

Nepenthes holdenii (Nepenthaceae), a new species of pyrophytic pitcher plant from the Cardamom Mountains of Cambodia

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ABSTRACT

A new species of pyrophytic *Nepenthes* L. (Nepenthaceae), *Nepenthes holdenii* Mey, from the Cardamom Mountains of Cambodia, is described and illustrated. *Nepenthes holdenii* and its relatives are reclassified here within the *N. thorelii* aggregate. A key to the pyrophytic species of Indochina is also presented.

សេចក្តីសង្ខេប

មានរុក្ខជាតិថ្មីមួយប្រភេទ ដែលដុះលើដីស្ងួតរោលភ្លើង នៅជួរភ្នំក្រវាញ ទើបមានឈ្មោះហៅថា *Nepenthes holdenii* Mey សសរដោយលោកនិពន្ធម្ចី ហ្វ្រង់ស្វ័យ សុខុម ក្នុងអត្ថបទនេះ។ អ្នក និពន្ធបានចាត់ថា ក្នុងចំណោម *Nepenthes* មានក្រុមប្រភេទមួយ ហៅថា ក្រុម *Nepenthes thorelii*។ ក្នុងក្រុមនេះមានប្រភេទ *Nepenthes holdenii* និងប្រភេទខ្លះទៀតដែលដុះលើដីស្ងួតរោលភ្លើងនេះ។ អ្នកនិពន្ធបានពន្យល់ភាព និងសសរជាសាមញ្ញ សំរាប់អ្នកឈ្មោះប្រភេទ ដែលដុះលើដីស្ងួតរោល ភ្លើង នៃចុង *Nepenthes* នៅជួរភ្នំក្រវាញ។

RESUME

Une nouvelle espèce pyrophyte de *Nepenthes* L. (Nepenthaceae), *Nepenthes holdenii* Mey, originaire de la chaîne des Cardamones au Cambodge, est décrite et illustrée. *Nepenthes holdenii* et les taxa voisins sont ici regroupés au sein de l'agrégat de *N. thorelii*. L'article propose également une clé des espèces pyrophytes d'Indochine.

Key words: Cambodia, Cardamom Mountains, Indochina, *Nepenthes*, pyrophytes, taxonomy, *N. thorelii*.

INTRODUCTION

Cambodia's previously understudied biological diversity received significant attention in the last decade as a result of the research carried out by consortia of international and local scientists. During this period, many areas have been explored for the first time, revealing a rich flora and fauna, including many first records for the country, and the discovery of several endemic taxa new to science (Daltry & Wüster, 2002; Liu & Chen, 2002; Haitlinger, 2004; Csorba *et al.*, 2005; Motomura & Mukai, 2006; Grismer *et al.*, 2007; Thomas *et al.*, 2007; Wilkie, 2007; Neang & Holden, 2008; Rawson & Roos, 2008). The increasing number of species recorded in Cambodia in recent time reflects the greater understanding of Cambodia's biodiversity, particularly when assessed in the context of Cambodia's near neighbours. Ashwell (1997) gathered all available information concerning Cambodia's natural resources including 2308 species of vascular plants and noted that, "it is clear that there are many more species yet to be discovered" (Ashwell, 1997). This assertion is even more pertinent when one considers the scattered or incompletely published information for many taxa. The majority of publications focused on birds, mammals and other vertebrates (Delacour & Jabouille, 1925; Engelbach, 1953; Saint Girons, 1972; Desay & Lic, 1996). In the editorial for the first issue of "*Cambodian Journal of Natural History*", Daltry (2008) stated that, "the number of known plants is also rising steadily, although many hundreds of specimens collected in recent years remain unidentified." Daltry (2008) emphasised that the number of documented

plant and animal species will continue to increase and that “Cambodia’s biodiversity is far from being fully documented and understood.”

As a result of these increased efforts, the *Nepenthes* flora of Indochina has recently received significantly more attention from experts, making up for critical lack of research over a period that spanned from the early 20th century through to the start of the 21st century (Mey, 2009). This has included the description of several new taxa, namely *N. bokorensis* Mey (Mey, 2009) from Cambodia; and *N. thai* Cheek (Cheek & Jebb, 2009) *N. andamana* M. Catal., *N. chang* M. Catal., *N. suratensis* M. Catal., *N. mirabilis* (Lour.) Druce var. *globosa* M. Catal. and *N. kerrii* M. Catal. & T. Kruetr. (Catalano, 2010) from Thailand.

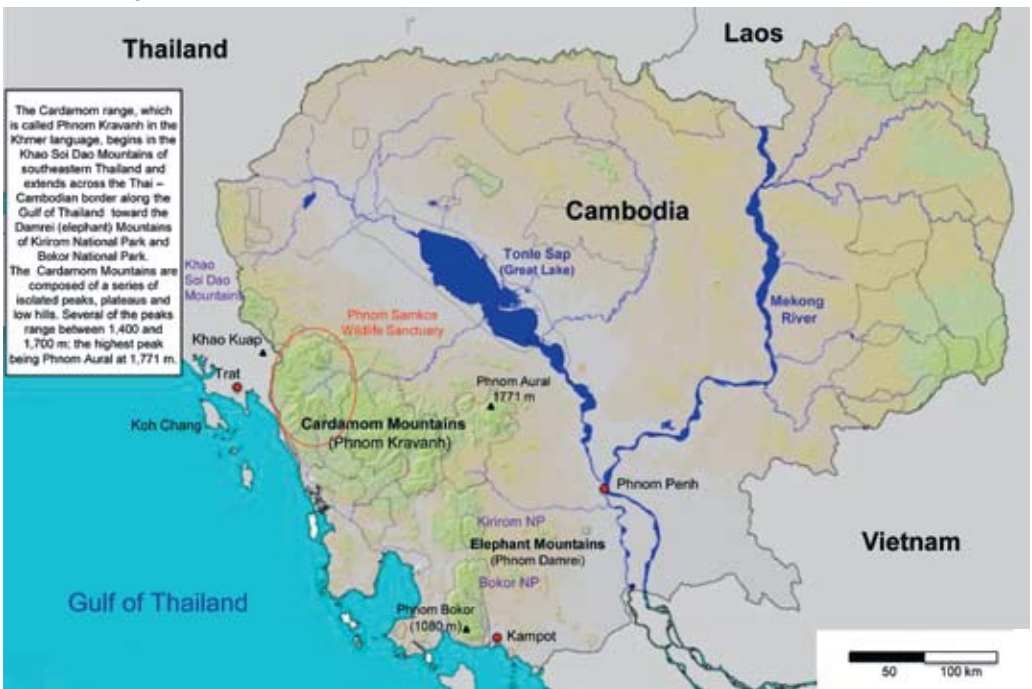
In 2008, photographer and biologist, Jeremy Holden, contacted the first author to study an apparently undiagnosed *Nepenthes* that he observed on an isolated peak from the Cardamom Mountains in Cambodia (Figure 767). This taxon was first observed during field surveys conducted for Fauna & Flora International (FFI) in the Phnom Samkos Wildlife Sanctuary in February 2006. Populations were seen in four different locations around a single mountain system (Figure 770), all in dry, steep terrain characterised by open areas of tall grasses and pine trees at 600-750 meters above sea level. Photographs were taken of these plants, but no specimens were collected until September 2008 (*Neang & Holden 1, 2, 3, 4, 5, 6* RUPP) (J. Holden, pers. comm.).

The Cardamom range, which is called Phnom Kravanh in the Khmer language, begins in the Khao Soi Dao Mountains of southeastern Thailand and extends across the Thai-Cambodian border along the Gulf of Thailand toward the Damrei (elephant) Mountains of Kirirom National Park and Bokor National Park. The Cardamom Mountains are composed of a series of isolated peaks, plateaus and low hills. Several of the peaks range between 1,400 and 1,700 m; the highest peak being Phnom Aural at 1,771 m. Vegetation in the range mainly consists of disturbed deciduous dipterocarp forests, in the lowland areas and evergreen hill forests along the slopes. Some of the peaks, such as Phnom Aural, to the northeast of the range, host undisturbed dipterocarp forests and

pristine evergreen forests, while the Central range includes pine forests and grasslands (Grismer *et al.*, 2008).

In August 2009, the author visited Cambodia together with J. Holden in order to study and collect the unidentified *Nepenthes*. During this expedition, a second population of the taxon was found on a neighbouring peak. Studies of the two populations *in situ* demonstrated that the taxon possesses a unique combination of features that distinguish it from all other known *Nepenthes* taxa. No other *Nepenthes* grow in the general vicinity of the two localities, much reducing the possibility of this taxon being a natural hybrid. Comparison of wild plants and herbarium material confirmed that this is an undescribed taxon. It appears to belong to a group of closely related Indochinese species that share similar ecological habitats; these taxa occur in seasonally dry savannahs or semi-deciduous monsoon forests prone to dry season fires (so-called “pyrophytes”). This group of pyrophytic *Nepenthes* is delimited and referred to in this paper as the *N. thorelii* aggregate.

Figure 767 (below). A Map of Cambodia. “Phnom” is the Khmer equivalent of the English “Mount”.



The description of the new taxon *Nepenthes holdenii* brings the number of Cambodian *Nepenthes* species to five, namely *N. bokorensis* Mey, *N. holdenii* Mey, *N. kampotiana* Lecomte, *N. mirabilis* (Lour.) Druce and *N. smilesii* Hemsl.

The description of *Nepenthes holdenii* is based upon the cited herbarium material as well as observations made of wild populations.

SPECIES DESCRIPTION

Nepenthes holdenii Mey, *spec. nov.* — Figures 767-782.

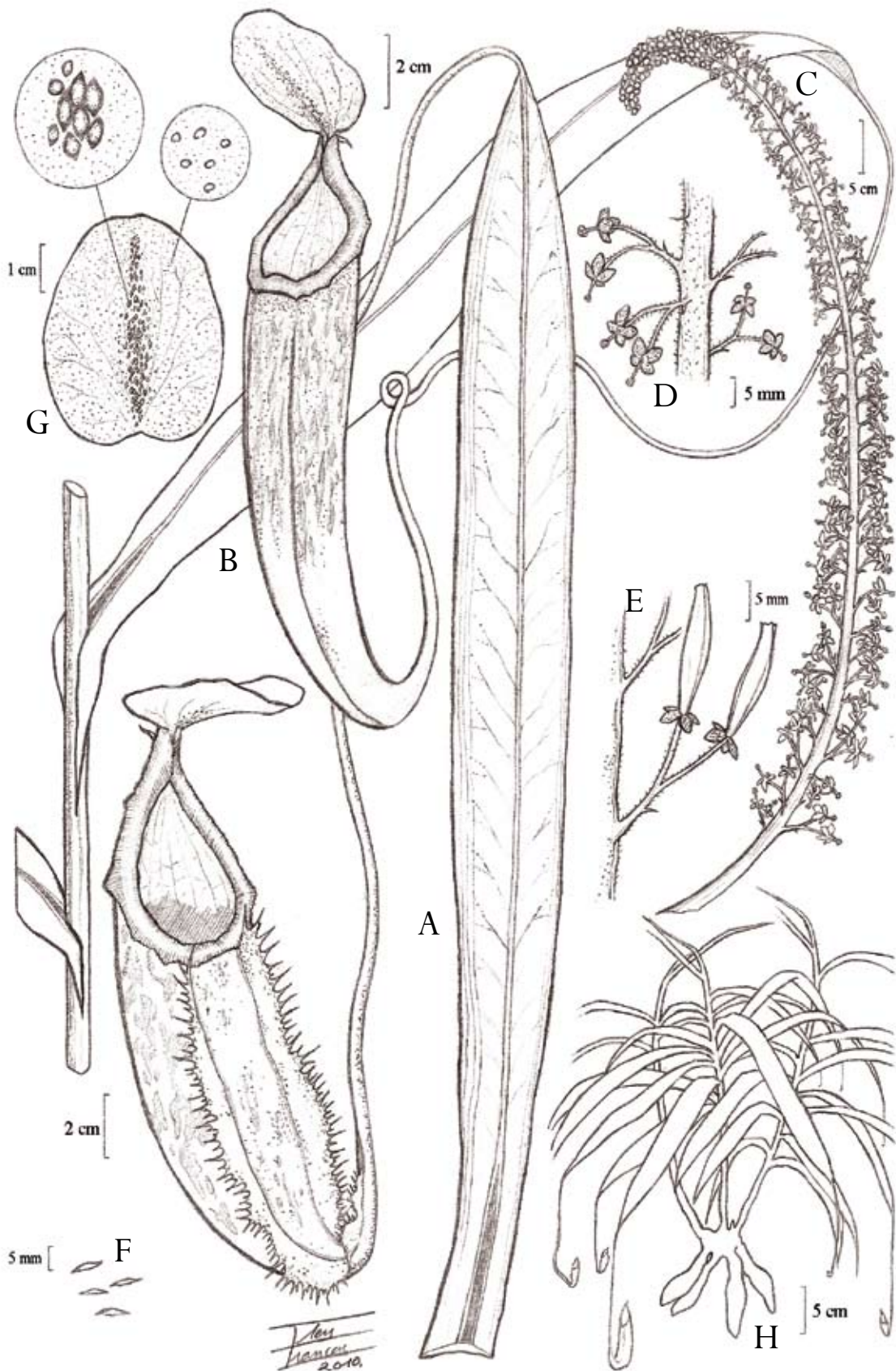
Diagnosis: *Nepenthi kampotianae* Lecomte similis sed floribus pedicellis 2-floris, foliis linearibus vel anguste-lanceolatis pubescentibus tantum ad axillas foliorum, ascidiis superioribus infundibuliformibus orificio dilatato et peristomio ascidii sinuolato differt.

Typus: *Mey 1A* (holotypus, RUPP; isotypi RUPP), western Cambodia, Cardamom Mountains, Province of Pursat, 653 m, 1 VIII 2009. Female plant with upper pitchers, infructescence and seed.

Nepenthes holdenii is most readily distinguished from its near relatives by the 2-flowered partial peduncles developed both in male and female inflorescences.

Terrestrial vine, with perennial rootstock producing annual large basal rosettes then climbing shoots to c. 5 m. over the course of the wet season. During the dry season, the plants lose most of their vegetative parts on account of drought and fires. **Roots** mainly composed of irregularly branched swollen tubers up to 25 mm thick. **Stem** terete, glossy, ca. 6-8 mm diam., internodes 2-3 cm long on rosette, 5-6 cm long on climbing stem. **Leaves** coriaceous, subpetiolate, lamina linear to linear-lanceolate, 25-40 cm long, 3.5-6 cm wide, apex acute, clasping the stem by 1/2 of its circumference, decurrent on rosette and on climbing stem on 3-4 cm projecting from the stem as wings; longitudinal nerves 3 (rarely 4) on each side of the midrib in outer third of

Figure 768 (facing page). An anatomical drawing of *Nepenthes holdenii* detailing (A) rosette leaf with lower pitcher, (B) climbing stem with upper pitcher, (C) rachis of male inflorescence, (D) detail of male inflorescence with bracts, (E) fruits, (F) seeds, (G) underside of lid with details of glands, (H) habit with rootstock.





May 1A

the lamina, inconspicuous, pennate nerves arising irregularly, oblique from midrib, sometimes branched, inconspicuous, midrib 1-2 mm wide; tendrils straight, terete, 1-2 mm in diameter, 15-25 cm in lower pitchers and 20-25 cm in upper pitchers, coiling. **Rosette and lower pitchers** 13-20 cm tall, 4-6 cm wide, ovate to ellipsoidal, not distinctly hipped; usually 50 to 60 % of the inner surface glandular in the basal half; two wings 15 mm wide run down ventral exterior surface from mouth to tendril, fringed with filiform segments up to 6-7 mm long; pitcher mouth steeply oblique, rising toward the lid; mouth ovate, peristome sinuate, striate, loosely cylindrical, up to 3 cm wide and flattened, ribs fine c. 0.6 mm apart and 0.3 mm tall; lid elliptic, base and apex slightly cordate, up to 5 cm long, 4 cm wide, not vaulted, margins slightly revolute, lower surface without appendage, but with numerous crateriform glands with striated sides, orbicular and larger, 0.8 mm across, along midrib, up to 130 per cm², elsewhere ovate, 0.2 mm across and up to 300 per cm²; spur 5-7 mm long, conical, simple or rarely bifurcated, inserted at base of lid, to 7 mm long. **Upper pitchers** similar, generally 25 cm tall, 6 cm wide, narrowly infundibular in the lower third, more broadly above, rarely slightly narrowed toward the mouth, not hipped, pitcher mouth less oblique than in lower pitcher; peristome sometimes slightly raised at the front to form a triangular point, sinuated, slightly striate, ribs fine c. 0.6 mm apart and 0.3 mm tall; lid elliptic, base slightly cordate, up to 5 cm long, up to 4 cm wide, not vaulted, margins not revolute, no appendage. **Male inflorescence** racemose, up to 90 cm, peduncle 30-40 cm long, 3-5 mm wide, rachis 40-50 cm long, up to 35 mm at the widest point, with ca. 150-200 flowers borne on 2-flowered partial peduncles, composed of pedicels 10-16 mm long, usually with a filiform basal bract 1-1.5 mm long; tepals elliptic, slightly acute at the apex, 4 mm long by 2.5-3 mm wide, densely covered with nectarioles 0.2-0.3 mm long, androphore 3.5-4.5 mm long, anther head subglobular, 1.5 mm long, 1.5 mm in diameter. **Female inflorescence** racemose, to 90 cm, peduncle 40-60 cm long, 4-6 mm wide, rachis 25-35 long, up to 60 mm at the widest point, with ca. 90-100 flowers borne on 2-flowered partial peduncles, composed of pedicels 12-13 mm long, usually with a filiform basal bract 1-1.5 mm long; tepals elliptic slightly acute at the apex, 4-6 mm long, up to 3 mm wide, densely covered with nectarioles 0.2-0.3 mm long, ovary unknown. **Infructescence** tepals persistent, capsule fusiform, fruit valves 4, 14-26

Figure 769 (facing page). The holotype of *Nepenthes holdenii* (Mey 1A) deposited at RUPP.

mm long, generally 16-20 mm long. **Seeds** fusiform, ca. 100 per fruit. c. 6 mm long, light brown. **Indumentum** of brown hairs 0.2 mm long covering the inflorescences and leaf axes; the tendrils, pitchers, leaves and stem virtually glabrous. **Colour** of living specimens: older leaves light green; young leaves of rosette glossy with a orange-brown hue to be developed, midrib pink-red with yellowish edges, forming near the leaf attachment a strongly acute pink-red triangle at the base of the lamina; lower pitcher exterior generally red, brown or purple, with faint purple blotching, rarely green with red peristome, interior yellowish green to creamy white, rarely blotched purple; upper pitchers entirely green or green with orange to red peristome or entirely brown, pink or red with faint purple blotching and red to orange peristome; interior yellowish green to creamy white, rarely blotched purple, peristome not striped; lid as for pitcher exterior; stem, dark purple, glossy; tepals brown or red; anthers yellow.

Additional material examined: *Nepenthes holdenii* - Godefroy 344 (P!), “ad montem Pusath Cambodiae”, Cambodia, 1875. *Mey 1A* (holo, RUPP!), Cardamom Mountains, 650 m, province of Pursat, Cambodia, 1 VIII 2009. *Mey 1B, 1C, 1D* (iso RUPP !), ibid. *Mey 7A, 7B, 7C* (RUPP!), Cardamom Mountains, 760 m, province of Pursat, Cambodia, 12 VIII 2009. *Neang & Holden 1, 2, 3, 4, 5, 6* (RUPP), Cardamom Mountains, between 600-750m, province of Pursat, Cambodia, VII 2008.

Material of other Indochinese species examined: *Nepenthes andamana* - Catalano 013395 (holo BCU), Takuapa, sea level, province of Phang-nga, Thailand.

Nepenthes bokorensis - M. Martin 1231 bis (holo P!), Bokor Hill, 800 m, province of Kampot Cambodia. *Chevalier 36411, 36429*, Damrei Mountains (P!) ; *Geoffray 324, 325, 326, 327, 328* (P!), Popokvil Falls, Bokor Hill, 960 m, province of Kampot, Cambodia. *Mey 3* (RUPP!), Phnom Bokor (Bokor Hill), 992 m. *Middleton & Monyrak 589* (P!), Bokor Hill, 944 m. *Poilane 206, 14728* (P!) ; *Smitinand 6496* (BKF; K) ; *Vidal 4780* (P!); *L. B. Abbe et al. 9617* (BK) ; *E. C. Ade et al. 9653* (BK) ; *Eryl Smiths* s. n.(K).

Nepenthes chang - Catalano 013394 (holo BCU), Ko Chang, 300



Figure 770 (above). One of the peaks of the Cardamom Mountains where *Nepenthes holdenii* occurs.



Figure 771 (above). *Nepenthes holdenii* growing at 700 m altitude on a sandstone ridge.

m, province of Trat, Thailand. *Kerr 17727* (BK), Khao Kuap, 600 m, province of Trat, Thailand.

Nepenthes geoffrayi - *Geoffray 84, 85, 87, 88, 91, 92, 93* (synt P!), Kampot, Cambodia.

Nepenthes kerrii - *Kerr 14127* (holo BK), Tarutao Marine Park, 500 m, province of Satun, Thailand.

Nepenthes kampfotiana - *Geoffray 89, 90, 191, 362* (synt P!), Kampot, Cambodia.

Nepenthes smilesii - *Charenphol, Larsen & Warncke 4623* (P!), Phu Kradung, Loei, Thailand. *Mey 2* (RUPP!), Kirirom National Park, 712 m, Province of Kampong Speu, Cambodia. *Mey 4* (RUPP!), town of Kampot, 16 m, province of Kampot, Cambodia. *Poilane 17457* (P!), south of Chambok, province of Kampong Speu, Cambodia.

Nepenthes smilesii x mirabilis - *Mey 6* (RUPP!), near town of Kampot, 14 m, province of Kampot, Cambodia.

Nepenthes suratensis - *Kerr 13136* (holo BK), Kanchadanit, sea level, province of Suratthani, Thailand.

Nepenthes thorelii - *Bois 2228, 2229* (P!), *Herbier Bonaparte*, Ong-iem swamps, Vietnam. *Thorel 903* (P!), Ti-Tinh, Vietnam. *Thorel 1032* (lecto P!), Lo-Thieu, Vietnam. *Thorel 1032* (iso P!), Guia-Toan, Vietnam. *Thorel 1032* (iso P) Ti-Tinh swamps, Vietnam.

The first author examined several *in situ* populations of *Nepenthes bokorensis* in July 2007 and August 2009 at the *locus classicus*, as well as populations of *Nepenthes smilesii* at Kirirom national park and Kampot province in August 2009 and February 2010.

Distribution: Western Cambodia, Pursat Province, from two peaks in the Cardamom Mountains (exact locality withheld for conservation purposes), between 600 and 800 m altitude. Further study might reveal that *Nepenthes holdenii* grows on other peaks of the extensive Cardamom range, but additional research may be hampered by the fact that Pursat province is remote and one of the most heavily mined parts of Cambodia.

Ecology: *Nepenthes holdenii* occurs in localities situated in the transitional zone between lowland evergreen forest and low montane evergreen



Figure 772 (above). The tuber rootstock of *Nepenthes holdenii*, typical of the *Nepenthes thorelii* aggregate.

forest. The lowland evergreen forest of the Cardamom range is mainly composed of tall trees such as *Lagerstroemia* (Lythraceae), *Anisoptera* and *Dipterocarpus* (Dipterocarpaceae), *Ficus* (Moraceae), as well as some emergent legumes, various species of bamboos, rattans and lianas are also very common. The hill evergreen forest, occurring more or less between 700 and 800 meters above sea level, is shorter and composed of trees like *Lithocarpus* (Fagaceae) and *Syzygium* (Myrtaceae) (Neang & Holden, 2008). In both localities, *N. holdenii* grows on steep ridges in peaty soil, in bright to fully exposed areas (Figure 771). The first locality (*Mey 1*, *Neang & Holden 1, 2, 3, 4, 5, 6*) is semi-exposed. Plants grow in full sun or under the part-shade of short trees. The forest floor is generally covered with leaf litter. Some small, undiagnosed lithophytic Orchidaceae, large succulent plants which look like species from the tribe Euphorbieae and a species of terrestrial mistletoe belonging to the genus *Dendrophthoe* Mart., occur in this area. The second locality (*Mey 7*) is open and drought appears to be severe in the dry season. *Nepenthes holdenii* occurs on steep ridges at the foot of a loose network of short trees and pines. A species of fern and species of myrmecophilous plants like *Hydnophytum* Jack (Rubiaceae), *Dischidia rafflesiana* Wall., as well as

the non myrmecophilous *Dischidia nummularia* R. Br. (Asclepiadaceae), can be found there growing as epiphytes. It is worth noting that no other genera of carnivorous plant have been found in either locality, whereas species like *N. bokorensis* and *N. smilesii* are usually found with various species of *Utricularia* (Lentibulariaceae) and *Drosera* (Droseraceae) (pers. observ.). The habitat is prone to frequent fires and the burned remains of many *N. holdenii* vines were found in the second locality. No climbing plants were observed there. Climbing plants were found in the first locality in semi-exposed spots. As with other Indochinese species such as *N. smilesii*, *N. holdenii* is able to survive a long extended drought and low intensity fires thanks to an underground tuber which seems to serve as a storage for water and nutrients (McPherson, 2009) (Figure 772). The average rainfall in the Western Cardamom where *N. holdenii* occurs is 3,000 mm and the dry season lasts more than 4 months each year (Anon, 2006) (Figure 773).

Nepenthes holdenii was observed on two neighboring peaks. Soil analysis provided by Dr. Eric Kohler (X-ray diffraction study of mineralogical composition of the rocks and quantification by Rietveld refinement) shows that both populations grow on sandstone in leached soils that include quartz and feldspar (potassic feldspar and sodic feldspar). The leaching process results in the formation of clays: illite and kaolinite. The small quantities of these minerals show the significant impact of the typically heavy, local monsoon rains. Soil analysis from the second locality (Mey 7) reveals a small percentage of carbonates, which are absent from the first locality. This might be the result of a number of causes, but is not indicative of limestone substrate like those in which *N. northiana*, a limestone specialist, occurs (E. Kohler, pers. comm.). According to data provided by the Geology Department, MIME (Anon, 2006: 57), the peaks where *N. holdenii* grows are part of an unmetamorphosed series of sandstone and shale considered to be of *Devonian-Carboniferous* age.

Botanical history: *Nepenthes holdenii* has been collected at least once previously by Godefroy in 1875 (*Godefroy 344 P!*). The single herbarium sheet indicates: “0.75 – 2 met. *Ad Montem pusath, Cambodia.*” This material



Figure 773 (above left). The habitat of *N. holdenii* can be very dry even during the wet season. **Figure 774 (above right).** A large rosette of *N. holdenii* growing back on the wet season. Note the dead climbing vines, remnants of the dry season.



Figure 775 (above). A rosette plant growing during the wet season. Note the pine leaves.

was previously diagnosed by Lecomte as *N. thorelii* (Lecomte, 1909). It is a flowering rosette stage specimen composed of a piece of rootstock, several rosette leaves, and two, long male inflorescences. The glabrous nature of the foliage and the long inflorescences with 2-flowered partial peduncles show that this material falls within *Nepenthes holdenii*. It is not known exactly which peak this specimen was collected from. It appears that until the 2006 FFI survey, *N. holdenii* has not been observed by scientists since Godefroy's initial collection. This is partly explained by past conflicts and the fact that Pursat province was a stronghold of the Khmer Rouge regime (Brocheux & Emery, 2001; Tertrais, 2004).

Etymology: The specific epithet *holdenii* commemorates photographer and biologist, Jeremy Holden, who first documented and recognised this plant as a possible new taxon. It honors Mr Holden's contribution to the promotion of wildlife knowledge in south-east Asia, especially, in Cambodia.

DISCUSSION

Definition of the *N. thorelii* aggregate

Nepenthes holdenii appears to be closely related to a group of Indochinese species namely:

- *N. andamana* M. Catal. (2010);
- *N. bokorensis* Mey (2009);
- *N. chang* M. Catal. (2010);
- *N. kampoiana* Lecomte (1909);
- *N. kerrii* M. Catal. & T. Kruetr. (2010);
- *N. smilesii* Hemsley (1897);
- *N. suratensis* M. Catal. (2010);
- *N. thorelii* Lecomte (1909).

We have decided to refer to this group as the “*Nepenthes thorelii* aggregate”. These nine taxonomically difficult species form an aggregate of closely allied taxa with affinities to *Nepenthes thorelii*, an Indochinese taxon, one of the first to be described, that has received a lot



Figure 776 (above). A detail of the flowers of *Nepenthes holdenii*. Note the 2-flowered partial peduncles.



Figure 777 (above). Lower pitchers of *Nepenthes holdenii* are often speckled with red blotches.

of attention by both *Nepenthes* taxonomists and horticulturists. Actually, *N. thorelii* has been the source of much confusion over the last century. It has never been officially relocated in the wild since its description by Lecomte in 1909 and is, thus, only known from herbarium specimens. Several taxa such as *N. smilesii*, *N. bokorensis*, *N. kamptoniana* have been incorrectly identified as *N. thorelii* in the past (Mey, 2009, 2010). The species of the *N. thorelii* aggregate are similar in overall appearance and share many features: long racemose inflorescence, flowering at rosette stage, seed with reduced filiform appendages, coriaceous narrow leaves, decurrent leaf attachment, and pyrophytic habit, with the production of a thickened rootstock. As it is often difficult to distinguish these species, a key is therefore proposed.

A number of features of this group can be linked to adaptations to a seasonally dry climate. Indochinese countries are strongly subject to the influence of monsoon with seasonal rainfall patterns: a dry season which begins in November or December and lasts until April or May, April usually being the hottest period of the year in Cambodia (Anon., 2006). Plants that occur in these strongly seasonal habitats generally exhibit adaptations to water stress and drought. These *Nepenthes* are no exception, with leaf, flower and pitcher production often ceasing during the dry season.

A striking feature of all members of this aggregate is that these species are able to flower at the rosette stage. Mature plants can flower without first producing upper pitchers and climbing stems. This is not a common feature among the genus (Jebb, 1991). Drought and fires appear to prevent most plants from entering the climbing stage, so this feature ensures successful reproduction. Species of the *N. thorelii* aggregate all develop a large tuber-like rootstock (Figure 772) which is otherwise found only in *Nepenthes rowanae* Bail. from Cape York, Queensland, Australia. *N. rowanae* is similarly able to recover from low intensity fires where it grows in the drier parts of swamps in Cape York (Clarke & Kruger, 2005). The tuberous rootstock is likely to act as a water and nutrient store for survival during periods of unfavorable conditions.



Figure 778 (above left). Most of the lower pitchers are ovate in shape and have a slightly sinuate peristome. **Figure 779 (above right).** A lower pitcher exhibiting prominent red colouration.



Figure 780 (above). An aerial rosette emerging from a dried climbing vine.

In the dry season, species of the *N. thorelii* aggregate will lose most of their leaves. Plants growing in more exposed locations even die back completely, entering a dormancy reminiscent of that seen in the tuberous *Drosera* (subgenus *Ergaleium*) (Tardieu-Blot *et al.*, 1965; McPherson, 2008); indeed, in Cambodia, small populations of *Drosera peltata* Thunb. grow on Mount Bokor sympatrically with *N. bokorensis* (Mey, 2009). It is not known if the dry season dormancy of *N. holdenii* is induced by unfavourable environmental conditions, and thus only occurs in response to the dry environment, or whether it is part of a genetically fixed seasonal growing cycle (like it is the case in tuberous *Drosera*). Other members of the species aggregate, such as *N. kampotiana*, *N. bokorensis* and *N. smilesii*, do not enter a dry dormancy in cultivation as long as the substrate is kept moist (pers. observ.). In the wild, plants grow back at the beginning of the wet season by developing many offshoots from the rootstock. In cultivation, specimens of *N. kampotiana*, are clearly able to grow back from divisions of the thickened rootstock that include neither foliage nor stem (T. Kahl, pers. comm.).

Nepenthes holdenii and its relatives may benefit from the drought and occasional fires, which will eliminate competing plants. The rosettes of the *Nepenthes* will develop quickly at the start of the wet season, producing many offshoots (Figure 772). This pyrophytic habit does not appear to be obligate however and fire is not required to trigger seed germination, as observed in many other pyrophytic plants. The seed of the other pyrophytic Indochinese *Nepenthes* does germinate without any special treatment (pers. observ.), though whether or not that is the case for this taxon is as yet unknown.

Although *N. holdenii* fits well in this group of species, it stands out because it is the only species of the aggregate which develops 2-flowered partial peduncles both on male and female inflorescences (Figure 776). Within the aggregate, closest relatives of *N. holdenii* appear to be *N. chang* which is known from the Thai locations of Ko Chang and Khao Kuap, and *N. kampotiana*, from the Cambodian province of Kampot, and the Thai province of Trat near the Cambodian southwestern border. The three species have in common the production of decurrent, long



Figure 781 (above left). A green upper pitcher with a reddish, sinuate peristome.

Figure 782 (above right). The upper pitcher of a pink variant of *Nepenthes holdenii*

linear to linear-lanceolate leaves and pitchers born on long tendrils. *Nepenthes holdenii* and *N. chang* also share similar habitat preferences as both species usually occur on open steep peaty terrain surrounded by forests. Although, flowering *N. holdenii* are readily distinguished from its closest relatives by its male and female inflorescence structure, it can be also be distinguished in vegetative conditions from *N. chang* by its infundibular upper pitchers (vs. tubulose), its glabrous stem and leaves (vs. hairs on all plants parts except adaxial surface of leaf) and the sinuated peristome (vs. cylindrical peristome and often larger at the sides of the pitcher opening); from *N. kampoiana*, it can be distinguished by the infundibular upper pitcher (vs. obovate or ovate in the lower

quarter to third and cylindrical above), and the sinuated peristome (vs. uniformly cylindrical peristome) (Figures 777-782).

Key to the *Nepenthes thorelii* aggregate species

- 1a. Raceme with 2-flowered partial peduncles.....2
- 1b. Raceme with 1-flowered pedicels.....3
- 2a. Partial peduncles 2-flowered on both male and female inflorescences; plants glabrous except on flowers, leaf axis, tendrils and pitchers; infundibular upper pitchers, sinuated peristome.....*N. holdenii*
- 2b. Male inflorescence bearing 2-flowered partial peduncles, female inflorescence bearing 1-flowered pedicels; short hairs on all aerial parts except upper surface of leaves; tubular upper pitchers..... *N. chang*
- 3a. Leaves obovate*N. kerrii*
- 3b. Leaves linear - lanceolate to oblong.....4
- 4a. Leaves lanceolate to oblong, vaulted lid, striped bulbous peristome...
.....*N. bokorensis*
- 4b. Leaves linear to linear-lanceolate, never oblong.....5
- 5a. All parts of leaves glabrous (pitcher and tendril excluded),.....
.....*N. kampotiana*
- 5b. Hairy on all or some parts of leaves.....6
- 6a. Short hairs on all vegetative parts.....7
- 6b. Short hairs on upper parts of plants, absent in lower part of plants...
.....8
- 7a. Long tendril, globose lower pitchers.....*N. thorelii*
- 7b. Short tendril, ovate to narrowly ovate lower pitchers.....*N. smilesii*
- 8a. Lid smaller than mouth, triangular mouth as large as 1/3 to 1/2 of the lower pitcher length, ovate lower pitcher, small glandular boss under the apex of pitcher lid.....*N. suratensis*
- 8b. Lid larger than mouth, ovate mouth as large as 1/4 of the lower pitcher length, lower pitcher ovate in the lower half and narrowing above, no boss under the lid..... *N. andamana*

Notes:

1. **Natural hybrids.** No natural hybrids including *N. holdenii* have been recorded. Hybrids with the widespread lowland *N. mirabilis* (Lour.) Druce are regularly found with species of the *N. thorelii*

aggregate (Catalano, 2010), but the very dry nature of the *N. holdenii* habitat, and the altitude where it occurs, makes this very unlikely.

2. ***Infafauna and carnivory.*** Dipteran larvae have been observed in great numbers in the pitcher fluid. Dead large crickets have also been found (J. Holden, pers. comm.). Entomological and botanical field research undertaken during the dry season, when pitcher production is very poor, would provide great insight into the life cycles of the various associated infauna.
3. ***Ethnobotany.*** People from the province of Pursat call *Nepenthes* pitcher plants “among sramoch”, which translates as “ants pit-hole” (or sometimes “among krâlaom”, (= “insects pit-hole”)) in Khmer. The villagers who live near the type location of *N. holdenii* reported that leaves and roots of the plant are used to make a decoction to cure fever and pain.
4. ***Conservation.*** Cambodia’s biodiversity is under pressure from threats that include logging, poaching, land speculation and encroachment in protected areas and forests, invasive alien species, transformation of natural habitats by roads, agricultural concessions, mines, and hydroelectric dams (Daltry, 2008). Protected Areas regulations have been established (Sok & Sarin, 1999) but are largely ignored since concessions are regularly granted. Despite the fact that the Western Cardamom are part of the Phnom Samkos Wildlife Sanctuary, logging is a plague in Pursat Province (Anon., 2006). Although *N. holdenii* occurs in two remote peaks in the Cardamom range (which present no immediate economic value and considering Pursat province is also known to be one of the most heavily mined parts of Cambodia it is afforded a degree of natural protection), the several known populations are scattered, localised and composed only of a few dozen specimens. In the short term, therefore, the main threat to these localised populations is likely to come from over-collection. Accordingly, *N. holdenii* is here assessed

using IUCN (2001) as NT (Near Threatened) according to the World Conservation Union (IUCN, 2001).

5. **Material deposition.** Half of the *N. holdenii* material, including the holotype *Mey 1A*, is in the process of being transferred to Paris herbarium (P).

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