

OBSERVATIONS OF SUBTERRANEAN PITCHERS
IN CULTIVATED *NEPENTHES RHOMBICAULIS*

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Abstract: The remarkable subterranean growth habit of *Nepenthes rhombicaulis* is described based on the examination of nine mature plants in the UK's National Plant Collection of *Nepenthes* at Chester Zoo. The species is found to produce most of its pitchers below ground, these being larger and sturdier than—and morphologically distinct from—its more familiar aboveground traps. The underground pitchers are borne on vertically orientated stems originating below the soil line, which are only transiently carnivorous and eventually develop into pitcherless lianas. As such, repeated subterranean branching is necessary to sustain concealed carnivory. Underground pitchers appear to have lengthy functional lifespans, likely reflecting their increased construction costs. The consistent production of plentiful underground pitchers even under conditions of artificially high light abundance points to the phenomenon being a genetically determined adaptation rather than a plastic response to shading. Suggestions are made for how to cultivate and display this unusual species to best effect.

Introduction

The reality of functional underground carnivory in *Nepenthes* (Nepenthaceae) only became widely known with the description of the Bornean *Nepenthes pudica* by Dančák *et al.* (2022). However, literature records of this phenomenon date back to at least the work of Salmon (1993), who—based on field observations made in 1989 with Ricky Maulder¹—noted that wild plants of *N. rhombicaulis*, a species endemic to northern Sumatra, routinely produce traps below the soil line and proposed that this species might be adapted to targeting subterranean prey. Surprisingly, this remarkable observation has received very little attention in the subsequent three decades.²

¹ These observations were made as part of a series of expeditions detailed in the trip report of Hopkins *et al.* (1990), which included perhaps the first published photograph of subterranean pitchers of *Nepenthes rhombicaulis*, albeit ones only shallowly buried in soft humus (see top-right photo on p. 21 therein; R. Maulder & B. Salmon, pers. comm.). Comparable photos of an excavated pitcher of this species appeared in Hernawati & Akhriadi (2006:61, fig. 25).

² To the best of our knowledge, the only other explicit reference in the published literature to ‘underground’ or ‘subterranean’ pitcher production in *Nepenthes rhombicaulis* is that by Robinson (1995), citing the original article of Salmon (1993), though other authors have noted this species’ tendency to produce pitchers under detritus (e.g., Clarke 2001:180).

In contrast to *Nepenthes pudica*, the subterranean carnivory of *N. rhombicaulis* has yet to be subjected to detailed field studies. Since the species entered cultivation several decades ago, examination of mature, artificially grown specimens offers an alternative means of investigating this phenomenon. However, *N. rhombicaulis* is generally considered a rather horticulturally unimpressive species (Clarke 1997, 2001) owing to its small and unremarkable aboveground rosette pitchers and the tendency for the visible parts of older specimens to consist solely of pitcherless climbing stems. For this reason, few growers have it in their collections and even fewer have large specimens, let alone the significant number that would be needed for a meaningful characterisation of the species' habitus. As such, the sizeable collection at Chester Zoo in the United Kingdom represents a valuable source of live material for study.

Nepenthes rhombicaulis at Chester Zoo

Two visits by the first author to the UK's National Plant Collection of *Nepenthes* at Chester Zoo, England (see Plant Heritage 2015, n.d.), in April and May 2022, offered a rare opportunity to unpot and inspect multiple large specimens of this seldom-grown species. In total, nine mature plants were examined, each more than 10 years old (collectively accessioned as ACC.2012.0320,

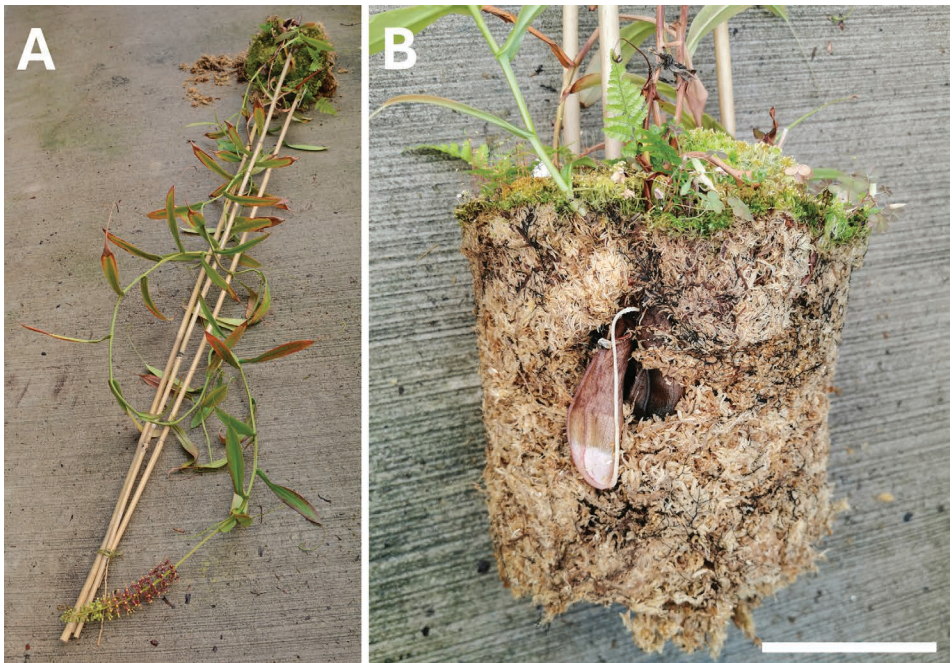


Figure 1. Typical growth habit of mature cultivated *Nepenthes rhombicaulis*. (A–B) Plant 1: male flowering plant with a single, small aboveground rosette pitcher and much larger and more numerous subterranean traps; note the long, entirely pitcherless climbing stems (>2 m long), typical of all the plants examined. The intact substrate mass in (B) shows the entirely concealed location of the underground pitchers within the pot. Scale bar: 10 cm. Photographs by M. Golos.

reflecting the year of acquisition; these plants were possibly all genetically identical). All plants bar one had climbing stems exceeding 2 metres in length (Fig. 1A) and all grew in a substrate consisting primarily of dead, long-fibre *Sphagnum* moss (Fig. 1B) in standard 5- or 7.5-litre opaque plastic pots under typical conditions for highland *Nepenthes*. Five bore active, fully subterranean pitchers and two more showed unambiguous evidence of their past presence. The lack of active underground pitchers in the remaining plants appeared to be at least partly attributable to unfavourable anoxic conditions resulting from substrate compaction and breakdown.

Interestingly, the abundant underground pitchers of this accession had remained entirely undetected at Chester Zoo prior to the first author's visit in 2022, despite all the plants having been repotted on multiple occasions during the previous decade. This is because particular care had always been taken to minimise root disturbance and consequently the entire root ball complete with compressed substrate had on each occasion been transplanted without further examination.

General observations

Though the following observations pertain to cultivated rather than wild material and the sample size is modest, some tentative conclusions can nonetheless be drawn.

Plant architecture and growth habit: *Nepenthes rhombicaulis* produces its underground pitchers on vertically orientated, initially achlorophyllous shoots (Fig. 2A–C) originating from just below the substrate surface to a depth of at least 20 cm. Once these shoots emerge above the soil line and chlorophyll production is established, they briefly produce aboveground rosette pitchers in the 'short stem' phase (*sensu* Cheek & Jebb 2001:5) and thereafter continue as pitcherless vines (Fig. 1A). Each stem is therefore transiently carnivorous and basal branching is generally necessary for continued carnivory, whether above or below ground.³

Since branching leading to the production of subterranean pitchers occurs from basally woody vines at some depth below the soil line (Fig. 2A–C), *Nepenthes rhombicaulis* plants must presumably reach a significant size before they can produce pitchers in this manner, which likely requires several years of growth. Individual shoots can bear many concurrently active underground pitchers, and up to 10 were observed on a single plant (Fig. 2B). It appears that mature specimens of this species produce the bulk of their pitchers underground and that—since these are generally larger and more robust than their terrestrial counterparts—they represent the overwhelming majority of the plant's total pitcher biomass over its lifetime.

Pitcher variability and carnivory: Generally speaking, subterranean pitchers of *Nepenthes rhombicaulis* become progressively less sturdy with decreasing substrate depth: initially rigid throughout, then remaining so only in the basal portion (that occupied by the digestive zone), and finally becoming flimsy throughout, as are the aboveground rosette pitchers (a fact already noted in the type description; Kurata 1973:231). The greater rigidity of pitchers produced at depth reflects their markedly thicker walls and is likely necessary to allow them to effectively displace surrounding substrate as they grow. Nevertheless, many subterranean pitchers assume a somewhat misshapen or deformed appearance as a result of their concealed development.

³ An exception to this is the production of rosette pitchers on *aerial* offshoots from the main climbing stem, which have occasionally been observed in the wild (J. Bae, pers. comm.; JIPS 2000). As far as the authors are aware, true upper pitchers of *Nepenthes rhombicaulis* have never been recorded in the field with certainty (see Schmid-Hollinger 1994; Clarke 1997, 2001) and only very rarely in cultivation (A. Robinson, pers. comm; Smith 2015).

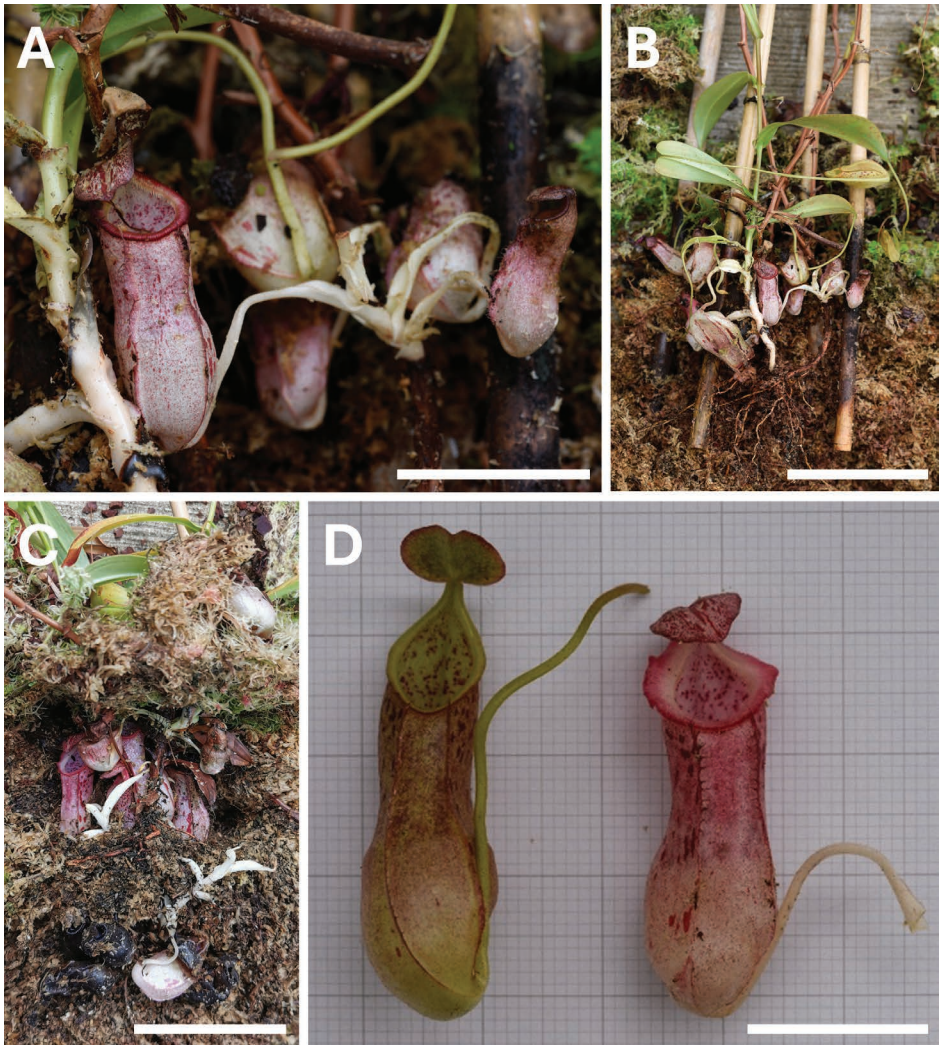


Figure 2. Underground and aboveground lower rosette pitchers of mature cultivated *Nepenthes rhombicaulis*. (A–B) Plant 2: this specimen bore seven active growth points, including four pitcherless, basally woody vines between 90 and 230 cm long and three younger shoots with active subterranean pitchers (10 in total). (A) shows an achlorophyllous, pitcher-bearing offshoot ca. 4 cm long produced just below the surface; note apical greening of the adjacent stem. In (B), note the emergence of the stem near the rootball and the profusion of pitchers just below the soil line. (C–D) Plant 3: large specimen bearing at least seven concurrently active subterranean pitchers. Note the black mass of rotten pitchers on either side of the lone live example near the bottom of (C). (D) shows an aboveground rosette pitcher (left) and an underground pitcher on 2 mm graph paper; note morphological differences and absence of chlorophyll in the latter. Here two pitchers of similar size are shown, but aboveground pitchers were generally found to be significantly smaller. Scale bars: (A,D) = 3 cm; (B,C) = 10 cm. Photographs by M. Golos.

Compared to aboveground rosette pitchers, underground pitchers tend to have markedly broader peristomes that are flattened (as opposed to subcylindrical) and bear longer teeth on the inner margin (Fig. 2D), as well as having greatly reduced spurs. Pigmentation is a vibrant red-on-white owing to the lack of green chlorophyll that, in combination with red anthocyanins (see Dávila-Lara *et al.* 2021), gives aboveground pitchers their characteristic muddy brown colour (Fig. 2D). These marked differences in pitcher morphology and pigmentation between below- and aboveground pitchers closely mirror field observations of *Nepenthes rhombicaulis* (R. Maulder, B. Salmon, A. Robinson & J. Bae, pers. comm.).

The development of the interior waxy zone in subterranean pitchers is similar to that of the aboveground rosette pitchers, comprising roughly half of the pitcher's height, suggesting a conventional pitfall trap mechanism. While it is tempting to speculate that some of the aforementioned morphological differences (particularly those of the peristome) might reflect specialisations for subterranean prey, this requires further investigation. The cultivated plants documented herein appeared to catch few prey in their underground pitchers, though several indeterminate arthropods and a small snail were recorded.

Developmental progression in a single stem: an illustrative example

Study plant and changes associated with shoot emergence: One of the plants examined (Plant 2; Fig. 2A–B) was notable for its numerous stems and abundance of underground pitchers. It bore seven active growth points, consisting of: four basally woody vines between 90 and 230 cm tall that lacked pitchers altogether; a green basal rosette *ca.* 4 cm long with one rigid subterranean pitcher and one flimsy aboveground pitcher; an almost entirely achlorophyllous underground offshoot *ca.* 4 cm long with four active subterranean pitchers (Fig. 2A); and a short stem with a combination of both functional underground and aboveground pitchers (Fig. 2B).

This last shoot is of particular interest as it was in a transitional stage, simultaneously bearing functional below- and aboveground pitchers. It was approximately 27 cm long as measured from its origin near the root ball: achlorophyllous for the basal *ca.* 8 cm and entirely green by *ca.* 11 cm. Close inspection of this stem revealed evidence of 16 past and present leaves⁴, including six underground pitchers (Fig. 3)—of which five at least partially active—and two aboveground rosette pitchers: one functional and one developing. Given the paucity of available information on the underground architecture of this species, the sequence of leaves is detailed in Table 1.

Pitcher lifespan and construction costs: It is notable that in the examined stem the oldest living underground pitcher was borne on the 14th phyllode when counting back from the youngest, inrolled leaf (Table 1). The significant longevity of these subterranean traps likely reflects their increased construction costs as compared to the thinner-walled and generally smaller aboveground traps. All else being equal, this would necessitate a longer functional lifespan to recoup the associated metabolic 'debt' (see Osunkoya *et al.* 2007, 2008; Karagatzides & Ellison 2009; Gilbert *et al.* 2025).

Interestingly, most of the live pitchers on this stem appeared to have transitioned to the late-stage 'digestion-only' phase, as evidenced by the browning of the upper portion of each trap (Fig. 3), which would have presumably precluded further prey capture.

⁴ Here 'leaf' is used in a broad sense to refer to the entire assimilatory structure consisting of the basal phyllode (often called the 'lamina' or 'leaf blade'), the intervening tendril, and the terminal pitcher.



Figure 3. Six subterranean *Nepenthes rhombicaulis* pitchers and their associated phyllodes removed from a single short stem of Plant 2, which concurrently also supported one functional aboveground rosette pitcher. The pitchers are arranged left to right from most to least basal according to their attachment point on the stem, and laid out on 2 mm graph paper. Numbers correspond to those given in red in Table 1. Note the achlorophyllous nanophylls associated with the first five pitchers and the contrasting green, enlarged phyllode of the final pitcher. Scale bar: 5 cm. Photograph by M. Golos.

Table 1. Sequence of leaves in a transitional shoot of Plant 2, from most to least basal. Pink-shaded rows indicate entirely subterranean leaves (both phyllode and pitcher), blue-shaded rows indicate entirely aboveground leaves, and white ones indicate the transition zone where phyllodes may be aboveground but pitchers subterranean. Subterranean pitchers are numbered in red and aboveground pitchers in blue.

Leaf no.	Description
1–2	leaf base remnants (remainder had rotted away)
3	semi-browned pitcher (1)
4	pitcher that had entirely browned out of sequence (2)
5	very rigid pitcher (3)
6	leaf severed at base
7	basally rigid pitcher with flimsy upper portion (4)
8	wholly flimsy pitcher (5)
9	first green subterranean leaf with pitcher (6)
10	green aboveground (?) leaf with undeveloped pitcher bud
11	green leaf with end of tendril missing (original pitcher development unknown)
12	green leaf with aboveground rosette pitcher (flimsy throughout, lid underdeveloped) (7)
13	green leaf with developing rosette pitcher (8)
14–16	green leaf with apparently activated pitcher bud (leaf 14); recently opened leaf (leaf 15); curled up developing leaf (leaf 16)

Nepenthes rhombicaulis remains a poorly documented species and little is known of its ecology, though in the wild it has typically been encountered in the deep shade of closed-canopy forest—a low-light environment that few other *Nepenthes* could tolerate—growing terrestrially among plentiful moss, detritus, and soft humus (R. Maulder, B. Salmon, A. Robinson & J. Bae, pers. comm.; Salmon 1993; Clarke 1997, 2001; McPherson 2009, 2023; Mio 2010). Under such conditions, it is easy to imagine that basal offshoots could be smothered by rapid growth of terrestrial mosses or else completely concealed under falling leaf litter or other detritus. Such an aphotic situation would invariably induce partial or complete achlorophylly in the affected shoots, which might nonetheless bear pitchers, especially since the production of photosynthetic tissue at ground level—where light penetrance is lowest—is likely to be only marginally profitable from the point of view of leaf economics.⁵ Though such concealed pitchers might be described as ‘subterranean’, they would only be so in a rather trivial sense, and would merely represent a plastic response to prevailing local conditions.

That the cultivated *Nepenthes rhombicaulis* plants described herein grew under strong natural light—in a situation that precluded significant shading by other plants or organic debris—yet consistently maintained abundant, truly subterranean pitcher production on achlorophyllous leaves borne on shoots originating at significant depth, suggests that the observed growth habit is instead a genetically determined adaptation. That is to say, an example of ‘true’ subterranean carnivory comparable to that documented in *N. pudica* by Dančák *et al.* (2022). Field studies will be needed to confirm this.

Cultivation and display of *Nepenthes* with subterranean pitchers

Nepenthes rhombicaulis has been in cultivation for many years, and *N. pudica*, though still something of a horticultural rarity, is becoming more widely available. Growers may wonder how best to display plants whose most interesting structures are ordinarily hidden from view. Enthusiasts of terrestrial *Genlisea* and *Utricularia* (both Lentibulariaceae) have long faced a similar problem. In that context, Geoff Wong’s famous transparent-bottomed *Genlisea* display case offers one innovative solution (Anon. 1995; D’Amato 1998:287). An analogous, if simpler, setup would likely work well for displaying *Nepenthes* with subterranean pitchers. Large-sized transparent orchid pots filled with loose substrate would be an obvious first choice.

Pure, long-fibre *Sphagnum* moss (as used at Chester Zoo) appears to be an ideal medium that closely mimics the natural growing conditions of *Nepenthes rhombicaulis*. However, semi-frequent repotting would likely be needed to prevent substrate compaction and to maintain the airy conditions presumably conducive to subterranean pitcher production. The latter property might be aided through the addition of coarse perlite.

Ideally, the transparent container would be covered when not being actively viewed (e.g., with blackout fabric or ‘double-potted’ in a removable opaque vessel of equivalent size), so as to simulate the total darkness experienced under natural conditions—light availability is likely to induce

⁵ Certain species of *Nepenthes* occurring in shady habitats—most notably *Nepenthes ampullaria*—habitually produce greatly reduced phyllodes (known as ‘nanophylls’) near ground level, presumably due to these structures’ poor return on investment in terms of fixed carbon (Green 1967:63; Jebb 1991:13; Cheek 2015:224; Golos *et al.* 2020:138).

aberrant underground growth, including chlorophyllous subterranean shoots. In a public display setting this variable concealment could be achieved with a sliding door.

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ADAPTIVE STRATEGIES OF *NEPENTHES*: A REVIEW

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Abstract: The evolution of *Nepenthes* pitcher plants illustrates a remarkable case of morphological innovation shaped by ecological pressures. Across the genus, diverse pitcher forms have emerged in response to nutrient-poor habitats, enabling both efficient carnivory as well as resource capture from other nitrogen sources. Variation in pitcher morphology aligns closely with environmental factors, reflecting intricate relationships between form, function, and survival strategy. These patterns reveal not only the adaptability of *Nepenthes* but also illuminate broader evolutionary processes such as convergence, niche specialization, and constraint-driven innovation.

Introduction

The greatest concentration of *Nepenthes* species is found in the Malay Archipelago, particularly Borneo, Sumatra, and the Philippines. *Nepenthes* are also found in Madagascar, Seychelles, Sri Lanka, India, Australia, and New Caledonia. *Nepenthes* pitcher plants have evolved a variety of tailored adaptations to survive in this highly diverse ecological region. As a review of the current literature, this paper explores some of these specialized adaptations shaped by ecological conditions.

The landscape of these regions varies greatly. In Borneo alone, the lowlands including Kota Kinabalu, Sandakan, and the coastal regions, experience average temperatures of 26–32°C, while the highlands maintain cooler conditions between 18–24°C. These temperature gradients, paired with the island's fragmented geography create a variety of distinct microenvironments, which in turn promote allopatric speciation among *Nepenthes*, the process by which geographic isolation ultimately results in genetically distinct species. As a result, plants in those types of environments have evolved in isolation, adapting to their niches (Thorogood *et al.* 2018). Thorogood notes that in addition to the different altitudes, the evolutionary path of *Nepenthes* is further shaped by varying rainfall, soil types, and sunlight in these regions, creating distinct species suited to the local ecological conditions. The combination of these environmental factors plays a crucial role in driving the evolutionary patterns seen in *Nepenthes*, highlighting how physical isolation and local climate differences foster diversity within the genus.

While *Nepenthes* vary heavily in shape and size, there are generally some characteristics shared between all species. *Nepenthes* utilize carnivory through highly modified leaves, which can trap and digest organisms for nutrients, a vital adaptation in environments where the soil lacks essential elements, namely nitrogen. They use a passive-trapping method—unlike the active thigmonastic traps employed by the famous Venus Flytrap. Their leaves attach to the pitcher cup through a tendril, which can wrap around other objects for stability. *Nepenthes* typically have a peristome, a slippery rim on the edge of the pitcher cup which may have specific coloring to help attract prey (Scott *et al.* 2000). The majority of *Nepenthes* have a lid which partially blocks the orifice of the pitcher, preventing rainwater from overflowing the cup, which, if absent, could lead to the loss of nutrients and dilution of digestive fluid. Like the peristome, the lid is often unique in color and

patterning, and in certain species, it serves as a major site of nectar production (Merbach *et al.* 2001). It is hypothesized by some that the nectar is intoxicating to insects, causing them to become uncoordinated – and increasing the chances of being captured (Lathika *et al.* 2000). According to anecdotal reports from some observers, as well as my own experience, insects found on the peristome react somewhat lethargically when touched, although conclusive research identifying what specific compounds might contribute to this effect is lacking at this time. The production of nectar, coupled with the slippery peristome, increases the likelihood of prey capture. While their primary prey consists of insects, larger *Nepenthes* species may also trap small vertebrates like frogs and lizards, further highlighting the diversity of their carnivorous diet. The combination of these adaptations makes *Nepenthes* plants efficient in nutrient acquisition, enabling them to thrive in otherwise nutrient-poor environments.

Specialized adaptations for carnivory

While all *Nepenthes* species are carnivorous to some degree, many have evolved extraordinary adaptations that significantly enhance their trapping efficacy. From potent nectar to deadly teeth and sticky fluids, these modifications enhance the ability to capture prey. Whether by luring insects to a slippery edge or forcing them into dangerous positions, many species have developed unique approaches to survival. These specialized traits underscore the evolutionary innovation of *Nepenthes* to the nutrient-poor environments where they thrive. One such adaptation is seen in *Nepenthes lingulata*, a rare highland species (Lee *et al.* 2006). Its most distinctive feature is a thin, tongue-like filament that juts out from the underside of the pitcher lid. Unlike the lid glands of most *Nepenthes*, which secrete nectar broadly across the surface, *N. lingulata* produces nectar exclusively at the tip of this long, dangling “tongue” (*lingua*). Lee and colleagues observed that insects must crawl out onto the slender projection, hanging directly over the pitcher’s deadly opening, to access the reward. A single misstep or gust of wind can easily send them tumbling into the trap below. While minor nectar-producing crests are common in species like *N. izumiae*, which has a short 1 cm ridge, *N. lingulata*’s extreme 2–4 cm extension represents an effective evolutionary tactic. In the nutrient-poor, high-altitude forests where it grows, and where prey is scarce, this strategy ensures that any insect drawn in is placed in maximum peril.

Most *Nepenthes* species have a ribbed peristome—small ridges that face inward toward the pitcher cup. These ridges make the surface difficult for insects to grip and help guide prey toward the trap opening. While in many species the ribbing is subtle (only fractions of a millimeter in size), others have evolved dramatic, tooth-like structures along the peristome. One striking example is *Nepenthes hamata*, whose fearsome, hook-shaped teeth can extend up to 7 mm from the pitcher rim (Cheek & Jebb 2001). These structures increase the effective surface area of the peristome, creating more opportunities for insects to lose their footing and fall in (Thorogood *et al.* 2018). The hooked shape of *N. hamata*’s teeth also serves to block escape, helping to ensure prey cannot climb back out once trapped (Fukushima 2023). Another species, *Nepenthes edwardsiana*, features similarly elaborate peristome ornamentation, though its teeth are flatter and more blade-like. These comb-like edges, when combined with nectar secretion and the slippery surface of the peristome, destabilize footing and further entice prey toward the trap. In extreme cases, like *Nepenthes macrophylla*, the teeth resemble interlocking spines, forming a jagged, almost cage-like barrier around the pitcher mouth (Cheek & Jebb 2001). These “toothy” *Nepenthes* species are all native to high-altitude environments, where insect life is less abundant, and nutrients are harder to come by. In such habitats,

every successful catch matters, and the evolution of complex peristome structures likely reflects strong selective pressures favoring efficient prey capture and retention.

The peristome, one of the most striking features of *Nepenthes*, is absent in some species. While the peristome functions to lure prey to the pitcher, provide a slippery surface, and prevent prey from escaping, *Nepenthes inermis* diverged evolutionary from most other *Nepenthes* species. The pitcher cup is funnel-shaped and relatively small—only 5 to 9 cm in height—and is fully green. The ends of the pitcher cup of this species simply taper off, forming a thin edge. It appears extremely delicate and inefficient at prey capture. Despite its appearances, *N. inermis* is lethal. Well described in Matt Candeias' blog (Candeias 2019), *In Defense of Plants*, to compensate for a lack of peristome, the pitcher fluid inside *N. inermis* is thick and viscous, and comparable to honey. When poured out, the fluid can stretch multiple meters before it breaks. Instead of elaborate trapping methods like other *Nepenthes*, once an insect steps inside the fluid of *N. inermis*, it gets trapped and begins to sink further into the cup. Additionally, the pitchers lack a waxy zone, demonstrating their reliance on the pitcher fluid. This strategy allows *N. inermis* to thrive in its misty, highland environment where heavy rainfall could otherwise dilute thinner pitcher fluids, especially since the lid, which usually can help protect the pitcher from rain, is essentially vestigial (Candeias 2019). Despite its pared-down structure, the trapping efficacy of *N. inermis* highlights the genus's wide range of adaptive strategies.

Many *Nepenthes* species attract insects with their enticing nectar. However, *N. albomarginata* has evolved a more deceptive strategy. At first glance, *N. albomarginata* does not appear particularly noteworthy, featuring a fully red pitcher cup and a somewhat plain shape. However, upon closer inspection, a distinct white “band” just below the peristome becomes visible. Described by Marlis Merbach and colleagues in the journal *Nature*, this band is made up of trichomes, small, hair-like structures, that specifically attract *Hospitalitermes bicolor*, a species of foraging termite (Merbach *et al.* 2002). The termites are drawn to the edible trichomes and begin to feast but in the chaos of competition, many fall into the pitcher's digestive fluid. In their scramble to reach the trichomes, termites push and shove each other, inevitably sending some to their deaths. Merbach noted *N. albomarginata* can capture up to 22 termites per minute, with each pitcher capable of trapping thousands of termites – most of which may be caught in a single night. Merbach reported that by morning, previously intact trichomes had been consumed, and the pitchers had filled with prey. This innovative method of prey capture makes *N. albomarginata* one of the only plants known to offer its own tissue as bait. The strategy proves highly beneficial: termites are not only among the most abundant insects in tropical rainforests but also provide a rich source of nitrogen compared to other insect prey.

Unique adaptations of lowland species

While many *Nepenthes* species have developed intricate ways to trap insects, others have evolved strategies to maintain viability in resource-limited surroundings. In the unpredictable and often harsh conditions of the rainforest, finding a consistent food source can be difficult. Research reveals how *Nepenthes* have adapted by shifting focus away from carnivory alone, developing traits that allow them to exploit new resources or thrive in a wider range of environments. These adaptations highlight the resilience and versatility of the genus in the face of constant environmental challenges. As insects can be a scarce resource for *Nepenthes*, instead other methods must be devised to acquire essential nitrogen for growth. For *Nepenthes ampullaria*, this means focusing its attention on falling leaves (Candeias 2016). *N. ampullaria* grows throughout the Malesian floristic region in southeastern Asia and can be found in lowland tropical forests including peat swamps and shaded

nutrient-poor areas (Kiew 2012). Kiew notes that while *N. ampullaria* may be observed climbing, growing “to about 15 m tall with a stem 1–1.5 cm thick,” its pitchers are most typically found covering the low-lying areas, forming dense regions of confluent growth. Falling leaves are abundant here with leaf litter coating the lowland rainforest floors of *N. ampullaria*’s home. The plant sits with its mouth wide open, letting the leaf litter pile in its cups. To maximize their adaptations, *N. ampullaria* has urn-like pitchers – its peristome forms a circle, and slopes downward toward the digestive fluid. Normally, the lid of *Nepenthes* would prevent leaves and water from falling into the pitcher, but for *N. ampullaria*, this is no issue. As reported by Candeias (2016), the lid of *N. ampullaria* is vestigial and lacks nectar production. The waxy layer that normally coats the inside of the pitcher to prevent bugs from leaving is not present, hinting at the plant’s unique method of survival. In fact, the pitchers of *N. ampullaria* make excellent and enduring homes for an inquiline community of insects and even frog larvae, lasting up to 6 months (Candeias 2016). With these novel adaptations, it is estimated that *N. ampullaria* receives 35.7% of its foliar nitrogen through leaf litter (Moran *et al.* 2003).

Nepenthes mirabilis is the most widespread species of pitcher plant – its species covers from China to Australia (Lavarack 1977). Unlike *N. ampullaria*, which supplements nutrients by capturing leaf litter, *N. mirabilis* relies more heavily on insect prey for nitrogen acquisition. Like many carnivorous species, its pitchers are adapted to efficiently trap insects using slippery surfaces and digestive fluids. However, its tolerance for varied habitats and soil conditions also hints at a flexible strategy for survival in nutrient-poor environments. Like *N. ampullaria*, *N. mirabilis* is a lowland species found typically from near sea level to 300 m (Druce 1917). While *N. mirabilis* grows pervasively in swampy locations of East Asia and Southeast Asia, it can also be occasionally found in drier areas and can tolerate a wide range of temperatures, demonstrating extraordinary survival capabilities (Lavarack 1977). Lavarack noted that the plants can withstand a great variety of soil types, ranging from peaty to gritty, remarking “I have quite often seen plants growing in dry sandy soil in full sun.” *N. mirabilis* prefers partial shade, growing up to 10 m in these conditions, but can grow healthily fully exposed, even in areas where the soil may completely desiccate during a long dry season (Lavarack 1997). Lavarack also notes a “peculiar relationship between insect larvae and the pitchers,” with certain species of mosquito breeding within the pitchers and other insects thriving in the “same fluid that means death to most.” *N. mirabilis* demonstrates considerable resilience in variable lowland climates, and alongside its sustained dependence on insect prey, highlights its dual strategy of environmental tolerance and efficient carnivory.

Mutualism with animal species

Nepenthes have adapted to their environment with the formation of complex symbiotic relationships with other organisms, including mammals and insects. These partnerships, which often involve the exchange of resources, underscore the plants’ ability to survive in rainforest environments. Through these symbiotic interactions, *Nepenthes* have developed tactics that increase the likelihood of survival and growth in challenging ecosystems. One of the most remarkable examples of mutualism described in the literature is found in *Nepenthes lowii*, which has co-evolved with tree shrews (*Tupaia montana*); the plant provides sugary nectar, attracting tree shrews that in return, deposit nutrient-rich feces into the pitcher. Over time, *N. lowii* has developed a distinctive toilet-shaped pitcher, complete with a large, flared peristome and a concave lid which invites and encourages “*T. montana* to sit astride the pitcher whilst feeding, facilitating fecal deposition” (Clarke

et al. 2010). This same shape can also be appreciated in *N. lowii*-hybrid cultivars, such as the author's *Nepenthes* 'Peter D'Amato' specimen (Fig. 1). Clarke notes that with this distinct shape, *N. lowii* is largely ineffective in capturing prey and relies heavily on this mutualistic relationship, with between 57% and 100% of its nitrogen intake derived from tree shrew feces. *Nepenthes lowii* is not the only "toilet pitcher." *Nepenthes macrophylla* and *Nepenthes rajah* have both evolved similar adaptations and have fine-tuned their relationship with *T. montana*. Notably, the distance from the end of the peristome to their lid is the exact average body length of the tree shrew. While the morphology of these three *Nepenthes* species correlates closely with that of the shrew, only *N. macrophylla* and *N. rajah* are closely related genetically to each other, an example of convergent evolution between those species and that of *N. lowii* (Thorogood *et al.* 2018). However, the reliance on *T. montana* comes with a major caveat: the "poop eaters" are essentially restricted to habitats above 1800 m in elevation. The tree shrew's diet mainly consists of figs and other fleshy fruits commonly found at lower elevations, but not abundant in the mountain environments. Since *T. montana* prefers these foods, the mutualistic relationship with pitcher plants does not occur at lower altitudes. As a result, *N. lowii*, *N. macrophylla*, and *N. rajah* are limited to alpine habitats, where *T. montana* must depend on them for food (Clarke *et al.* 2010).

In a similar fashion, *Nepenthes hemsleyana* relies on feces as its primary source of nitrogen but has adapted to attract a different partner – the Hardwicke's woolly bat (*Kerivoula hardwickii*). As reported in *National Geographic* by Ed Yong (2015), instead of offering nectar, *N. hemsleyana* provides shelter for the woolly bat, functioning almost like a "bat landlord" renting out a property. Its pitchers have abnormally low digestive fluid level, yet are extremely tall and cylindrical, making it ideal to accommodate its tenants. Yong's research reveals that woolly bats contribute nutrient-rich droppings, whose nitrogen is absorbed by the plant and used to grow. To ensure its guests find the right home, *N. hemsleyana* has evolved a unique auditory adaptation: the back wall of its pitcher is widened and curved, acting "like a parabolic dish...[which] strongly reflects incoming ultrasound" of the bat's echolocation calls, an adaptation that guides the bat to safe shelter in the vast rainforests of Borneo (Yong 2015).

Vincent Bazile and colleagues (2012) investigated *Nepenthes bicalcarata*, which has forged a remarkable partnership with ants, using its two fang-like protrusions to house some of the largest nectar glands of any plant and support symbiosis with *Camponotus schmitzi*, a species of carpenter ant native to Borneo. *Nepenthes bicalcarata* provides *C. schmitzi* with both food and



Figure 1. *Nepenthes* 'Peter D'Amato' specimen, a hybrid of *N. lowii* and *N. ventricosa*. The toilet-shaped peristome configuration of the "poop eater" *N. lowii* persists in this hybrid cultivar.

shelter, offering a swollen tendril ideal for housing ant larvae and a constant supply of nectar. Unlike other pitcher plants, *N. bicalcarata* is relatively ineffective at capturing prey on its own. Bazile found that its pitcher fluid is less acidic and viscous than that of other *Nepenthes* species, and it contains fewer digestive enzymes. Additionally, its pitcher walls are not particularly slippery, allowing some insects to climb out of what could otherwise be a deadly trap. This favors a mutualistic interaction with ants, contributing significantly to nutrient uptake in the plant species. Colonies of *Camponotus schmitzi* live exclusively on *N. bicalcarata* in the wild, making them dependent on the plant for survival. Bazile also observed the ants roosting inside the plant's tendril, which provides an ideal shelter for their queen and larvae. The fangs of *N. bicalcarata* contain massive nectar glands that feed the entire colony. In return, worker ants clean the plant's peristome, removing fungi and pests, which increases the effectiveness of the trap (Thornham *et al.* 2011). Most importantly, *C. schmitzi* aids in digestion. The prey insects that hang precariously on the fangs, lured by the sweet nectar, often lose their footing and tumble into the trap. When prey falls into the pitcher, the ants attack—demonstrating “an unusual and specific swimming behaviour” (Bazile *et al.* 2012). They break down the captured insects into smaller pieces and consume what they need, leaving behind nutrient-rich undigested remnants, as well as the ant's feces that *N. bicalcarata* then digests. This highly productive partnership may contribute to *N. bicalcarata*'s exceptional tenacity, as its vine can climb up to 20 m high (Bazile *et al.* 2012; Clarke 1997).

Conclusion

The adaptations seen across *Nepenthes* species highlight that evolutionary success in nutrient-poor habitats is not driven by a single strategy, but by a wide range of distinctive innovations. Whether it is through slippery peristomes and viscous digestive fluids to mutualistic relationships with mammals and insects, each species reflects a tailored response to ecological challenges. Even species like *Nepenthes inermis*, which at first appear minimalistic and ill-equipped, reveal complex and highly specialized strategies beneath their simple appearance. These diverse strategies not only underscore the ecological versatility of the genus but also provide valuable insight into broader evolutionary processes. Future research into the genetic and biochemical mechanisms underlying the traits will deepen our understanding of plant adaptations. Ultimately, *Nepenthes* stands as a compelling model for how life evolves to meet adversity through innovation.

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Chlorophyll-free underground shoots and pitchers of *Nepenthes rhombicaulis*, a species apparently specialised for subterranean carnivory. Photograph of a cultivated plant by M. Golos. Article on page 122.