

OBSERVATIONS OF THE NATURAL HISTORY AND ECOLOGY OF
NEPENTHES CAMPANULATA

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Abstract: *Nepenthes campanulata* is a little known species from limestone cliff habitats in Borneo. In this study, we conducted the first field-based survey of pitcher dimensions and the prey and invertebrate fauna in *N. campanulata* pitchers, sampled from plants growing on the cliff face above Deer Cave in Gunung Mulu National Park. We found that the dominant prey taxon is Diptera, followed by Formicidae. The metazoan community that inhabits the pitchers consists of just three species, making it one of the simplest in the genus. The pitchers of *N. campanulata* have a unique structure among *Nepenthes*, which may be related to the highly specialized habitat that the plant occurs in. Prior to this study, *N. campanulata* had been recorded at just two localities: Mt. Ilas Bungan in East Kalimantan, and Gunung Mulu National Park in Sarawak. However, on a recent expedition to Palawan, we observed plants that we identified as *N. campanulata*, which represents a remarkable extension to the geographical range of this species.

Introduction

Nepenthes campanulata is one of the most unusual and poorly documented of all *Nepenthes* species. It is remarkable for the compact stature of the plant and its small, yellow, bell-shaped pitchers, which give the plant its species name (Fig. 1). In terms of pitcher structure, the most similar species appears to be *Nepenthes inermis* from Sumatra, but these similarities are superficial – the upper pitchers of *N. inermis* lack a peristome entirely, and the inner surfaces are entirely glandular, lacking a layer of wax crystals. By contrast, the pitchers of *N. campanulata* have a minute, toothed peristome and a well-developed waxy zone that covers most of the inner surfaces of the pitchers. As we shall see below, the structure of *N. campanulata*



Figure 1: Close-up of a *Nepenthes campanulata* plant growing on a sheer limestone cliff face above Deer Cave, Gunung Mulu National Park, Sarawak.

pitchers is in fact unique among *Nepenthes*, and the results of recent ecological research into the genus allows us to propose – for the first time – how they might have evolved.

Nepenthes campanulata was first described by Kurata (1973). The description was based on a specimen collected in 1957 by A.J.G.H. Kostermans (*Kostermans 13764*, SIN) that was deposited at the Singapore Herbarium. The type locality was stated as “Mt Ilas Bungaan” in eastern Borneo. According to Kurata (1973), Kostermans trekked for 14 days to reach Mt. Ilas Bungaan, the face of which was said to be “completely overgrown with flowers”. The “flowers” were in fact pitchers of *N. campanulata*. Until relatively recently, the precise location of Mt. Ilas Bungaan remained unknown to all but Kostermans. Eventually, the location was rediscovered, but recent visits to the type location (Mt. Ilas Bungaan) in eastern Borneo revealed that much of the vegetation on the mountain has been burned off, and no *N. campanulata* plants remained. As no other populations of *N. campanulata* were known at that time, it was thought that the species might be extinct.

In 1997, one of us (CL) discovered a population of *N. campanulata* in Gunung Mulu National Park in Sarawak. As with the type locality, the plants were found to be growing on steep limestone cliffs (Fig. 2). Remarkably, the distance between the Sarawak population and the type locality was over 400 km, with no obvious sites in between that could feasibly be colonized by *N. campanulata*. In 1998, voucher specimens were obtained from the Mulu site and deposited in the Kuching Herbarium (Borneo, Sarawak, Taman Negara Mulu, Batu Pajing, *C. Lee S 87440* (SAR); *C. Lee S 87441* (SAR)). Subsequent expeditions to Gunung Mulu National Park by C. Lee revealed that *N. campanulata* grows on several sheer limestone cliffs there, but nowhere easily accessible, with all plants growing between 100-300 m above sea level.

Within this habitat, *N. campanulata* is apparently quite specialized, and has been observed to grow only on sections of the cliff, which are rarely exposed to rain. These sites are easily distinguished by the white color and relatively smooth surface of the rock as opposed to a gray and often sharply eroded surface. Such zones remain dry either due to the overhanging angle of the cliff or the fact that rain predominantly blows from a direction which does not often strike the vertical face. Plants of *N. campanulata* typically grow with their roots embedded within spongy, often moist, tufa formations, and therefore must derive much of their water from that which seeps through the limestone.

Although *N. campanulata* has been rediscovered and its habit and habitat observed through binoculars and telephoto lenses, many aspects of its natural history have yet to be documented, because of the extreme challenges associated with physically reaching the plants on the high, vertical cliffs



Figure 2: Plants of *Nepenthes campanulata* growing on the limestone cliff near the entrance of Deer Cave in Gunung Mulu National Park, Sarawak.

Table 1. Average dimensions of <i>Nepenthes campanulata</i> pitchers.		
Pitcher characteristic	Mean	Standard deviation
Capacity (ml)	24.06	11.77
Height (mm)	9.31	1.80
Orifice diameter (front to rear) (mm)	3.68	0.94
Orifice diameter (side to side) (mm)	4.19	0.86
Lid length (mm)	3.44	0.80
Lid width (mm)	2.92	0.57
Hip position (distance from base to hip) (mm)	3.74	0.61
Hip diameter (front to rear) (mm)	2.37	0.46
Hip diameter (side to side) (mm)	2.44	0.51

on which they grow. For several years, it seemed that the logistical challenges to studying this plant in the wild could never be overcome, but in 2011, we had a unique opportunity to study *Nepenthes campanulata* in its natural habitat.

During filming for a television documentary, a film crew managed to abseil down the cliff above Deer Cave to film millions of free-tailed bats emerging from the cave at sunset. Several plants of *N. campanulata* grow on this cliff face, and as one of us (CL) also has the necessary skills and experience to abseil down this cliff, we managed to obtain permission to visit these plants and collect the contents of some pitchers, so that we could learn more about what sorts of insects *N. campanulata* traps, and what sorts of animals live in its pitcher fluid.

In addition, during a recent field trip to Palawan in the southern Philippines, we observed plants growing on limestone cliffs that we identified as *N. campanulata*. This represents a remarkable extension to the geographical range for this species, and gives us cause to reconsider the phylogeographic relationships between Borneo and Palawan with regards to the evolution and diversification of *Nepenthes*.

Methods

The habitat of *N. campanulata* is virtually inaccessible to humans. Aside from a small number of stray plants, the majority of plants grow approximately 200 m above the ground on sheer limestone cliffs above the entrance to Deer Cave in Gunung Mulu National Park. The only way to reach them is to abseil down to them from the top of the cliff, some 50 m above the plants. The undulating surface of the rock, along with sharp ridges and shelves, makes this a perilous activity. To survey the plants in their natural habitat, rope lines were anchored near the top of the cliff and Ch'ien abseiled down to the plants (Front Cover). Due to the slightly overhanging slope, it was necessary to use multiple anchor points down the cliff face in order to stay in close proximity with the rock. After surveying the plants and obtaining prey samples, Ch'ien ascended the fixed lines back to the top of the cliff.

A total of 17 *N. campanulata* pitchers were observed, measured, and their contents analyzed using a Nikon Stereomicroscope. Identifiable prey were sorted, counted and identified to Order. Infaunal organisms were identified to genus (or species) where possible. The food web diagram was drawn in accordance with the methods of Clarke & Kitching (1993). Pitcher dimensions were measured to the nearest mm, using the methods of Chin *et al.* (2010).

Field work was conducted in accordance with Sarawak Forestry Permit Number 22/2011. Permission to abseil down the cliff face above Deer Cave was granted by the management of Gunung Mulu National Park.

Results & Discussion

Pitcher dimensions

The pitchers of *N. campanulata* are comparatively small (Table 1), with a height similar to that of *N. gracilis* pitchers (Clarke & Kitching 1993). However, the average (± 1 S.E.) capacity of *N. campanulata* pitchers appears to be somewhat greater than *N. gracilis* (24.06 ± 2.68 ml versus 14.40 ± 1.17 ml ($n = 20$)), due to the bell-shaped structure of *N. campanulata*. The waxy zone of *N. campanulata* pitchers extends from the orifice down to the hip, which is located approximately one third of the way up from the base. The position of the hip, coupled with the narrow dimensions of the pitcher in the lower third, strongly constrains the volume of fluid that the pitchers can accommodate. Although we were unable to accurately measure pitcher fluid volumes, these appear to be consistently less than 5 ml.

Prey capture

N. campanulata traps mostly small flies and ants, along with the occasional beetle, cricket, or moth (Fig. 3). This prey-capture profile is typical for a species with small, yellow pitchers that are produced at or above canopy level (Moran 1996; Bonhomme *et al.* 2011). However, it is highly atypical for a species that has a reduced peristome and well-developed waxy zone. The small peristome/well-developed waxy zone character combination has been referred to in recent ecological studies as “dry type”. The pitchers of most *Nepenthes* species can be divided into two groups, called “wet type” and “dry type” (Bauer *et al.* 2012; Moran *et al.* 2013). Wet type pitchers tend to have a broad peristome and a reduced (or no) waxy zone. The peristome relies on moisture to function, and so species with “wet type” pitchers are confined to habitats that are almost permanently moist. By contrast, dry type pitchers have narrower peristomes and well-developed waxy zones. While the peristomes of dry type pitchers are less effective than those of wet type ones, the waxy zone remains effective even if the weather is dry. Furthermore, the wax crystals are better at retaining water than glandular surfaces, so dry type pitchers are more efficient in places where occasional, short term water deficiencies occur.

One thing that is intriguing about the prey caught by *N. campanulata* pitchers is that dry type pitchers are thought to be more effective

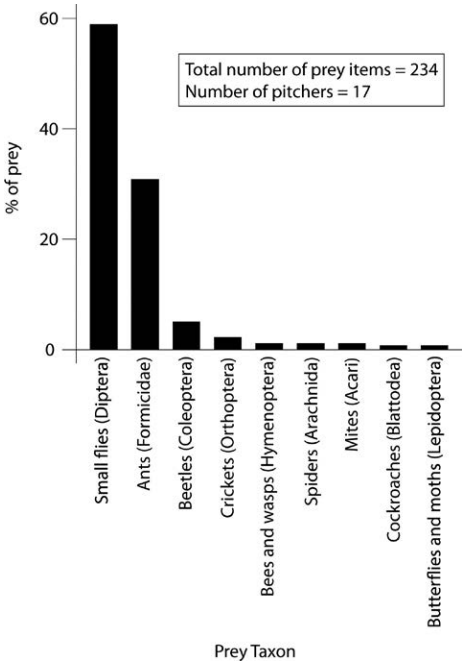


Figure 3: Histogram showing the proportional composition of arthropod prey taxa in *Nepenthes campanulata* pitchers.

at trapping crawling prey, such as ants, and less effective at trapping flying prey, such as small flies (Bonhomme *et al.* 2011; Bauer *et al.* 2012; Moran *et al.* 2013). In this respect, our findings for *N. campanulata* pitchers are counter-intuitive and suggest that the dry-type pitcher format may also be highly effective at trapping flying prey. Moran *et al.* (2013) contend that the geographical distribution of trap types is governed solely by climate. Our findings support this assertion – most likely, the structure of *N. campanulata* pitchers reflects the highly specialized environment that *N. campanulata* occurs in, rather than specializations to target any specific type of insect prey.

It should be noted that our sample size is small, and our observations were based on a single sampling event, so there is potential for error in our findings and interpretations. That said, similar sample sizes have been used in other surveys of prey capture by *Nepenthes* and we feel that our results are likely to be representative, at least as far as rates of capture of Diptera and Formicidae are concerned. While there is a patent need for further, more detailed observations of prey capture by *N. campanulata* pitchers, the logistical challenges to doing this are extreme, and at present, there is little chance of these being overcome.

Invertebrate fauna

With only three species, the metazoan infauna of *N. campanulata* pitchers is one of the simplest recorded to date (Fig. 4) (Beaver 1985). Larvae of the mosquito, *Tripteroides nepenthis*, feed on the remains of captured insects, breaking down the carcasses and increasing the rate of digestion of prey. This species is a common inhabitant of lowland *Nepenthes* pitchers in open, disturbed habitats throughout Borneo, as are mites of the genus *Zwickeya*. Somewhat surprisingly, we found that *N. campanulata* pitchers are also colonized by a species of *Toxorhynchites*, whose larvae are predators, feeding on the larvae of other mosquitoes and midges. Although the pitchers of several *Nepenthes* species from Borneo are colonized by *Toxorhynchites*, these larvae are generally found only in pitchers of *Nepenthes* species that have a rich infaunal community that contains several other mosquito and midge species. It remains to be seen whether *Toxorhynchites* is a regular colonist of *N. campanulata* pitchers, or whether it is an “accidental” colonist – with gravid females occasionally laying their eggs in *N. campanulata* pitchers, rather than larger congeners from nearby habitats, such as *N. faizaliana*, *N. reinwardtiana*, *N. ampullaria*, and *N. bicalcarata*.

Of the 17 pitchers we examined, nine had no metazoan infauna and a further two were colonized only by *Zwickeya* sp. mites. Compared to other lowland *Nepenthes* species from nearby Brunei, this is an extremely low rate of pitcher colonization (Clarke & Kitching 1993) and is similar to pitchers from sites that are the most marginal for infaunal organisms. This result suggests that the environment in which *N. campanulata* grows is extremely challenging for invertebrate larvae, and that only the most resilient species are able to colonize and persist in them.

The geographical range of *N. campanulata*

N. campanulata pitchers represent an extreme development of the dry type pitcher format. The peristome is reduced to such an extent that it is barely visible, but the waxy zone is very highly developed. This makes the pitchers

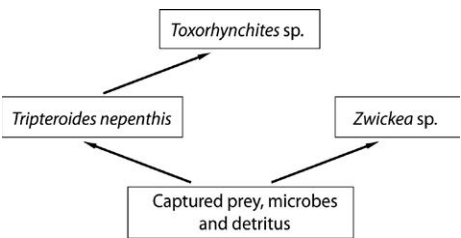


Figure 4: Summary metazoan food web for *Nepenthes campanulata* pitchers. Boxes represent metazoan species or sources of nutrition. Arrows show the directional transfer of energy/nutrients from one trophic level to the next.

effective arthropod traps even when the weather is comparatively dry. Water loss from pitchers is minimized by reducing the digestive zone to a small area at the bottom of the pitcher, with a correspondingly small quantity of pitcher fluid. In other words, most of the surface area of the trap is devoted to capturing and retention of prey, whereas only a small part is devoted to the digestion of prey. The bell-shaped structure does not prevent rainfall from entering, but because the plants often grow beneath overhangs on the cliff face, they rarely receive large quantities of direct rainfall, so a bell-shaped pitcher with a small lid is not a disadvantage. These pitcher characteristics are instructive with regards to the niches that *N. campanulata* colonizes on limestone cliff faces. If *N. campanulata* grew on the most exposed parts of the cliff faces, the pitchers would often overflow whenever it rains, and the plants would be subjected to far greater water stress during dry spells. By growing beneath rocky shelves (whose surfaces stay moist longer than in exposed sites) the pitchers are protected from direct rainfall.

Few limestone escarpments in Borneo have cliffs with the type of shelves and overhangs that *N. campanulata* colonizes, which is why the recorded range of this species is not greater (Fig. 5). However, a wider geographical range within Borneo is possible, for two reasons: (1) large areas of karst terrain exist in eastern Borneo, and few of these have been explored in any detail for *Nepenthes*, and (2) *N. campanulata* only colonizes sites with a specific combination of features (see above). Cliffs that lack these features are devoid of *N. campanulata* plants, and probably always have been.

In July 2013, during an expedition to Palawan, we surveyed a number of sheer limestone cliffs that form part of the Saint Paul formation, which seemed to possess similar characteristics of the



Figure 5: The extraordinary habitat of *Nepenthes campanulata*. Note the angle of the cliff face, which slopes inwards.



Figure 6: Plants that we identified as *Nepenthes campanulata* growing on a limestone cliff in the Saint Paul limestone region of Palawan.

cliffs at Gunung Mulu National Park above Deer Cave (including being several hundred meters in height!). Scanning the cliffs with binoculars, we found a *Nepenthes* growing in precisely the same habitat niche as *N. campanulata*. Furthermore, the plant stature and growth habit, leaf shape, short tendrils, and bell-shaped pitchers corresponded to *N. campanulata*. Although we were unable to get close enough to the plants to make detailed observations of minor morphological characteristics (Fig. 6), we concluded that they represent *N. campanulata*. Of course, it is feasible that closer examination of these plants could show them to be an undescribed, closely related species, but we are comfortable with our identification, which allows the Palawan populations to be included in existing frameworks for conservation assessments (such as the IUCN Red List). We acknowledge that our identification of these populations is likely to cause debate, but we view that as a good thing and look forward to seeing our judgment put to test in the near future!

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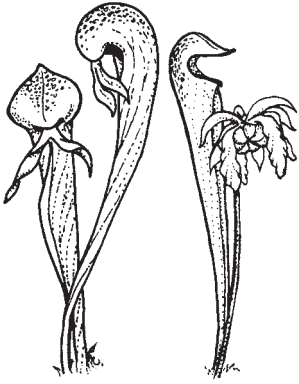
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Front Cover: Ch'ien Lee in the habitat of *Nepenthes campanulata*, suspended approximately 200 m above the ground, on the rock face above Deer Cave in Gunung Mulu National Park, Sarawak. Ch'ien removed his safety helmet to pose for this photograph. Article on page 7.

Back Cover: Geoff Wong at the Bay Area Carnivorous Plant Society Show and Sale June 15, 2013. Geoff was talking about the *Utricularia quelchii* that he donated to the auction. Photo by Jeremiah Harris. Article on page 4.

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