

Nepenthes megastoma (Nepenthaceae), a micro-endemic pitcher plant from Puerto Princesa Subterranean River National Park, Palawan, Philippines



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Abstract

Nepenthes megastoma is described and illustrated as a new species from the Puerto Princesa Subterranean River National Park, a UNESCO World Heritage Site in Palawan Philippines. This carnivorous tropical pitcher plant is currently known from just three locations in the Mount Saint Paul karst formation, where it grows on vertical limestone walls. Morphologically, *N. megastoma* is characterised by its highly branched stems, campanulate pitchers, peltate tendril exsertion, dimorphic upper pitchers, and unidirectionally upturned female flowers. It is assessed as Critically Endangered under the IUCN Red List criteria, based on its restriction to three subpopulations comprising few total individuals. Pitcher morphology suggests a degree of ecological-functional convergence with *N. campanulata* of Borneo, though overall morphology indicates a probable close affinity with the widespread Palawan endemic *N. philippinensis*.

Key words: Malesia, new species, non-core Caryophyllales, taxonomy

Introduction

Nepenthes Linnaeus (1753: 955) (Caryophyllales Juss. ex Bercht. & J.Presl, Nepenthaceae Dumort.) is a genus of carnivorous tropical pitcher plants comprising 200 accepted species (Clarke *et al.* 2018, POWO 2025) which are naturally distributed throughout the Palaeotropics, primarily within the Malesian and Papuasian biogeographic regions but ranging from Madagascar to New Caledonia and several outlying western Pacific islands (Jebb & Cheek 1997). *Nepenthes* are terrestrial or epiphytic vines or subscandent shrubs that produce a characteristic leaf structure comprising a leaf-like phyllode (modified leaf base) from the apex of which a tendril (the true petiole) emerges, giving rise to an epiascidiate lamina or “pitcher” (representing the true leaf), evolved primarily as the means of attracting, capturing and digesting prey (Kubitzki 2002, Bauer & Federle 2009, Moran & Clarke 2010).

Historically regarded as having centres of diversity in Borneo and Sumatra (Clarke 2001), research carried out across the archipelago mainly since 2007 has shown that *Nepenthes* also has a significant centre of species diversity in the Philippines, the majority of that diversity being localised to ultramafic soils where *Nepenthes* diversity is disproportionately high (Robinson *et al.* 2019, Damit *et al.* 2024, Lagunday & Amoroso 2025).

However, across the range of the genus, a dozen *Nepenthes* are known to occur obligately on limestone, including *Nepenthes biak* Jebb & Cheek (2018: 175), *N. calcicola* Wilson, Venter & Damas (2023: 106), *N. campanulata* Kurata (1973: 227), *N. epiphytica* Robinson, Nerz & Wistuba (2011: 36), which despite its name is now known to occur abundantly on limestone substrates within its range (Michal Golos, pers. comm.), *N. faizaliana* Adam & Wilcock

(1991: 123), *N. krabiensis* Nuanlaong, Onsanit, Chusangrach & Suraninpong (2016: 128), *N. mapuluensis* Adam & Wilcock (1990: 265), *N. northiana* Hooker (1881: 717), *N. rosea* Catalano & Kruetreepradit (2014: 30), *N. thai* Cheek (2009: 321), *N. treubiana* Warburg (1891: 318), and *N. viridis* Micheler, Gronemeyer, Wistuba, Marwinski, Suarez & Amoroso (2013: 4). In addition to these, a range of species occurs facultatively on limestone (Lee 2004), including *N. albomarginata* Lobb ex Lindley (1849: 580), recorded on limestone in Borneo only, *N. ampullaria* Jack (1821: 23), *N. boschiana* Korthals (1839: 25), *N. gracilis* Korthals (1840: 22), *N. lowii* Hooker (1859: 420), *N. mirabilis* (Loureiro) Druce (1917: 637), *N. reinwardtiana* Miquel (1852: 168), *N. stenophylla* Masters (1890: 240), *N. tentaculata* Hooker (1873: 101), *N. veitchii* Hooker (1859: 421), and *N. vogelii* Schuiteman & de Vogel (2002: 537).

In July 2013, surveys of limestone cliffs by ecologists Charles Clarke and Chien Lee within the Mount Saint Paul karst formation—the central feature of the UNESCO World Heritage listed Puerto Princesa Subterranean River National Park (PPSRNP) in Palawan, Philippines (Fig. 1a)—revealed the presence of a *Nepenthes* species growing high on the vertical walls of the massif (Clarke *et al.* 2014). Observed at great distance through binoculars, the plants were tentatively determined to be *N. campanulata*, hitherto regarded as a Borneo endemic, based on the comparable karstic habitat and apparently similar habit and morphology, in particular, the presence of campanulate pitchers. In 2014, local nature guide Roy Moyano informed Palawan naturalist Will Cabanillas of another location well-known to local karst explorers for its overhanging *Nepenthes* on limestone, resulting in a visit to that locality (W. Cabanillas, pers. comm.). Images subsequently shared on Facebook by Cabanillas (Fig. 1b) were seen by the authors, depicting what was recognised to be the same *Nepenthes* but from a more accessible vantage point and with consequently greater magnification. With this added insight, it became clear that the plant exhibited a range of characteristics different to those of *N. campanulata*, leading the authors to hypothesise that it was an undescribed taxon.

Following consecutive delays caused by the COVID-19 pandemic (2020 onwards) and then Typhoon Rai (known in the Philippines as Super Typhoon Odette) in 2021, a category 5 storm that resulted in extensive damage across PPSRNP and closure of key access trails for more than two years (see “Conservation Status”), an expedition was made in May 2023 to study the plants *in situ*, and a follow up visit made in June 2023 to collect voucher material.

Morphological and ecological observations confirmed that the taxon has multiple unique characteristics and that it can be considered endemic to PPSRNP. Despite its comparable ecology and superficial similarity to *Nepenthes campanulata*, comparative studies of its morphology suggest a possible relationship with the widespread Palawan-province endemic *N. philippinensis* Macfarlane (1908: 43). Consequently, the taxon is described here as new to science.

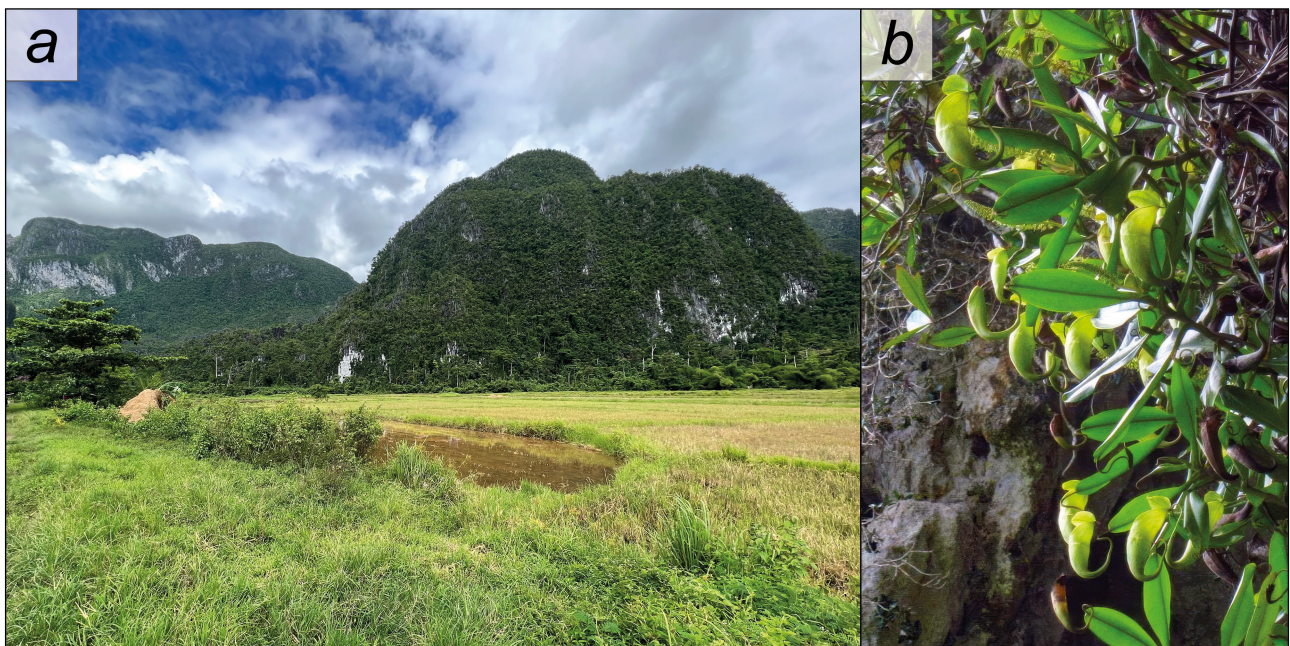


FIGURE 1. *a.* General landscape of the Mount Saint Paul karst formation, Puerto Princesa Subterranean River National Park, as observed from the roadside. *b.* The first published close-up image of *Nepenthes megastoma*. Photographs by A. Robinson (a) and Will Cabanillas (b).

Materials and Methods

Exploratory *in situ* observations were made with PPSRNP staff by authors A. Robinson, J. Altomonte, and R. Bustamante at two of the plant's known locations (precise localities withheld for conservation reasons) on 23 May 2023 to evaluate the feasibility and safety of accessing material and to record ecological details. Access was granted under PPSRNP Protected Area Management Board clearance order no. 051-2023 issued to A. Robinson. Detailed images of the plants were captured using a Mini 3 Pro drone (SZ DJI Technology Co., Ltd., China) and Canon 5D Mk IV (Canon Inc., Japan) with Sigma AF 150–600mm f/5–6.3 DG OS HSM C telephoto lens (Sigma Corporation, Japan).

Voucher material was collected in a single gathering from adjacent male and female plants by J. Collantes and A. Langbao on 23 June 2023. Vouchers were taken in the form of cuttings to avoid impacting the naturally small population of wild plants. Material was collected under Wildlife Gratuitous Permit (GP) no. 2023-15 issued to V. Mangussad. The specimens were pressed as per genus-specific recommendations made in Clarke & Moran (2011) and material lodged at PPC prior to transfer to PNH and MEL (herbarium codes follow Thiers 2025+).

Transfer of herbarium material to PNH from PPC was authorised under licence PAL-0021 from the Department of Agriculture Bureau of Plant Industry (Manila), and authorisation from the Palawan Council for Sustainable Development, both issued to V. Mangussad. Clearance to export to MEL from the Philippines was provided under CITES Permit No. 31144/P-2025, issued to Jhaydee Ann F. Pascual (PNH) by the Department of Environment and Natural Resources Biodiversity Management Bureau (Republic of the Philippines).

The species description is based on measurements of living material made *in situ* and from prepared herbarium specimens. Fine measurements were made using a vernier calliper (Mitutoyo Corporation, Japan) and a Zeiss Stemi 2000 stereo microscope with table stand (Carl Zeiss AG, Oberkochen, Germany). Scanning electron microscopy (SEM) was performed using a TM4000Plus II low-vacuum SEM (Hitachi Co. Ltd., Tokyo, Japan) with 15 kV accelerating voltage in mix mode (secondary electron + backscattered electron detection) with a 30 Pa vacuum.

Taxonomy

Nepenthes megastoma A.S. Rob., R. Bustam. & Altomonte, *sp. nov.* (Figs 1b, 2, 3, 4b–d, 5b–e, 6, 7a,b).

Type:—PHILIPPINES. Palawan, Barangay Cabayugan: Mount St Paul, on limestone cliffs, 200 m a.s.l., 23 June 2023, *Collantes & Langbao 1* (holotype PNH 259144 [one sheet, barcode 01-001582]; isotypes PNH 259145 [three sheets, barcodes 01-001583 (sheet 1 of 6), 01-001584 (sheet 2 of 6), 01-001585 (sheet 3 of 6)]; MEL 2541012A [sheet 4 of 6], MEL 2541013A [sheet 5 of 6], MEL 2541014A [spirit collection from sheet 5 of 6], MEL 2541015A [sheet 6 of 6]).

– *Nepenthes campanulata sensu* Clarke *et al.* (2014: 7–13, fig. 6).

– *Nepenthes* sp. ‘Saint Paul Cliffs’ *sensu* McPherson (2023: 1988–1991, figs. 2395–2398).

Diagnosis:—*Nepenthes megastoma* superficially resembles *N. campanulata* but differs in the production of (differences in parentheses): large growths, individual stems to 2.8 m long and 1.2 cm in dia., branching basally or medially to form pendent clumps to 10 m long (to ~35 cm, mostly basally branching to form short clumps, stems to 0.4 cm dia.), phyllodes elliptic-subobovate and 20–38 cm long with shortly decurrent base and slight abaxial basal swelling (spatulate-lanceolate, to 9 cm long, base amplexicaul without swelling), pitchers trimorphic, comprising uniform lower pitchers and two forms of upper pitcher (pitchers monomorphic), pitchers brittle, peristome pronounced, to 5.5 mm wide, lid \pm suborbicular, to 5 cm dia. (pitchers flexible, peristome very narrow, typically \leq 2 mm, lid ovate-elliptic, to 2 cm long), inflorescences to 48 cm long, partial peduncles dense, mostly 2-flowered, female flowers ascending, unidirectionally upturned (Fig. 6f) but borne on pedicels evenly distributed about rachis (inflorescences \leq 20 cm long, lax with few flowers, partial peduncles mostly 1-flowered, female flowers spreading, not unidirectionally upturned), and an indumentum of dimorphic trichomes present on most surfaces (almost entirely glabrous except below peristome and around spur).

Description:—Lithophytic shrub. *Stems* 30–70(–280) cm long, terete, 0.8–1.2 cm in dia., internodes 1.1–2.1 cm, prolifically branched basally and medially with 1–30(–70) growing points, individual clumps to 10 m in length, pendent but with terminal portion of growths horizontal to suberect. *Phyllodes* coriaceous, marcescent, petiolate, petiole winged, margins often wavy, 4–7 cm long, c. 1 cm wide, base clasping stem for 1/2 its circumference and shortly decurrent for c. 0.5 cm, often slightly swollen abaxially. Lamina narrowly elliptic-subobovate, 20–30(–38) cm

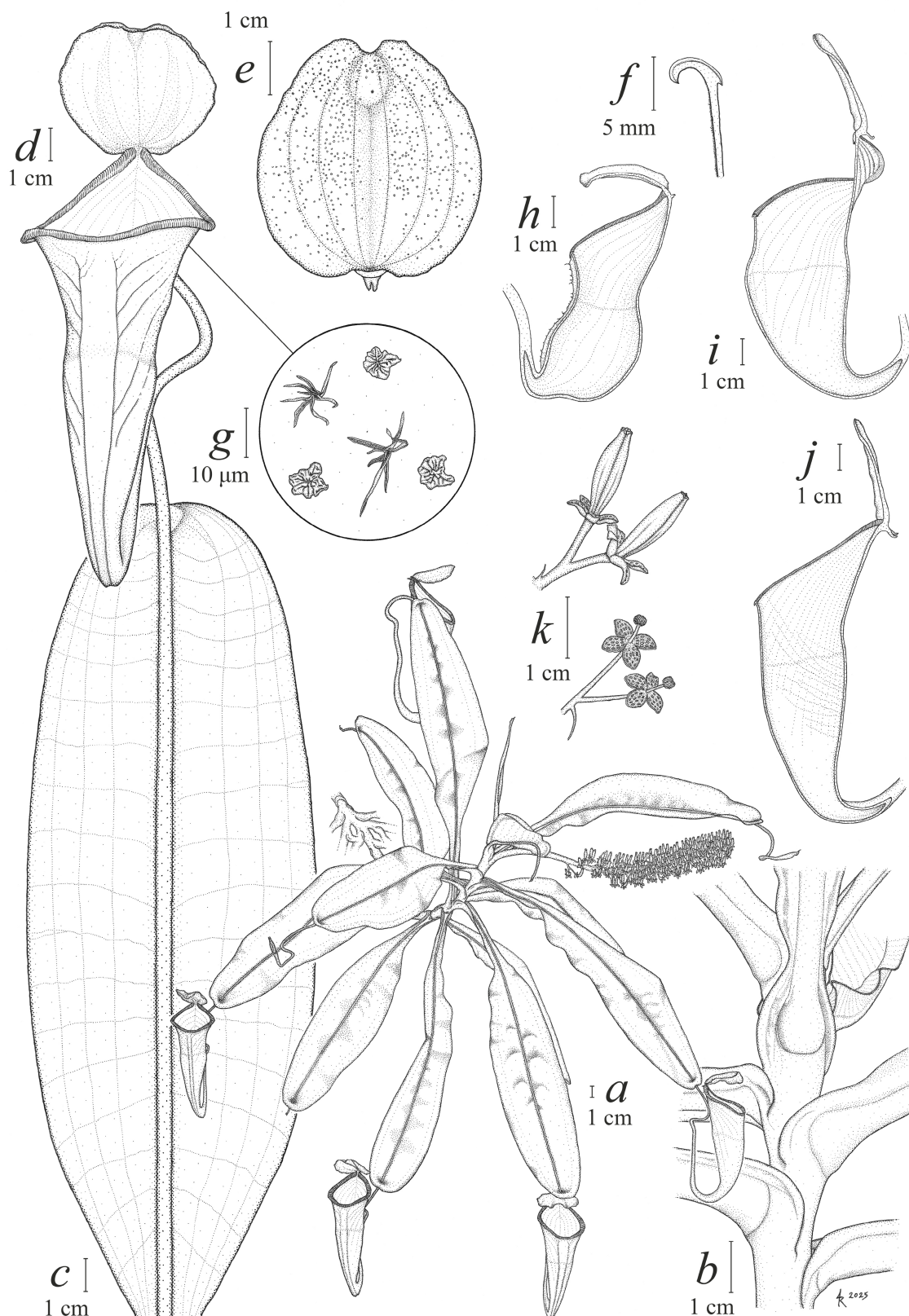


FIGURE 2. *Nepenthes megastoma* A.S.Rob., R.Bustam. & Altomonte. *a.* Habit, suberect terminal growth bearing upper pitchers and female inflorescence. *b.* Section of stem showing characteristic phyllode bases which are shortly decurrent and slightly swollen. *c.* Abaxial view of phyllode with most prominent venation indicated. *d.* Attached elongate form of upper pitcher. *e.* Lower surface of lid showing general distribution of glands. *f.* Profile section through peristome and upper wall of pitcher. *g.* Magnification of trichomes, with stellate trichomes and peltate scales (lepides) shown. *h.* Dissected lower pitcher in profile. *i.* Stout form of upper pitcher in profile. *j.* Elongate form of upper pitcher in profile. *k.* Female flowers with developing fruit (above) and male flowers at anthesis (below). Based on *Collantes & Langbao 1* and supplemented with photographs and measurements made of material *in situ*. Illustration by A. Robinson.

long, 7–10 cm wide, midrib 2.5–4.0 mm wide, (3–)4 longitudinal veins either side of midrib in outer 2/3 of lamina, transverse veins 15–25 pairs per phyllode, both fairly conspicuous on both adaxial and abaxial surfaces, base attenuate, apex of basal phyllodes broadly acute to narrowly obtuse and sometimes retuse, tendril exertion not or only very slightly peltate, and in rosette phyllodes associated with upper pitchers becoming rounded, or obtuse and slightly retuse, tendril exertion markedly peltate and emergent 0.7–1.5 cm from apex, tendrils 7–11 cm long, 3–4 mm dia., adaxially flattened, straight in basal pitchers, in rosette pitchers sinuous, forming a spring-like half-coil, rarely a full, single coil. *Lower pitchers* basally narrowly infundibular, rarely subventricose, with a median hip, then cylindric to widely infundibular above, ventrally attached to tendril, 4.5–9.3 cm tall excluding lid, 3.0–4.8 cm wide at the pitcher opening, opening round to rhomboid, pitcher walls 0.7–1.0 mm thick, interior surface glandular below hip, gland density c. 700 cm⁻², waxy above, exterior ventral surface with a pair of fringed wings 2–4 mm wide running from base of pitcher to mouth, fringe elements 1–5 mm long, 2–3 mm apart, peristome oblique throughout, c. 35° from horizontal, 3.0–5.5 mm wide, more or less uniform in width but often slightly narrower and slightly depressed at front between the wings, opposing margins below lid not appressed, with a gap of 1–4 mm, and often broader but lacking a rear column of any kind, ribs fine, c. 0.4 mm apart, c. 0.3 mm tall, teeth of inner margin minute, acute, generally ±0.3 mm long. Lid suborbicular to very broadly ovate, 3.1–4.4 cm long, 3.8–5.0 cm wide, typically 20–50° from horizontal, slightly domed overall but furrowed along the midline with slight concave bulge at apex, apex retuse, occasionally deeply notched, base cordate, lower surface without pronounced median rib, with large, crateriform glands sparsely scattered across surface, absent from midline, more dense towards base, edges, and on apical bulge, glands 0.2–0.5 mm dia. with a broad, flat rim. Spur 1–4 mm long, often flattened, 1–3 mm wide, (1–2)–3-fid, branching basally or distally. *Upper pitchers* dorsally attached to tendril, base tubulose into tendril for 2–4 cm, expanding into pitcher to become basally narrowly infundibular below, with a median hip, and then either wholly infundibular-campanulate and mediolaterally flaring or shortly cylindric and infundibular above, apparently depending on season (see “Discussion”), 7.7–14.2 cm tall excluding lid, 3.1–5.6 cm wide at the pitcher mouth, pitcher opening round to somewhat rhomboid, peristome 1.5–7.0 mm wide, lid 3.2–4.8 cm long, 2.9–4.5 cm wide. *Inflorescences* marcescent, ±1 per growing point per flowering season. Male inflorescence 31.5–43.5 cm long, 80–250 flowers, peduncle 7–15 cm long, 5–7 mm diam. at base, rachis 17–30 cm long, partial peduncles (1–)2-flowered, 6–8 mm long, bifurcating 1–2 mm from base, each with simple, terete, abaxial filiform bract 4–5 mm long, 0.3 mm dia., emergent from base or slightly above, tepals very broadly ovate to suborbicular, 3–4 mm long, to 3 mm wide, concave, adaxial surface with 40–60 elliptic pitted glands, largest in middle, to 0.15–0.25 mm long, c. 0.1 mm wide, apex obtuse; staminal column 1.6–2.5 mm long, anther head 1.2–1.5 mm dia., anthers (6–)7(–10), bilocular, extrorse, thecae pale yellow, pollen grains deep yellow. Female inflorescence 30–48 cm long, (40–)80–150(–200) flowers, peduncle 10–16 cm long, 6–7 mm diam. at base, rachis 16–25 cm long, partial peduncles evenly distributed about rachis, but either erect or ascending so that all female flowers are similarly orientated upwards, 2-flowered, 7–14 mm long, bifurcating 2–3 mm from base, basal filiform bract 2(–4) mm long, simple, free or partially adnate to partial peduncle, tepals ovate, 4–6 mm long, 3 mm wide, apex subacute, fruit 13–20 mm long, 4–5 mm dia., valves 4. *Seeds* fusiform, 4–6 mm long, wings somewhat reduced. *Indumentum* of dimorphic, eglandular, compound trichomes present on most surfaces, comprising a mix of sessile, basally branched stellate, multiangulate trichomes, each with (6–)7(–8) rays 0.05–0.12 mm long, and peltate scales (lepides) with angular processes c. 0.7 mm dia., but most dense on stems, inflorescences, partial peduncles, abaxial tepal surfaces and external surfaces of pitchers, trichomes largely absent from adaxial phyllode surface where mainly peltate scales are only sparingly scattered towards base, abaxial phyllode surface with densely arranged trichomes comprising predominantly scales, stellate hairs becoming simpler, longer and ±erect along curved margins of decurrent phyllode bases, underside of lid with peltate scales only, and trichomes reduced to simple hairs 0.1–0.2 mm long on valves of fruit. *Colour* of all plant parts initially bright chartreuse green, adaxial lamina surface of senescing phyllodes becoming forest green with age, pitchers becoming yellowish green, lower pitchers splotched or suffused with red, mainly along tendril, towards pitcher opening, and either side of midrib of lid, upper pitchers without any red colouration but parts of the pitchers orientated parallel to the line of sight appearing orange-tinged due to density of indumentum, pitcher interior yellow in the lower, digestive portion, whitish above owing to covering of epicuticular wax.

Etymology:—The epithet *megastoma* is constructed from the Greek-derived prefix *mega-* (large) and the Greek word *stoma* (mouth), meaning ‘large mouth’, a reference to the diameter of the pitcher opening, which is greater than that of the rest of the pitcher in all pitcher forms.

Phenology:—Infructescences observed nearing maturity at end May, suggesting maturity in mid-June, two months after end of dry season. At this time, 80% of all males were observed to have already senesced.

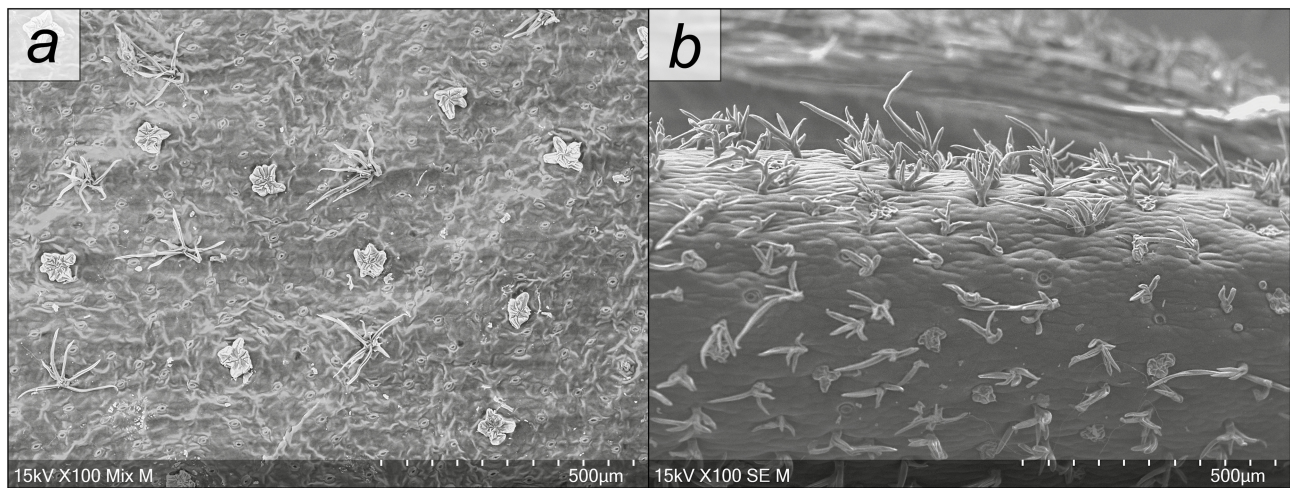


FIGURE 3. *a.* Equally distributed stellate hairs and peltate scales on abaxial surface of phyllode. *b.* Abundant stellate hairs with few scales on valves of fruit. Micrographs by A. Robinson.

Distribution and ecology:—*Nepenthes megastoma* is known from only three locations, growing on cliff walls within PPSRNP (R. Moyano, pers. comm.); only two locations were accessible to us. Even at these locations, plants are difficult to access, being situated tens to hundreds of metres above ground level. At Location 1, all observed individuals occurred in a band at approximately 250 m elevation and could only be studied by drone. These plants grew on exposed cliffs with a full southwesterly aspect, receiving intense afternoon insolation. In contrast, at Location 2, plants were found at 91–115 m a.s.l., growing on the walls of sheltered, overhanging cliffs with a northwesterly aspect, subject to only diffuse evening light later in the day. At both locations, the rock underlying the *Nepenthes* was dark and encrusted with humic material, likely indicative of long periods of time in association with the plants and the communities that form amongst their tangled stems. Tracts of this dark rock were observed fully exposed in places where plants were found to have fallen from the walls (see “Conservation status”).

Co-occurring flora in the general vicinity of *Nepenthes megastoma* includes *Amorphophallus palawanensis* (Araceae Juss.), *Begonia taraw* (Begoniaceae C.Agardh), *Cycas saxatilis* (Cycadaceae Pers.), *Dracaena* sp. (Asparagaceae Juss.), *Gynura* sp. (Asteraceae Bertch. & J.Presl), *Paphiopedilum philippinensis* (Orchidaceae Juss.) and *Ridsdalea philippinensis* (Rubiaceae Juss.).

Numerous small (c. 5 mm) ants were observed feeding at large crateriform glands beneath the lids of many pitchers. Larvae tentatively identified as blow flies (Calliphoridae) and a *Dasyhelea* sp. (Ceratopogonidae) (Charles Clarke pers. comms.) were observed in the basal cavity of several dissected pitchers (Figs. 7a, b) and, in the case of the former, were seen to be actively engaged in macerating and swallowing fragments of large (c. 1 cm) ants (*Camponotus* sp.). Solitary black wasps (Pompilidae) with iridescent blue wings were also observed resting on the phyllodes or pitcher peristomes of several plants, though specific interactions with the plants or their pitcher communities could not be deduced.

Conservation status:—Observations of *Nepenthes megastoma*, together with discussions with local rangers, suggest the species has a naturally small range and population. At Location 1, only four distinct individuals could be identified in our drone footage. Notably, the image of this species published in Clarke *et al.* (2014: fig. 6), taken in July 2013, shows the same rock formations—and thus the same population—with six to seven individuals visible, indicating a decline in numbers in this subpopulation since that time. At Location 2, there were 15 large and presumably clonal individual clumps recorded, along with a small number of scattered, smaller plants, resulting in an estimated total subpopulation size of fewer than 25 individuals. Three large, fallen piles of mature *Nepenthes* vines were found at the base of the cliffs in an advanced state of decomposition, with corresponding growth scars of dark rock visible on the rock face directly above (Fig. 7c–e), and were identified by our guides as remains of direct damage caused by Typhoon Rai. The third location, which could not be visited owing to the perilous limestone terrain, is home to just two or three plants (R. Moyano, pers. comm.).

Our observations have identified a *Nepenthes megastoma* functional population size (IUCN 2012) of approximately 19 known mature clumps, believed to represent highly branched single plants, and approximately 12 non-flowering (putative juvenile) plants. Given the complex nature of this karst formation—a limestone ridge 11 km long, 3–5 km wide on average, with an area of 35 km², comprising steep-sided towers, cones, and pinnacles, interspersed with

cockpits and dolines (Piccini & Landelli 2011)—the presence of additional *N. megastoma* subpopulations cannot be ruled out. The interior of the range that can be accessed without specialist climbing equipment has been relatively well-explored by park rangers and official guides, who have indicated that there are currently no other casual records of this distinctive plant elsewhere in the park, though the plant has not previously been the subject of a targeted search.

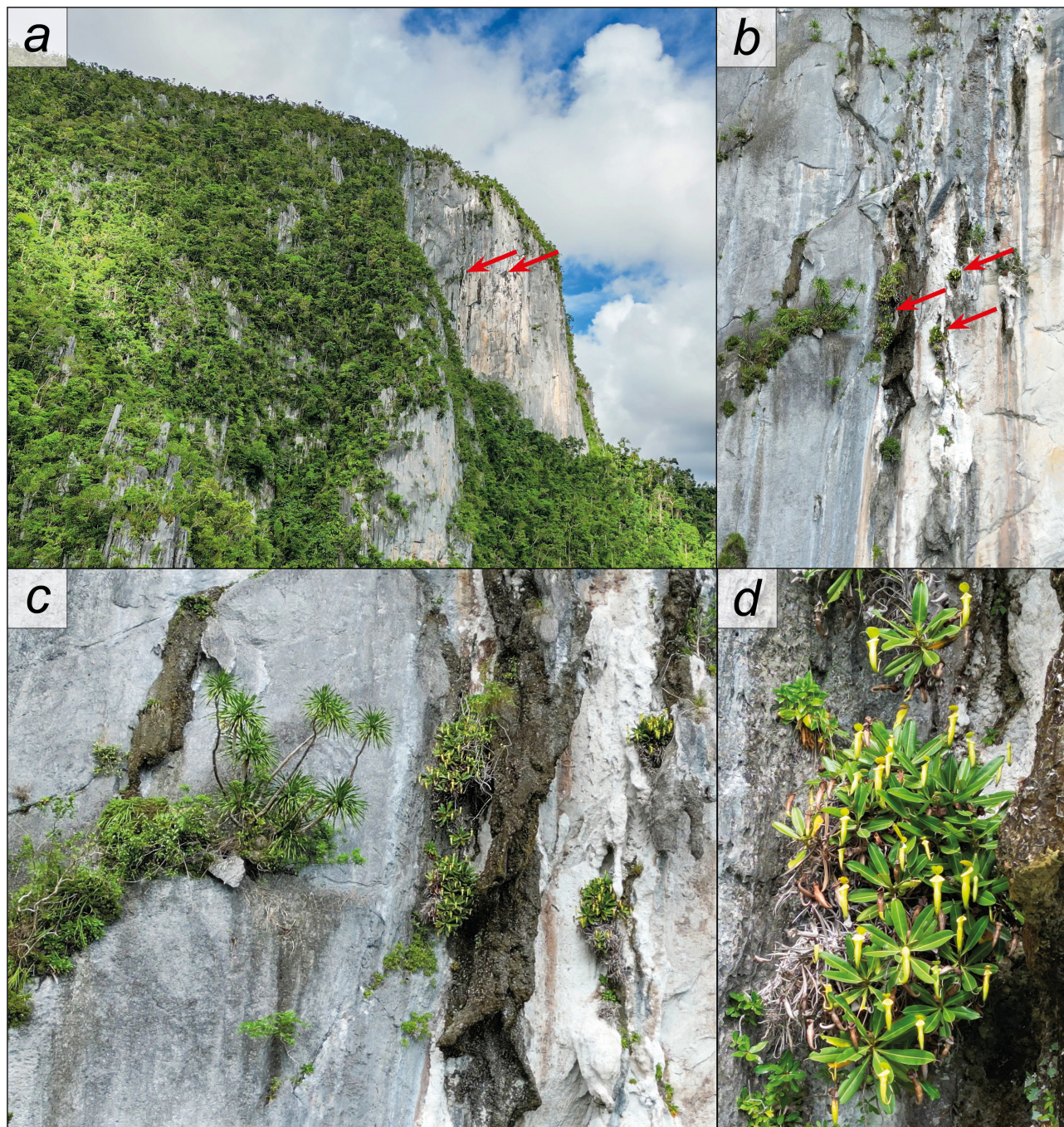


FIGURE 4. Drone views of *Nepenthes megastoma* Location 1 with red arrows indicating plants. *a.* Habitat on vertical limestone walls at c. 250 m elevation. *b.* Clumps of plants appear to follow vertical seams in the rock wall *c.* On approach the yellowish green pitchers become apparent, as do co-occurring plants like *Dracaena* sp. At both locations, the plants appear associated with dark rock that has become encrusted and discoloured over time through accumulation of organic matter. Note that this is the same subpopulation featured in Clarke *et al.* 2014: fig. 6, confirming a decline in total individuals. *d.* Closest possible approach without digital magnification. Photographs by J. Altomonte.

Based on current knowledge, *Nepenthes megastoma* satisfies the IUCN 3.1 Red List CR (*Critically Endangered*) criteria B1ab(ii,v)+B2ab(ii,v)+C2a(i) (IUCN 2012), i.e., it has an extent of occurrence (EOO) <100 km² and is known to exist at only a single location (comprising three subpopulations), with projected declines in the number of mature individuals owing to increasing frequency and severity of extreme weather events, particularly droughts and typhoons, as well as poaching, which has already been documented through several sales of illegally harvested plants via a vendor

in Manila; has a known area of occupancy (AOO) $<10\text{ km}^2$ at a single location, again with the same projected decline in number of mature individuals; and a population size estimated at well below the threshold of 250 mature individuals, with no subpopulation estimated to contain more than 50 mature individuals. The small AOO is a particular concern since it makes the taxon particularly vulnerable to destructive stochastic events like fire. The clearing of forest for agriculture and development adjacent to the boundaries of the PPSRNP represent a risk that cannot be fully assessed here. Such land conversion may affect the natural, historic patterns of orographic lift across the limestone massif, affecting rates and patterns of precipitation and thence the hydrological stability of the limited cliffside habitats that have fostered the evolution of this microendemic species. While criterion D (population size estimated to number fewer than 50 mature individuals) may well be satisfied by the cumulative total of 19 mature individuals, this is not assessed as such here owing to the uncertainties resulting from insufficient exploration of the karst formation specifically targeting this taxon.

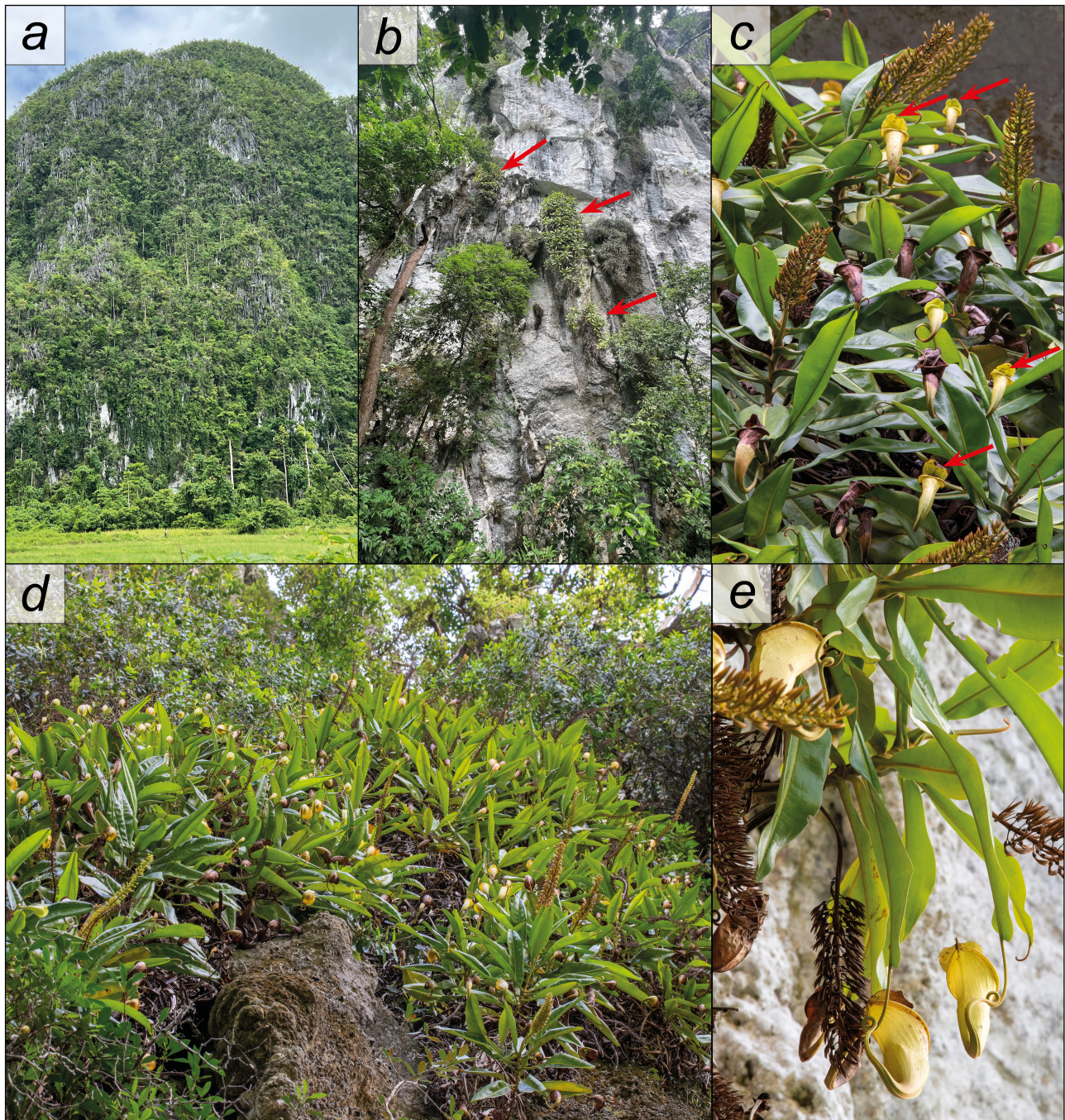


FIGURE 5. *a.* Generalised view of the type of habitat that comprises Location 2. *b.* Individual clumps of *N. megastoma* (red arrows) growing overhead on sheltered cliff walls. *c.* Groups of ants (red arrows) were frequently observed feeding beneath the lids. *d.* Large clump of plants observed from below, comprising what appeared to be two multibranching males and one female. *e.* Female plant viewed from below, showing various inflorescences and pitchers with uncommon single coils. Photographs by A. Robinson.

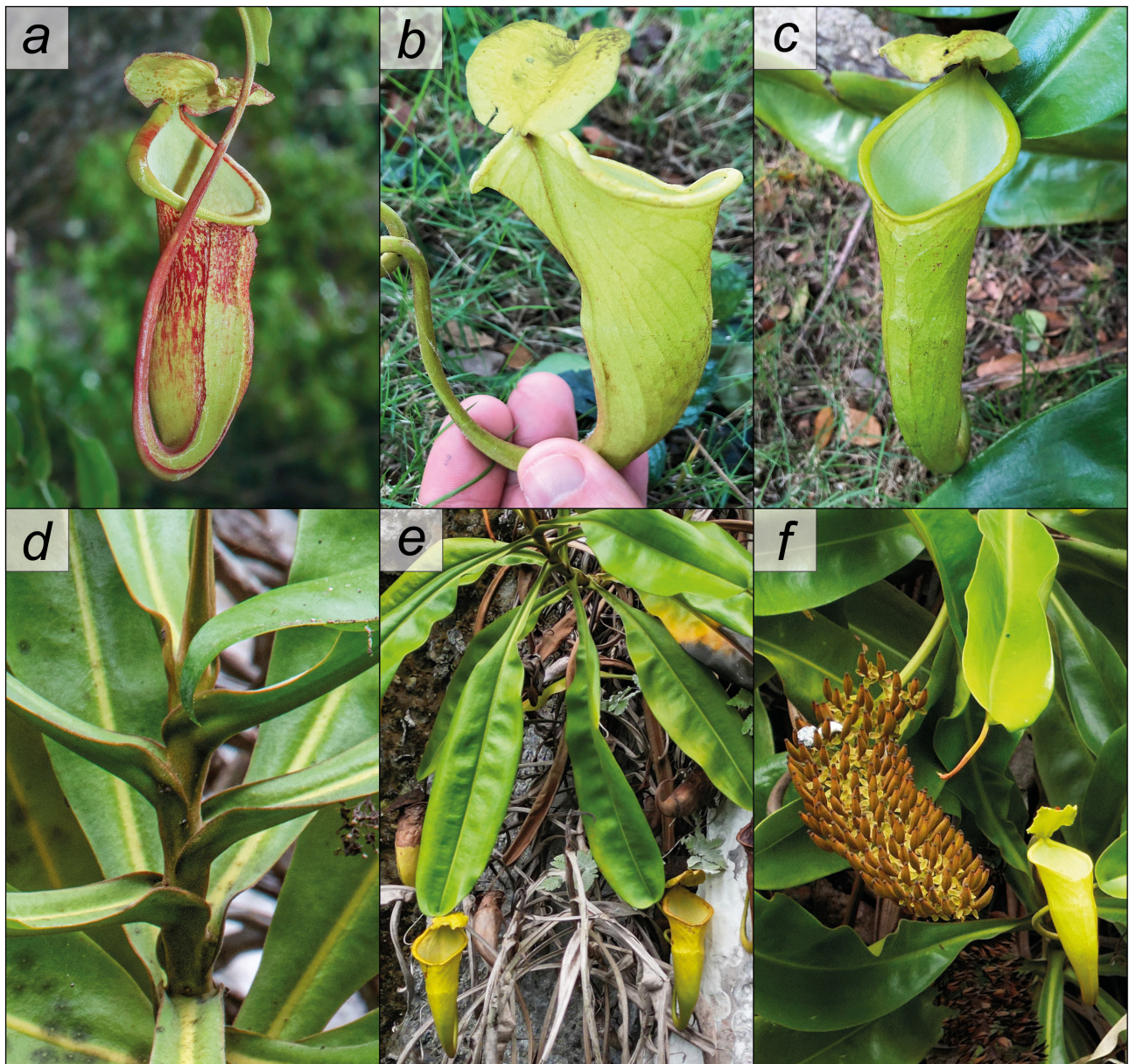


FIGURE 6. *Nepenthes megastoma* characteristics. *a.* Lower-intermediate pitcher with strong colouration. *b.* Stout form of upper pitcher with mediolateral flaring. *c.* Elongate form of upper pitcher. *d.* Magnification of stem showing winged phyllode bases with slight basal swelling. *e.* Suberect terminal growth showing peltate phyllode tips. *f.* Female inflorescence demonstrating universally upturned flowers with fruit in advanced development. Photographs by J.P. Collantes (a) and A. Robinson (b–f).

Specimens examined:—*Nepenthes megastoma*: PHILIPPINES. **Palawan:** Barangay Cabayugan: Mount St Paul, on limestone cliffs, 200 m a.s.l., 23 June 2023, *Collantes & Langbao 1*, detail of type materials referenced in protologue (holotype PNH 259144! [stem fragment bearing 8 phyllodes with one intact upper pitcher and a female infl. with dehiscent capsules]; isotypes PNH 259145! [3 detached phyllodes, bearing a lower pitcher, upper pitcher, and partially developed pitcher respectively, and a detached male infl. at anthesis (sheet 1 of 6); 1 detached phyllode bearing upper pitcher (sheet 2 of 6); 2 detached phyllodes bearing upper pitchers, one sectioned to reveal interior (sheet 3 of 6)]; MEL 2541012A! [stem fragment bearing 6 phyllodes with 3 whole or partial lower pitchers, and a detached phyllode with a lower pitcher (sheet 4 of 6)], MEL 2541013A! [stem fragment bearing 3 phyllodes and a female infl. with dehiscent capsules (sheet 5 of 6)], MEL 2541014A! [spirit collection containing intact upper pitcher, one detached lid, and several dehiscent valves with few seeds], MEL 2541015A! [stem fragment bearing 8 phyllodes with one partially developed pitcher and a male infl. at anthesis (sheet 6 of 6)]).

Nepenthes campanulata: INDONESIA. Borneo, E. Kalimantan, **Berau:** foot of Mt Ilas Bunga on steep limestone walls, upriver from Sangkulirang, 300 m, 9 Sept. 1957, *Kostermans 13764* (holo photo SING!; iso A *n.v.*; photo BM!; photo BO!; CANB *n.v.*; K!; photo KEP!; L!; photos NY! [2 sheets]; photos P! [2 sheets]; photo US!)

[single stem with two branches bearing *ca.* nineteen pitchers/pitcher fragments (SING 0046768); branched, sterile stem bearing *ca.* twenty pitchers and six pitcher fragments in an envelope (BM 000522420); length of stem with one attached and one detached rosettes of leaves bearing pitchers (BO 1300380); short, sterile stem bearing *ca.* eight pitchers and two leaf and pitcher fragments (K 000651541); two stems, left bearing one large pitcher and a number of juvenile sized pitchers, right with few small basal pitchers (KEP 13190); two stems, top with numerous intact leaves and pitchers, bottom with leaves and fragmented pitchers (L 0281510); at least three overlayed stems bearing numerous pitchers, three dehiscent infructescences apparent (NY 00039331 photo); single rosette bearing *ca.* ten pitchers (NY 00039332); two stems, left depauperate, right with *ca.* nine pitchers (P 00686448); one? branched stem bearing massed large leaves and pitchers, *ca.* five infructescences apparent (P 00686449); three? sterile stems bearing numerous pitchers (US 00516982)].

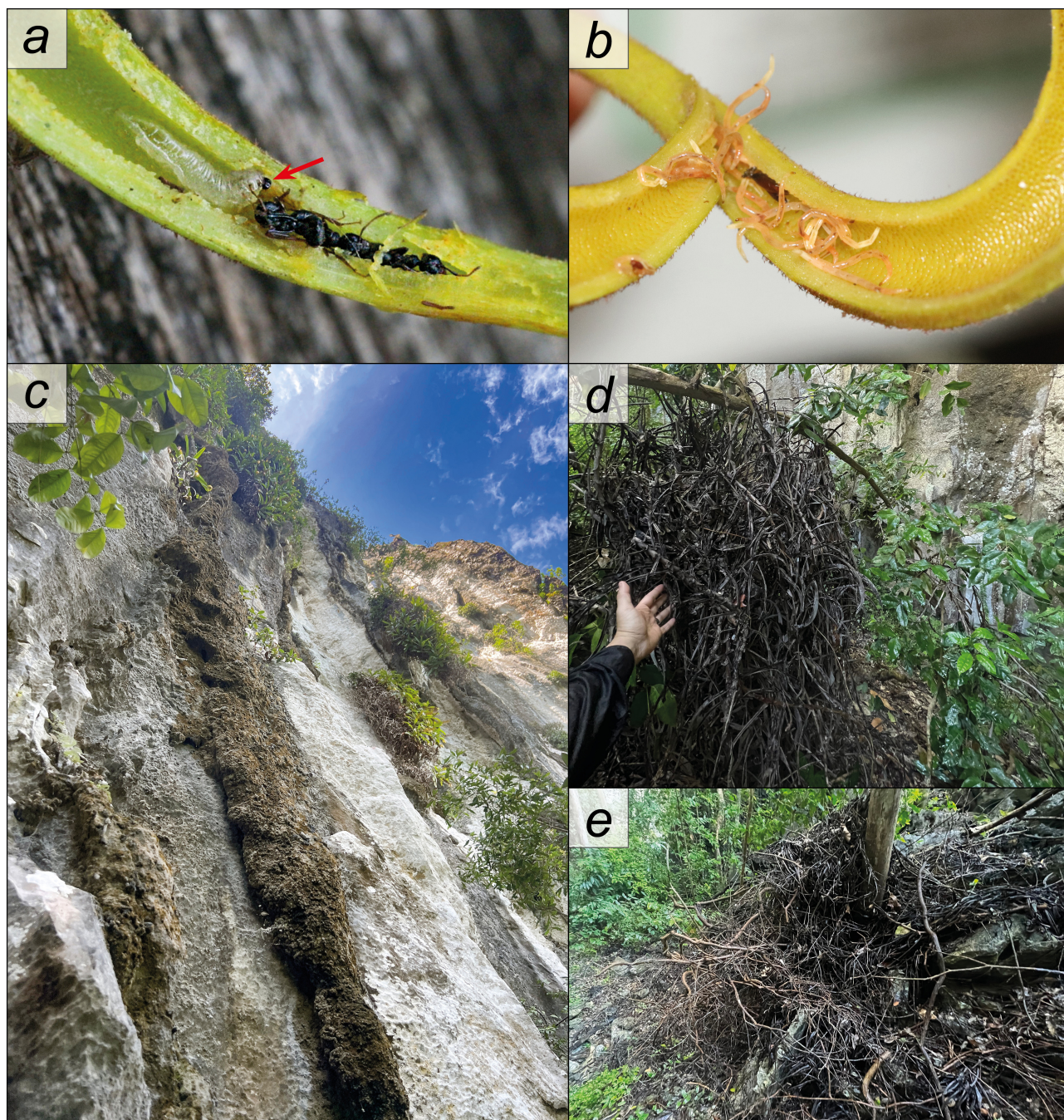


FIGURE 7. *a.* Dissection of upper pitcher tendril showing translucent white Calliphorid larva with macerated fragment of ant (red arrow) in its mandibles. Three ants appear to have been pushed into the narrow lumen of the pitcher base. *b.* Larvae of a *Dasyhelea* sp. in the base of another dissected pitcher. *c.* Humus encrusted rock immediately above fallen *Nepenthes megastoma* plants dislodged by Typhoon Rai. *d.* Fallen plants at base of cliff trapped by vegetation. *e.* Downslope view showing additional *Nepenthes* killed by storm damage. Photographs by A. Robinson (a, c–e) and J.P. Collantes (b).

***Nepenthes philippinensis*:** PHILIPPINES. **Palawan:** Mt. Pulgar [Thumb Peak], *Curran 3896* (lectotype K *n.v.*); waterfall 2 km west of Sabang, Barangay Cabayugan, *M. Mendum, D.J. Middleton & R. Fuentes 25545* (holotype K!; iso photos E! [2 sheets]; PNH *n.v.*) [stem with six phyllodes, one upper pitcher and male inflorescence (K 382198); stem with six phyllodes and two lower pitchers, with sketch of lid nectar gland (E 281569); two stems, one bearing a single phyllode, other with six phyllodes and two lower pitchers (E 281570)]; above waterfall 2 km west of Sabang, Barangay Cabayugan, *M. Mendum, D.J. Middleton & R. Fuentes 25551* (paratype K!; photo E!) [rosette with nine phyllodes and four lower pitchers (K 382199); rosette with seven small lower pitchers (E 281568)]; Between Culion and the “Negative Barrio,” Culion Island, Calamian Group, *H. H. Bartlett 15544* 26 July 1935 (photo GH!; NY 1628539 *n.v.*) [rosette with numerous phyllodes and pitchers, as well as male inflorescence, originally as ‘*Nepenthes ventricosa* Blanco’, annotated ‘*N. sp. not N. ventricosa* Blanco Cheek 1994’ (GH 01871616)]; Brookes Point, Caramay, forest road to Bulho, about 8 km off Abo-Abo to Brookes Point main road, at Malalung River bridge, rocky river bank in partially logged lowland mixed forest, *D.D. Soejarto 6546* with E. Reynoso, E. Sagcal, & R. Edrada 12 April 1989 (NY 1628545 *n.v.*); Puerto Princesa, exposed ridge between Mt. Viadunga and Mt. Beaufort, chromite mining site, *D.D. Soejarto 6431* with E. Reynoso, E. Sagcal, & R. Rutz 06 April 1989 (NY 1628546 *n.v.*); Silanga, *E.D. Merrill 9588* May 1913 (photos BK!; NY!; US!) [stem with upper pitchers and simultaneous pair of fragmented infructescences, originally labelled ‘*Nepenthes brachycarpa*’ but identified as ‘isotype of *Nepenthes brachycarpa* Merrill = *N. philippinensis* Macfarl.’ by Cheek, 23.iii.2000 (BK 235337); stem with numerous phyllodes, single, folded upper pitcher and detached infructescence (NY 00387787); stem one immature and one mature infructescences (US 100638)]; Puerto Princesa, Bacuñgan [Bacungan] ‘along river in forest’, originally as ‘*Nepenthes alata* Blanco’, *G. E. Edaño 259* March 26 1947 [stem with large upper pitcher pair and immature infructescence (A 01871597)]; Puerto Princesa, Bacuñgan [Bacungan] ‘above river in secondary growth’, originally as ‘aff. *hirsuta* Hk f. [Hooker f.] of Borneo’, *G.E. Edaño 325* March 23 1947 [pair of rosettes bearing numerous, small lower pitchers and intact roots (A 01871596)]; Victoria Mountains [Victoria-Anepahan Mountain Range], Panacan, Aborlan, ‘Mt. Victoria (SE slope) Panacan, upper source of Karaniagan River, open bank where boulders abound’, 350 m asl, *M.D. Sulit 12441* May 17 1950 [stem with three upper pitchers and male inflorescence (A 01871614)]; Mt. Mantalingajan, submontane ridge, ultrabasic soil, 1100 m, *G. Argent & E.M. Romero 92150* 4 March 1992 [stem with two phyllodes bearing a mature upper pitcher and a partially formed upper pitcher (E 32648)]. Note that *H.H. Bartlett 15544* shares some features in common with *Nepenthes abalata* Jebb & Cheek (2012: 3), apparently flowering in the rosette stage, however, the specimen is notably lacking nectar glands along the midline of the lower surface of the lid and is at least partly 2-flowered. Moreover, *N. philippinensis* has on several occasions been noted to flower in the rosette stage along the boulder-strewn lowland floodplain of Mt Victoria’s Buhawi River, along the principal route of access to the peak of that mountain (A. Robinson pers. observ.).

Discussion

In this work, *Nepenthes megastoma* is diagnosed against *N. campanulata* owing to their superficial morphological similarities and near identical habitat types. However, the authors neither perceive nor imply a relationship between these taxa, though the similarities do raise interesting questions about how such habitats might influence growth habits and pitcher shapes, particularly factoring in the comparable pitcher form of another karst endemic, *N. epiphytica*, from East Kalimantan. In fact, despite certain exaggerated characteristics, in morphological terms *N. megastoma* appears to be related to *N. philippinensis*: lid and lid gland morphology appear similar, minor differences in gland size and distribution notwithstanding; both produce inflorescences that are 1- and 2-flowered and bracteate in both males and females [1(–2)-flowered in *N. philippinensis*, (1–)2-flowered in *N. megastoma*]; peristome structure is similar, particularly in the region of the column; and phyllode bases are also similar, though larger and thicker with a distinctive basal swelling in *N. megastoma* that is not found in *N. philippinensis*.

In morphological terms, *Nepenthes megastoma* is notable for three peculiarities. First, the species has a distinctive indumentum, comprising stellate trichomes and peltate scales (lepides) in various ratios depending on the organ in question (Figs. 2g, 3). The precise function of these is unknown, but they may be implicated in water conservation and moisture regulation given the comparatively well-characterised role of comparable scales in lepidote rhododendrons (Nilsen *et al.* 2014, Desch 1983), or possibly prey attraction given the presence of only scales on the lower surface of the lid. Following submission of this manuscript, new research was published demonstrating the presence of endodermal cells, transfer cells, cuticular discontinuities, and osmiophilic material in *Nepenthes* peltate trichomes

(Płachno *et al.* 2025), supporting the theory that these structures might serve a water capture and absorption role in species like *N. megastoma* that experience seasonal decreases in rainfall. Second, the authors are not aware of any other *Nepenthes* in which the flowers—in this instance the female flowers only—are universally upturned so that they are similarly orientated (Figs. 5c,e, 6f), a character absent from *N. campanulata* and *N. epiphytica* that one might otherwise ascribe to the facilitation of pollination in cliffside habitats. And third, during fieldwork it was noticed that the upper pitchers occur in two forms, one slightly stouter and mediolaterally flaring, the other narrower, more elongate, and less widely flaring (Fig. 2i,j, 6b,c). Interestingly, these two forms do not transition permanently from one form to the other as plants lengthen, as in most other *Nepenthes* with different pitcher types, but they instead appear in like-series that infrequently alternate, with the form of the upper pitchers more or less concurrent on adjacent plants as determined by counting backwards from the most recently produced leaf (the assumption being that growth rate is more or less uniform between plants). This observation might suggest that there is some seasonal variation in upper pitcher shape. A possible influence may be monthly variations in rainfall and temperature, since this region of Palawan has a pronounced dry season from January to April (climate data from Worldbank.org 2025). Notably, at Location 1, which is exposed to more sun and wind than Location 2, the pitchers appear to be entirely of the elongate form, possibly indicating that more drying conditions may give rise to the narrower pitcher form, which possibly serves to reduce water loss through evaporation.

TABLE 1. Morphological comparison between *Nepenthes megastoma*, *N. campanulata*, and *N. philippinensis*.

	<i>N. campanulata</i>	<i>N. megastoma</i>	<i>N. philippinensis</i>
Known geographical range	Sarawak and East Kalimantan (where possibly extinct), Borneo	Central Palawan, Philippines	Palawan province, including Palawan, Linapacan and the Calamian islands
Substrate	Karst limestone	Karst limestone	Typically degraded ultramafic rock and clay laterite, rarely in humus over limestone or on shoreline quartzitic sand
Habitat	Lithophytic on vertical limestone walls, typically sheltered beneath overhangs, on white, spongy moist tufa	Lithophytic on vertical limestone walls in sheltered to open aspects, on tufa, which it appears to modify over time	Terrestrial in scrubby grasslands, floodplains, and cleared areas, mid-montane forest clearings
Elevation (m)	100–500	90–250	0–600(–1200)
Stems	To 35 cm long and 0.4 cm dia.	To 2.8 m long and 1.2 cm dia.	To 10 m long and 0.7 cm dia.
Branching	Common, basal, forming several growing points	Prolific, basal and medial, forming tens of growing points	Occasional, mostly basal
Phyllodes	Spathulate-lanceolate, to 9 cm long, base without swelling	Elliptic-subobovate, 20–38 cm long, base with basal abaxial swelling	Linear to elliptic-subspathulate, to 35 cm long, base without swelling
Apex of phyllodes bearing upper pitchers	Rounded, tendril exertion peltate, 0.1–0.4 cm from apex	Rounded or obtuse and slightly retuse, tendril exertion markedly peltate, 0.7–1.5 cm from apex	More or less acute, tendril exertion not peltate
Indumentum	Glabrous except for below peristome and around spur, hairs short, brown, <0.1 mm long	Dense covering of sessile, basally branched stellate trichomes and/or peltate scales on most surfaces	Stems glabrous, usually glaucous, pitchers and inflorescences with minute reddish hairs
Pitcher forms	Essentially monomorphic, campanulate	Trimorphic (lowers and two types of uppers), uppers either campanulate or infundibular, with possible seasonal variation	Dimorphic (lowers and uppers), ovate below, more or less cylindric-infundibular above
Partial peduncles	1-flowered, female flowers spreading (orientated away from axis)	2-flowered, female flowers ascending (unidirectionally upturned)	2-flowered, female flowers spreading (orientated away from axis)

Conflicts of interest

The authors declare no known conflicts of interest.

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Author contributions

The project was conceptualised by R. Bustamante, J. Altomonte, and A. Robinson; applications for applicable permits were made by A. Robinson and V. Mangussad; expedition logistics were arranged by J. Collantes; funding was acquired, project administered, manuscript prepared, and figures and illustration generated by A. Robinson; material collections made by J. Collantes with A. Langbao; analyses conducted by A. Robinson and J. Collantes; review and editing of the manuscript was overseen by all co-authors.

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