



## *Nepenthes erucooides* (Nepenthaceae), an ultramaficolous micro-endemic from Dinagat Islands Province, northern Mindanao, Philippines

ALASTAIR S. ROBINSON<sup>1,\*</sup>, SARAH GRACE ZAMUDIO<sup>2,3</sup> & ROLLY BALAGON CABALLERO<sup>4</sup>

<sup>1</sup> National Herbarium of Victoria, Royal Botanic Gardens Melbourne, Melbourne, VIC 3004, Australia;

e-mail: [alastair.robinson@rbg.vic.gov.au](mailto:alastair.robinson@rbg.vic.gov.au)

<sup>2</sup> The Graduate School, University of Santo Tomas, España Boulevard, 1015 Manila, Philippines.

<sup>3</sup> Research Center for the Natural and Applied Sciences, University of Santo Tomas, España Boulevard, 1015 Manila, Philippines.

<sup>4</sup> DENR-PENRO Dinagat Islands, Caraga Region Purok 2, Barangay Santa Cruz, San Jose, Province of Dinagat Islands, Mindanao, Philippines.

\*Author for correspondence

### Abstract

A new species of *Nepenthes*—*N. erucooides*—is described and illustrated from a single ultramafic peak in the Dinagat Islands Province of northeastern Mindanao. It is a distinctive component of a relatively low-elevation, highly biodiverse montane elfin forest that has evolved in association with a particularly thin and extremely hostile substrate. Plant habit, and leaf, inflorescence, indumentum and peristome-column morphology appear superficially similar to those of the ultramaficolous montane species of Palawan, implicating an environmental basis for a syndrome of shared characteristics.

**Keywords:** Philippines, Malesia, new species, non-core Caryophyllales, taxonomy, ultramafic

### Introduction

*Nepenthes* Linnaeus (1753b: 955) is a genus of tropical pitcher plants comprising *ca.* 160 species (see e.g., Clarke *et al.* 2018), with a wide distribution across the Malesian and Papuan biogeographic regions, with recognised centres of diversity in Borneo, the Philippines and Sumatra, where the greater proportion of species are represented by microendemic taxa from individual mountains or mountain ranges (Cheek & Jebb 2001, Clarke 2001, Robinson *et al.* 2009).

In 2001, only 12 species of *Nepenthes* were recognised from the Philippines (Cheek & Jebb 2013), but 44 further species have been described from the country since then. This marked increase stems from a number of factors, including novel discoveries resulting from increased exploration of the archipelago by botanists and *Nepenthes* enthusiasts alike; a concomitant increase in familiarity with the genus amongst Filipino botanists and, particularly, a Kew-led project that has elevated a raft of taxa to species rank, mainly from overlooked specimens in herbaria around the world, and raised others from synonymy (e.g., Cheek & Jebb 2014, 2013a, 2013b, 2013c, 2013d).

When excluding those newly described Filipino species that are not accepted by various authors (e.g., Clarke *et al.* 2018), the total number of good species recognised from the archipelago still stands at approximately 45. Out of the 56 taxa described at specific rank, *ca.* 30 are either ultramafic endemics or largely restricted to mafic substrates or surface laterites with associated open canopies. A further *ca.* 20 taxa are associated with more general mid-montane and montane habitats, mainly in association with mossy forest where they predominantly grow as epiphytes or in pockets of humus. Though many in this group are recorded from volcanoes, few Filipino *Nepenthes* are actually recorded growing directly in volcanic substrates, rather occurring in humic material overlying volcanic substrata. In fact, the only Filipino *Nepenthes* verifiably documented as facultatively growing directly in volcanic substrates are *N. ventricosa* Blanco (1837: 807), e.g. on the lava tube walls of the Mayon volcano, and *N. copelandii* Merrill ex Macfarlane (1908: 51), e.g. on volcanic rubble on the slopes of the Camiguin and Mt. Apo volcanoes (A. Robinson, pers. observ.). The few other non-ultramaficolous terrestrial species known are typically recorded from other substrates, such as weathered granites [e.g., *N. mira* Jebb & Cheek (1998: 966), Cleopatra's Needle], degraded shale and mudstone [e.g., *N. robcantleyi* Cheek (2011: 678) at one of two mountain locations above the Compostela Valley, also epiphytic at lower elevations]

and limestone [e.g., *N. viridis* Micheler *et al.* (2012: 4), coastal Dinagat] (all A. Robinson, pers. observ., but see also Encarnación & Mukasa 1997, and Suerte *et al.* 2009).

Within the Philippines, the highest *Nepenthes* species diversity is recorded on Mindanao, where 30 species occur and 18 of them are ultramaficolous. This high species diversity correlates with the spatial heterogeneity of exposed ultramafic terranes on Mindanao, which include numerous isolated mountain peaks. The edaphic effects of nutrient-poor, broadly phytotoxic, cation-imbalanced and frequently water-stressed soils combined with the particular climatic factors associated with individual ultramafic outcrops are disproportionately associated with high levels of speciation and endemism (Galey *et al.* 2017). The eastern half of Mindanao is home to the largest tracts of exposed ultramafic regolith on that island, and the prominent outcrops of Surigao del Norte Province, Dinagat Islands Province and the Pujada Peninsula (Davao Oriental, including Mt. Hamiguitan) are all derived from the same belt of Cretaceous ophiolite complexes (Balce *et al.* 1976, Yumul *et al.* 2003, 2008, Tamayo *et al.* 2004), a geological feature associated with a range of endemic *Nepenthes* including *N. bellii* Kondo (1969: 653), *N. hamiguitanensis* Gronemeyer *et al.* (2010: 1296), *N. merrilliana* Macfarlane (1911: 207), *N. micramphora* Heinrich *et al.* (2009: 1315), *N. mindanaoensis* Kurata (2001: 32), *N. peltata* Kurata (2008: 12), *N. ramos* Jebb & Cheek (in Cheek & Jebb 2013d: 108), *N. surigaoensis* Elmer (1915: 2785) and *N. truncata* Macfarlane (1911: 209). Six *Nepenthes* species, i.e. *N. bellii*, *N. merrilliana*, *N. mindanaoensis*, *N. mirabilis* (Loureiro 1790: 606) Rafarin (1869: 270), *N. truncata*, and *N. viridis* (only on limestone within this region), have been recorded just from the fraction of the relatively small Dinagat Islands Province (ca. 1036 km<sup>2</sup>) already investigated by the first author.

In November 2014, an unidentified species of *Nepenthes* was photographed from a conserved, relatively low-elevation ‘montane forest’ on Dinagat Island by botanists J. Barcelona and P. Pelsler (University of Canterbury, New Zealand) as part of their ongoing work to catalogue the entire flora of the Philippines (Pelsler *et al.* 2011+). Images of the plant were shared with AR, who confirmed its undescribed status. Assessments of the plant were carried out in 2018, after which representative material was collected and accessioned, allowing for its description, presented here.

## Materials and methods

*In situ* studies of *Nepenthes* were made on Dinagat by AR in July 2014, and specific morphological and ecological studies of *N. erucoides* and its habitat were conducted by AR and Brian Quinn (New Zealand) with the support of RC in June 2018 after a permit for access to the habitat was granted. Material of the plant was collected by SZ (under DENR Region XIII Wildlife Gratuitous Permit No. R13-2018-0053 and Wildlife Transport Permit No. 2018-10-01) and subsequently deposited at the herbaria PNH and UST (acronyms follow Thiers 2019+). Fine measurements were made using a Mitutoyo vernier calliper (Mitutoyo Corporation, Japan).

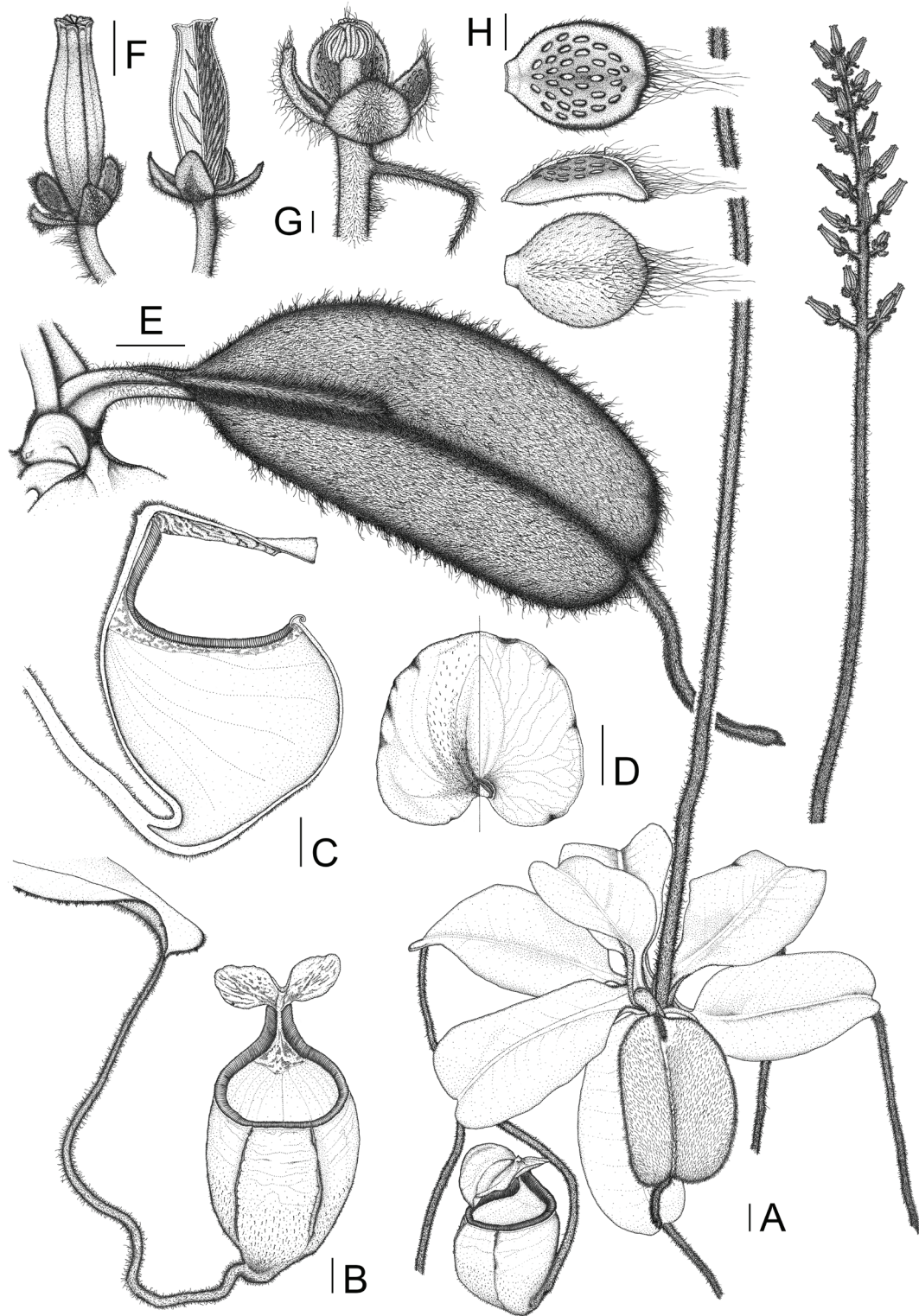
Initial *de novo* georeferencing was made using a Garmin Oregon 600 GPS unit with dual GPS and GLONASS telemetry enabled. Key measurements were made with 3 averaged waypoint readings over the course of a 15 minute period, with an estimated accuracy of  $\pm 3$  m.

## Taxonomy

*Nepenthes erucoides* A.S.Rob. & S.G.Zamudio, *sp. nov.* (Figs 1–3).

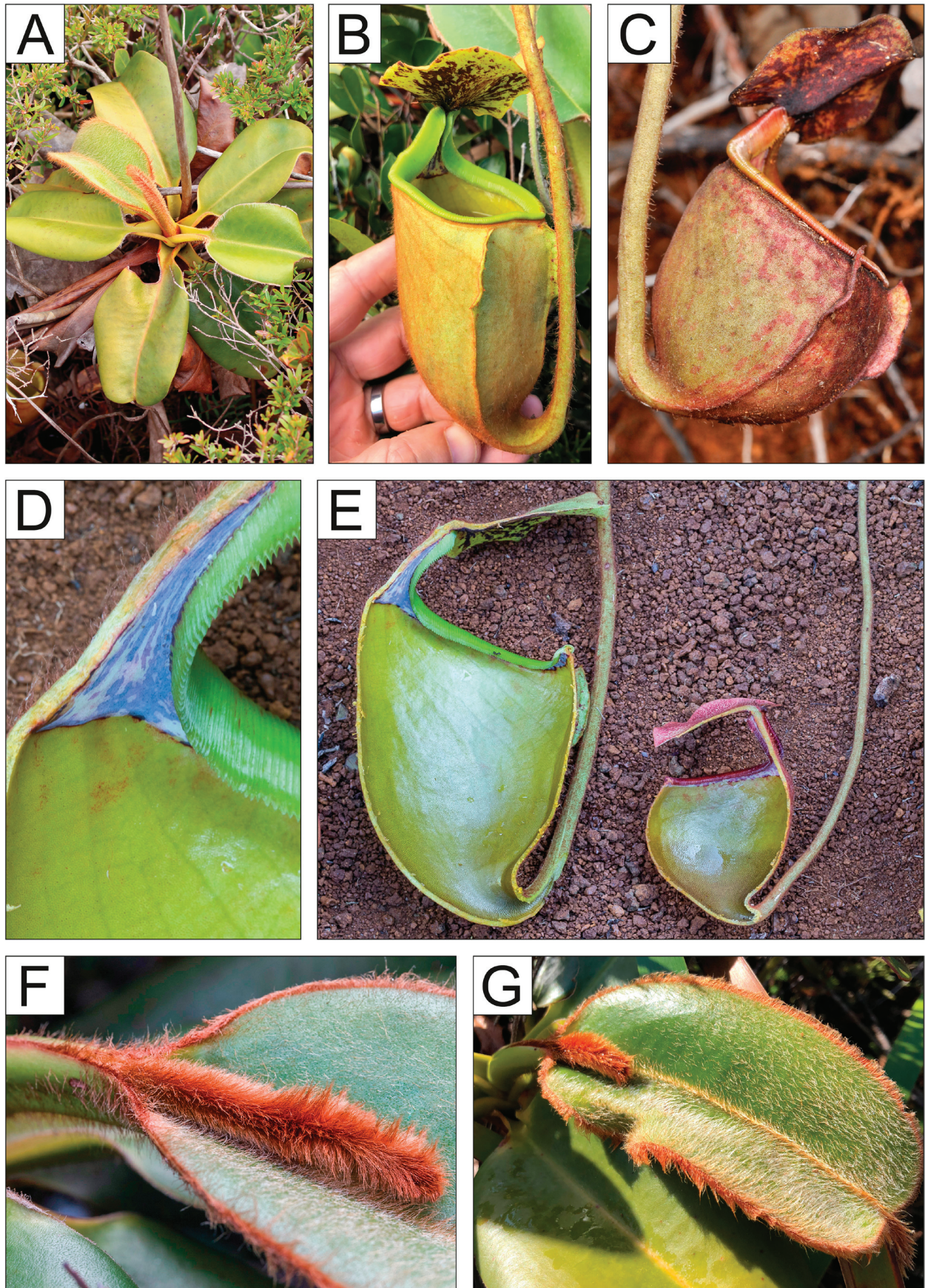
**Type:**—PHILIPPINES. Mindanao: Dinagat Province, Mt. Redondo, 839 m elevation, 13 October 2018, Zamudio, Apo, Gonzales & Tan 257395 (holotype, PNH!) [mature rosette bearing three lower pitchers]; *ibidem* Zamudio, Apo, Gonzales & Tan 014747 [detached upper pitcher], 014749 [three sheets: mature rosette with tendrils; lower pitcher  $\times$  2; upper pitcher], 014753 [intermediate pitcher] and 014754 [small rosette with very dense indumentum] (all isotypes, UST!).

**Diagnosis:**—*Nepenthes erucoides* is similar to *N. mantalingajanensis* Nerz & Wistuba (2007: 17) in overall plant form, but differs from that species by way of its (differences in parentheses) long, dense indumentum of rufous hairs (predominantly glabrous), production of lower and upper pitchers (lower pitchers only), urceolate to sub-campanulate pitcher shape (ovate-obconic), finer peristome with small teeth along the inner margin (broader with clearly defined ribs and long teeth), very large bracts 8–15 mm long produced from some partial peduncles and the rachis of male inflorescences (bracts on most partial peduncles, ca. 1 mm long, never from the rachis), and seeds without well-developed filaments (filaments well-developed).



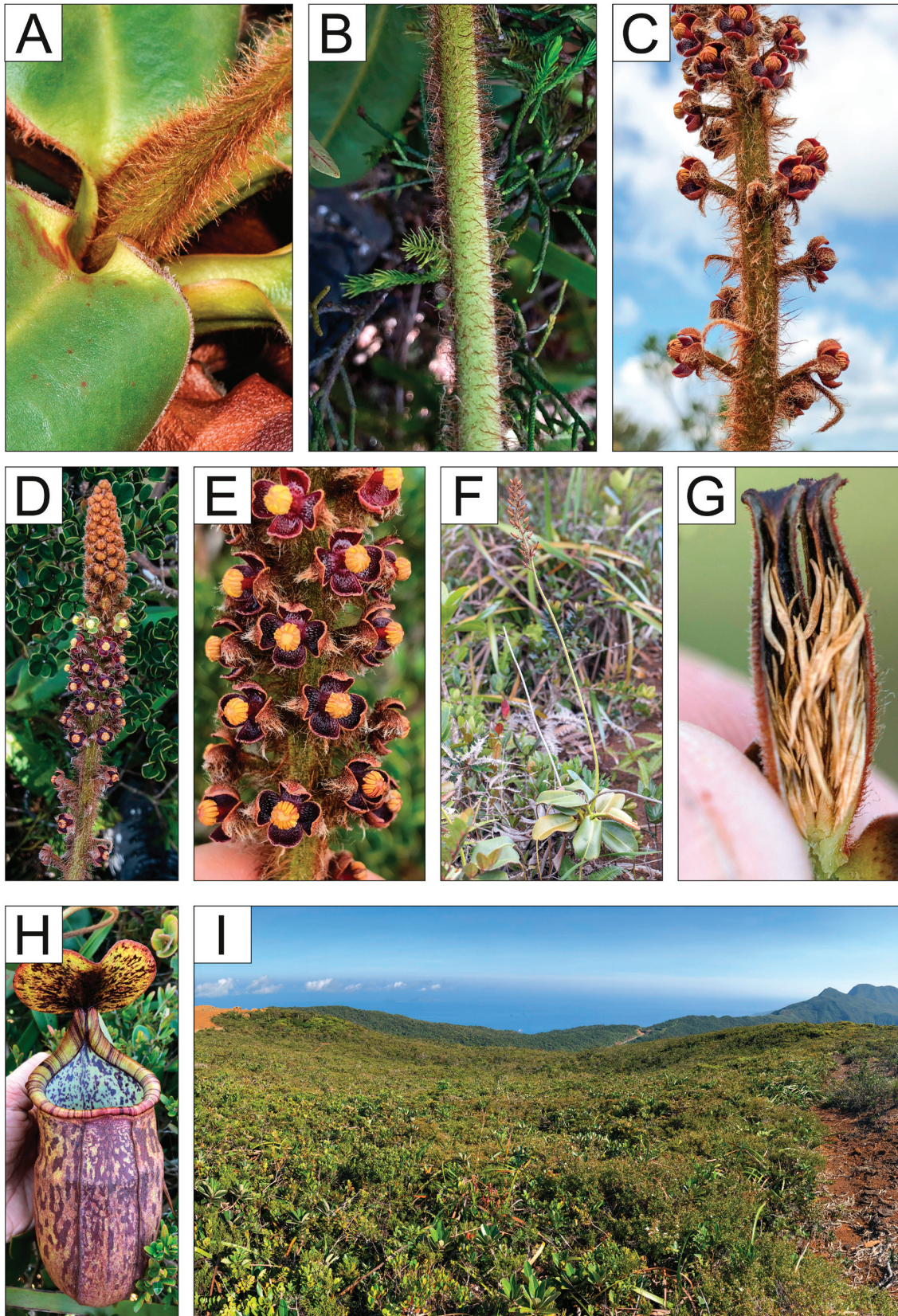
**FIGURE 1.** *Nepenthes erucoides*. A) mature rosette bearing female inflorescence and upper pitcher; the prominent, dense, adaxial indumentum of the newest leaf soon becomes caducous. B) lower pitcher. C) upper pitcher in section; the waxy zone is present only on the column and just below the peristome. D) adaxial (left) and abaxial (right) surfaces of a pitcher lid. E) detail of a newly formed leaf with its dense indumentum and a developing leaf; the stem indumentum is variably caducous between individuals. F) entire (left) and sectioned (right) indehiscent fruit. G) male flower with very large bract. H) adaxial (top), lateral section (middle) and abaxial (bottom) detail of tepal from male flower. Scale bars: A, B, C, D, E = 1 cm, F = 5 mm, G, H = 1mm. Based on Zamudio, Apo, Gonzales & Tan 257395 and 014754, as well as on photographs and measurements made *in situ*. Illustrated by A. Robinson.





**FIGURE 2.** A) mature rosette emergent from elfin vegetation. B) lower pitcher. C) upper pitcher. D) the limited waxy zone. E) transverse sections of (left) lower and (right) upper pitchers showing the almost entirely glandular interior. F) detail of the superficially caterpillar-like (erucoid) developing leaf emergent from the petiolar-laminar groove of the preceding leaf. G) a recently unfurled leaf; the dense adaxial indumentum has already begun to be shed towards the leaf base. Photographs A, C by P. Pelsler; B, D–G by A. Robinson.





**FIGURE 3.** A) the indumentum of juvenile stem and leaf parts is abruptly caducous. B) the largely persistent indumentum of the tendril. C) the extremely dense indumentum of a senescent male inflorescence; note the large bracts on the rachis and partial peduncles. D) sequential anthesis and development of tepal colouration in the male inflorescence. E) detail of male flowers at anthesis. F) a female rosette in fruit. G) transverse section of fruit with seeds; note the relatively short, broad form of the seeds. H) the natural hybrid *Nepenthes erucoides* × *mindanaensis*. I) the elfin ‘forest’ at the summit of Mt. Redondo, formed in response to the inorganic, granular, ultramafic substrate and associated conditions. Photograph A by P. Pelsler; B–H by A. Robinson.



**Description**<sup>1</sup>:—An upright to subscandent sub-shrub 10–50(–120) cm tall. *Stems* terete, 0.9–1.8 cm in diameter, internodes 0.5–3 cm long, climbing stems absent. *Leaves* coriaceous, petiolate, emerging pliant, becoming brittle on maturity, lamina broadly sub-elliptic to oblong, 8–15 cm long, 4.5–8.5 cm wide, apex retuse-emarginate and often unequal either side of midrib, base of lamina abruptly attenuate into petiole, petioles 0.8–1.8 cm long initially, but up to 3.8 cm long on taller stems, without wings, base sheathing the stem and amplexicaul for 1/2–4/5 of the stem circumference, initially tubular, wholly enclosing primordium of subsequent leaf, opening to form a canaliculate petiolar-laminar groove. Longitudinal veins 2(–3), more conspicuous on abaxial surface, situated on either side of midrib in outer 1/3 of lamina, parallel to margin, with fine, ±simple transverse venation running between longitudinal veins and midrib. Tendrils rarely peltate from apex of large leaves, *ca.* 2.5 times longer than the laminae, 25–38 cm long, uncoiled in lower and upper pitchers. *Lower pitchers* urceolate to broadly sub-cylindric or sub-campanulate, 6–10(–15) cm tall, 4.5–8.5 cm wide, typically widest at the mouth, tendril ventrally attached, ventral surface between wings flattened, largest pitchers becoming angular, wings poorly developed, present only in the most basal lower pitchers, thereafter reduced to pronounced ridges, restricted to upper 1/3 of ascidium if manifested at all, and 1–4 mm wide, fringe elements absent or sparse and tubercle-like, 0.5–1.2 mm long, 4–6 mm apart; pitcher interior almost entirely glandular, bar a scant waxy zone arising only near the base of the column and continuing to its apex, also contiguous but hidden beneath inner margin of peristome, glands in lower 1/6 of pitcher slate grey to brown in colour, elliptic, 0.3–0.5 mm long, 0.2–0.3 mm wide, with a density of *ca.* 330 glands per cm<sup>2</sup>, glands in upper 5/6 of pitcher of same colour as pitcher interior, 1/3 smaller and more densely arranged, with a density of *ca.* 400 glands per cm<sup>2</sup>; peristome slightly raised to ±horizontal at front of pitcher between wings, thereafter rising at an angle of 20°–25° towards pitcher rear, becoming abruptly vertical at column, column itself typically recurved forwards over pitcher opening at an angle of *ca.* 30° from vertical, peristome in section moderately curved to sub-cylindric at the front, 2–4(–6) mm wide, rear part broadening only slightly by less than 1/3, becoming flattened and appressed from the base of the column to its apex, external marginal lobing absent, ribs fine but pronounced, *ca.* 0.2–0.4 mm high, *ca.* 0.8 mm apart, teeth triangular-acuminate, 0.8–1 mm long along inner margin. Lid positioned between horizontal and 45°, cordate, sometimes ±complanate in smaller pitchers, but typically broadly canaliculate along the midvein, canaliculum occupying central 1/3 of lid between a pair of perfect or imperfect, basal to supra-basal acrodromous veins, one each side of the canaliculum furrow, apex retuse to obtuse, 2.5–5 cm long, 3.2–5.8 cm wide, abaxial surface without midline rib protuberances, but densely, uniformly covered with minute, elliptic to round pitted glands. Spur vestigial to simple and short, 1–2.8(–5) mm long, rarely bifurcating. *Upper pitchers* globose to sub-campanulate, attenuating into the dorsi-basally attached tendril in the lower 1/6, 4.5–9(–11) cm tall, 4–8 cm wide, usually widest just above the midsection, ventral surface gibbous to slightly flattened, wings usually reduced to ridges, rarely expressed towards peristome, if so 0.5–3 mm wide, fringe elements usually absent; pitcher interior almost entirely glandular, scant waxy zone arising only near the base of the column and continuing to its apex as well as immediately beneath teeth of peristome, glands in lower 2/5 of pitcher slate grey to brown in colour, elliptic, 0.7 mm long, 0.3–0.45 mm wide, with a density of *ca.* 165 glands per cm<sup>2</sup>, glands in upper 3/5 of pitcher of same colour as pitcher interior, 1/3 smaller and more densely arranged, with a density of *ca.* 320 glands per cm<sup>2</sup>; peristome ±horizontal at front of pitcher between wings, thereafter rising at an angle of 15–20(–40)° towards pitcher rear, becoming abruptly vertical at column, column itself typically recurved forwards over pitcher opening at an angle of *ca.* 30° from vertical, peristome in section sub-cylindric at the front, *ca.* 2–3.5 mm wide, rear part broadening by up to 1/2, otherwise similar to lower pitchers. Lid similar to lower pitchers but often slightly shorter and broader, (3–)4.2–5 cm long, (3.5–)4.8–5.8 cm wide. Spur vestigial, simple, 0.2–1.2 mm long. *Inflorescences* marcescent, ±emergent from axil at base of preceding leaf. *Male inflorescence* 45–55 cm long, 60–80 flowers, peduncle 30–40 cm long, *ca.* 5–6 mm in diameter at the base, rachis 15–20 cm long, partial-peduncles 1-flowered, stout, to 1.2 mm in diameter, pedicels 7–9 mm in length, bracts prominent, simple, terete, *ca.* 0.35 mm in diameter, 8–15 mm long, produced from underside of only lowermost pedicels or emergent directly from rachis, adnate to stem, tepals opening yellowish green on the adaxial surface, rapidly turning deep red to blackish maroon, broadly elliptic, *ca.* 4.5 mm long, 3 mm wide, concave throughout, adaxial surface with 30–70 elliptic pitted glands, those closest to the base larger than the more distal glands, to 0.4 mm long and 0.18 mm wide, tepal apex acute; staminal column 2.4–2.8 mm long, anther head *ca.* 2.3 mm in diameter, anthers ±14, bilocular, extrorse, thecae pale yellow, pollen grains deep yellow. *Female inflorescence* *ca.* 70 cm long, 20–28 flowers, peduncle 55 cm long, 5–6 mm in diameter at the base, rachis 15–18 cm long, partial-peduncles 1-flowered, bracts infrequent on lowermost pedicels, filiform-subulate, 4–7 mm long, pedicels to 1 mm in diameter, 4–6 mm long, flowers with a scent of murine urine, fruit 17–20 mm long, 4–5 mm in diameter, tepals as per male flowers but apices acute to

1 This description incorporates details from observations made of living material *in situ* on Mt. Redondo, as well as from the holotype (*Zamudio, Apo, Gonzales & Tan 257395*) and the associated listed isotype materials.



obtuse, glands restricted to central part of adaxial surface, and adaxial surface yellowish green in the proximal 1/3, and reddish ageing to grey-black in the distal 2/3. *Seeds* fusiform, *ca.* 5 mm long, without well-developed filaments. *Indumentum* of dense, villous, rufous hairs 2–6 mm long covering all terminal developing parts, tomentose along leaf margins and abaxial midrib, with downy, rufous to straw-coloured or white hairs 2.5–3 mm long additionally covering adaxial surface of lamina of most recent leaf; indumentum thereafter abruptly caducous, preceding foliage being adaxially glabrous and stems frequently so, with indumentum persistent on abaxial surface of lamina and midrib, on tendril, and more sparsely so on external surface of pitchers, where it is most persistent towards dorsal midrib, as well as around spur and proximal adaxial surface of lid, with additional dark, minute, stiff hairs contributing to a slightly scabrous pitcher texture. Indumentum of abaxial lamina surface differs in being predominantly covered with brown, bristly, curved hairs *ca.* 2 mm long. Inflorescence indumentum is persistent along the rachis, where it is especially long and dense in males versus slightly more sparse in females, and close to the base of the peduncle, the peduncle itself becoming variably sub-glabrous, partial-peduncles with longer hairs on the abaxial surface. The abaxial surface of the tepals is particularly hairy close to its base and along the midline. *Colour* of mature stems and leaves a deep, glossy green, emerging leaves yellowish green, pitchers yellowish olive-green to yellow or orange, sometimes suffused with red, with or without highly variable amounts of red stippling, peristome colour generally congruent with base colour of pitcher, adaxial surface of lid similar, but abaxial surface invariable stippled with red, particularly towards base and midline.

**Etymology:**—The specific epithet *erucoides* is derived from the Latin *eruca* (caterpillar) and the Greek suffix *-oides* (resembling), in reference to the densely hairy developing leaves which, when still appressed within the petiolar-laminar groove of the preceding leaf, resemble the exuberantly hairy caterpillars of certain erbid macromoths from the subfamily Arctiinae, such as those of the genus *Arctia* Schrank (1802: 152) [e.g. *Arctia opulenta* Edwards (1881: 38)].

**Phenology:**—Anthesis in *Nepenthes erucoides* has been observed in June (AR, RC & Brian Quinn, pers. observ.) and as late as November (Pieter Pelsler & Julie Barcelona, pers. comms.), but patterns of inflorescence development and senescence suggest that the majority of inflorescences emerge in response to increases in rainfall immediately following the February to April dry season, with peak flowering from late May to early July, and maturation of seed from late July to early September, immediately preceding the height of the October to January wet season (climate data from Worldbank.org 2019), favouring establishment of seedlings.

**Distribution and ecology:**—*Nepenthes erucoides* is endemic to Dinagat Island's highest peak, Mt. Redondo, where it occurs from *ca.* 800 m elevation to the 929 m summit in a dark, materially dense, inorganic, granular, clinker-like substrate of lateritic nickel ore and decomposed chromite rubble, through to a clay derived thereof, certainly the most extreme ultramafic substrate observed by the first author for any *Nepenthes* across the entire range of the genus. This species is a notable component of the extremely stunted [25–70(–150) cm tall] elfin ('bonsai') forest that covers the upper reaches of Mt. Redondo from about 750 m elevation. The forest, which occupies an estimated area of *ca.* 5.2 km<sup>2</sup>, is characterised by a shrub-like covering of stunted trees ranging in height from 3 m, at its lowest elevations, to less than 50 cm in the summit region. Notable plants observed in this region included *Dacrydium beccarii* Parlatores (1869: 494) (Podocarpaceae Endl.), *Fagraea gitingensis* Elmer (1910: 859) (Gentianaceae Juss.), *Leptospermum amboinense* Blume (1826: 1100) (Myrtaceae Juss.), *Psychotria surigaoensis* Sohmer & Davis (2007: 100) (Rubiaceae Juss.), *Rhodomyrtus surigaoensis* Elmer (1914: 2344) (Myrtaceae), *Scaevola micrantha* Presl (1831: 58) (Goodeniaceae R.Br.), *Elaeocarpus* Linnaeus (1753a: 515) spp. (Elaeocarpaceae Juss.), several species of *Syzygium* (Myrtaceae), and a range of herbaceous plants including *Paphiopedilum ciliolare* (Reichenbach filius 1882: 488) Stein (1892: 462) and miniature *Dendrochilum* Blume (1825: 398) spp. (both Orchidaceae Juss.), *Dischidia major* (Vahl 1810: 110) Merrill (1917: 437) (Apocynaceae Juss.), *Freycinetia* Gaudichaud-Beaupré (1824: 509) (Pandanaeae R.Br.) and, of course, other *Nepenthes* species, most notably the co-localising *N. bellii* (where protected from desiccation by thick vegetation) and *N. mindanaoensis* (which also hybridises with *N. erucoides*). *N. truncata* also occurs in the bonsai forest; however, within the constraints of the limited observations made during our field studies, this giant species seems to occupy an adjacent but distinct elevational band mainly below 800 m where the soil profile is deeper and water-holding capacity greater—*N. erucoides* is absent from this lower elevation zone. *N. merrilliana*, which frequently approaches *N. truncata* in terms of sheer pitcher size, occurs almost entirely below 600 m elevation in this region.

Within its habitat, *Nepenthes erucoides* occurs mainly in very open, low growing (<50 cm), scrubby vegetation, where it is most easily located via its emergent inflorescences. In this situation, shelter from the extremes of intense sunlight, heat and high rates of evapotranspiration experienced in adjacent open ground likely favours the recruitment of seedlings. However, scattered plants were also observed growing in apparent good health on rocky, open ground that was too hot to touch beneath the midday sun, while a minority of plants occurred in denser thickets of taller vegetation

(up to 1.7 m) where the diminutive *N. bellii* was occasionally found, if far more difficult to discern. These represented the tallest and most robust *N. erucoides* plants (up to 120 cm), however seedling recruitment appeared to be reduced by low levels of light at ground level as a result of the higher vegetation density.

**Conservation Status:**—*Nepenthes erucoides* has been directly impacted by mining activities which have resulted in clearing of part of the Mt. Redondo bonsai forest habitat. However, as part of this work, the mining corporation overseeing the site (Krominco, Inc.) have set aside a portion of this very important and highly biodiverse habitat for preservation. The corporation currently acts as conservator of the habitat, critically preventing further damage to the site and reducing the likelihood of biopiracy by unscrupulous plant and animal collectors by limiting general access only to permitted and supervised groups.

Direct observations of *Nepenthes erucoides* made *in situ* satisfy the IUCN 3.1 Red List CR (Critically Endangered) Criteria B1ab(ii,iii)+2ab(i,ii,iii) (IUCN, 2012), i.e. the species has an EOO < 100 km<sup>2</sup> and is known from only a single location with documented decline in area of occupancy and quality of habitat, and an AOO < 10 km<sup>2</sup> at the single location with a reduction in area of occurrence, occupancy, and extent and quality of habitat.

**Notes:**—Although partly caducous, the indumentum of *Nepenthes erucoides* is the most highly developed in the genus, being remarkably long and dense on all parts of any primordia, across the entire adaxial surface of the most recent leaf, and persistent on all floral parts, but particularly the male rachis. This adaptation is presumed to both protect exposed or developing organs from intense solar radiation and to reduce water loss, particularly during the very hot dry season (see discussion below). The production of seeds without developed filaments is presumed to be an adaptation to the species' island habitat, similar to that seen in *N. argentii* Jebb & Cheek (1997: 19), *N. kerrii* M.Catal. & Kruetr. in Catalano (2010: 30) and *N. pervillei* Blume (1852: 10); the lack of prominent seed filaments presumably serves to prevent the dispersal of seeds away from the extremely limited summit elfin forest habitat by strong winds (A. Robinson, pers. observ.).

*Nepenthes erucoides* co-occurs with *N. mindanaoensis*, which also has markedly petiolate leaves, but that species differs in having a narrower peristome with finer ribs, far less discernible teeth and no column, an abaxially ribbed lid, as well as 2-flowered partial peduncles and a poorly developed indumentum. Also present, albeit at a far lower density, is *N. bellii*, the diminutive sister species to *N. merrilliana* (which is virtually identical in pitcher, leaf and to some extent floral characteristics, but differs in its overall miniature form and more sheltered forest ecology), to which *N. erucoides* is similar in terms of its lid and the structure of the peristome ribs, but *N. bellii* has no peristome column, sessile leaves, and only a sparse indumentum on developing foliage. There are no significant indications that *N. erucoides* has a hybrid origin involving these or any of the other species present on Dinagat, and the hybrids observed between it and *N. mindanaoensis* show unmistakably intermediate foliar and floral characteristics (Fig. 3H) as well as, in some cases, extreme hybrid vigour.

The precise nature of the relationship of *Nepenthes erucoides* with its other congeners is likewise unclear. In this work it is compared with *N. mantalingajanensis* based on striking but presumably superficial similarities, particularly its mostly dwarf, upright habit, its 1-flowered inflorescences, petiolate leaves, the absence of any keel or processes on the abaxial surface of the lid, and its robust, sometimes markedly-angular pitchers. In this respect, *N. erucoides* is similar to another Mindanao *Nepenthes*, *N. peltata* of Mt. Hamiguitan, in sharing many characteristics in common with the ultramaficolous montane species of Palawan and Borneo but differing in ways that cannot easily be reconciled. The authors are obliged to contend that certain environmental selection pressures common to extreme ultramafic habitats (e.g., rhizospheric water stresses of largely inorganic substrates, associated hyper-concentrations of phytotoxic soil cations, exposed habitat-associated transpiration and solar radiation stresses, pronounced temperature fluctuations even at high elevations) may favour the emergence of a fairly uniform syndrome of robust, ultramafic-associated morphological characteristics in *Nepenthes* that confound accurate placement of all of these species based on morphology alone, highlighting the great need for improved resolution in the markers used to generate meaningful *Nepenthes* phylogenies.

Historically, these phylogenies have been poor, however, a recently published analysis using genome skimming has provided dramatically improved and highly credible phylogenetic and temporal resolution in *Nepenthes* (Nauheimer *et al.* 2019), with the clear potential to address both this suggestion and to more accurately represent the relationships between members of the genus. A recent preprint (Murphy *et al.* 2019) also places the robust, morphologically similar *N. mantalingajanensis*, *N. attenboroughii* Robinson *et al.* (2009: 196), *N. deania* Macfarlane (1908: 57), *N. leonardo* McPherson *et al.* (2011: 5) and *N. palawanensis* McPherson *et al.* (2010: 1332)—all strictly endemic to the very summits of ultramafic Palawan mountains subject to annual fluctuations in rainfall—as sister to the slender-pitched, scrub- to forest-dwelling *N. philippinensis* Macfarlane (1908: 43), itself sister to *N. alata* Blanco (1837: 805); it also places the robust Mindanaoan ultramafic endemic *N. peltata*, which also resembles the aforementioned Palawan



ultramafic species, in a different clade close to the slender-pitched *N. justinae* Gronemeyer *et al.* (2016: 6) and *N. micramphora*. These data seem to support the notion that this syndrome of morphological characteristics may have a higher likelihood of developing in response to the common environmental challenges of specific ultramafic habitats irrespective of the clade within which a given species may fall.

The particularly low-elevation elfin forest of Mt. Redondo represents an unusual and especially extreme example of an ultramafic habitat, the rigours of which may account for the development of this species' compact and extremely hirsute characteristics. The occurrence of so extremely stunted a forest at such low elevation cannot be entirely attributed to the Massenerhebung (mountain mass) effect (Schroter 1926), the elfin forest of Mt. Redondo differing markedly from the typically wet, lower elevation mossy forests that result from the lowered cloud base that this phenomenon typically brings about (e.g. Gunung Santubong, Sarawak), particularly in terms of its distinctly sclerophyllous character (Fig. 3I). Rather, the elfin forest is likely to have formed in response to a range of factors, namely: the geology of Mt. Redondo, the main prominence of which comprises an 87 million year old exposed ultramafic terrane that affords an extremely thin, hostile surface substrate of exposed podiform chromite and the unconsolidated weathering products of the olivine-rich tectonic rock dunite (Dickey 1975, Madrona *et al.* 1980, David 1994); seasonal rainfall patterns, which include a pronounced dry season with average rainfall of *ca.* 130 mm and particularly hot days of average *ca.* 27 °C (see Worldbank.org 2019), the effects of which are compounded by the low water-holding capacity of the almost entirely inorganic soil; and finally by the phytotoxic nature of the soil itself.

The stunting of forests in response to periodic water shortage, but particularly in shallow and stony soils in more windy and exposed montane situations, is well documented (Van Steenis 1972, Whitmore 1984, Proctor *et al.* 1988, 1999). The Mt. Redondo elfin forest is exemplary in this regard; the *ca.* 30 cm deep rhizospheric soil contains, on average, *ca.* 396,024 ppm iron (Fe), 1,344 ppm nickel (Ni), 425 ppm copper (Cu), 10,875 ppm chromium (Cr), and 4,453 ppm manganese (Mn) (Fernando *et al.* 2018), and 94% of the trees have a stem diameter of just 1–10 cm (Fernando *et al.* 2017). Given the rocky, granular nature of ultramafic soils, morphological adaptations to minimise water requirements and water loss—including reduced leaf morphologies, sclerophyllous characteristics, hirsuteness and small stature—are particularly well-documented amongst ultramafic-growing plants (Brady *et al.* 2005); like the unusual, ultramafic-growing high-montane species *N. argentii*, *N. erucooides* appears to represent an extreme, ultramafic-adapted *Nepenthes*, albeit one that is specialised to tolerate the added rigours of periodic water stress, marked temperature fluctuations and high levels of solar radiation, all of which are associated with the low levels of cloud cover resulting from its windy, relatively low elevation near-coastal habitat.

## Acknowledgements

We thank the Department of Environment and Natural Resources (DENR)—Provincial Environment and Natural Resources Office (PENRO), Province of Dinagat Islands, especially Mr Leo Joseph E. Oconer, for arranging access permits and providing key logistical support; Mayor Erwin San Juan and Vice Mayor Pretsy Semorlan of Loreto for facilitating and seeking to understand the value of our research; and Krominco Inc., particularly staff Gay Espinal and Rove Cagas, for considering and granting access to the protected forest area within the Mt. Redondo chromite mining concession. Permission to collect plant specimens from Dinagat Island for scientific study was covered by Gratuitous Permit No. R13-2018-0053 issued by the Department of Environment and Natural Resources (DENR), Region 13, CARAGA Regional Office, Butuan City, Philippines. Finally, we thank Julie Barcelona and Pieter Pelsler (University of Canterbury, New Zealand), both for providing data specifically about this new species and for accessory data supplied via the Co's Digital Flora of the Philippines database ([www.philippineplants.org](http://www.philippineplants.org)), Brian Quinn for assistance with field measurements and logistics, and the Philippine Taxonomic Initiative, Inc. ([phtaxa.org](http://phtaxa.org)) for bringing together and supporting the expertise of the researchers and institutions involved in this study.

## References

- Balce, G.R., Alcantara, P.H., Morante, E.M. & Almogela, D.H. (1976) Tectonic Framework of the Philippine Archipelago (A Review). *In: Philippine Bureau of Mines Report*. 59 pp.
- Blanco, F.M. (1837) *Nepenthes*. *Flora de Filipinas. Segun el Sistema sexual de Linneo*. Santo Thomas [printers] por D. Candido Lopez, Manila, 619 pp.

- Blume, C.L. von (1825) *Dendrochilum*. *Bijdragen tot de Flora van Nederlandsch Indie* 8: 398–400.  
<https://doi.org/10.5962/bhl.title.6656>
- Blume, C.L. von (1826) *Leptospermum*. *Bijdragen tot de Flora van Nederlandsch Indie* 17: 1100–1101.  
<https://doi.org/10.5962/bhl.title.6656>
- Blume, C.L. (1852) *Museum Botanicum Lugduno-Batavum, sive stirpium exoticarum novarum vel minus cognitarum ex vivisautsicis brevis expositio*, vol. 2. E.J. Brill, Lugduni-Batavorum [Leiden], 256 pp.
- Brady, K.U., Kruckeberg, A.R. & Bradshaw, Jr H.D. (2005) Evolutionary ecology of plant adaptation to serpentine soils. *Annual Review of Ecology, Evolution, and Systematics* 36: 243–266.  
<https://doi.org/10.1146/annurev.ecolsys.35.021103.105730>
- Catalano, M. (2010) *Nepenthes kerrii* M. Catal. et T. Kruetr. sp. nov. In: Catalano, M. (Ed.) *Nepenthes della Thailandia: Diario di viaggio*. WOW s.r.o., Prague, p. 32.
- Cheek, M. (2011) *Nepenthes robcantleyi* sp. nov. (Nepenthaceae) from Mindanao, Philippines. *Nordic Journal of Botany* 29 (6): 677–681.  
<https://doi.org/10.1111/j.1756-1051.2011.01449.x>
- Cheek, M.R. & Jebb, M.H.P. (2001) *Flora Malesiana. Series I – Seed plants*, Vol. 15: *Nepenthaceae*. Nationaal Herbarium Nederland, Leiden, iv + 164 pp.
- Cheek, M. & Jebb, M. (2013a) Typification and redelimitation of *Nepenthes alata* with notes on the *N. alata* group, and *N. negros* sp. nov. from the Philippines. *Nordic Journal of Botany* 31: 616–622.  
<https://doi.org/10.1111/j.1756-1051.2012.00099.x>
- Cheek, M. & Jebb, M. (2013b) Recircumscription of the *Nepenthes alata* group (Caryophyllales: Nepenthaceae), in the Philippines, with four new species. *European Journal of Taxonomy* 69: 1–23.  
<https://doi.org/10.5852/ejt.2013.69>
- Cheek, M. & Jebb, M. (2013c) *Nepenthes alzapan* (Nepenthaceae), a new species from Luzon, Philippines. *Phytotaxa* 100 (1): 57–60.  
<https://doi.org/10.11646/phytotaxa.100.1.6>
- Cheek, M. & Jebb, M. (2013d) *Nepenthes ramos* (Nepenthaceae), a new species from Mindanao, Philippines. *Willdenowia* 43 (1): 107–111.  
<https://doi.org/10.3372/wi.43.43112>
- Cheek, M. & Jebb, M. (2014) Expansion of the *Nepenthes alata* group (Nepenthaceae), Philippines, and descriptions of three new species. *Blumea-Biodiversity, Evolution and Biogeography of Plants* 59 (2): 144–154.  
<https://doi.org/10.3767/000651914X685861>
- Clarke, C.M. (2001) *Nepenthes of Sumatra and Peninsular Malaysia*. Natural History Publications (Borneo), Kota Kinabalu, x + 326 pp.
- Clarke, C.M., Schlauer, J., Moran, J.A. & Robinson, A.S. (2018) Systematics and evolution of *Nepenthes*. In: Ellison, A.M. & Adamec, L. (Eds.) *Carnivorous Plants: physiology, ecology, and evolution*. Oxford University Press, Oxford, pp. 58–69.  
<https://doi.org/10.1093/oso/9780198779841.003.0005>
- David, C.P.C. (1994) The chromite deposits of the Dinagat Ophiolite Complex--Contributions to chromite genesis. *Journal of the Geological Society of the Philippines* 49 (4): 263–279.
- Dickey, Jr J.S. (1975) A hypothesis of origin for podiform chromite deposits. *Geochimica et Cosmochimica Acta* 39: 1061–1074.  
[https://doi.org/10.1016/0016-7037\(75\)90047-2](https://doi.org/10.1016/0016-7037(75)90047-2)
- Edwards, H. (1881) Descriptions of new species and varieties of Arctiidae. *Papilio* 1 (3): 38–39.  
<https://doi.org/10.5962/bhl.part.23310>
- Elmer, A.D.E. (1910) Notes on *Fagraea*. *Leaflets of Philippine Botany* 3: 857–860.
- Elmer, A.D.E. (1914) Myrtaceae from Mount Urdaneta. *Leaflets of Philippine Botany* 7: 2343–2358.
- Elmer, A.D.E. (1915) Nepenthaceae. Two Hundred Twenty Six New Species—II. *Leaflets of Philippine Botany* 8: 2785–2787.
- Encarnación, J.P. & Mukasa, S.B. (1997) Age and geochemistry of an ‘anorogenic’ crustal melt and implications for the origin of I-type granites. *Lithos* 42 (1–2): 1–13.  
[https://doi.org/10.1016/S0024-4937\(97\)00026-1](https://doi.org/10.1016/S0024-4937(97)00026-1)
- Fernando, E.S., Quakenbush, J.P., Lillo, E.P. & Ong, P.S. (2018) *Medinilla theresae* (Melastomataceae), a new species from ultramafic soils in the Philippines. *PhytoKeys* 113: 145–155.  
<https://doi.org/10.3897/phytokeys.113.30027>
- Galey, M.L., Van der Ent, A., Iqbal, M.C.M. & Rajakaruna, N. (2017) Ultramafic geoecology of South and Southeast Asia. *Botanical Studies* 58 (1): 18.  
<https://doi.org/10.1186/s40529-017-0167-9>
- Gaudichaud-Beaupré, C. (1824) Descriptions du *Pinonia*, du *Schizoloma*, de l'*Adenophorus* et du *Freycinetia*, nouveaux genres de Plantes recueillies. *Annales des sciences naturelles; comprenant la physiologie animale et végétale, l'anatomie comparée des deux règnes, la*



zoologie, la botanique, la minéralogie et la géologie (Paris) 3: 507–510.

- Gronemeyer, T., Wistuba, A., Heinrich, V., McPherson, S., Mey, F. & Amoroso, V. (2010) *Nepenthes hamiguitanensis* (Nepenthaceae), a new pitcher plant species from Mindanao Island, Philippines. In: McPherson, S.R. (Ed.) *Carnivorous Plants and their Habitats*, Vol. 2. Redfern Natural History Productions, Poole, pp. 1296–1305.
- Gronemeyer, T., Suarez, W., Nuytemans, H., Calaramo, M., Wistuba, A., Mey, F.S. & Amoroso, V.B. (2016) Two new *Nepenthes* species from the Philippines and an emended description of *Nepenthes ramos*. *Plants* 5 (2): 23.  
<https://doi.org/10.3390/plants5020023>
- Heinrich, V.B., McPherson, S., Gronemeyer, T. & Amoroso, V. (2009) *Nepenthes micramphora* (Nepenthaceae), a new species of *Nepenthes* L. from southern Mindanao, Philippines. In: McPherson, S.R. (Ed.) *Pitcher Plants of the Old World*, Vol. 2. Redfern Natural History Productions, Poole, pp. 1314–1319.
- Hooker, J.D. (1852) *Nepenthes villosa* [tab. 888]. In: Hooker, W.J. (Ed.) *Icones Plantarum*, vol. 9. Reeve & Co., London, tabs. 801–900.
- IUCN (2012) *IUCN Red List Categories and Criteria Version 3.1, 2nd ed. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK*. Available from: [http://www.iucnredlist.org/static/categories\\_criteria\\_3\\_1](http://www.iucnredlist.org/static/categories_criteria_3_1) (accessed 04 May 2019).
- Jebb, M.H.P. & Cheek, M.R. (1997) A skeletal revision of *Nepenthes* (Nepenthaceae). *Blumea* 42 (1): 1–106.
- Kondo, K. (1969) A new species of *Nepenthes* from the Philippines. *Bulletin of the Torrey Botanical Club* 96 (6): 653–655.  
<https://doi.org/10.2307/2483544>
- Kurata, S. (2001) Two new species, *Nepenthes pyriformis* from West Sumatra (Indonesia) and *Nepenthes mindanaoensis* from Mindanao (Philippines). *The Journal of the Insectivorous Plant Society* 52 (2): 30–35.
- Kurata, S. (2008) *Nepenthes peltata* (Nepenthaceae), a new species of pitcher plant from the Philippines. *The Journal of the Insectivorous Plant Society* 59 (1): 12–17.
- Linnaeus, C. (1753a) *Species Plantarum*, vol. 1. Impensis Laurentii Salvii, Holmiae [Stockholm], 560 pp.
- Linnaeus, C. (1753b) *Species Plantarum*, vol. 2. Impensis Laurentii Salvii, Holmiae [Stockholm], 640 pp.
- Loureiro, J. de (1790) Genus IV *Phyllamphora*. *Flora cochinchinensis: sistens plantas in regno Cochinchina nascentes. Quibus accedunt aliae observatae in Sinensi imperio, Africa Orientali, Indiaeque locis variis. Omnes dispositae secundum systema sexuale Linnæanum. Ulyssipone* 2: 606–607.  
<https://doi.org/10.5962/bhl.title.40199>
- Macfarlane, J.M. (1908) Nepenthaceae. In: Engler, A. (Ed.) *Das Pflanzenreich: regni vegetabilis conspectus IV, III*, vol. 36. Wilhelm Engelmann, Leipzig, pp. 1–92.
- Macfarlane, J.M. (1911) New Species of *Nepenthes*. *Contributions from the Botanical Laboratory of the University of Pennsylvania* 3 (3): 207–210.
- Madrona, J.D. & Villamor, R.T. (1980) 1M--The chromite deposit of Malayan Wood Products, Inc., Loreto, Dinagat Island, Surigao Del Norte. In: Geology and mineral resources of Surigao Del Norte (Eds.), *Philippines Bureau of Mines Report of Investigation* 102: 6–7.
- McPherson, S.R. (2010) *Carnivorous Plants and their Habitats*, vol. 2. Redfern Natural History Productions, Poole. 719 pp.
- McPherson, S., Cervancia, J., Lee, C., Jaunzems, M., Fleischmann, A., Mey, F., Gironella, E. & Robinson, A.S. (2010) *Nepenthes palawanensis* (Nepenthaceae), a new pitcher plant species from Sultan Peak, Palawan Island, Philippines. In: McPherson, S.R. (Eds.), *Carnivorous Plants and their Habitats*, vol. 2. Redfern Natural History Productions, Poole, pp. 1332–1339.
- McPherson, S., Bourke, G., Cervancia, J., Jaunzems, M., Gironella, E., Robinson, A.S. & Fleischmann, A. (2011) *Nepenthes leonardoii* (Nepenthaceae), a new pitcher plant species from Palawan, Philippines. *Carniflora Australis* 8 (1): 4–19.
- Merrill, E.D. (1917) Asclepiadaceae. *An Interpretation of Rumphius's Herbarium Amboinense*. Bureau of Printing, Manila, 595 pp.  
<https://doi.org/10.5962/bhl.title.79163>
- Micheler, M., Gronemeyer, T., Wistuba, A., Marwinski, M., Suarez, W. & Amoroso, V. (2012) *Nepenthes viridis*, eine neue *Nepenthes*-Art von der Insel Dinagat, Philippinen. *Das Taublatt* 76: 4–21.
- Murphy, B., Forest, F., Barraclough, T., Rosindell, J., Bellot, S., Cowan, R., Golos, M.R., Jebb, M.H.P. & Cheek, M.R. (2019) A phylogenomic analysis of *Nepenthes* (Nepenthaceae). Biorxiv preprint, Cold Spring Harbor, 43 pp.  
<https://doi.org/10.1101/680488>
- Nauheimer, L., Cui, L., Clarke, C., Crayn, D., Bourke, G. & Nargar, K. (2019) Genome skimming provides well-resolved plastid and nuclear phylogenies revealing patterns of deep reticulate evolution in the tropical carnivorous plant genus *Nepenthes* (Caryophyllales). *Australian Systematic Botany* 32 (3): 243–254.  
<https://doi.org/10.1071/SB18057>
- Nerz, J. & Wistuba, A. (2007) *Nepenthes mantalingajanensis* (Nepenthaceae), eine bemerkenswerte neue Spezies aus Palawan (Philippinen). *Das Taublatt* 55 (3): 17–25.
- Parlatore, F. (1868) Coniferae. In: Candolle, A.P. de. (Ed.) *Prodromus Systematis Naturalis Regni Vegetabilis*, vol. 16. Victoris Masson et Filitii, Paris, pp. 493–521.

- Pelser, P.B., Barcelona, J.F. & Nickrent, D.L. (Eds.) (2011+) *Co's Digital Flora of the Philippines*. Available from: [www.philippineplants.org](http://www.philippineplants.org) (accessed 07 May 2019).
- Presl, C. B. (1831). Goodeniaceae. In: Presl, K.B. (Ed.) *Reliquiae Haenkeanae, seu, Descriptiones et icones plantarum: quas in America meridionali et boreali, in insulis Philippinis et Marianis collegit*. Thaddeus Haenke, Prague, 152 pp.
- Proctor, J., Lee, Y.F., Langley, A.M., Munro, W.R.C. & Nelson, T. (1988) Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia, I. Environment, forest structure and floristics. *Journal of Ecology* 76: 320–340.  
<https://doi.org/10.2307/2260596>
- Proctor, J., Bruijnzeel, L.A. & Baker, A.J.M. (1999) What causes the vegetation types on Mount Bloomfield? *Global Ecology & Biogeography Letters* 8: 347–354.  
<https://doi.org/10.1046/j.1365-2699.1999.00147.x>
- Rafarin, C. (1869) Des *Nepenthes*. *Revue horticole* 40: 268–271.
- Reichenbach, H.G. (1882) New Garden Plants. *The Gardeners' chronicle: a weekly illustrated journal of horticulture and allied subjects*, vol. 18. Bradbury, Agnew & Co., London, 488 pp.
- Robinson, A.S., Fleischmann, A.S., McPherson, S.R., Heinrich, V.B., Gironella, E.P. & Peña, C.Q. (2009) A spectacular new species of *Nepenthes* L. (Nepenthaceae) pitcher plant from central Palawan, Philippines. *Botanical Journal of the Linnean Society* 159 (2): 195–202.  
<https://doi.org/10.1111/j.1095-8339.2008.00942.x>
- Schrank, F. von Paula (1802) Spinnerförmige Schmetterlinge. In: Schrank, F. von Paula (Ed.) *Favna Boica: Durchgedachte Geschichte der in Baiern einheimischen und zahmen Thiere*, Band 2 (2). Johann Wilhelm Krüll, Ingolstadt, pp. 149–156.
- Schroter, C. (1926) *Das Pflanzenlebender Alpen. Eine Schilderung der Hochgebirgsflora*. Albert Raustein, Zurich, 1288 pp.
- Sohmer, S.H. & Davis, A.P. (2007) The Genus *Psychotria* (Rubiaceae) in the Philippine Archipelago. *Sida, Botanical Miscellany* 27: 1–247. Botanical Research Institute of Texas, Fort Worth, U.S.A.
- Stein, B. (1892) *Stein's Orchideenbuch*. Verlag von Paul Parey, Berlin, 604 pp.
- Suerte, L.O., Imai, A. & Nishihara, S. (2009) Geochemical Characteristics of Intrusive Rocks, Southeastern Mindanao, Philippines: Implication to Metallogenesis of Porphyry Copper-gold Deposits. *Resource Geology* 59 (3): 244–262.  
<https://doi.org/10.1111/j.1751-3928.2009.00094.x>
- Tamayo, Jr R.A., Maury, R.C., Yumul, Jr G.P., Polve, M., Cotton, J., Dimalanta, C.B. & Olaguera, F.O. (2004) Subduction-related magmatic imprint of most Philippine ophiolites: Implications on the early geodynamic evolution of the Philippine archipelago. *Bulletin de la Société Géologique de France* 175 (5): 443–460.  
<https://doi.org/10.2113/175.5.443>
- Thiers, B. (2019+) *Index Herbariorum. A global directory of public herbaria and associated staff*. New York Botanical Garden's virtual Herbarium. Available from: <http://sweetgum.nybg.org/science/ih> (accessed 6 May 2019)
- Vahl, M. (1810) *Collyris. Skrifter af Naturhistorie-selskabet* 2: 109–112.
- Van Steenis, C.G.G.J. (1972) *The Mountain Flora of Java*. E.J. Brill, Leiden, 90 pp.
- Whitmore, T.C. (1984) *Tropical Rain Forests of the Far East, 2<sup>nd</sup> ed.* Clarendon Press, Oxford, 352 + xvi pp.
- Worldbank.org (2019) *Climate Change Knowledge Portal: Average Monthly Temperature and Rainfall for Philippines from 1901–2016*. Available from: <https://perma.cc/LK9G-V6HW> (accessed 23 May 2019)
- Yumul, Jr G.P., Dimalanta, C.B., Maglambayan, V.B. & Tamayo, Jr R.A. (2003) Mineralization controls in island arc settings: Insights from Philippine metallic deposits. *Gondwana Research* 6 (4): 767–776.  
[https://doi.org/10.1016/S1342-937X\(05\)71023-6](https://doi.org/10.1016/S1342-937X(05)71023-6)
- Yumul, Jr G.P., Dimalanta, C.B., Maglambayan, V.B. & Marquez, E.J. (2008) Tectonic setting of a composite terrane: A review of the Philippine island arc system. *Geosciences Journal* 12 (1): 7–17.  
<https://doi.org/10.1007/s12303-008-0002-0>