only a single forested mountain or hill. Examples are *N. aristolochioides* Jebb & Cheek (Jebb & Cheek 1997), *N. alzapan* Jebb & Cheek (Cheek & Jebb 2013b) and *N. extincta* Jebb & Cheek (Cheek & Jebb 2013h). The last is already thought to be globally extinct due to open-cast nickel ore mining of the ultramafic substrate that forms its habitat (Cheek & Jebb 2013h).

Reductions in the population of *N. weda* by the project additional to those caused by the test pit drilling and road clearance have been caused by drilling operations in the exploration phase of the project. These serve to produce cores, which when analysed, give data on the depth of the deposit and the extent of its mineralisation, necessary in order to plan extraction of the ore in an efficient manner. Holes are drilled in ever-intensifying densities. Ultimately, hundreds of holes and their associated drill pads can be expected. Although, commendably, small, lightweight drills have been used in the project, of great benefit in reducing the need for the usual forest clearance, some disturbance of the understorey has still occurred, resulting in damage to *N. weda* individuals. This can be seen in the photograph of the Wikipedia entry for Halmahera, in the entry for mining, where a small drill rig is shown being moved through a forest, damaging and destroying rosette shoots of what appears to be *N. weda* (http://en.wikipedia.org/wiki/Halmahera#mediaviewer/File:Rig_Crew_on_Halmahera_Island.jpg).

DISCUSSION

The earlier phase of botanical studies at WBNP were summarised and analysed in an Environment and Social Impact Study (ANDALAS) published by ERM (2010). This document contains valuable geological, climatological and social data. However the botanical studies, while not without value, are evidently incomplete, with many taxa not identified to species, without indication as to whether or where specimens were preserved, and in the case of *Nepenthes*, very likely with important misidentifications. For example, *N. papuana* Danser (endemic to New Guinea) and *N. maxima* (Sulawesi to New Guinea) both reported in ERM (2010) appear not to be present at Weda Bay Nickel Project on the basis of the intense subsequent sampling by the study initiated in 2012 (referred to above, and also, below under *N. weda*). It is likely that *N. papuana* and *N. maxima* were misidentifications for the two species described below as *N. halmahera* and *N. weda*.

The Nepenthes danseri group

Among the SE Asian paniculate species of *Nepenthes*, *N. weda* and *N. halmahera* appear to form a natural, morphologically coherent and probably monophyletic group with *N. danseri.* All three are set apart by sharing simple, straight, acute, multicellular hairs which are also shared with the basal Indian Ocean

paniculate species (Jebb & Cheek 1997, Mullins & Jebb 2009). Other paniculate *Nepenthes* species have branched or stellate hairs. A second feature uniting these three species are the leaves of the climbing stems, which have moderately broad blades contracting into ± well-defined canaliculate-winged petioles. These petioles broaden abruptly at the junction with the stem, partly girdling it with a broad patent wing which equally abruptly becomes very shortly- to long-decurrent, depending on the species. This abrupt widening of the petiole at the node, together with patent wings, and a red colouration of the petiole midrib area and stem, are most distinctive, and appear to represent apomorphies which are otherwise unknown in the genus. Thirdly, these three species, uniquely among all paniculate species, share the characteristic of having only 15–30(–50) lower surface lid nectar glands which are large ((0.2–)0.5–1.25 mm diam) with overarching borders, rather than having hundreds of minute nectar glands which have erect, non-overarching bordering walls. However, outside the paniculate group, such nectar gland characteristics can be found in *N. gracilis* Korth. (Malaysian Peninsula to Borneo and Sumatra) which has even fewer, larger, more strongly overarched glands.

Multiseriate fringed elements on pitcher wings

In most species of *Nepenthes*, perhaps all, the lower pitchers (and in a few species the upper pitchers also) have two fringed, more or less parallel wings that descend from the peristome at the mouth of the pitcher towards the base of the pitcher at the insertion of the tendril. These 'fringe elements' are fimbriae, multicellular extensions from the margin of the wings themselves. They bear hairs of the same sort as the wings and the external surface of the pitcher. The fringe elements occur in a single plane (i.e. they are uniseriate), usually extending from the wing edge, in the same plane, or in the case of the species with incurved wings, the same arc as the wing. Exceptions are rare, one being the rosette pitchers of *N. ampullaria* Jack. Here the fringe elements on one wing are held in four different planes (i.e. they are multiseriate). The elements in a row alternate with each other so that only one in every four elements in a row along the fringe edge are in the same plane. The same phenomenon occurs in the nanophyll rosette pitchers of *N. weda* (*Phillipson 6430*, MO sheet 1 of 2, see Fig. 3a and http://www.tropicos.org/ImageFullView.aspx?imageid=100205863). In contrast, the normal rosette and short stem lower pitchers of *N. weda* and the lower pitchers of the short stems of *N. ampullaria* have uniseriate fringe elements. It can be speculated that the function of the fringed wings may be to guide ground-dwelling insects and at the same time to protect them from competing animal predators, as they climb from the litter of the forest floor towards the peristome of the mouth of the pitcher. Such insects climb to the pitcher mouths either by chance or possibly when they are attracted by scent, in the case of *N. ampullaria* (in which nectar glands are absent from the pitchers) or in the case of *N. weda*, the lure of nectar glands staged along the inner surface of the wings (Fig 3a). Multiseriate elements would function better at both tasks compared with the uniseriate character state, presenting a more impenetrable barrier to traverse, and offering cover from predators in the air above.

Detection of the orientation of the fringe elements is difficult in herbarium specimens due to their conversion to two dimensions in the preservation process. Instead field observations and photographs, study of the live *Nepenthes* species collection at the Royal Botanic Gardens, Kew, and inspection of the hundreds of published photographs of species taken in the wild (e.g. Clarke 2001, McPherson 2009) have served as the basis for the observations made here.

With the benefit of these, it has been possible to confirm that it is the uniseriate, rather than the multiseriate state, that occurs in the nanophyll rosette pitchers of *N. gracilis* and *N. pectinata* Danser. We have not had sufficient access to data on any of the other species which also have nanophyll rosette pitchers (see below) to elucidate which character state is present in them.

The multiple planar orientation of the fimbriae in *N. weda* and *N. ampullaria* is partly the result of two unusual circumstances: 1) the fimbriae do not only occur along the very edge of the wing, as in all other species investigated, but also in a row on the abaxial (outer) surface of the wing, set back from the apex itself by < 1 mm; and 2) the wing edge alone (and not the remainder of the wing) involutes by 90°, so taking the fimbriae it bears out of alignment with the subterminal row(s) of fimbriae by 90° of arc.

Nanophyll rosette shoots

Photographs taken of *N. weda* (*Phillipson et al. 6430*) show horizontal, woody stems in the leaf litter layer that have sprouted vertical rosette shoots along their length. This phenomenon is not unusual in *N. ampullaria*, and occurs when climbing stems fall to the ground after their support collapses (Cheek & Jebb pers. obs.).

The current classification of *Nepenthes* architecture is based on Danser (1928). He recognised and defined 'rosette shoots', 'short shoots' and 'climbing stems', each with their own characteristics. Rosette shoots develop first as 'primary rosette shoots' from seedlings in many species (other species instead develop short shoots from seedlings) and can in turn develop into the 'climbing stem' stage. Only in some unusual species such as *N. argentii* Jebb & Cheek do rosette shoots directly produce inflorescences (Cheek & Jebb 2001).

The secondary rosette shoots of *N. weda* referred to above, are of two sorts both of which can arise from the same stem in close proximity (see http://www.tropicos.org/Image/100205859):

1. 'normal' rosette shoots of the type produced commonly in the genus. These have internodes so short that the nodes are congested and the leaves form a more or less compact rosette, radiating in all directions and completely covering the ground below. The blades bear a terminal tendril that descends vertically to the ground, ending in a lower pitcher, never an upper pitcher. This sort of rosette shoot is almost identical to those primary rosettes produced from seedlings. Such secondary rosette shoots are most frequently produced adventitiously in mature plants from the basal portion of an older climbing stem, and may then give rise to a new climbing stem, rejuvenating the individual or increasing its size by adding additional stems.
2. nanophyll ('dwarf leaf') rosette shoots are here named and defined for their dwarf leaf-blades, < 5 % of the size of 'normal' rosette leaf-blades, and often < 1 % of the area as in *N. weda*. These can be seen in *Phillipson et al. 6430* (Fig 2e, http://www.tropicos.org/Image/100205864). The 'normal' rosette leaves (e.g. *Bidault et al. 1129*) are instead elliptic, measuring 9–12 by 3–4 cm, while nanophyll blades are different in shape and size: linear-oblong and 2–2.7 by 0.2–0.4 cm long. Tendril lengths are similar in both 'normal' and nanophyll rosette leaves, 7–8.7 cm long in the first and 6–8 cm long in the second. Nanophyll shoots have never been observed to develop into 'normal rosette shoots', 'short shoots' or 'climbing stems'.

It has been hypothesised in *N. ampullaria* in New Guinea (Jebb 1991) that nanophyll leaf rosettes are an evolutionary adaptation to low light levels on the forest floor. Here we hypothesise that the energetic rewards from photosynthesis might be less than the expenditure on constructing and operating full-sized rosette leaf blades. In contrast the pitchers can still function in capturing nutrients from either animal prey (numerous ants

are seen trapped in nanophyll rosette pitchers of *N. weda*), or perhaps also from leaf litter, as is reported in *N. ampullaria* (Clarke 2001).

Nanophyll leaf rosettes are not usual in the genus *Nepenthes.* They are best known in *N. ampullaria* in which they are abundantly produced. They also occur in the following species (source of data indicated in brackets):

– *N. danseri* Jebb & Cheek (Jebb & Cheek 1997)
– *N. glabrata* J.R.Turnbull & A.T.Middleton (Cheek & Jebb 2001)
– *N. gracilis* Korth. (Kurata 1976)
– *N. gymnamphora* Nees (Cheek & Jebb 2001)
– *N. hispida* Beck (pers. obs. Cheek, cultivated plants at RBG, Kew, Jan. 2015)
– *N. neoguineensis* Macfarl. (*Kloss s.n.*, 9 Jan. 1913, K)
– *N. pectinata* Danser (Cheek & Jebb 2001)
– *N. tentaculata* Hook.f. (pers. obs. Cheek, Santubong, Sarawak)

Lid appendages in Nepenthes weda

Appendages on the lower surface of the pitcher lid are characteristic of the *Nepenthes Regiae* group, and of the *Nepenthes alata* group (Cheek & Jebb 2013h, 2014). They also occur in three of the Sumatran species of the *Montanae* group of Danser. Their occurrence in *N. weda* (this paper) is their first documented occurrence in any of the paniculate species. The distal (inserted near the lid apex), forward-facing and concave lid appendages of *N. weda* are most similar to, and may be homologous with, those recently reported in *N. tboli* Jebb & Cheek (Cheek & Jebb 2014) which have been observed in other members of the *N. alata* group such as *N. robcantleyii* Cheek (Cheek 2011).

The change in morphological character states from those in lower pitchers to those of upper pitchers is well known in general terms, that is: from tendril straight to coiled; from fringed wings to wings reduced to non-winged ridges; pitcher shape from ovoid-cylindric to cylindric or funneliform; pitcher posture from facing the main axis and tendril to facing away from main axis and tendril; from pitcher size large to smaller (Cheek & Jebb 2001). However, the concomitant change in character state of lower surface lid appendages appears never to have been remarked upon. This may be because they rarely occur. Be that as it may, stage-related heteromorphy of the lid appendage is marked in *N. weda* and is recorded here for the first time in the genus. Below are recorded the differing morphologies of the lid appendage at four different stages of the pitcher in *N. weda*:

1. Nanophyll rosette pitchers. In *Phillipson et al. 6430* the lid apex appears to be emarginate due to a folding, downwards, of a triangle of tissue. On the lower surface a U-shaped, walled structure, which is hair-filled is developed at the apex (Fig. 3b, c).
2. Normal rosette pitchers. In *Bidault et al. 1129*, the folding of the lid is absent, instead the curved wall structure noted in 1. above, is set back from the apex by 3–4 mm, its arc is widened to a crescent-shape, and the walls become concave, producing a shallow 'scuttle' shape to the appendage.
3. Lower pitchers. In *Mahroji et al. 70* lid appendages are absent, but in *Bangun et al. 218*, a small transverse rectangular boss 0.3 by 0.8 mm is present on the midline, 9 mm from the apex.
4. Upper pitchers. In *Phillipson et al. 6417* the subapical appendage is 4–5 mm long, placed along the midline, its apex with a concave, forward-facing appendage c. 2 by 1.5 mm, the proximal part of which is a plateau 0.75 mm high, 1 mm long, with a central, bordered, nectar gland 0.5 mm diam (Fig. 3d, http://www.tropicos.org/ImageFullView.aspx?imageid=100206237).

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