Observations of subterranean pitchers in cultivated *Nepenthes rhombicaulis*

Michal R. Golos • Department of Biosciences • University of Exeter • Stocker Road • Exeter EX4 4QD • UK • m.golos@exeter.ac.uk
Paul Leach • The Plant Project • Chester Zoo • Cedar House • Caughall Road • Upton-by-Chester • Chester CH2 1LH • UK • p.leach@chesterzoo.org

Keywords: carnivory, cultivation, ecology, growth habit, leaf economics, Nepenthaceae, pitcher polymorphism, plant architecture, Sumatra, underground
Received: 29 August 2025
https://doi.org/10.55360/cpn544.mg739

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 Maulder[1]—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,

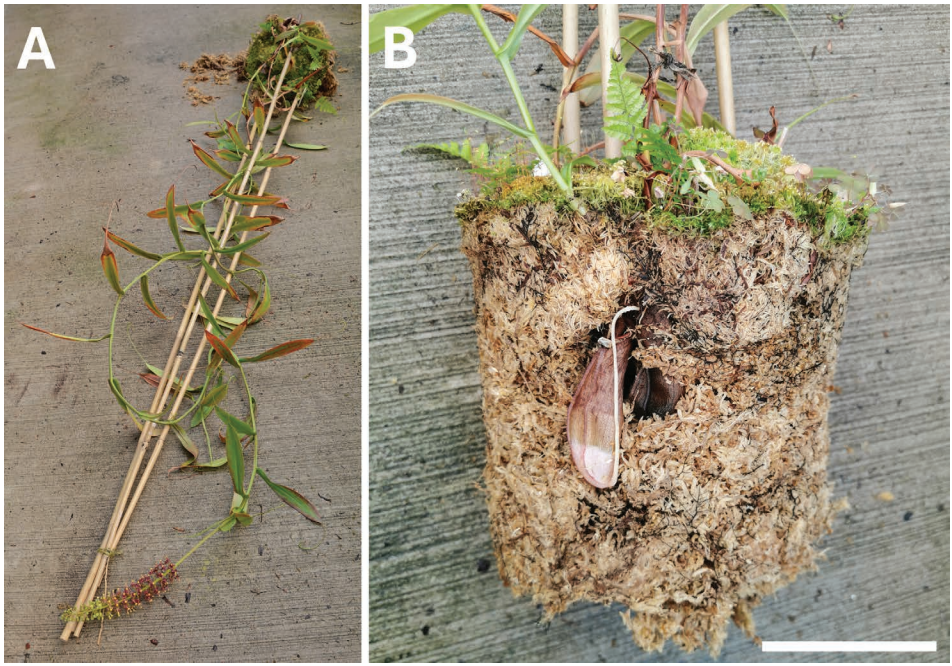

Figure 1. Typical growth habit of mature cultivated *Nepenthes rhombicaulis*. (A–B) Plant 1: male flowering plant with a single, small aboveground rosette pitcher and much larger and more numerous subterranean traps; note the long, entirely pitcherless climbing stems (>2 m long), typical of all the plants 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).

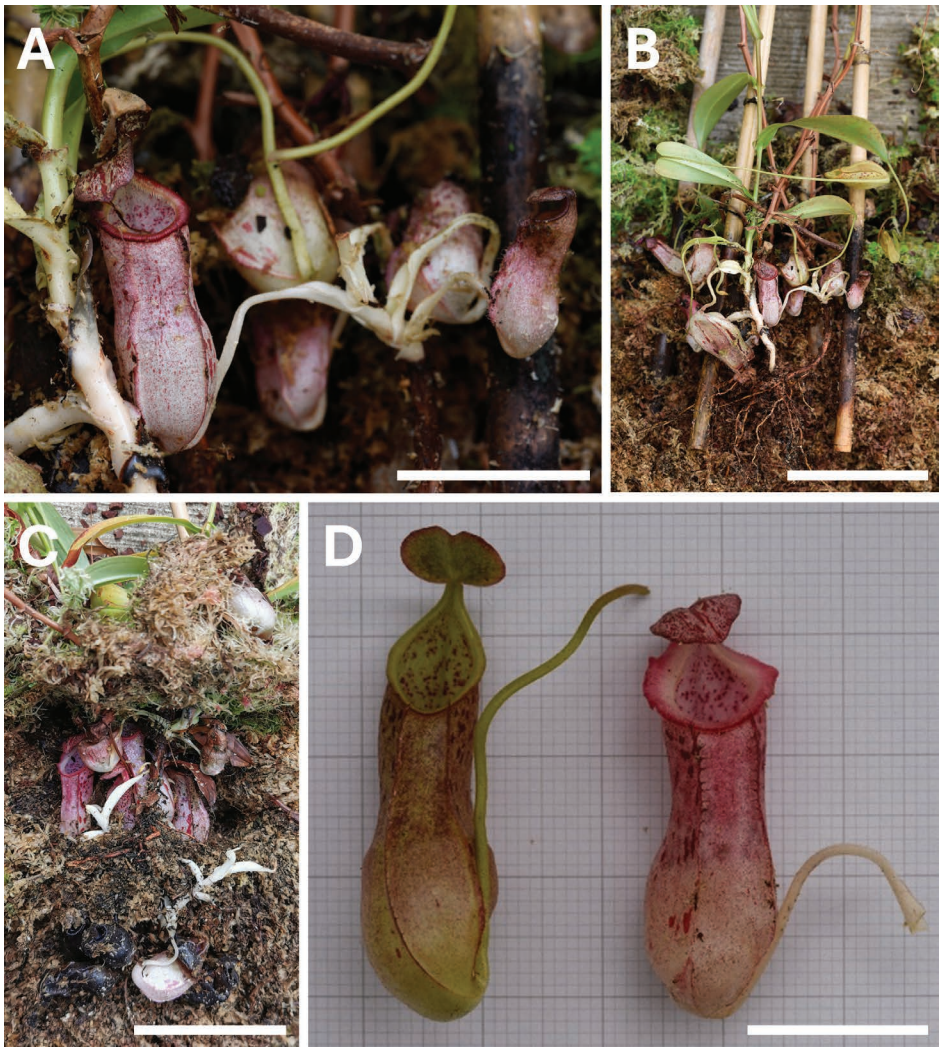

Figure 2. Underground and aboveground lower rosette pitchers of mature cultivated *Nepenthes rhombicaulis*. (A–B) Plant 2: this specimen bore seven active growth points, including four pitcherless, basally woody vines between 90 and 230 cm long and three younger shoots with active subterranean pitchers (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 leaves[4], 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)

Ecological context

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.

Acknowledgements: We gratefully acknowledge Jaehan Bae, Ricky Maulder, Alastair Robinson, and Bruce Salmon for sharing information and photographs of their field observations of *Nepenthes rhombicaulis*. François Sockhom Mey and Alastair Robinson are thanked for useful comments that helped to improve the manuscript. Mitsuyasu Hasebe is thanked for help with tracking down sources. P. Leach additionally wishes to thank Chester Zoo for their continued support over many years.

References

Anon. 1995. About our covers this month. Carnivorous Plant Newsletter 24(2): 31+ fig. on front cover. https://doi.org/10.55360/cpn242.pd956

Cheek, M.R. 2015. *Nepenthes* (Nepenthaceae) of Halmahera, Indonesia. Blumea 59(3): 215–225. https://doi.org/10.3767/000651915X689091

Cheek, M.R., and Jebb, M.H.P. 2001. Flora Malesiana. Series I – Seed plants. Volume 15: Nepenthaceae. Nationaal Herbarium Nederland, Leiden.

Clarke, C.M. 1997. Another nice trip to Sumatra. Carnivorous Plant Newsletter 26(1): 4–10. https://doi.org/10.55360/cpn261.cc173

Clarke, C.M. 2001. *Nepenthes* of Sumatra and Peninsular Malaysia. Natural History Publications (Borneo), Kota Kinabalu.

D'Amato, P. 1998. The Savage Garden: Cultivating Carnivorous Plants. Ten Speed Press, Berkeley.

Dančák, M., Majeský, L., Čermák, V., Golos, M.R., Płachno, B.J., and Tjiasmanto, W. 2022. First record of functional underground traps in a pitcher plant: *Nepenthes pudica* (Nepenthaceae), a new species from North Kalimantan, Borneo. PhytoKeys 201: 77–97. https://doi.org/10.3897/phytokeys.201.82872

Dávila-Lara, A., Reichelt, M., Wang, D., Vogel, H., and Mithöfer, A. 2021. Proof of anthocyanins in the carnivorous plant genus *Nepenthes*. FEBS Open Bio 11(9): 2576–2585. https://doi.org/10.1002/2211-5463.13255

Gilbert, K.J., Armitage, D., Bauer, U., Fukushima, K., Gaume, L., Love, R., Lin, Q., Liu, S., Martin-Eberhardt, S., Millett, J., Renner, T., Scharmann, M., and Thorogood, C. 2025. Construction costs and tradeoffs in carnivorous pitcher plant leaves: towards a pitcher leaf economics spectrum. Annals of Botany 135(7): 1261–1280. https://doi.org/10.1093/aob/mcaf024

Golos, M.R., Robinson, A.S., Barer, M., Dančák, M., De Witte, J., Limberg, A., Noorhana, M.S., and Tjiasmanto, W. 2020. *Nepenthes fractiflexa* (Nepenthaceae), a new Bornean pitcher plant exhibiting concaulescent metatopy and a high degree of axillary bud activation. Phytotaxa 432(2): 125–143. https://doi.org/10.11646/phytotaxa.432.2.3

Green, S. 1967. Notes on the distribution of *Nepenthes* species in Singapore. The Gardens' Bulletin Singapore 22(1): 53–65. https://biodiversitylibrary.org/page/43647258

Hernawati, and Akhriadi, P. 2006. A Field Guide to the *Nepenthes* of Sumatra. PILI-NGO Movement, Bogor.

Hopkins, M., Maulder, R., and Salmon, B.R. 1990. A real nice trip to Southeast Asia. Carnivorous Plant Newsletter 19(1–2): 19–28. https://doi.org/10.55360/cpn191-2.mh330

Jebb, M.H.P. 1991. An account of *Nepenthes* in New Guinea. Science in New Guinea 17(1): 7–54.

JIPS. 2000. *Nepenthes rhombicaulis* Sh.Kurata. JIPS Carnivorous Plant Database. (in Japanese) https://web.archive.org/web/20021119140228/http://www.cam.hi-ho.ne.jp/jips/NepPhoto/Spec/rhombica.html

Karagatzides, J.D., and Ellison, A.M. 2009. Construction costs, payback times, and the leaf economics of carnivorous plants. American Journal of Botany 96(9): 1612–1619. https://doi.org/10.3732/ajb.0900054

Kurata, S. 1973. *Nepenthes* from Borneo, Singapore and Sumatra. The Gardens' Bulletin Singapore 26(2): 227–232. https://www.biodiversitylibrary.org/page/43625346

McPherson, S.R. 2009. Pitcher Plants of the Old World, 2 vols. Redfern Natural History Productions, Poole.

McPherson, S.R. 2023. *Nepenthes*: The Tropical Pitcher Plants, 3 vols. Redfern Natural History Productions, Poole.

Mio, K. 2010. 三尾和久: 北スマトラ·トバ湖周辺の *Nepenthes* を訪ねて [Visiting *Nepenthes* around Lake Toba, North Sumatra]. The Journal of Insectivorous Plant Society 61(3): 59–60 + figs. on front & back covers. (in Japanese)

Osunkoya, O.O., Daud, S.D., Di Giusto, B., Wimmer, F.L., and Holige, T.M. 2007. Construction costs and physico-chemical properties of the assimilatory organs of *Nepenthes* species in northern Borneo. Annals of Botany 99(5): 895–906. https://doi.org/10.1093/aob/mcm023

Osunkoya, O.O., Daud, S.D., and Wimmer, F.L. 2008. Longevity, lignin content and construction cost of the assimilatory organs of *Nepenthes* species. Annals of Botany 102(5): 845–853. https://doi.org/10.1093/aob/mcn162

Plant Heritage. 2015. UK's largest collection of carnivorous plants at Chester Zoo awarded National Plant Collection status. NCCPG News, 23 February 2015. https://www.nccpg.com/news/uks-largest-collection-of-carnivorous-plants-at-c.html

Plant Heritage. n.d. National Plant Collections: *Nepenthes*. Plant Heritage. https://www.plantheritage.org.uk/national-plant-collections/search-the-national-plant-collections/collection/1735/nepenthes

Robinson, A.S. 1995. *Nepenthes rhombicaulis.* CPS News [1995](3): 10.

Salmon, B.R. 1993. Some observations on the trapping mechanisms of *Nepenthes inermis* and *N. rhombicaulis*. Carnivorous Plant Newsletter 22(1–2): 11–12. https://doi.org/10.55360/cpn221-2.bs260

Schmid-Hollinger, R. 1994. More knowledge about *Nepenthes rhombicaulis*. Carnivorous Plant Newsletter 23(3): 62–63. https://doi.org/10.55360/cpn233.rs994

Smith, A. 2015. First time for me….an upper pitcher on *Nepenthes rhombicaulis*. Facebook, 30 November 2015. https://www.facebook.com/groups/292670740824091/permalink/894202797337546/