JOURNAL OF
INTERDISCIPLINARY
PERSPECTIVES

ISSN Print: 2984-8288, ISSN Online: 2984-8385
Vol. 2, No. 8, pp. 422-440, August 2024

A Historical Review of the Molecular Phylogeny of the Philippine *Nepenthes* L. (Nepenthaceae) with Notes for Unsampled Taxa

Samuel C. Brillo[1,2*], Julius John D. Salamanes[1], Eleanor S. Austria[1]
[1]Biology Department, College of Science, Adamson University, Metro Manila, Philippines
[2]Biology Department, College of Science, Pamantasan ng Lungsod ng Maynila, Metro Manila, Philippines

[*]Corresponding Author Email: scbrillo@plm.edu.ph, sambrillo24@gmail.com

Date received: June 20, 2024
Date revised: July 4, 2024
Date accepted: July 7, 2024

Originality: 92%
Grammarly Score: 99%
Similarity: 8%

Recommended citation:
Brillo, S., Salamanes, J.J., Austria, E. (2024). A historical review of the molecular phylogeny of the Philippine *Nepenthes* L. (Nepenthaceae) with notes for unsampled taxa. *Journal of Interdisciplinary Perspectives*, 2(8), 422-440. https://doi.org/10.69569/jip.2024.0298

Abstract. Despite advances in molecular phylogenetics, the genus *Nepenthes* L., comprising about 180 species, presents a challenging phylogenetic puzzle due to morphological convergence. The Philippines (PH), a hotspot for pitcher plant diversity with 61 species, faces unclear evolutionary relationships due to insufficient taxon sampling. This historical review compiled the phylogenetic studies concerning Philippine *Nepenthes* from various molecular studies using nuclear or plastid markers. Here, we identified that the molecular phylogeny constructed from the angiosperms353 probe set used by Mullins et al. (2020) has given the most comprehensive results, with most samples from the Philippines and a total of 35 species compared to previously conducted phylogenies since 2000. It was revealed that these species form a large Philippine clade, split into three groups: Mindanao, Palawan, and Graciliflora, with other PH taxa belonging to the Insignes Clade. This study noted the possible clades of 26 unsampled PH taxa based on morphology and geography. Lastly, we created a distribution map of Philippine *Nepenthes* to support these placements. This study will help future research determine the phylogeny of *Nepenthes* in the Philippines, understand their evolutionary relationships with other paleotropical species, and assist policymakers in conserving these species from extinction.

Keywords: *Nepenthes*; Pitcher plant; Angiosperms353; Philippine endemic; Phylogenetic relationship; Molecular phylogeny.

1.0 Introduction

Nepenthes L. (Linnaeus, 1737) is the sole genus within the family Nepenthaceae, the largest carnivorous plant family of the eudicot order Caryophyllales (McPherson, 2009a; McPherson, 2009b; Cheek and Jebb, 2013a). *Nepenthes* has an exceptional and remarkable biology compared to its carnivorous relatives within the Caryophyllales (McPherson, 2009a; McPherson, 2009b). Except for a few epiphytes, all *Nepenthes* species are evergreen climbers or scrambling shrubs. They can be found from sea level up to 3000–4000 m in elevation, mostly in humid montane rainforests or open swamp areas where the canopy is generally thin and the soil is sparse. One of the significant factors in the evolution of the genus is the adaptation of the species to different soil types (serpentine, granite, limestone, or sandstone) with low nutrient levels (Cheek et al., 2019).

Regarding pitchers, certain species evolved and mutated into complex morphological varieties due to differences in ecological adaptations for acquiring prey from the environment. Recently, researchers classified pitchers based on their functions and prey-specific trapping syndromes to collect nutrients from distinct species (Cheek et al., 2019). In addition to this, factors such as the location of species at elevations above sea level and mountain altitudes, the type of substrate, such as *Nepenthes*, a genus known for its high-level adaptive radiation, and tight isolation may also play a significant role (Thorogood et al., 2018; Murphy et al., 2020).

Researchers thought that abiotic environmental variables, sympatric speciation, and natural hybridization all contributed to the emergence of new species. *Nepenthes* is distributed in paleotropics, with a global count of 181 species as of 2020 (King & Cheek, 2020; Murphy et al., 2020). Southeast Asian rainforests are home to most of them, with the Philippines alone recording 61 species (Table 1). *Nepenthes* primarily inhabit ultramafic mountain ranges and submontane forests in the Philippines, exhibiting similarities in pitcher morphology with other nearby species. According to studies by Mansell and Suarez (2016), Cheek and Jebb (2014), Gronemeyer et al. (2016), and Mansell and Jebb (2014), *Nepenthes* predominates in ultramafic mountain ranges and submontane forests in the Philippines. However, phylogenetic relationships and species delimitation within the Nepenthaceae need to be clarified, particularly in Philippine taxa. Previous studies typically used a small number of samples and loci.

The systematic constraints within the family Nepenthaceae include the following: (1) taxonomic position, (2) subgeneric or infrageneric classification within the family, and (3) species delimitation.

Based on taxonomy, the Nepenthaceae, Ancistrocladaceae, Dioncophyllaceae, Droseraceae, and Drosophyllaceae all belong to the Caryophyllales, and they all have different types of carnivorous syndromes (Heubl et al., 2006; Walker et al., 2018). Researchers have reliably restored only the sister relationship between Ancistrocladaceae and Dioncophyllaceae, albeit with varying degrees of success among these five families. Heubl et al. (2006), Meimberg et al. (2000), Soltis et al. (2011), and Walker et al. (2018) identify this combined clade as sister to the rest of the Caryophyllales and the carnivorous clade as sister to the Frankeniaceae, Tamaricaceae, Plumbaginaceae, and Polygonaceae clades. The unique characteristics of modern *Nepenthes*, like strict dioecious reproduction and carnivorous pitchers, cannot be traced back to a missing link in the tree of life (Meimberg et al., 2001; Meimberg & Heubl, 2006; Clarke et al., 2018). Even *Nepenthes*' carnivorous relatives, *Drosera, Dionaea, Aldrovanda,* and *Drosophyllum*, lack those traits (Heubl et al., 2006). The absence of significant variation or primitive *Nepenthes* forms implies that all extant species may have radiated from a single close ancestor with all modern traits.

The second constraint would be the designation of subgeneric or infrageneric classification. Taxonomists have attempted to classify *Nepenthes* species according to their physical characteristics, particularly their pitchers, and their geographic distribution within the paleotropical region. They did this to figure out how the species evolved (Danser, 1928; Cheek and Jebb, 2013h; Cheek and Jebb, 2014; Cheek and Jebb, 2015; Cheek and Jebb, 2016a; Cheek and Jebb, 2016b; Clarke et al., 2018). Danser (1928) proposed six infra-generic groups. These are *Insignes*, *Montanae*, *Nobiles*, *Regiae*, *Urceolatae*, and *Vulgatae*), though he admitted that none of these reflected evolutionary links. Considering modern molecular discoveries and taxonomic work, there have been two primary competing methods for updating this classification: Cheek and Jebb (2013h; 2014; 2015; 2016a; 2017b) and Clarke et al. (2018). While reordering several species, Cheek and Jebb (2013h; 2014; 2015; 2016a; 2017b) added five new sections to Danser's (1928) classification: *Alatae*, *Micramphorae*, *Pyrophytae*, *Tentaculatae*, and *Villosae*, as well as the informal *Danseri* and subsection *Poculae-ovis*. Clarke et al. (2018) acknowledge only three sections, excluding Danser's Nobiles. *Montanae* and *Regiae* from Danser (1928) are significant groups for Cheek and Jebb (2013h; 2014; 2015; 2016a; 2017b) and Clarke et al. (2018), albeit their interpretations disagree. Clarke et al. (2018) placed all taxa from Peninsula Malaysia and Indochina (including some Bornean species) in an enlarged sect. *Pyrophytae*. Cheek and Jebb (2013h; 2014; 2015; 2016a; 2017b) created the *Pyrophytae* group for Indochinese species adapted to fire-prone and dry environments. Clarke et al. (2018b) need to recognize the sects Alatae and Micramphorae of Cheek and Jebb (2013h; 2014; 2015; 2016a; 2017b), which contain various Philippine taxa from Mindanao Island. However, both recognize small sects, *the Insignes* and *Tentaculatae*, which cross Wallace's line. The minor Urceolatae group, which includes other common, widespread lowland species, has assigned several species, including *Nepenthes gracilis, Nepenthes mirabilis, and Nepenthes papuana. Nepenthes campanulata, Nepenthes mapuluensis*, and *Nepenthes northiana*, the limestone species, create gray areas, defying taxonomic classification by any authority.

Species delimitation is also a controversial subject. These questions are made more complicated by the fact that there are a lot of natural hybrids, there don't seem to be any natural barriers to reproduction between species, there is a lot of infraspecific morphological diversity, and taxonomists rely on pitchers. For example, the recent separation of *Nepenthes orbiculata, Nepenthes parvula, Nepenthes rowaniae*, and *Nepenthes tenax* from *Nepenthes* *mirabilis* makes taxonomists wonder how the remaining species fit together (Catalano, 2018; Clarke and Kruger, 2005, 2006; Wilson and Venter, 2016). Previous molecular investigations have seldom sequenced many individuals (although see Kurata et al. (2008)). So, it's unknown if huge geographical populations of ubiquitous species form clades or how much gene flow connects them. Many recently described species, particularly from the Philippines and Indochina, are synonyms of other taxa, based on Clarke et al. (2018).

Molecular approaches have overcome challenges in the taxonomy and systematics of *Nepenthes*. However, using more than one or two markers results in low branch support needs for more currently known species (Murphy et al., 2020) and is continuously growing in number. On the other hand, the formation of three separate evolutionary lineages from the Philippines and two from Borneo and Sulawesi suggests that the Philippines, together with Sulawesi, is an essential center of variety and evolution (Meimberg et al., 2001; Meimberg and Heubl, 2006). Despite this, phylogenetic studies underrepresent the Philippine taxa, with the discovery of 43 new species in the last two decades. This accounts for about 70% of all Philippine *Nepenthes* today (see Table 1). Furthermore, some populations of the Philippine *N. mirabilis* exhibit variable morphologies, indicating the presence of natural hybrids, or possibly, new species. Once proven by molecular methods, the existence of such hybrids may indicate new species. However, some Philippine *Nepenthes* are considered extinct in the wild, while others face extinction because of anthropogenic activities. These demonstrate that the Philippine taxa are an essential part of the Nepenthaceae systematics.

This paper reviewed the historical advancements in the molecular phylogeny of Philippine *Nepenthes* taxa by conducting a highly sensitive literature search, selection, and analysis, addressing significant developments and gaps in the phylogeny of Nepenthaceae with a focus on the Philippine *Nepenthes* taxa, identifying the most comprehensive phylogenetic study to date, and providing notes on the possible phylogenetic positions of unsampled Philippine *Nepenthes* species based on morphological and geographical similarities to nested species from the most comprehensive study identified in this review. This paper also provided an updated distribution map for Philippine *Nepenthes* in relation to their nested clades based on the most comprehensive phylogenetic study to date.

2.0 Methodology

2.1 Literature Search

Electronic literature searches were conducted in the following journals and taxonomic databases relevant to plant systematics: For our research, we utilized Co's Digital Flora of the Philippines, Philippine Journal of Systematic Biology, Phytotaxa, PeerJ, Carnivorous Plants Newsletter, Willdenowia, Blumea, Nordic Journal of Biology, Planta Carnivora, Bulletin du Jardin Botanique du Buitenzorg, Plants, Gardens' Bulletin Singapore, and Molecular Phylogenetics and Evolution. The researchers also utilized Google Scholar, ScienceDirect, and Scopus.

"*Nepenthes*," "Nepenthaceae," "Phylogeny," "Phylogenetic," and derivatives of these terms were among the search terms used. This study only included phylogenetic studies that used molecular methods and included many representative *Nepenthes* species from across the paleotropical region and at least one Philippine species.

2.2 Selection Criteria

This study used secondary data from selected molecular phylogeny studies of Nepenthaceae. The following are important details to note: (1) nested sampled species within clades formed using nuclear and/or plastid markers; (2) morphological characteristics; and (3) geographical distribution. The data identified breakthroughs and systematic gaps. Furthermore, the most comprehensive phylogenetic study of Nepenthaceae to date was identified in terms of (1) the greatest number of species sampled, as well as multiple individuals of several widespread taxa; (2) the most advanced and efficient DNA sequencing method used; (3) less gene conflict encountered; and (4) most findings confirmed and resolved.

All six studies (Mullins, 2000; Meimberg et al., 2001; Meimberg & Heubl, 2006; Golos, 2012; Alamsyah & Ito, 2013; Murphy et al., 2020) met the selection criteria. This study also involved retrieving published descriptions of *Nepenthes* species. We retrieved only Philippine taxa for this study. We extracted and analyzed data from these articles.

2.3 Data Extraction and Analysis

This study used secondary data from selected molecular phylogeny studies of Nepenthaceae. The following are important details to note: (1) nested sampled species within clades formed using nuclear and/or plastid markers; (2) morphological characteristics; and (3) geographical distribution. The data identified major breakthroughs and systematic gaps. Furthermore, the most comprehensive phylogenetic study of Nepenthaceae to date was identified in terms of: (1) the greatest number of species sampled, as well as multiple individuals of several widespread taxa; (2) the most advanced and efficient DNA sequencing method used; (3) less gene conflict encountered; and (4) most findings confirmed and resolved.

Sets of taxonomic information from published descriptions were listed in a table to create a checklist of all Philippine *Nepenthes* species, including taxonomic author(s), year of publication, morphology, geographical distribution data, conservation status, and notes on diagnostic characters with an emphasis on possible speciation. The validity of each species' taxonomic status and information was confirmed using ICBN nomenclature codes and taxonomic database systems. The checklist was used to double-check the Philippine species used in selected molecular phylogenetic studies of Nepenthaceae and to update the geographical distribution map of Philippine *Nepenthes* species. Minor limitations on journals regarding amended species types, natural hybrids, or section regroupings related to Philippine taxa were considered, as these works of literature may be helpful in comparing taxonomic information professed by authors. However, these will not be discussed in depth in this review.

3.0 Results and Discussion

3.1 Geographical Distribution and Notes on Morphology of 61 Philippine *Nepenthes* Species

Currently, there are 181 species of *Nepenthes* globally (King & Cheek, 2020). Reports indicate the occurrence of 61 species of *Nepenthes* in the Philippines (Pelser et al., 2024). Fifty-nine (59) of these are endemic to the Philippines, while the remaining two (2) are native or indigenous (see Table 1).

Table 1. Checklist of *Nepenthes* species of the Philippines.[1]

Species		Geographical Distribution	Notes on Morphology
1.	*Nepenthes abalata Jebb & Cheek*	(VISAYAS) Malalison Island, Panay, Antique (PALAWAN) Culion Island	Related to *N. philippinensis* Macfarl. but with similarities to grassland species of Indochina; differs from *N. alata* in that it flowers as a terrestrial subshrub, not known to climb, growing in open grassy slopes near sea level, absent, petiole absent, blade tapers to stem, pitcher lid nectar glands dimorphic, midband with large perithecoid glands.
2.	*Nepenthes abgracilis Jebb & Cheek*	(MINDANAO) Mt. Legaspi, Surigao	Terrestrial shrub or climber with glabrous stems, leaves, and pitchers (except under peristome); leaves with no distinct petiole (sessile); Upper pitchers are subcylindric, with a base width of about 16 cm.
3.	*Nepenthes aenigma Nuytemans, W.Suarez & Calaramo*	(LUZON) Ilocos Norte	Morphologically, it falls within a Philippine group revolving around *N. ventricosa*, which in turn is included in Danser's rather loosely defined Insignes group but is unusual in having only 3 to 4 longitudinal leaf nerves and consistently branched fringed elements; not known to produce lower pitchers.
4.	*Nepenthes alata Blanco*	(LUZON, Northeastern, Central Cordillera) Burgos, Ilocos Norte; Benguet; Bontoc; Nueva Vizcaya; Mountain Province; Ifugao; Mt. Pinatubo, Zambales; Sierra Madre, San Luis, Quezon (PALAWAN) Silanga	The pitcher appeared stoutly subcylindric, with a modest contraction at the waist. Fringed wings that run from the pitcher's base to the tip. Even if reduced elsewhere, fringes are always present below the peristome; Small white stellate hairs, 0.2 mm wide, are densely covered and almost touch one another; Small white stellate hairs, 0.2 mm wide, are densely covered and almost touch one another; Young leaves and stems are densely covered with fine white hairs, which often obscure the skin. Bracts typically present, partial-peduncles 1-flowered.
5.	*Nepenthes alfredoi V.B.Amoroso & Lagunday*	(MINDANAO) Mt. Hamiguitan Range Wildlife Sanctuary Expansion Site, Brgy Luzon, Davao Oriental.	It differs from *N. mindanaoensis* in having an upper pitcher with fringed wings reaching for some distance along the tendril. The upper pitcher has well-expressed fringed wings extending for some distance along the tendril and a lengthier habit.
6.	*Nepenthes alzapan Jebb & Cheek*	(LUZON) Mt. Alzapan, Tayabas Province	*N. alzapan* has oblong, glabrous, ligulate, sessile leaf blades with 5–7 pairs of relatively uniformly spaced longitudinal nerves.
7.	*Nepenthes argentii Jebb & Cheek*	(VISAYAS) Mt. Guiting-guiting, above Magdiwang on ridge leading to Mayo's Peak, Sibuyan.	The absence of climbing habit and the subpetiolate, oblanceolate leaves with truncate apices distinguish *N. argentii* from *N. bellii*. This species is unique in that it possesses a subterranean rhizome that is long and vertical. The stem is slowly growing higher, keeping up with the buildup of organic debris on the surface, which continues to bury the lower half of the stem.
8.	*Nepenthes armin Jebb & Cheek*	(VISAYAS) Magdiwang, Sibuyan	*N. armin* varies from *N. graciliflora* in that the pitchers are as wide at the apex as they are at the base (not the broadest at the base); the convex lid appendage is absent (not present); androecium: tepal length ≤ 1:1 (not 2:1). Male pedicels are 3.5–4.5 mm long, with angular stems and no convex basal appendage on the lid.
9.	*Nepenthes attenboroughii A.S.Rob., S.McPherson & V.B.Heinrich*	(PALAWAN) Mt. Victoria	Habit resembles *N. rajah* and *N. mira*; sub petiolate blade oblong to elliptic, obtuse, occasionally blunt, short-narrowing base never very robust spirally, leaves modest in size, although it varies substantially from it.
10.	*Nepenthes barcelonae Tandang & Cheek*	(LUZON) Sierra Madre Mountain Range, Aurora	The inset mouth and dichromic upper pitchers (first-produced pitchers red, later-produced pitchers green) that are also

			dimorphic distinguish *N. barcelonae* as part of species within sect. *Insignes*. The primary upper pitchers (primary upper pitchers) are red, larger, stouter, and have an uncoiled long tendril. In contrast, the secondary upper pitchers (secondary upper pitchers) are green, smaller, slenderer, and have a coiled tendril.
11.	*Nepenthes bellii Kondo*	(MINDANAO) Surigao del Norte; Surigao Del Sur; DINAGAT	*N. bellii* is closely related to *N. merrilliana* and *N. surigaoensis* which share a similar morphology of the pitchers and laminae and a reddish coloration of the top leaves. The inferior pitcher of *N. bellii is* ovate ellipsoid in shape and ventricose in the middle. Compared to *N. merrilliana*, the plant body is substantially smaller.
12.	*Nepenthes burkei Hort.Veitch ex Mast.*	(VISAYAS) Mt. Halcon, Mindoro Oriental; Mt. Madia-as, Panay, Antique	*N. ventricosa* is a closely related to *N. burkei* having large, flaring peristomes on waxy pitcher bodies, just like the rest of the family.
13.	*Nepenthes cabanae Lagunday & V.B.Amoroso*	(MINDANAO) Pantaron Mountain Range, Mt. Malimumu, San Fernando, Bukidnon.	*N. cabanae* belongs to Danser's Insignes group, characterized by a lack of petiole, broadly subcylindrical pitchers, broad peristomes, lids with no appendages, and transversely elliptic nectar glands. It is most closely related to *N. surigaoensis* also found in this section.
14.	*Nepenthes campanulata Sh. Kurata*^{N}	(PALAWAN) Saint Paul Limestone Formation	The lid is quite small in some species with extremely infundibuliform pitchers, such as *N. dubia, N. eymae,* and *N. inermis*, and the pitcher is laterally flattened along its length before opening. The lid of *N. campanulata*, is tiny and elliptic. As a result, the mouths of these pitchers must extend significantly more than is typical in the genus after opening. They are like *N. reinwardtiana* pitchers in this regard, which have a broad infundibuliform pitcher with a wide mouth, but a short lid and a severely reduced peristome. The pitchers are not divided into upper and lower pitchers.
15.	*Nepenthes candalaga Lagunday & Amoroso*	(MINDANAO) Davao de Oro	*N. candalaga* resembles *N. justinae* but can be easily distinguished by its lamina with 2–3 longitudinal nerves, orbicular lid, non-bifid lid spur tip, triangular lid appendage, short banner-shaped trap wings, and absence of an upper pitcher rim.
16.	*Nepenthes ceciliae Gronem., Coritico, Micheler, Marwinski, Acil & V.B.Amoroso*	(MINDANAO), Mt. Kiamo, trail from Brgy. Kibalang, Malaybalay City, Bukidnon	*N. ceciliae* resembles *N. alata, N. copelandii*, and *N. micramphora* the most superficially, and appears to be related to this group of related Philippine-endemic species. The infundibular upper pitchers of *N. ceciliae* are similar to those of *N. copelandii*, but they differ in relative proportions and overall size.
17.	*Nepenthes cid Jebb & Cheek*	(MINDANAO) Dalvangan, Bukidnon	Leaf blade shape widest in the middle, upper pitchers broadest at base and apex, peristome width longer, thinly bordered lid nectar glands, and entire spur distinguish *N. cid* from *N. micramphora*.
18.	*Nepenthes copelandii Merr. ex Macfarl.*	(MINDANAO) Mt. Apo, Davao del Sur; Camiguin	Winged petioles, lower lids with basal ridges on the lower surface (often elaborated into appendages), and upper pitchers that are usually broadest near the base are all morphological characters that *N. copelandii* shares with the *N. alata* group.
19.	*Nepenthes cornuta Marwinski, Coritico, Wistuba, Micheler, Gronem., Gieray & V.B.Amoroso*	(MINDANAO) Pantaron Mountain Range, Brgy. St. Peter, Malaybalay City, Bukidnon.	This species is closely related to the Mindanao species *N. ceciliae* and *N. copelandii*. All three are members of the "*N. alata* group" which is much larger.
20.	*Nepenthes deaniana Macfarl.*	(PALAWAN) Mt. Pulgar	The non-climbing habit, glabrous stems that spread by shoots, much more minor pitchers, relatively narrower peristomes, and one-flowered pedicels distinguish this species from the Philippine (Palawan) representatives (*N. mantalingajanensis* and *N. mira*).
21.	*Nepenthes erucoides A.S.Rob. & S.G.Zamudio*	(MINDANAO) Mt. Redondo, Dinagat	The species has an overall plant form like *N. mantalingajanensis* (a member of Palawan Clade) but differs in such a way that it has indumentum that is long, dense, rufous hairs, produces both upper and lower pitchers, pitcher shape urceolate to sub-campanulate, finer peristome with small teeth through the inner margin, some partial peduncles and the rachis of male inflorescences produce very large bracts 8–15 mm long, and seeds lacking well-developed filaments
22.	*Nepenthes extincta Jebb & Cheek*	(MINDANAO) boundary between Surigao del Norte and Surigao del Sure.	It is most likely confused with *N. mindanaoensis*; both have robust, ovoid-cylindric pitchers that emerge from thickly leathery blades with longitudinal nerves that emerge from the blade's base. The blade is not decurrent to the petiole in both species, and the petiole has involute wings, making it appear cylindric.
23.	*Nepenthes gantungensis S.McPherson, Cervancia, Chi.C.Lee, Jaunzems, Mey & A.S.Rob.*	(PALAWAN) Mt. Gantung	The lower pitchers are entirely ovate or urceolate, and never completely red or purple. Upper pitchers, which are either completely infundibular or partially cylindrical, are very common. The apex is acute or rounded, the base is attenuate or obtuse, and two or three-thirds of its circumference clasp the stem. The inflorescence is usually made up entirely of 1-flowered pedicels, but 1- and 2-flowered pedicels are also common. The stem can grow up to 3.5 meters long and is commonly used for scrambling or climbing. The indumentum is a collection of simple, densely arranged, caducous reddish-copper hairs found on the lower part of tendrils and the margins of the lamina, with the hairs transforming silver as they age.
24.	*Nepenthes graciliflora Elmer*	(VISAYAS) Mt. Giting-giting, Sibuyan (LUZON) Mt. Makiling, Laguna; Sorsogon; Zambales; Quezon	Unlike *N. alata*, it has a ventricose base that is abruptly constricted above to a narrower subcylindric upper part; fringed wings are present only on the basal part; upper pitchers are reduced to ribs. Subglabrous, stellate hairs absent, scattered red, bun-like glands 0.05 mm diam, and very sparse simple hairs absent except for the bun-like glands
25.	*Nepenthes hamiguitanensis Gronem., Wistuba, V.B.Heinrich, S.McPherson, Mey & V.B.Amoroso*	(MINDANAO) Mt. Hamiguitan, Davao Oriental	*N. hamiguitanensis* was compared to *N. micramphora, N. mindanaoensis,* and *N. peltata,* which the authors classified as "closely related species." This plant was once thought to be a natural hybrid between *N. micramphora* and *N. peltata*, but it is a hybridogenic species. It produces squat upper pitchers with pigmentation ranging from red speckled to yellow all over. In addition, unlike *N. peltata, N. hamiguitanensis* forms upper pitchers and a climbing stem with relative ease.
26.	*Nepenthes justinae Gronem., Wistuba, Mey & V.B.Amoroso*	(MINDANAO) Mt. Hamiguitan, Davao Oriental	*N. justinae* differs from *N. mindanaoensis* by having lower pitchers that are bulbous in the lower two-thirds and slightly infundibulate in the upper one-third; upper pitchers that are strongly dimorphic;

			pitcher openings that are strongly oblique in the lower pitcher; monomorphic nectar glands; and upper pitchers that have an appendage.
27.	*Nepenthes kampalili Lagunday & Amoroso*	(MINDANAO) Davao de Oro	*N. kampalili* differs from *N. peltata* by having tendrils that are apically attached to the leaf, densely pubescent ground pitchers and pitcher lid, and occasionally two pitcher spurs arising from the posterior midsection of the peristome neck. In contrast, N. peltata features peltate tendril-leaf attachment, glabrous ground pitchers and pitcher lid, and a single unbranched pitcher spur.
28.	*Nepenthes kitanglad Jebb & Cheek*	(MINDANAO) Mt. Kitanglad, Bukidnon	It differs from *N. saranganiensis* in having angled (rather than winged) stems, lower and upper pitchers that are strongly dimorphic (rather than subdimorphic), being a climbing epiphyte of forest (rather than a terrestrial shrub of open areas), and having a strongly concave pitcher mouth with a long neck (rather than having a pitcher mouth that is flat or only slightly concave and lacking a neck Upper pitcher has a lid that is about as long as the mouth; the mouth is highly concave; a column is present; and the lid base is cordate.
29.	*Nepenthes leonardoi S.McPherson, Bourke, Cervancia, Jaunzems & A.S.Rob.*	(PALAWAN) Narra, summit of Schom-carp Peak	It is related to several other Palawan endemics, including *N. deaniana, N. gantungensis,* and *N. mira*. This species' traps stand at least 24 cm tall. Some specimens are known to produce upper pitchers that are incredibly dark, almost black.
30.	*Nepenthes leyte Jebb & Cheek*	(VISAYAS) Mt. Lobi, Leyte	Except in the hairy axils, the stems of *N. alata* are glabrous (not densely white hairy); upper pitchers lack fringed wings (versus with fringed wings); nectar glands on lower surface of lid dimorphic, concentrated around margin and appendage (not monomorphic, uniformly dense and distributed); Largest pitchers are 12 cm long; the peristome is 2–3 mm wide, narrowly cylindrical, with no visible teeth (unless dissected), and the outer edge is not lobed.
31.	*Nepenthes malimumuensis Lagunday, Acma, Cabana, Sabas & V.B.Amoroso*	(MINDANAO) Mt. Malimumu, San Fernando, Pantaron Range, Bukidnon	*N. malimumuensis* is distinct from *N. sumagaya* in having upper pitcher wings that are reduced to ribs or not visible; having four to five nerves on either side of the midrib; lid appendage is reduced to a keel, and lid appendage is reduced to a keel.
32.	*Nepenthes manobo Lagunday, Acma, Cabana, Sabas & V.B.Amoroso*	(MINDANAO) Mt. Malimumu, San Fernando, Pantaron Range, Bukidnon	It is distinct from *N. surigaoensis* in having sessile leaves clasping half of the stem diameter with three nerves on either side of the midrib; lower pitcher bulbous to ovate bottom half, cylindrical towards the opening; upper pitchers with a distinct hip; lid shape orbicular to ovate; peristome inner margin with short teeth-like projections.
33.	*Nepenthes mantalingajanensis Nerz & Wistuba*	(PALAWAN) Mt. Mantalingajan	The size, shape, and lack of indumentum on the pitchers distinguish it from *N. mira*, as does the operculum that is as wide as the mouth and the extreme rarity (possibly total absence) of upper pitchers (both lower and upper pitchers are produced at the same time in mature plants of *N. mira*).
34.	*Nepenthes maximoides Cheek*	(LUZON) Mt. Banahaw, Quezon	Upper pitchers narrowly infundibulate, widest in the distal half at the peristome (not ovoid-cylindric, widest in the proximal half), peristome broad, flattened, and lobed on the outer edge (not narrowly cylindrical and entire on the outer edge), and lid with asymmetrically hooked basal appendage and filiform apical appendage (not ovoid-cylindric, widest in (not symmetrical non-hooked, and absent, respectively).
35.	*Nepenthes merrilliana Macfarl.*	(MINDANAO) Mt. Urdaneta, Agusan del Norte, Surigao. (DINAGAT)	Long, narrow spathulate leaves with an obtuse or slightly emarginate apex, 5-7 longitudinal nerves on each side of the midrib in the outer 2/3 of the blade, and an ellipsoid to obovoid pitcher with a broad sinuous peristome distinguish it.
36.	*Nepenthes micramphora V.B.Heinrich, S.McPherson, Gronem. & V.B.Amoroso*	(MINDANAO) Mt. Hamiguitan, Davao Oriental	*N. micramphora* is closely related to *N. abgracilis* and *N. cid*, both of which are native to Mindanao. These species are like the *N. alata* group but lack a basal ridge or appendage on the lower surface of the lid.
37.	*Nepenthes mindanaoensis Sh.Kurata, J.*	(MINDANAO) Surigao del Sur	The pitcher lids, which have poorly developed to non-existent median keels and basal appendages, and the dimorphic lid glands distinguish this species from *N. alata*.
38.	*Nepenthes mira Jebb & Cheek*	(PALAWAN) Cleopatra's Needle	The long, rather stiff indumentum on the younger leaves, the pitcher lids with poorly developed to non-existent median keels nor basal appendages, and the dimorphic lid glands distinguish it from *N. alata.*
39.	*Nepenthes mirabilis (Lour.) Rafarin*^{N}	(MINDANAO) Camp Keithley, Lanao del Sur, Zamboanga; Surigao	*N. mirabilis* differs from *N. rowaniae* by having slender pitchers with the hip about a third of the way up from the pitcher base (vs. halfway or more), laxer, chartaceous leaves (vs. rigid, arcuate, coriaceous), and longer scandent or climbing aerial stems (vs. erect to subscandent).
40.	*Nepenthes nebularum G.Mansell & W.Suarez*	(MINDANAO) Mt. Mayo, Davao Oriental	The only differences between this species and *N. truncata* and *N. robcantleyi* are the plants' smaller stature, more pronounced peristome teeth, and the bronzy, dense, and woolly indumentum found on the petiole wings, tendrils, and traps.
41.	*Nepenthes negros Jebb & Cheek*	(VISAYAS) Biliran, Negros	Upper pitchers are wider at the swollen base, gradually narrowing to the slenderer, subcylindric upper two-thirds (not subcylindric overall, slightly constricted in the middle); partial-peduncles of the inflorescence are 2-flowered (not 1-flowered).
42.	*Nepenthes palawanensis S.McPherson, Cervancia, Chi.C.Lee, Jaunzems, Mey & A.S.Rob.*	(PALAWAN) Sultan Peak, Narra	*N. attenboroughii*, which grows near Mount Victoria, appears to be the most closely related to *N. palawanensis*. It can be distinguished from *N. attenboroughii* by its larger pitchers, which can reach 35 cm in height. The pitchers of *N. palawanensis* are lined with orange to red hairs, distinguishing them from *N. attenboroughii.*
43.	*Nepenthes pantaronensis Gieray, Gronem., Wistuba, Marwinski, Micheler, Coritico & V.B.Amoroso*	(MINDANAO) Pantaron Mountain Range, Bukidnon	Upper pitchers can be up to 40 cm long and 5 cm wide, with glands distributed densely and evenly over the lower surface. The lid has a bright red lower and upper surface. The lower pitchers have narrow orange-red blotches on their greenish or slightly orange exteriors. The lid is ovate in shape, measuring up to 7cm in length

			and 6cm in width. The pitcher's interior is white or light yellowish green, with small purple-red blotches running down the sides.
44.	*Nepenthes peltata Sh.Kurata, J*	(MINDANAO) Mt. Hamiguitan, Davao Oriental	A peltate tendril attachment and prominent indumentum distinguish it. Upper pitchers of *N. peltata* have never been observed and are either very rare or absent altogether; the species typically produces ovoid pitchers with a prominent basal crest and large nectar glands on the lower surface of the lid. It's been suggested that the species, like the closely related *N. deaniana* and *N. mira,* may only produce aerial pitchers in deep shade or if provided with enough vegetation to support a climbing stem.
45.	*Nepenthes petiolata Danser*	(MINDANAO) Mt. Urdaneta, Agusan del Norte, Surigao del Sur.	Slender pitchers with no appendages on the lower surface, thin, profoundly flanged peristome ribs with long flattened teeth, and petiolate leaves characterize this species. Other Mindanaoan species are unlikely to be confused with *N. petiolata*. The most similar Philippine species is N. *mira*, which has broadly ellipsoid lower pitchers and infundibuliform upper pitchers.
46.	*Nepenthes philippinensis Macfarl.*	(PALAWAN) Mt. Pulgar Thumb Peak; Mt. Victoria	*N. philippinensis* is most closely related to *N. macrovulgaris,* a Sabah-only species that appears to be restricted to ultramafic areas like *N. philippinensis*. Based on the description, it was ascribed to synonymy under *N. alata* Blanco, to which it is superficially similar but lacks a lid appendage.
47.	*Nepenthes pulchra Gronem., S.McPherson, Coritico, Micheler, Marwinski & V.B.Amoroso*	(MINDANAO) trail from Brgy. Kibalabag, Mt. Kiamo, Malaybalay, Bukidnon	*N. pulchra* is closely related to *N. petiolata*, and their pitchers have very similar morphology and coloration. The petioles of *N. pulchra* are winged, and the wings extend the entire length of the internode and a portion of the preceding internode The leaf base of *N. petiolata* clasps the stem and is petiolate.
48.	*Nepenthes ramos Jebb & Cheek*	(MINDANAO, Camuigin) Misamis Occidental, Surigao del Norte	The upper pitchers lack fringed wings; the peristome is flattened, not cylindrical; the lower surface of the lid has strongly dimorphic nectar glands, not uniform; and the inflorescences have partial peduncles that are 2-flowered, not 1-flowered, as in *N. alata.*
49.	*Nepenthes robcantleyi Cheek*	(MINDANAO) exact location not specified by authors	It is related to *N. truncata* and was considered a dark, highland form of that species. Borneo's *N. veitchii* is a close relative. *N. robcantleyi* pitchers are enormous, measuring up to 40 cm in length and 10 cm in width. The inflorescence is the tallest among known *Nepenthes* species, reaching up to 2.5 m in length. However, the plant does not grow very tall and that is not identified to climb.
50.	*Nepenthes samar Jebb & Cheek*	(VISAYAS) Samar	*N. samar* differentiates from *N. merrilliana* in that it has a winged climbing stem, an obtuse, rounded, or retuse leaf apex, and a leaf base that is slightly attenuate but almost as wide as the rest of the blade, and a 1.5-3cm broad leaf base at the stem junction. Leaf texture and surface are leathery and glossy, with higher pitchers being infrequently produced, the inner part of the peristome of upper pitchers revolute, the edge not visible without dissection, and the outer tepal surface being hairy.
51.	*Nepenthes saranganiensis Sh.Kurata*	(MINDANAO) Sarangani	The pitchers' morphology is quite like *N. alata*, and it is known for its very decurrent leaf attachment that runs a long distance down the stem, often continuing into the next internode. Its frequent characteristics include winged petioles, lids with basal ridges on the lower surface (sometimes expanded into appendages), and upper pitchers that are normally largest toward the base.
52.	*Nepenthes sibuyanensis Nerz*	(VISAYAS) Mt. Gitging-giting, Sibuyan	*N. insignis* has also been compared to *N. sibuyanensis.* The pitcher mouth of *N. sibuyanensis* is virtually horizontal, compared to oblique in the latter, and the former produces one-flowered pedicels. Peristome creates a short neck and longer than *N. insignis*. The pitchers of *N. sibuyanensis* are also ovate or somewhat infundibulate in form. The pitcher shape of *N. sibuyanensis* distinguishes it from *N. burkei* and *N. ventricosa*; the traps of *N. burkei* and *N. ventricosa* are oblong to slightly infundibulate while pitchers are smaller.
53.	*Nepenthes sumagaya Cheek*	(MINDANAO) Mt. Sumagaya, Claveria, Misamis Oriental	It is sympatric with *N. pantaronensis*, and there have been reports of hybrids between the two species. *N. sumagaya* has no clear close relatives in the genus due to its uncommon combination of morphological features.
54.	*Nepenthes surigaoensis Elmer*	(MINDANAO) Mt. Urdaneta, Agusan del Norte	At an early growth, plants begin to grow erect and are supported by the surrounding vegetation, which is largely low bushes. The vines and short stems have broad spathulate-ovate leaves that are 10 cm long and 3.5 cm wide, with a broad, winged and 1 cm wide petiole. Short and ascending stems have upper pitchers that are 10–15 cm tall and 3 cm wide. The upper pitchers have a yellowish green to orange appearance that is irregularly stained with crimson or has red spots. The pitcher's interior is pale, with large purple spots visible through the pitcher wall. The lid is yellow, with numerous red blotches and a tiny appendage near the base that has been reduced to a keel. The pitcher lid spur is 3 mm long, unbranched, filiform, and unbranched. The mouth of a pitcher is circular, slightly elevated in front and elongated in rear, with a slightly developed neck and a small appendage in the back. The inflorescence is a panicle with a 15-centimeter scape and a 15-centimeter rachis. The anther column can be up to 14 mm long, and the ovary can be up to 5 mm long, with mature seeds inside. Across the leaf, there is a conspicuous indumentum.
55.	*Nepenthes talaandig Gronem., Coritico, Wistuba, Micheler, Marwinski, Gieray & V.B.Amoroso*	(MINDANAO) Pantaron Mountain Range, Brgy. St. Peter, Malaybalay, Bukidnon	*N. talaandig* differs from *N. cornuta* by having bulbous lower pitchers with a flattened, crenellated peristome and a winged petiole that clasps the stem.
56.	*Nepenthes tboli Jebb & Cheek*	(MINDANAO) Lake Parker, T'Boli, South Cotabato	*N. tboli* differs from *N. saranganiensis* in having stems are terete (not 4-winged), the leaf blade midribs and margins are hirsute (not glabrous), and the pitcher lid apices are retuse (not rounded).
57.	*Nepenthes truncata Macfarl.*	(MINDANAO) Agusan del Norte, Surigao del Norte near Samsolang	Because of its conspicuously truncate to severely notched leaf blade apex, huge size, and lid with a basal glandular crest, *N. truncata* is unlikely to be confused with any other species. The species, like *N. bellii, N. merrilliana,* and *N. petiolata,* appears to have

			a very limited distribution, being found only in the very ultramafic north-eastern corner of Mindanao. In its highly petiolate leaves, appendaged pitcher cover, 2-flowered partial peduncles, and venation of the leaf blade, *Nepenthes truncata* reveals affinities to the *N. maxima* group. Only a few incomplete collections of *N. truncata* exist.
58.	*Nepenthes ultra Jebb & Cheek*	(LUZON) Aurora; Isabela; Zambales	*N. ultra* differs from *N. alata* in having upper pitchers lack fringed wings entirely; outer pitcher surface sparsely and minutely stellate hairy, 10–15 percent of surface covered with red-translucent hairs 0.06–0.1 mm diam; stems glabrous or sparsely hairy at apex.
59.	*Nepenthes ventricose Blanco*	(LUZON) Aurora; Cagayan; Ilocos Norte; Ifugao; Nueva Ecija; Nueva Vizcaya; Mountain Province; Bataan; Quezon; Rizal; Camarines; Albay; Sorsogon	*N. ventricosa* is easily recognized by its angular stems and white, hourglass-shaped upper pitchers. *N. ventricosa* is similar to *N. burkei* of Mindoro and *N. sibuyanensis* of Sibuyan, but neither species has the white, constricted pitchers of *N. ventricosa.*
60.	*Nepenthes viridis Micheler, Gronem., Wistuba, Marwinski, W.Suarez & V.B.Amoroso*	(VISAYAS) Samar (MINDANAO) Dinagat	Regarding pitcher morphology, *N. viridis* differs from *N. alata* in various ways. The front section of the peristome in *N. viridis* is elevated and crenellated. The pitcher lid is likewise unusual, with a noticeable keel or keeled appendage and a highly domed cover. *N. alata*, on the other hand, has a triangular appendage or a shortened keel and no domed lid. The development of the ventral pitcher wings also differs significantly. Lower and intermediate pitchers of *N. viridis* are only found in the upper third of the pitcher cup and have large, widely spaced filaments.
61.	*Nepenthes zygon Jebb & Cheek*	(MINDANAO) Mt. Pasian; Agusan del Norte; Davao Oriental	Leaf blades narrowly oblong-elliptic (not ovate-lanceolate), petiole with wings patent (not severely involute, seeming cylindric), and basal lid appendage present in upper pitchers, noticeable, strongly convex or hooked, distinguish *N. zygon* from *N. mindanaoensis* (not inconspicuous or weakly developed).

^{1} = Data extracted from published description paper, literature, and online databases of each species; ^{N} = native/indigenous

3.2 Resolving the molecular phylogeny of the Philippine *Nepenthes*

Mullins (2000) made the first attempt to resolve phylogenetic relationships within the genus *Nepenthes* using both the chloroplast and nuclear genome: the nuclear 5S-NTS non-transcribed spacer region and the chloroplast's trnL-F intron plus intergenic spacer (5S-NTS and trnL-trnF). Nepenthaceae lacks identifiable morphological features and exhibits extreme polymorphism, preventing the creation of a phylogenetic tree. At that time, there were a total of 87 species that originated from different biogeographic regions, with the goals of testing the monophyly of the genus and constructing a hypothesis of species relationships, evaluating the taxonomic circumscription of poorly known species, and investigating character evolution and biogeographic patterns (Mullins, 2000). DNA sequencing analysis has revealed the evolutionary tree for the first time, proving the Nepenthaceae to be monophyletic. The 5S-NTS tree exhibits more strongly supported clades, suggesting a faster evolutionary rate for *Nepenthes* than the more difficult-to-resolve trnL-trnF tree.

Table 2. Nested sampled species within Clade C, Clade E1, and Clade F1 using nuclear 5S-NTS and chloroplast trnL-F intron with notes on morphological characteristics and geographical distribution.^{1}

Clade	Morphological Characteristics	Geographical Distribution	Nested Species
Section V, subsection C (Clade C)	The pitcher lid among nested species is morphologically similar but lacks petiolate leaves and an abaxial appendage.	Widely distributed; not monophyletic. Species originating from Mindanao (a), Mindoro (b), Luzon (c), and Sibuyan Island (d).	(a) *N. merilliana, N. bellii* (b) *N. burkei* (c) *N. ventricose* (d) *N. sibuyanensis*
Section V, subsection E series 1 (Clade E1)	Morphologically identical to one another, with petiolate leaves; no unique synapomorphy.	Restricted; monophyletic. Species within Mindanao (a). Purely ultramafic species. *N. petiolata* is sister to *N. truncata* and *N. copelandii*, both of which are endemic to Mindanao and grow sympatrically.	(a) *N. petiolata, N. truncata, N. copelandii*
Section V, subsection F series 1 (Clade F1)	*N. mira* is morphologically distinct to *N. argentii* and *N. philippinensis* but does not share any synapomorphies. *N. mira* is more similar to Bornean *N. villosa.*	Restricted within Palawan (a) and Sibuyan Island (b).	(a) *N. mira, N. philippinensis* (b) *N. argentii*

^{1} = Data from 11 Philippine *Nepenthes* species sampled by Mullins (2000). Clades with nested species outside Philippines are excluded here.

Mullins (2000) used molecular data sets from two opposing and separate gene areas. Then a third data set was analyzed and merged with the molecular data sets, consisting of distinct morphological characters. As a result, the understanding of character evolution and biogeographic trends proposed by Danser (1928) and Jebb and Cheek (1997) in questionnaire classification systems was clarified and improved. Out of 19 recorded Philippine *Nepenthes* in 2000, only 12 were sampled in his study. Three Philippine-restricted clades were formed from these sampled species: Section V Subsection C (Clade C), Section V, Subsection E Series 1 (Clade E1), and Section V, Subsection F Series 1 (Clade F1). These clades are separated by differences in their morphological characteristics and geographical distributions (see Table 2). However, the Philippine *N. alata* sampled was not assigned to any clade, suggesting that the specimen was a hybrid at the time its DNA was sequenced. This is valid since *N. alata* is a highly variable taxon that is vulnerable to natural hybridization (Cheek and Jebb, 2014; Murphy et al., 2020). All species of *Nepenthes* are obligate outbreeders, being dioecious plants. Because numerous taxa are strikingly similar, all are interfertile. Isolated hybrid swarms are regularly encountered in sympatric species areas, it has long been assumed that hybridization has a role in the diversification of *Nepenthes* (Mullins, 2000; McPherson, 2009a; McPherson, 2009b; Cheek and Jebb, 2013f; Handayani, 2017; Murphy et al., 2020).

At the time, the phylogeny derived from the trnK intron data was partial to *Nepenthes*' current infrageneric taxonomy. Meimberg et al. (2001) constructed three clades using only trnK as a marker for phylogenetic analysis. The first clade (Clade I) consisted of all species from Sumatra, the Malay Peninsula, Thailand, Cambodia, and Vietnam, as well as Philippine species with three nested species. The second clade (Clade II) appeared to have included all the descendants of Mullins' Clade C (2000). The third clade (Clade III) showed no any nested Philippine species. For these species, the markers trnK intron, 5S-NTS, and trnL-trnF show the same grouping, confirming a morphologically monophyletic group. Meimberg et al. (2001) distinguished the lineages of Philippine taxa based on morphological characters rather than geography. When compared to the results of Mullins (2000), it appears to have limited geographical specifications; Meimberg et al. (2001) did not elaborate on specific Philippine Island restrictions for Clades I and II (see Table 3). Molecular evidence from Meimberg et al. (2001) suggests that Southeast Asian colonization began with the introduction of ancient Indian ancestors. Later, due to this development, a new secondary center of diversity arose in the Malay Archipelago. Migration across land bridges most likely reached Madagascar, the Seychelles, and New Caledonia (Raven and Axelrod, 1974), starting with widely dispersed common ancestors and ending with extinction, leading to the extinction of the current taxa. Furthermore, evidence does not support long-distance dispersal.

Table 2. Nested sampled species within Clade I and Clade II using trnK intron with notes on morphological characteristics and geographical distribution.[1]

CLADE	MORPHOLOGICAL CHARACTERISTICS	GEOGRAPHICAL DISTRIBUTION	NESTED SPECIES
CLADE I	Morphologically dissimilar as per groupings of Danser (1928) having characteristics of *Vulgatae*, *Insignes*, and *Regiae* sects.		*N. mirabilis, N. petiolata, N. truncata*
CLADE II	Morphologically similar to *Insignes* group of Danser (1928). *N. alata* was placed in this, showing relationship to *Regiae* group of Danser (1928).	Clade I and II are widely distributed throughout the Philippines.	*N. ventricosa, N. merilliana, N. bellii,* and *N. globamphora*[2]

[1] = Data from 7 Philippine *Nepenthes* species sampled by Meimberg et al. (2001). Clades with nested species outside Philippines are excluded here.

[2] = *N. globamphora* sampled by Meimberg et al. (2001) is now recognized as *N. bellii.*

Using the peptide transferase 1 (PTR1) locus in several species, Meimberg and Heubl (2006) created a new nuclear marker for phylogenetic analysis of *Nepenthes*. Mullins (2000) had already used a nuclear marker in his study. In terms of biogeographical evolution, the PTR1, unlike the previously studied translocated copy of trnK, has proven useful. These findings are supported by the major clades visible in the trnK intron phylogeny and the PTR1 phylogenetic reconstruction. Although most species from the Sunda Shelf, the Philippines, and other regions of Southeast Asia are very similar, most Bornean species form a monophyletic group. Even with the presence of the nuclear marker PTR1 for phylogenetic analysis, it fails to identify specific geographic clades within the Philippines (refer to Table 4), and the sampling of Philippine taxa still seems to be inadequate compared to other paleotropical taxa.

Table 3. Nested sampled species within Clade I and Clade II trnK intron and PTR1 with notes on morphological characteristics and geographical distribution. [1]

CLADE	MORPHOLOGICAL CHARACTERISTICS	GEOGRAPHICAL DISTRIBUTION	NESTED SPECIES
CLADE I	Clade I and II are similar to Meimberg et al. (2001).	Includes all species found on the Sumatra mainland in Southeast Asia.	*N. mirabilis, N. petiolata, N. truncata*
CLADE II		Species from Borneo and the Philippines predominate.	*N. alata, N. mira, N. bellii, N. burkei, N. merilliana, N. sibuyanensis, N. ventricosa*

[1] = Data from 10 Philippine *Nepenthes* species sampled by Meimberg and Heubl (2006). Clades with nested species outside Philippines are excluded here.

The published description of *Nepenthes* peaked in 2010 with eight new species, and in 2011 with 10 new ones (Golos, 2012). In the Philippines, researchers discovered seven new species between 2010 and 2012. *Nepenthes gantungensis* S.McPherson, Cervancia, Chi.C.Lee, Jaunzems, Mey & A.S.Rob. (2010), *Nepenthes hamiguitanensis* Gronem., Wistuba, V.B.Heinrich, S.McPherson, Mey & V.B.Amoroso (2010), *Nepenthes palawananensis* S.McPherson, Cervancia, Chi.C.Lee, Jaunzems, Mey & A.S.Rob. (2010), *Nepenthes leonardoi* S.McPherson, Bourke, Cervancia, Jaunzems & A.S.Rob. (2011), *Nepenthes pulchra* Gronem., S.McPherson, Coritico, Micheler, Marwinski & V.B.Amoroso (2011), *Nepenthes robcantleyi* Cheek (2011), and *Nepenthes ceciliae* Gronem., Coritico, Micheler, Marwinski, Acil & V.B.Amoroso (2011). But Philippine taxa were still undersampled. Golos (2012) used the same markers as Meimberg et al. (2001) and Meimberg and Heubl (2006). Golos (2012) only sequenced and nested three of the seven Philippine endemics in their respective clades (see Table 5). Golos (2012) did not sequence samples of *N. deaniana, N. hamiguitanensis, or N. mantalingajanensis*. It's hard to amplify PTR1 even from living things, and PTR1 primers often get mixed up, which leads to common banding patterns in gel results (Meimberg and Heubl, 2006; Golos, 2012).

Table 4. Nested sampled species within Clade I and Clade II using trnK intron and PTR1 with notes on morphological characteristics and geographical distribution. [1]

Clade	Morphological Characteristics	Geographical Distribution	Nested Species
Clade I	Similar findings to Meimberg et al. (2001) and Meimberg and Heubl (2006).		*N. copelandii*
Clade II			*N. argentii, N. philippinensis*

[1] = Data from 7 Philippine *Nepenthes* species sampled by Golos (2012). Clades with nested species outside Philippines are excluded here.

[2] = Four out of seven nested species within Clade I and Clade II from Golos (2012) were the same species nested in the same clades from the Meimberg et al. (2001) and Meimberg and Heubl (2006) results using trnK intron and PTR1 markers. *N. copelandii, N. argentii, and N. philippinensis* were added to their respective clades using the same markers employed by Golos (2012).

Instead of being useless for phylogenetic analysis, as previously thought, the PTR1 locus proved to be extremely helpful in this study. The main groups seen in the trnK intron phylogeny also show up in the PTR1 phylogenetic reconstruction, which backs up this conclusion (Meimberg et al., 2000; Meimberg and Heubl, 2006; Golos, 2012). The Sunda Shelf and Southeast Asian species are highly convergent, while Bornean species form a distinct monophyletic group (Meimberg and Heubl, 2006). However, preliminary results from the PTR1 gene locus remain. Currently, we cannot make a firm estimate about Nepenthes' ancestry due to the failure to include an outgroup for the PTR1 locus, which includes outgroup taxa from Droseraceae (*Drosera*), Dioncophyllaceae (*Triphyophyllum*), and Ancistrocladaceae (*Ancistrocladus*).

According to the findings of Alamsyah and Ito (2013), *Nepenthes* has most likely moved to the Philippines from Borneo, which contradicts the conclusion of Meimberg and Heubl (2006) regarding the colonization of Southeast Asian species. They demonstrated this by using ITS nRDNA sequences, the internal transcribed spacer of the nuclear ribosomal DNA, as markers for their phylogenetic study of 56 *Nepenthes* species (nested in 7 different monophyletic subclades), and by finding *Nepenthes campanulata* at the base of their tree in Subclades III and IV, sister groups to Subclade II, which includes Borneo and Sulawesi species. Furthermore, Alejandro et al. (2008), using the same marker, strongly supported the placement of *N. alata* and *N. ventricosa* in Subclade IV. Alamsyah and Ito (2013) found that ITS nrDNA sequences did not form any unique Philippine island-specific groups or lineages, despite the strong basis of morphological similarities. Alamsyah and Ito (2013) restricted their phylogenetic research to major biogeographical areas of *Nepenthes* in Southeast Asia, and focused on evolutionary trends in peristome morphologies based on Danser (1928). This may have led them to overlook or not investigate other character states of nested species within Subclade IV, their Philippine-restricted clade, and Subclade III, which could have revealed island-specific distribution within the archipelago. However, Table 6 indicates that Subclade III appears to restrict nested species to Mindanao, while Subclade IV exhibits widespread distribution throughout the Philippines.

Table 5. Nested sampled species within Subclade III and Subclade IV using ITS nRDNA sequences with notes on morphological characteristics and geographical distribution. [1]

Subclade	Morphological Characteristics	Geographical Distribution	Nested Sampled Species
Subclade III	Species have small peristomes (suggesting peristomes is plesiomorphic state in *Nepenthes*)	Limited to Philippine islands, but authors did not specify restrictions on specific Philippine islands.	*N. copelandii, N. mindanaoensis, N. truncata*
Subclade IV	There were intermediate and broad peristomes in some species.		*N. alata, N. bellii, N. burkei, N. merrilliana, N. ventricosa*

[1] = Data from 8 Philippine *Nepenthes* species sampled by Alamsyah and Ito (2013). Clades with nested species outside Philippines are excluded here.

The Southeast Asian *Nepenthes* clades diversified into two major clades, according to the most recent phylogenetic study by Murphy et al. (2020). Southeast Asia is home to nearly all of the known *Nepenthes* species, making it the epicenter of the genus' diversity. Murphy et al., 2020 consistently found the two sister clades of Southeast Asian *Nepenthes* together. Clade 1 includes common and lowland species from Sulawesi and Papua, as well as a few high-altitude species from Sulawesi and Papua. Clade 2 contains the most distinct clades from Sumatra-Java, Indochina, Peninsular Malaysia, Mindanao, and Palawan. Both Clade 1 and Clade 2 included Borneo, Sulawesi, and Papua New Guinea species, which were less clearly differentiated than those from other regions. These findings demonstrate the resolution of most *Nepenthes* species into well-supported clades, and the presented phylogeny can enhance our understanding of *Nepenthes* lineage evolution, particularly for geographically defined clades. Murphy et al. (2020) demonstrated a strong geographical delimitation among Philippine taxa, supporting a monophyletic pan-Philippine clade that reveals three exclusive lineages and the widespread Insignes clade (see Table 7). The study also showed that N. pervillei from Seychelles is related to the rest of the genus and N. danseri from Waigeo island is related to all other Asian species (Murphy et al., 2020). This supports what other researchers have found about Western taxa that split off early on (Mullins, 2000; Meimberg et al., 2001; Meimberg and Heubl, 2006; Golos, 2012; Alamsyah and Ito, 2013). When comparing Alamsyah and Ito's (2013) study with Murphy et al.'s (2020) study, it appears that all nested species within Subclade III from Alamsyah and Ito (2013) are Mindanaoan taxa, which aligns with Murphy et al.'s Mindanao Clade, while the species nested within Subclade IV (Alamsyah and Ito, 2013) appeared to be polyphyletic in Murphy et al.'s (2020) trees.

Table 6. Nested sampled species within Mindanao Clade, Palawan Clade, Graciliflora Clade, and Insignes Clade using angiosperms353 probe set with notes on morphological characteristics and geographical distribution.[1]

Clade	Morphological Characteristics	Geographical Distribution	Nested Sampled Species
Mindanao Clade	Most Mindanaoan taxa were classified into sect. *Alatae* by Cheek and Jebb. For *N. micramphora,* lid appendage absent and slender peristomes present.	Mindanao Island only	*N. ceciliae* *N. copelandii* *N. cornuta* *N. hamiguitanensis* *N. justinae* *N. micramphora* *N. mindanaoensis* *N. pantaronensis* *N. peltata* *N. petiolata* *N. pulchra* *N. robcantleyi* *N. sumagaya* *N. talaandig* *N. truncata* *N. zygon*
Palawan Clade	Distinctive blade-like peristome ridges. No lid appendage. Members of Palawan Clade placed under Sect. *Villosae* of Cheek and Jebb are similar to type species *N. villosae*. Filiform bracts and hipped pitchers for *N. philippinensis*.	Palawan Island only	*N. attenboroughii* *N. deaniana* *N. leonardoi* *N. mantalingajanensis* *N. mira* *N. palawanensis* *N. philippinensis* *N. sp.* Anipahan
Graciliflora Clade[2]	Nested sampled species within this clade having characteristics similar to the sect. Alatae (*N. alata* group) of Cheek and Jebb.	Luzon, Visayas (Sibuyan), and Dinagat	*N. alata* *N. argentii* *N. armin* *N. graciliflora* *N. viridis*
Insignes Clade[3]	Nested sampled species within this clade having characteristics similar to the sect. Insignes (*N. insignis* group) such as pitchers without lid appendages, sparse indumentum, and large sessile leaves.	Luzon, Visayas (Mindoro and Sibuyan), and Northern Mindanao	*N. barcelonae* *N. bellii* *N. burkei* *N. merrilliana* *N. sibuyanensis* *N. surigaoensis* *N. ventricosa*

[1] = Data from 35 described and 1 undescribed (*N.* sp. Anipahan) Philippine *Nepenthes* species sampled by Murphy et al. (2020). Clades with nested species outside Philippines are excluded here.

[2] = Probable type species for this clade is *N. graciliflora.*

[3] = Probable type species for this clade is *N. insignis.*

Nepenthes species from Mindanao and Palawan belong to consistent and well-supported clades while remaining geographically distinct. The Mindanao Clade is sister to the Palawan and Graciliflora Clades (Murphy et al., 2020). Cheek and Jebb (2013f) confirmed that most species assigned to the section Alatae in the Cheek and Jebb classification, including its type species (*N. alata*), are members of the Mindanao Clade. Instead, these taxa formed the Graciliflora Clade. The Mindanao, Palawan, and Graciliflora Clades form the entire monophyletic Philippine Clade. Murphy et al., 2020 confirmed the geographical heterogeneity of the Insignes Clade alongside the section Tentaculatae, which includes Borneo and Sulawesi species. This is linked to widespread species in Luzon (*N. barcelonae, N. ventricosa*), the Visayan Islands (*N. burkei, N. sibuyanensis*), and Mindanao (*N. bellii, N. surigaoensis).*

3.3 Phylogenetic status of Philippine *Nepenthes mirabilis*

Murphy et al. (2020) sampled many *N. mirabilis* from various countries and biogeographical hotspots but did not sample any species from the Philippines. It is true that *N. mirabilis* is the most widespread and likely abundant species of all *Nepenthes*. Furthermore, it has the most synonyms of all *Nepenthes* species and demonstrates remarkable variety in pitcher form and color across its range, resulting in diverse hybrids (Catalano, 2009). Despite its wide distribution, this species likes to live in coastal marshes where there are few other *Nepenthes* species (Clarke, 1997; Clarke, 2001). It would be fascinating to learn whether *N. mirabilis* has acquired particular adaptations to help with migration or if existing in coastal wetlands is enough. This corresponds to the distribution of N. mirabilis in the Philippines, primarily in swamps, marshes, and forests from sea level to 900 meters (Pelser et al., 2021).

Murphy et al., 2020 recently classified several *N. mirabilis* species as distinct species. There were at least three recorded *N. mirabilis* natural hybrids in the Philippines: *Nepenthes mirabilis* × *N. alata* Sh. Kurata & Toyoshima (1972) (*N. mirabilis* × *N. alata*); *Nepenthes* × *mirabilata* Hort. ex Lauffenburger (1995) (*N. alata* × *N. mirabilis*); and *Nepenthes* × *tsangoya* Tsang ex Lauffenburger (1995) nom.nud (*N. alata* × *N. merrilliana*) × *N. mirabilis*. However, Lauffenburger (1995) localizes these hybrids to Mindanao, where the parent species overlap. Murphy et al. (2020) sampled the Philippine *N. mirabilis* using the angiosperms353 probe set. They expected the following results: 1) Samples from various locations may be nested in any of the Philippine clades identified by Murphy et al. (2020), and 2) sampling different Philippine hybrids could yield different results, potentially indicating their species. Despite their obvious paraphyly, these related species form a clade when considering their extensive range, lack of apparent long-range dispersal mechanisms, and proclivity for hybridization. The paraphyletic results may be due to noise or a lack of support and resolution in the gene trees, among other things (Mullins, 2000; Alamsyah & Ito, 2013; Murphy et al., 2020). Based on the trees from Meimberg et al. (2001) and Meimberg and Heubl (2006), Murphy et al. (2020) placed Philippine *N. mirabilis* within the group of *N. petiolata* and *N. truncata*, both species belonging to the Mindanao clade. It is most likely that the native *N. mirabilis* is a Mindanaoan taxon (see Table 1).

Possible clades of unsampled Philippine Nepenthes species following angiosperms353 of Murphy et al., 2020

Murphy et al. (2020) were confident in placing of most species and unsampled taxa in broad clades, at least in terms of the nuclear genome, since their phylogenetic trees were relatively stable compared to previous studies. So far, the use of the angiosperms353 probe set for the 151 *Nepenthes* species included in Murphy et al.'s phylogenetic tree (2020) has had the most advanced resolution. The method divided most species into well-supported lineages, revealing new information about *Nepenthes* evolution. Several clades, especially those from Mindanao and Palawan, are geographically distinct. There are still some worries about individual gene trees, but their results show that the angiosperms353 probe collection has the most potential for species-level systematics compared to other molecular approaches.

Since their research began in 2018, there have been gaps in sampling, especially for newly described species (Murphy et al., 2020). Murphy et al. (2020) acknowledged that challenges in collecting and retrieving samples, like leaf tissues or herbarium specimens, prevented them from sampling some Philippine species. For example, *Nepenthes extincta* Jebb & Cheek, a published species in 2013, was described using only a single existing herbarium-type specimen collected in 1978 (Cheek and Jebb, 2013f). Although the authors classified it as critically endangered, it is believed to be extinct in the wild due to mining companies exploiting its natural habitat, which is rich in ultramafic substrate, and the lack of sightings of this species since then. These findings are almost identical to those of *Nepenthes alzapan*, Jebb & Cheek, and other species thought to be extinct in the wild. Future phylogenomic studies, grounded in the methods of Murphy et al. (2020), may include some species if existing wild or cultivated specimens exist. Unsampled species are almost certainly extinct as a result of human disturbances in their natural habitats. Time of species publication, availability of specimens, and potential conflicts of interest are all potential barriers to conducting comprehensive phylogenetic research (Mullins, 2000; Meimberg et al., 2001; Meimberg and Heubl, 2006; Golos, 2012; Alamsyah and Ito, 2013; Murphy et al., 2020).

Table 8. Summary of unsampled species to their possible clades based on morphological characteristics and geographical distribution similarities to clades formed by Murphy et al. (2020).

Clade	Unsampled Philippine Species
Mindanao Clade = 13 taxa	*N. abgracilis, N. alfredoi, N. candalaga, N. cid, N. extincta, N. kitanglad, N. malimumuensis, N. nebularum, N, ramos, N. saranganiensis, N. tboli,* *N. erucoides*[1], *N. kampalili*[1]
Palawan Clade = 7 taxa	*N. abalata, N. gantungensis* *N. erucoides*[1], *N. campanulata*[2], *N. kampalili*[1]
Graciliflora Clade = 4 taxa	*N. maximoides, N. ultra* *N. leyte, N. negros, N. samar*[3] *N. erucoides*[1]
Insignes Clade = 7 taxa	*N. aenigma, N. alzapan, N. manobo, N. cabanae* *N. leyte, N. negros, N. samar*[3]

[1] = *N. erucoides* can be potentially nested in either of three clades: Mindanao, Palawan, or Graciliflora; *N. kampalili* can be potentially nested in Palawan clade.

[2] = *N. campanulata* can be potentially nested in Palawan clade with considerations.

[3] = *N. leyte, N. negros,* and *N. samar* can be potentially nested in either Graciliflora clade or Insignes clade.

We must sample and analyze the remaining 26 Philippine species (Appendix 2) to fully understand the phylogenetic relationship between the Philippine *Nepenthes* and its relatives. We noted a possible phylogenetic position for these species based on morphology and geographical distribution similarities to nested species from the most comprehensive phylogeny to date (Murphy et al., 2020). To confirm this, a government-funded research extension must be considered. We can use type specimens, vouchers, and tissue samples to conduct DNA sequencing for phylogenetic analysis. We can use the results for conservation efforts. Table 8 shows a list of species that haven't been sampled yet that might belong to the same clades as species from Murphy et al. (2020) based on their physical features and where they live. Figures 1 and 2 show the distribution of 61 *Nepenthes* species in the Philippines.

Mindanao Clade

***Nepenthes abgracilis* Jebb & Cheek.** It is a species found in Surigao, Mindanao, and has similarities to *N. micramphora*, a nested species within the Mindanao Clade. It differs from *N. micramphora* in longer stem diameter, 3-4 mm width of decurrent leaf wings at node, larger leaf blade size, upper pitchers slightly broadest base about 16 cm long: longer peristome width, lid nectar gland type thinly bordered, and entire spur (Cheek and Jebb, 2013g).

***Nepenthes alfredoi* V.B.Amoroso & Lagunday.** It is possible to have *N. alfredoi* in Mindanao Clade because it differs from *N. zygon* having both pitchers with fringed wings, extending along the tendril for some distance; two-flowered and rarely one flowering for male and female inflorescences (Jebb and Cheek, 2014). *N. alfredoi* is distributed on Mt. Hamiguitan, Davao Oriental, Mindanao. Since *N. zygon* was included in the Mindanao Clade (Murphy et al., 2020) these morphological differences strongly support the suggestion.

***Nepenthes candalaga* Lagunday & Amoroso.** *N. candalaga* is located in Davao de Oro, Mindanao and is closely related to *N. justinae* but differs in several key features: it has a lamina with 2–3 longitudinal veins parallel to the midrib (*N. justinae* has 3 veins). It also has an orbicular pitcher lid, a non-bifid lid spur tip, a triangular lid appendage, short banner-shaped wings below the peristome covering a sixth of the trap's anterior and becoming ridges toward the base, and an absent upper pitcher rim that is widest near the peristome. Locality and morphological features like *N. justinae* (a species nested in Mindanao clade of Murphy et al. (2020)) indicates possible placement of *N. candalaga* in the same clade.

***Nepenthes cid* Jebb & Cheek.** The species is distributed in Northcentral Mindanao, specifically in Bukidnon Province, which happens to be around other *N.* species such as *N. ceciliae, N. cornuta,* and *N. pantaronensis.* It is like *N. micramphora* having terete stem in cross-section, stem diameter, width of decurrent leaf wings at node nil, teeth not visible peristome inner edge, and >100 lid nectar glands (Cheek and Jebb, 2013g). This geographical and morphological data considers *N. cid* to be nested within the Mindanao Clade.

***Nepenthes extincta* Jebb & Cheek.** Although thought to be extinct by the authors because of rampant open-cast mining in its natural habitat, its placement within the Mindanao Clade is in no doubt. It is found along the border of Surigao del Sur and Surigao del Norte. It differs from *N. mindanaoensis* (a nested species within the Mindanao Clade) in lacking fringed wings in its pitchers, a cordate lid base, and the indumentum of dense minute grey-white stellate hairs in the midrib (Cheek and Jebb, 2013f).

***Nepenthes kampalili* Lagunday & Amoroso.** *N. kampalili* is found in Davao de Oro, Mindanao which resembles *N. peltata,* a nested species within Mindanao clade of Murphy, 2020. The geographical distribution of *kampalili* and *peltata* strongly supports its placement within the Mindanao Clade. However, according to Lagunday & Amoroso (2024), it is placed in *Nepenthes* section *Villosa.* The features that classify it within this section include blade-like teeth on the peristomes, absence of central basal appendages on the pitcher lid, as well as developed pitcher lids, and preference for high-altitude ultramafic habitats. Phylogenetic analysis by Murphy et al. (2020) indicates that species in section *Villosa* (or *Villosae*) are nested within the Palawan clade. Morphologically, *N. kampalili* could be nested within the Palawan clade.

***Nepenthes kitanglad* Jebb & Cheek**. It differs from *N. saranganiensis* (Table 1) in terms of stems, pitchers, habit, pitcher mouth, lid, and pitcher base. It is found in Bukidnon, Mindanao (Cheek and Jebb, 2013f). The geographical distribution of this species is a strong cause of its placement within the Mindanao Clade.

***Nepenthes malimumuensis* Lagunday, Acma, Cabana, Sabas & V.B.Amoroso**. It belongs to the Villosae group (type species: *Nepenthes villosa*) (Cheek and Jebb, 2013f) according to Lagunday et al. (2017) and differs from *N. sumagaya* in having broadly spathulate to ovate leaves, rounded leaf apex, 4 to 5 longitudinal nerves, wings of upper pitchers not apparent or reduced to ribs and reduced to a keel lid appendage. It also differs from *N. truncata* Macfarl. in terms of the lamina, pitcher peristome, and lid appendage. *N. sumagaya* and *N. truncata* were placed in the Mindanao Clade. The comparative morphology of *N. malimumuensis, N. sumagaya,* and *N. truncata* and the phylogenetic data of the latter species suggest its potential placement in the Mindanao Clade.

***Nepenthes nebularum* G.Mansell & W.Suarez**. It was assigned by Mansell and Suarez (2016) to putative *Regiae* group (Danser, 1928). The species is closely related to *N. robcantleyi* and *N. truncata* and grows sympatrically in lower elevations with *N. truncata* and *N. cfr. cornuta* (Mansell and Suarez, 2016). The placement of *N. robcantleyi* and *N. truncata* in the Mindanao Clade (Murphy et al., 2020) supports our proposal to place the species in the same clade.

***Nepenthes ramos* Jebb & Cheek**. It differs from *N. alata* Blanco (Table 1) in terms of upper pitchers, peristome, lower lid surface, nectar glands, and inflorescences. Although this species was compared to *N. alata* (a nested species within Graciliflora Clade), *N. ramos* is found in Surigao, Mindanao and, having characteristics like other Mindanaoan taxa that were considered part of Danser's and Cheek and Jebb's *N. alata* group (Danser, 1928; Cheek and Jebb, 2013f) the placement of *N. ramos* within the Mindanao Clade is highly considered.

***Nepenthes saranganiensis* Sh. Kurata**. It is the only Philippine species reported to be found in the Sarangani Province, Mindanao. *N. saranganiensis* is a potential species within the Mindanao Clade, just as *N. ramos* is morphologically like *N. alata* with few differences.

***Nepenthes tboli* Jebb & Cheek**. It is the only Philippine species reported to be found in South Cotabato, Mindanao. It is like *N. saranganiensis* with a few differences (Table 1). This species can be nested within the Mindanao Clade, as supported by its morphology and distribution.

Palawan Clade

***Nepenthes abalata* Jebb & Cheek**. It can be found on Panay's Malalison Island, Antique and Culion, Palawan. *N. abalata* has a closer geographical and taxonomic relationship to *N. philippinensis*, which Cheek and Jebb restored from synonymy in 2001 (Cheek and Jebb, 2001). Even though both species live in the western Visayas, they do not appear to be sympatric. Both live at low elevations, lack a distinct petiole, have a midline area on the bottom surface of the lid that is free of typical glands (although *N. abalata* has a few larger perithecoid glands), and have no basal lid appendage. *N. abalata* may be nested within the Palawan clade.

***Nepenthes gantungensis* S.McPherson, Cervancia, Chi.C.Lee, Jaunzems, Mey & A.S.Rob**. It is the only Philippine species reported to be found on Mt. Gantung, Palawan (McPherson et al., 2010). In comparison to *N. deaniana* of the Palawan Clade, the inflorescence of *N. gantungensis* is usually much longer. There are also differences in pitcher morphology, with *N. gantungensis* having a more pronounced peristome. Whereas the lower pitchers of *N. deaniana* and *N. mira* may be reddish-purple all over, *N. gantungensis* does not have this dark pigmentation. Unlike its close relatives, it frequently produces upper pitchers.

Graciliflora Clade, Insignes Clade, and considerations for N. campanulata

***Nepenthes aenigma* Nuytemans, W.Suarez & Calaramo** and ***Nepenthes alzapan* Jebb & Cheek**. These are Luzon species distributed in Ilocos Norte and Mt. Alzapan in Tayabas respectively. The former was placed in a weakly defined Insignes group of Danser, in which *N. ventricosa* was confirmed to be part of the phylogenetically supported Insignes Clade of Murphy et al. (2020). In addition, *N. alzapan* has similar affinities with *N. aenigma* (Table 1) as reported by their authors. We suggest that both species can be potentially nested within the Insignes Clade.

***Nepenthes cabanae* Lagunday & V.B.Amoroso**. It was reported that *N. cabanae* is not a hybrid species because of its unique characters delineating it from others and has a stable population (Lagunday and Amoroso, 2019). Also, it is morphologically close to *N. surigaoensis* under sect. Insignes of Danser (1928) having sessile leaves unevenly clasping up to half of the stem that runs down the internode, four longitudinal nerves, subcylindrical lower pitchers, and a peristome with short triangular teeth not projecting beyond the margin (Cheek et al., 2018). These findings would suggest *N. cabanae* and *N. manobo* are placed together with *N. surigaoensis* under morphologically defined Insignes Clade of Murphy et al. (2020). From a geographical perspective, *N. cabanae* and *N. manobo* might be nested within Mindanao Clade with a small probability, since both species are found in Pantaron Range, Mindanao although the latter was reported to occur in an ultramafic substrate, unlike the former.

***Nepenthes erucoides* A.S.Rob. & S.G.Zamudio**. It was discovered in Dinagat where *N. viridis* of Graciliflora Clade and *N. mindanaoensis* of Mindanao Clade were found. It can be understood that *N. erucoides* could be placed in either of the clades based on geographical distribution. In contrast, *N. erucoides* might also be placed in the Palawan Clade, morphology-wise. The species has an overall plant form similar to *N. mantalingajanensis* (a nested species in Palawan Clade) but differs in such a way that it has an indumentum that is long, hair rufous and dense, produces both upper and lower pitchers, pitcher shape urceolate to sub-campanulate, more fine peristome with small teeth through the inner margin, some partial peduncles and the rachis of male inflorescences produce very large bracts 8–15 mm long, and seeds lacking well-developed filaments (Robinson et al., 2019).

***Nepenthes leyte* Jebb & Cheek**, ***Nepenthes negros* Jebb & Cheek**, and ***Nepenthes samar* Jebb & Cheek**. The species' specific epithet is used as a noun in apposition to the island of that name, to which the species appears to be unique (Cheek and Jebb, 2013d; Cheek and Jebb, 2013f). For the exact geographical distribution of these species, see Table 1. Based on the geographical distribution patterns of species nested within the Graciliflora and Insignes clades of Murphy et al. (2020), the former clade appears to have nested species found in the Visayas and Dinagat, except for the widely distributed species, *N. alata* of Luzon. The latter consists of morphologically similar nested species found in three major island groups of the Philippines (i.e., *N. barcelonae* and *N. ventricosa* of Luzon, *N. burkei* and *N. sibuyanensis* of Visayas, and *N. bellii* and *N. surigaoensis* of Mindanao). We are confident that *N. leyte, N. negros,* and *N. samar* could be nested either within Graciliflora or Insignes.

***Nepenthes manobo* Lagunday, Acma, Cabana, Sabas & V.B.Amoroso**. Morphologically, *N. manobo* belongs to sect. Insignes (Cheek and Jebb, 2013f; Lagunday et al., 2017) and differs from *N. surigaoensis* in having 3 longitudinal nerves, sessile petiole clasping ½ of stem diameter, lower pitcher having bulbous to ovate bottom half, cylindrical to the opening, upper pitcher having distinct hip, lid shape orbicular to ovate, and peristome inner margin with teeth-like projections that are short (Lagunday et al., 2017).

***Nepenthes maximoides* Cheek**. It is likely a part of the Graciliflora Clade since it was discovered on Mt. Banahaw, Luzon and it differs from *N. graciliflora* in terms of the upper pitcher, peristome, lid, and basal appendage (King & Cheek, 2020). A sample of *N. alata* sourced from Bontoc, Mountain Province, Luzon, and *N. graciliflora* from Sibuyan was placed in Graciliflora Clade (Murphy et al., 2020).

***Nepenthes ultra* Jebb & Cheek**. For geographical distribution and morphology of *N. ultra*, see Table 1. Having few similarities and differences to *N. alata, N. ultra* can most likely be nested within Graciliflora Clade.

***Nepenthes campanulata* Sh. Kurata**. It is a Borneo-endemic limestone specialist pitcher plant (Clarke et al., 2014). Additionally, the count of 61 total Philippine species from King & Cheek (2020) and Pelser et al. (2020) list may include this species. In this paper, we consider *N. campanulata* as a Philippine species based on Clarke et al. (2014) report of *N. campanulata* sighting in Saint Paul, Palawan wherein groups of these pitcher plants from the limestone cliff formation are similar to Bornean population in terms of habitat niche, plant stature, habit, leaf form, bell-shaped pitchers, and short tendrils. According to Mullins (2000), the sampled *N. campanulata* was nested to Clade (F3), which includes a Philippine group (Clade F3a) and a big Bornean and Sulawesian group (F3c), although it is sister to a separate clade of Philippine and Bornean species in the nuclear tree (Glade D). Furthermore, Murphy et al. (2020) discovered no evidence of a close relationship between sect. *Insignes* and *N. campanulata*, contrary to claim of Clarke et al. (2018). The small Villosae Clade is more closely related to the major *Regiae* Clade, with *N. maxima* and its allies forming a subclade amid the other Bornean *Regiae* taxa (Murphy et al., 2020). The Regiae Clade is sister to the combined Palawan and Graciliflora Clades, which is sister to the Mindanao Clade *and N. campanulata* in their derived 177-supermatrix tree (Murphy et al., 2020). Therefore, Mullins' (2000) and Murphy et al.'s (2020) phylogenetic analyses tend to corroborate the report of Clarke et al. (2014) regarding the existence of *N. campanulata* in the Philippines, at least in Palawan. The Philippine *N. campanulata* is potential species within the Palawan clade based on geographical data presented by Clarke et al. (2014).

3.4 Distribution of Philippine *Nepenthes*

An updated distribution maps of Philippine *Nepenthes* were created. The map illustrates the distribution of species based on Murphy et al.'s molecular phylogeny of Nepenthaceae (See Figure 2 and 3).

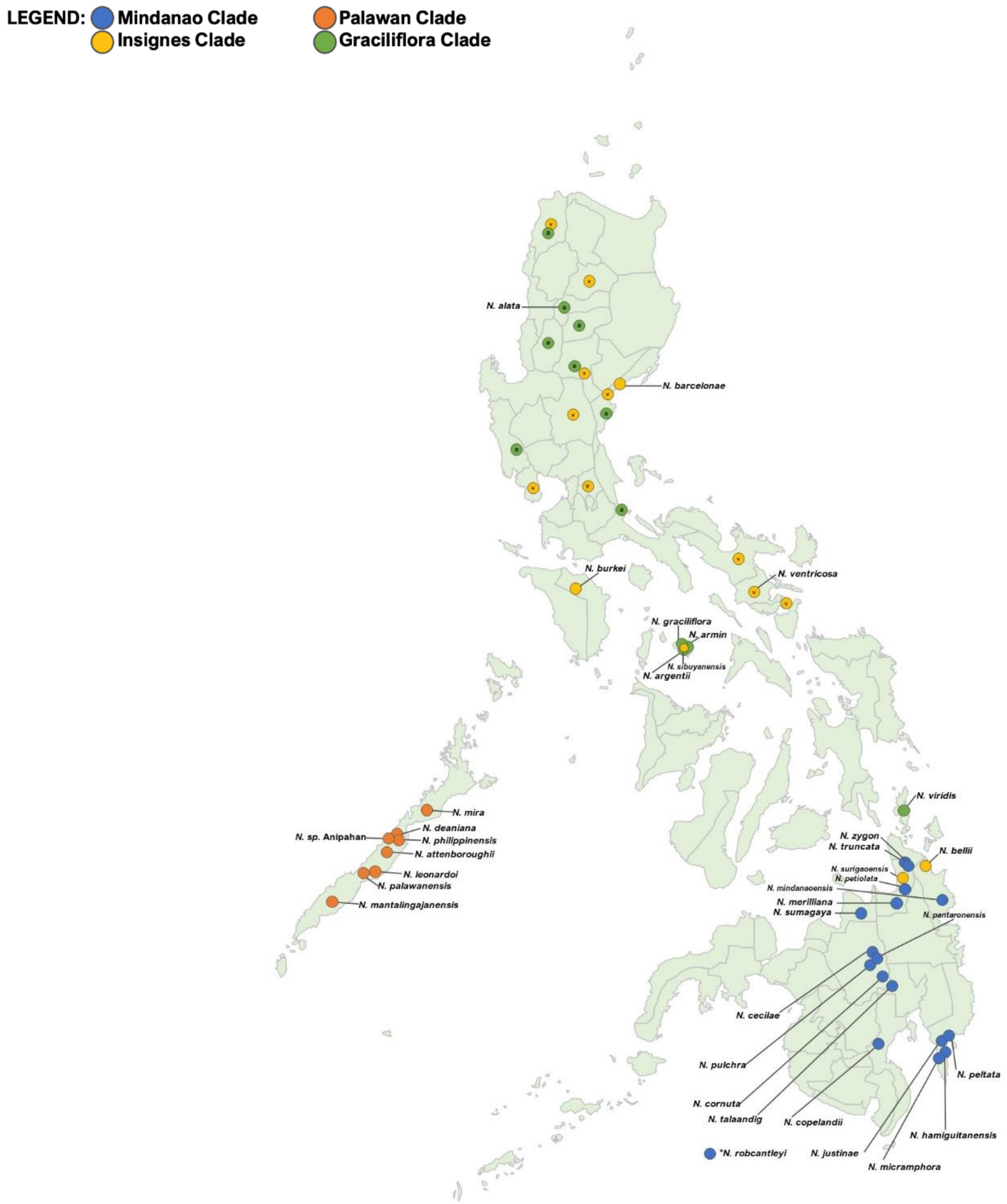

Figure 1. Geographical distribution of 35 Philippine *Nepenthes* species with respect to their nested clades from Murphy et al. (2020) using angiosperms353 probe set.
Note: *N. sibuyanensis location unknown is not included in this map.*

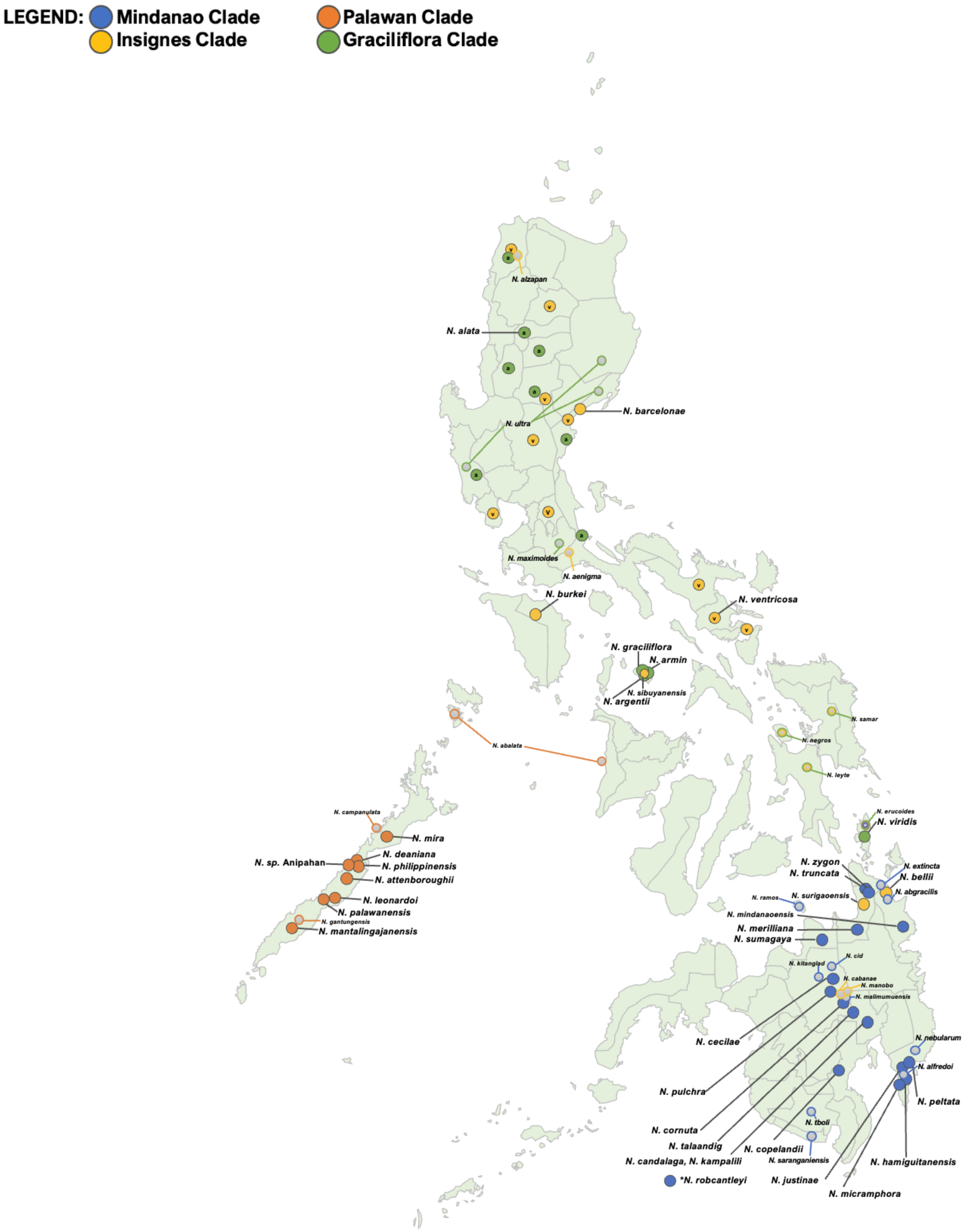

Figure 2. Geographical distribution of 61 Philippine *Nepenthes* species with respect to their nested clades from Murphy et al. (2020) using angiosperms353 probe set. Note: Unsampled species are represented by gray bordered circles and colored lines. These correspond to placement of these species to potential clades. Asterisk at the end of binomial name (*) indicate native/indigenous species. *Distribution data of *N. robcantleyi* was not disclosed by taxonomic authors due to conservation concerns.

4.0 Conclusion

Phylogenetic analyses revealed evolutionary relationships between *Nepenthes* species and their ties to biogeographical ranges and morphological differences. Molecular markers and sequencing methods used in these analyses made use of either nuclear or plastid DNA, including 5S-NTS, chloroplast trnL-F intron, trnK intron, PTR1 (peptide transferase 1), ITS nrDNA, and the angiosperms353 probe set. Previous studies left gaps due to limited sampling, markers with insufficient branching support, trees that could be interpreted differently, and sequencing issues. However, despite the problems with gene conflicts and variable tree interpretations, linkages are still identified, as indicated by the vast agreement between trees built by different approaches and datasets. Using DNA sequencing, most *Nepenthes* species were resolved into well-supported clades, providing novel topological information about lineage evolution.

Murphy et al. (2020) performed the most comprehensive phylogenomic analysis regarding the number of samples, DNA sequencing method and marker used (angiosperms353 probe set), tree construction, and interpretation of all studies addressed in this review. Using 35 recognized Philippine *Nepenthes* species, they revealed a large monophyletic Philippine Clade composed of Mindanao Clade, Palawan Clade, and Graciliflora Clade. The rest of the PH taxa not present in these clades were nested in the Insignes Clade. Although several Philippine species have yet to be sampled, it has been discovered that geographical distribution appears to be a better indication of Philippine species connections than morphology. In this review, we found 25 Philippine species that had never been sampled in any phylogenetic research and hypothetically assigned them to their possible clades formed from Murphy et al.'s tree (2020) using morphological characteristics and geographical distribution. Future studies should consider using molecular analyses to confirm clade placements and demonstrate stronger evolutionary links between Philippine taxa and the rest of the paleotropical species.

Phylogenetics is vital in conserving Philippine endemic plants since the intricate evolutionary history has resulted in a diverse flora with many relicts and derived traits. Phylogenetics based on sequence data explains relatedness patterns more accurately than previously available. When conservation biologists must decide which species to save from extinction, phylogenetics can help them make better choices. The benefits of phylogenetic analysis for plant conservation include clarification of taxonomic status, identification of unique evolutionary lineages, determination of relictual and recently derived species, determination of phylogenetic value for conservation priority setting, and identification of phylogenetically independent comparisons between rare and widespread species.

Because of the growing global biodiversity catastrophe, scientists must devise strategies for effectively allocating conservation efforts. Among these is the suggestion to include information on species' evolutionary relationships directly in the definition of biodiversity conservation priorities and policies. Tissue samples from previously unsampled taxa must be used in future phylogenetic analyses to confirm clade placements and demonstrate stronger evolutionary relationships between Philippine taxa and the rest of the paleotropical species. However, researchers will face numerous challenges due to the changing world, including threats to the species' survival. To name a few examples of human-caused environmental abuse, plant poaching, mining, deforestation, and land conversion for agricultural and industrial use are all threats to extinction.

5.0 Contributions of Authors

S. C. Brillo – conceptualizing, writing, and editing; J. J. D. Salamanes and E. S. Austria – commenting and supervising.

6.0 Funding

Pamantasan ng Lungsod ng Maynila funded the publication of this study.

7.0 Conflict of Interests

The author declares no conflict of interests.

8.0 Acknowledgment

The corresponding author would like to acknowledge Adamson University and Pamantasan ng Lungsod ng Maynila for their support.

9.0 References

Alamsyah, F., & Ito, M. (2013). Phylogenetic analysis of Nepenthaceae, based on internal transcribed spacer nuclear ribosomal DNA sequences. Acta Phytoaxonomica et Geobotanica, (64), 113–126.

Alejandro, G., Madulid, R., & Madulid, D. (2013). The utility of internal transcribed spacer (nrDNA) sequence data for phylogenetic reconstruction in endemic Philippine *Nepenthes* L. (Nepenthaceae). Philippine Journal of Science, (45), 99–110.

Amoroso, V. B., Lagunday, N., Coritico, F., & Colong, R. (2013). *Nepenthes alfredoi* (Caryophyllales, Nepenthaceae), a new species of pitcher plant from Mindanao, Philippines. Philippine Journal of Systematic Biology, (11), 14-19.

Barcelona, J., Nickrent, D., LaFrankie, J., Callado, J., & Pelser, P. (2013). Co's digital flora of the Philippines: Plant identification and conservation through cybertaxonomy. Philippine Journal of Science, (142), 57-67.

Berendsohn, W. (2017). Compilation of *Nepenthes* data for the Caryophyllales taxonomic backbone.

Catalano, M. (2009). *Nepenthes. Growing carnivores — an Italian perspective* (pp. 50–57). Prague.

Cheek, M., & Jebb, M. (2001). *Flora Malesiana – Nepenthaceae*. Series I, Volume (15).

Cheek, M. (2011). *Nepenthes robcantleyi* sp. nov. (Nepenthaceae) from Mindanao, Philippines. Nordic Journal of Botany, (29)6, 677–681.

Cheek, M., & Jebb, M. (2013a). Identification and typification of Nepenthes blancoi, with *N. abalata* sp. nov. from the western Visayas, Philippines. Nordic Journal of Botany, (31)2, 151-156.

Cheek, M., & Jebb, M. (2013b). *Nepenthes alzapan* (Nepenthaceae), a new species from Luzon, Philippines. Phytotaxa, 100(1) 57-60. http://dx.doi.org/10.11646/phytotaxa.100.1.6

Cheek, M., & Jebb, M. (2013c). *Nepenthes ramos* (Nepenthaceae), a new species from Mindanao, Philippines. Willdenowia, (43)(1), 107-111.

Cheek, M., & Jebb, M. (2013d). *Nepenthes samar* (Nepenthaceae), a new species from Samar, Philippines. Blumea, (58)1, 82-84.

Cheek, M., & Jebb, M. (2013e). *Nepenthes ultra* (Nepenthaceae), a new species from Luzon, Philippines. Blumea, (58) 241-244.

Cheek, M., & Jebb, M. (2013f). Recircumscription of the *Nepenthes alata* group (Caryophyllales: Nepenthaceae), in the Philippines, with four new species. European Journal of Taxonomy, (69), 1–23. doi: http://dx.doi.org/10.5852/ejt.2013.69

Cheek, M., & Jebb, M. (2013g). The *Nepenthes micramphora* (Nepenthaceae) group, with two new species from Mindanao, Philippines. Phytotaxa, (151)1, 25-34.

Cheek, M., & Jebb, M. (2013h). Typification and redelimitation of *Nepenthes alata* with notes on the *N. alata* group, and *N. negros* sp. nov. from the Philippines. Nordic Journal of Botany, (31)5, 616-622.

Cheek, M., & Jebb, M. (2014). Expansion of the *Nepenthes alata* group (Nepenthaceae), Philippines, and descriptions of three new species. Blumea, (59), 144-154.

Cheek, M., & Jebb, M. (2015). *Nepenthes*, three new infrageneric names and lectotypifications. Planta Carnivora, (37), 34-42.

Cheek, M., & Jebb, M. (2016a). A new section in *Nepenthes* (Nepenthaceae) and a new species from Sulawesi. Blumea, (61), 59-62.

Cheek, M., & Jebb, M. (2016b). *Nepenthes* section *Pyrophytae*. *Planta Carnivora, 38*, 44–45.

Cheek, M., Tandang, D., & Pelser, P. (2015). Nepenthes barcelonae (Nepenthaceae), a new species from Luzon, Philippines. Phytotaxa, (222)(2), 145-150.

Clarke, C. M. (1997). *Nepenthes* of Borneo. Natural History Publications (Borneo).

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

Clarke, C., Lee, C., & Enar, V. (2014). Observations on the natural history and ecology of *Nepenthes campanulata*. Carnivorous Plant Newsletter, (43)(1), 7-13.

Clarke, S., Moran, J., & Robinson, A. (2018). Systematics and Evolution of Nepenthes. OUP.

Danser, B. (1928). The Nepenthaceae of the Netherlands Indies. Bulletin du Jardin Botanique de Buitenzorg, 249–438.

Golos, M. (2012). Reassessing the phylogeny of *Nepenthes* (Nepenthaceae). Retrieved April 2021, from researchgate.net.

Gronemeyer, T., Coritico, F., Micheler, M., Marwinski, D., Acil, R., & Amoroso, V. B. (2011). *Nepenthes ceciliae*, a new pitcher plant from Mount Kiamo, Mindanao. McPherson, S. R., New Nepenthes, (1), 312-324.

Gronemeyer, T., Coritico, F., Wistuba, A., Marwinski, D., Gieray, T., Micheler, M., Mey, F. S., & Amoroso, V. B. (2014). Four new species of *Nepenthes* L. (Nepenthaceae) from the Central Mountains of Mindanao, Philippines. Plants (Basel), (3)2, 284-303.

Gronemeyer, T., Coritico, F., Wistuba, A., Marwinski, D., Gieray, T., Micheler, M., Mey, F. S., & Amoroso, V. B. (2016). Two new *Nepenthes* species from the Philippines and an emended description of *Nepenthes ramos*. Plants, (5)23.

Gronemeyer, T., Wistuba, A., Heinrich, V. B., McPherson, S. R., Mey, F. S., & Amoroso, V. B. (2010). *Nepenthes hamiguitanensis* (Nepenthaceae), a new pitcher plant species from Mindanao Island. Carnivorous Plants and Their Habitats, (2), 1296-1305.

Handayani, T. (2017). Flower morphology, floral development and insect visitors to flowers of *Nepenthes mirabilis*. Biodiversitas, 1624-1631.

Heinrich, V. B., McPherson, S. R., Gronemeyer, T., & Amoroso, V. B. (2013). *Nepenthes micramphora* (Nepenthaceae), a new species of *Nepenthes* L. from southern Mindanao, Philippines. Phytotaxa, (151)1, 25-34.

Heubl, G., Bringmann, G., & Meimberg, H. (2006). Molecular phylogeny and character evolution of carnivorous plant families in Caryophyllales – revisited. Plant Biology, 821-830.

Jebb, M., & Cheek, M. (1997). A skeletal revision of *Nepenthes* (Nepenthaceae). *Blumea,* (42), 1-106.

Johnson MG., Pokorny L, Dodsworth S, Botigué LR., Cowan RS, Devault, A., Eiserhardt WL, Epitawalage N, Forest F, Kim JT, Leebens-Mack JH, Leitch IJ, Maurin O, Soltis DE, Soltis PS, Wong GK, Baker WJ, Wickett NJ. (2018). A universal probe set for targeted sequencing of 353 nuclear genes from any flowering plant designed using k- medoids clustering. Systematic Biology. doi: https://doi.org/10.1093/sysbio/syy086.

Johnson MG, Gardner EM, Liu Y, Medina R, Goffinet B, Shaw AJ, Zerega NJC, Wickett NJ. (2016). HybPiper: extracting coding sequence and introns for phylogenetics from high throughput sequencing reads using target enrichment. Applications in Plant Sciences. (4), 1600016. doi: https://doi.org/10.3732/apps.1600016

King C, Cheek M. (2020) *Nepenthes maximoides* (Nepenthaceae) a new, critically endangered (possibly extinct) species in Sect. Alatae from Luzon, Philippines showing striking pitcher convergence with *N. maxima* (Sect. Regiae) of Indonesia. PeerJ. doi: 10.7717/peerj.9899

Kurata S, Toyoshima. (1972a). *Nepenthes mirabilis* X *N. alata* Sh. Kurata and Toyoshima, a natural hybrid. Gardens' Bulletin, Singapore, (26), 157.

Kurata S, Toyoshima. (1972b) *Nepenthes petiolata* X *N. alata* Sh.Kurata and Toyoshima, a natural hybrid. Gardens' Bulletin, Singapore, (26), 158.

Lagunday NE, Amoroso, VB. (2019). *Nepenthes cabanae* (Caryophyllales, Nepenthaceae), a new species of pitcher plant from Central Mindanao, Philippines. Philippine Journal of Systematic Biology, doi: DOI 10.26757/pjsb2019a13005

Lagunday N, Acma F, Cabana V, Sabas N, Amoroso VB. (2017). Two New *Nepenthes* Species from the Unexplored Mountains of Central Mindanao, Philippines. Philippine Journal of Science, (146)2, 159-165.

Lagunday, N. E., Rosa, S. D., Cleofei, C. M. B., Jr, R. P., Coritico, F. P., & Amoroso, V. B. (2022). *Nepenthes candalaga* (Nepenthaceae), a new species from eastern Mindanao, Philippines. Phytotaxa, (554)3, 285–292. https://doi.org/10.11646/phytotaxa.554.3.7

Lagunday, N. E., Yurong, A., & Amoroso, V. B. (2024). *Nepenthes kampalili* (Nepenthaceae), a new species of pitcher plant from the eastern mindanao biodiversity corridor, Philippines. Phytotaxa, (644)2, 163–170. doi: https://doi.org/10.11646/phytotaxa.644.2.8

Lauffenburger, A. (1995). Guide to *Nepenthes* Hybrids. OmnisTerra

Linnaeus C. (1737). *Nepenthes*. Hortius Cliffortianus.

Mansell G, Suarez, W. (2016). *Nepenthes nebularum*, A New Species From Mindanao, Philippines. Carnivorous Plants Newsletter, (45)4, 130-139.

McPherson SR. (2009a). Pitcher Plants of the Old World (1)

McPherson SR. (2009b). Pitcher Plants of the Old World (2)

McPherson SR, Bourke G, Cervancia J, Jaunzems M, Robinson AS, Fleischmann AS. (2011). *Nepenthes leonardoi* (Nepenthaceae), a new pitcher plant species from Palawan, Philippines. – Carniflora Australis; (8)1, 4-19

McPherson SR, Cervancia J, Jaunzems M, Fleischmann AS, Mey FS, Gironella EP, Robinson AS. (2010). *Nepenthes palawanensis* (Nepenthaceae), a new pitcher plant species from Sultan Peak, Palawan Island, Philippines. in: McPherson, S. R., Carnivorous plants and their habitats (2); 1332-1339.

McPherson SR, Cervancia J, Lee CC, Jaunzems M, Mey FS, Robinson AS. (2010) *Nepenthes gantungensis* (Nepenthaceae), a new pitcher plant species from Mount Gantung, Palawan, Philippines. in: McPherson, S. R., Carnivorous Plants and their Habitats (2); 1286-1295.

Meiberg H, Heubl G. (2006). Introduction of a nuclear marker for phylogenetic analysis of Nepenthaceae. Plant Biology, doi: https://doi.org/10.1055/s-2006-924676

Meimberg H, Wistuba A, Dittrich P, Heubl G. (2001). Molecular Phylogeny of Nepenthaceae Based on Cladistic Analysis of Plastid trnK Intron Sequence Data. Plant Biology, (3), 164–175. doi: https://doi.org/10.1055/s-2001-12897

Micheler M, Gronemeyer T, Wistuba A, Marwinski D, Suarez W, Amoroso VB. (2013). *Nepenthes viridis,* eine neue *Nepenthes* Art von der Insel Dinagat, Philippinen. Das Taublatt, (76)2, 4-14

Mullins JT. (2001). Molecular Systematics of Nepenthaceae. University of Reading; Retrieved from https://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.271202

Murphy B, Forest F, Barraclough T, Rosindell J, Bellot S, Cowan R, … Cheek, M. (2020). A phylogenomic analysis of Nepenthes (Nepenthaceae). Molecular Phylogenetics and Evolution, (144), 106668. doi: https://doi.org/10.1016/j.ympev.2019.106668

Pelser PB, Barcelona JF, Nickrent DL. (2021). Nepenthaceae. Retrieved June 10, 2021, from Co's Digital Flora of the Philippines: https://www.philippineplants.org/Families/Nepenthaceae.html

Raven, PH, Axelrod, DI. (1974). Angiosperm biogeography and past continental movements. Annals of the Missouri Botanical Garden, (61)3, 539. doi: 10.2307/2395021

Robinson AS, Zamudio SG, Caballero RB. (2019), *Nepenthes erucoides* (Nepenthaceae), an ultramaficolous micro-endemic from Dinagat Islands Province, northern Mindanao, Philippines. Phytotaxa; doi: https://doi.org/10.11646/phytotaxa.423.1.3

Robinson AS, Fleischmann AS, McPherson SR, Heinrich VB, Gironella EP, Peña CQ. (2009). A spectacular new species of *Nepenthes* L. (Nepenthaceae) pitcher plant from central Palawan, Philippines. Botanical Journal of the Linnean Society, (159)2, 195-202

Schwallier R, Raes N, de Boer HJ, Vos RA, van Vugt RR, Gravendeel B. (2016). Phylogenetic analysis of niche divergence reveals distinct evolutionary histories and climate change implications for tropical carnivorous pitcher plants. Diversity and Distributions, (22), 97–110. https://doi.org/10.1111/ddi.12382

Thorogood CJ, Bauer U, Hiscock SJ. (2018). Convergent and divergent evolution in carnivorous pitcher plant traps. New Phytologist, (217), 1035–1041.