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Nepenthes minima (*Nepenthaceae*), a new pyrophytic grassland species from Sulawesi, Indonesia

M. Cheek[1], M.H.P. Jebb[2]

Key words

carnivorous plants
fire
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Abstract *Nepenthes minima* is the first known pyrophytic grassland *Nepenthes* species from outside Indochina and the Philippines. A member of the sect. *Regiae* (Borneo, Wallacea, New Guinea) it is restricted to the highland grasslands of Central Sulawesi (Celebes) and has close affinities with *Nepenthes maxima*. The existence of *Nepenthes minima*, unique to these grasslands, suggests that they may be natural and predate the human influences that expanded them beginning 2000–3000 BP.

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INTRODUCTION

Although most frequently encountered in disturbed lowland forest in S.E. Asia, most species of *Nepenthes* are in fact terrestrial climbers or shrubs of submontane or montane forest, especially of stunted forest on montane ridges. Some other species occur in scrub or thicket, induced by altitude or ultramafic or limestone substrate, and a few species are epiphytes or lithophytes. In Indochina three or four species associated with sect. *Montanae* Danser, including *N. smilesii* Hemsl., occur in grassland, woodland and deciduous woodland as pyrophytes and have been placed in the recently defined sect. *Pyrophytae* (Cheek & Jebb 2016a).

In these habitats, dry-season fires burning the grassland do not kill the *Nepenthes* as might be expected. Instead these pyrophytic species persist as underground tuberous rootstocks, which, after the fires have passed, sprout new shoots, leaves and flowers (obs. MC). A similar but unrelated pyrophyte, *N. abalata* Jebb & Cheek, has been recorded in the drier parts of the Philippines (Cheek & Jebb 2013d). Pyrophytic *Nepenthes* share attributes otherwise unusual in the genus:

1. subterranean fleshy, tuberous rootstocks;
2. production of new stems after fire has removed previous growth (shown by the existence of several old carbonised stem bases next to the current season's growth);
3. stems short, free-standing, or shortly climbing (also seen in species of montane ultramafic scrub);
4. growing in seasonally dry habitats subject to inundation or fire.

All these attributes are shared by the species newly described here, from the submontane grasslands (1000–1700 m asl) of Sulawesi. The species resembles a miniature form of *Nepenthes maxima* Reinw. ex Nees and has been circulating in horticultural circles as the cultivar *N. maxima* 'Lake Poso' (Evans 2009). A lucid description of the Lake Poso plants is given by McPherson (2009: 248–249; 1019–1020 and (photos) 1022–1023):

"In Central Sulawesi a diminutive form of *N. maxima* occurs in seasonally dry grasslands between 1400–1700 m (pers. obs.). This variant is very distinct from the typical variety of *N. maxima* since it is consistently minute and produces leaves and pitchers just a few centimetres long. I observed populations of this taxon growing amidst low grasses forming small clumps of short, erect, self-supporting stems up to 35 cm tall. Each clump usually consisted of multiple living stems as well as the remains of dead and often burnt old growth.

This habitat type may be subjected to temperatures in excess of 38 °C, and may receive little or no rain for many weeks during the height of the dry season (May until September). The diminutive *N. maxima* plants grow in a lateritic substrate that becomes baked hard during the dry period. The grasslands are also prone to seasonal burning. The populations that I observed had evidently survived several successive fires, since the dead portions of each clump consisted of charred stems that were clearly of a few different ages. It would appear that each plant must periodically regrow after wild fires take place or once rains return. Ch'ien Lee (pers. comm.) reported observing similar populations of minute *N. maxima* in Central Sulawesi a few months after a wild fire had taken place, and observed that the plants were in the process of regrowing from the rootstock.

The consistently diminutive size of the savannah *N. maxima* plants may be an indication that these populations have responded to the dry conditions of their habitat by becoming reduced in size to minimise evapo-transpiration. It would appear that the small stature of the savannah plants is stable, since specimens growing in nearby wet savannahs do not produce foliage that is appreciably larger in size. No observations have been made of the underground parts of these plants, and so it is not known if they produce underground storage organs."

In fact, underground storage organs are produced (Fig. 1a and description below). Seed of this 'diminutive form of *N. maxima'* collected in Sulawesi by John Turnbull in the 1980s and donated to the Royal Botanic Gardens, Kew, germinated readily in 1985. The resultant 14 plants were remarkable for flowering when only c. 30 cm tall, in some cases within 18 months of sowing (observed by MC at the Tropical Nursery RBG, Kew, 1987–2016) rather than the more usual 5–8 years in *Nepenthes.* In cultivation over 30 years, plants have maintained the

[1] Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK; corresponding author e-mail: m.cheek@kew.org.
[2] National Botanic Gardens, Glasnevin, Dublin 9, Ireland.

Table 1 Characters differentiating *Nepenthes minima* from *Nepenthes maxima.*

	Nepenthes minima	*Nepenthes maxima*
Habitat	Open *Imperata* grassland	Forest
Underground perennating tuberous rootstocks	Present	Absent
Number of flowers per partial-peduncle	1	2
Bracts present or absent on partial-peduncles	Absent	Present
Number of aerial stems per plant	Multiple	Single
Shape and, length : breadth ratio of lid of upper pitchers	Narrowly ovate, 1 : < 0.5 < 2 : 1	Ovate, 1 : > 0.5 > 2 : 1

original miniature size and features seen in the wild plants even when grown in identical conditions and side-by-side with other *Nepenthes* including *N. maxima*. The taxon has been circulating amongst growers for some years as the named variety of *N. maxima* 'Lake Poso' (Evans 2009). A dwarf variety *N. maxima* var. *minor* Macfarl. has been described from New Guinea (Gibbs 1917) but was simply a category of diminutive plants without defining characters, and does not share the pyrophytic characters of the present species.

Characters separating this species from *N. maxima* are listed in Table 1. These are sufficient to merit recognition of the taxon at species level, which we therefore name below as *Nepenthes minima* Jebb & Cheek.

Nepenthes section *Regiae* Danser

The presence of both a basal and apical appendage on the lower surface of the lids of the upper pitchers of *N. minima,* together with the U-shaped petioles (in transverse section), clearly indicates placement in sect. *Regiae.* This section occurs in Borneo, throughout Wallacea and on the island of New Guinea. The section was lectotypified and redelimited in Cheek & Jebb (2016b).

Nepenthes maxima has the largest range of any species of sect. *Regiae.* Absent from Borneo, it occurs from Sulawesi to New Guinea. In Sulawesi, which includes the type locality of *N. maxima,* the species is morphologically rather uniform, while in New Guinea it is by contrast rather variable (Jebb 1991) and after further studies it may be necessary to resurrect some of the names synonymised under *N. maxima* by Danser (1928), such as *N. oblanceolata* Ridl. or *N. maxima* var. *minor*. Despite this variability no entity has been found that matches *N. minima.*

This paper forms part of studies towards a World Monograph of *Nepenthes* L. building on a Skeletal Revision of *Nepenthes* (Jebb & Cheek 1997) and the Flora Malesiana account (Cheek & Jebb 2001).

MATERIALS AND METHODS

Herbarium material was examined with a Leica Wild M8 dissecting binocular microscope fitted with an eyepiece graticule measuring in units of 0.025 mm at maximum magnification. The drawing was made with the same equipment with a Leica 308700 camera lucida attachment. The format of the description follows Cheek & Jebb (2013a–h). The conservation assessment follows the IUCN (2012) standard. Herbarium codes follow Index Herbariorum (Thiers, continuously updated).

KEY TO SPECIES OF NEPENTHES SECTION REGIAE IN SULAWESI

1. Plants of grassland, erect, self-supporting, subshrubs with underground tuberous rootstocks, 0.3–0.6 m tall; upper pitchers 1.2–1.5(–2.05) cm broad; inflorescence partial-peduncles 1-flowered, ebracteate . . . . . *N. minima*

1. Plants of forest or scrub (in Sulawesi), climbers or scramblers, lacking underground tuberous rootstocks, 2–4 m tall; upper pitchers 3–8 cm broad; inflorescence partial-peduncles 2-flowered, bracteate or ebracteate 2

2. Upper pitchers narrowly tubular below, abruptly bowl-shaped above; lids narrowly hastate; partial-peduncles ebracteate . . . . . *N. eymae*

2. Upper pitchers narrowly infundibuliform, never abruptly bowl-shaped; lids elliptic to ovate; partial-peduncles bracteate . . . . . *N. maxima*

Nepenthes minima Jebb & Cheek, *sp. nov.* — Fig. 1

Similar to *N. maxima* Reinw. ex Nees but differs in possessing fleshy underground perennating tuberous rootstocks (not without tubers), flowers one per partial-peduncle (not two), bracts absent from partial-peduncles (not present). — Type: *Ramadhanil et al. 280* (holotype K; isotypes BO not seen, CEB not seen), Indonesia, Sulawesi, Tengah Tamadue, Napu, Lore Utara, Poso, fl. 15 May 2001.

Etymology. Minima meaning 'small', in contradistinction to 'maxima' the epithet of the species to which it is most similar, yet much smaller in all its parts.

Pyrophytic dioecious, terrestrial subshrub 0.3–0.6 m tall. *Stems* annual, erect, arising from a fleshy-leathery, vertical underground rootstock c. 8 by 2 cm, the upper part densely covered in the carbonised bases of stems resulting from fires in previous dry seasons. *Rosette* and c*limbing stems* unknown and probably not produced. *Short stems* terete or slightly rounded-angular 3–5 mm diam, internodes (3.2–)4.5–5.2(–6) cm long, indumentum a mixture of dendritic and stellate hairs 0.2–0.7 mm long, dull white to orange-grey, 50–80 % cover at stem apex, decreasing to 10 % cover at the fourth internode from the apex. *Leaves* petiolate, blades elliptic-oblong, (4.8–)5–9(–12.5) by (1.3–)1.8–2(–3.5) cm, apex acute, tendrils apical 7–10 cm long, base cuneate; longitudinal nerves 3 on each side of the midrib in the outer third of the blade, all arising from the proximal two-thirds of the blade midrib; pennate nerves irregular, patent; indumentum inconspicuous, dull white simple (or inconspicuously branched), and 2–4-armed sessile hairs 0.15–0.3 mm long, mixed with sessile depressed-globose glands 0.05 mm diam, indumentum covering c. 10 % of both upper and lower surface of young leaves, glabrescent. *Petiole* canaliculate, (2–)3–5 cm long, 0.2 cm wide, 0.2 cm high, indumentum as the blade, but slightly denser, and longer (to 0.6 mm long). *Lower pitcher* not recorded. *Intermediate pitchers* infrequently produced in mature plants, narrowly infundibulate-cylindrical c. 9 cm long, c. 2 cm wide below peristome, c. 1.5 cm diam half way between base and apex, with two fringed wings running from the peristome, 9/10 the length of the way to the base of the pitchers; fringed wings 2 mm wide, fringe-elements 1–3 mm long, 2–3 mm apart; outer surface of pitcher with similar indumentum to that of the upper pitchers (see below); mouth narrowly ovate, concave, arising abruptly at the rear into a column, oblique, inner surface not recorded; peristome rounded, 3–4.5 mm wide, ribs 0.4 mm apart, 0.1 mm high, separated by c. 12

Fig. 1 *Nepenthes minima* Jebb & Cheek. a. Habit, female plant, showing remains of carbonised stems from previous seasons growth, and part of the underground tuberous rootstock; b. detail of indumentum from adaxial (upper) leaf-blade surface; c. indumentum from abaxial (lower) leaf-blade surface; d. fruit; e. indumentum from outer pitcher surface (mid-lateral portion); f. fringe element and part of wing from intermediate pitcher; g. peristome of upper pitcher, transverse section, outer pitcher surface to left; h. peristome, viewed from inside pitcher; i. peristome, viewed from above; j. lower surface of lid, upper pitcher; k. detail of j, showing detail of apex; l. detail of j, showing margin of lid; m. detail of j, showing dense nectar glands around the raised, glandless midline (all: *Ramadhanil et al. 280* K000224710). — Scale bars: a = 5 cm; b–c, e–f = 1 mm; d = 5 mm; g–i, k–m = 2 mm; j = 1 cm. — Drawn by Andrew Brown.

well-marked parallel ridges, outer edge entire, recurved, inner edge recurved and with teeth inconspicuous, column triangular, c. 18 by 7 mm at the base; lid narrowly ovate, c. 25 by 16 mm, apex acute, base rounded, upper and lower surface similar to the upper pitchers (see below), apical appendage c. 4 mm long; spur simple, 6 mm long, indumentum of short black hairs. *Upper pitchers* (tendrils coiled, dorsal to pitcher), green, slightly curved along main axis, narrowly infundibuliform, rarely cylindrical (5–)6–10.5(–12) by 1.2–1.5(–2.05) cm, narrowing to 1–1.2 cm wide halfway between base and peristome, the 'hip' not developed, wings absent; indumentum of the outer surface 10–30 % covered in three types of indumentum, large 3–5-branched, dendritic hairs 0.2–0.5(–0.7) mm long, (2–)5(–7) per mm^2; small 4-armed stellate hairs (rarely bifid or trifid) 0.1 mm diam, 1–6 per mm^2; sessile depressed-globose glands 0.05 mm diam, 4–7 per mm^2; mouth narrowly ovate, flat and oblique in the frontal half, slightly concave in the rear part, rising to form a weakly defined column, inner surface at mouth with upper exposed half waxy, the lower half glandular, glossy; peristome flattened-cylindric in transverse section, 3–4.5 mm wide, ridges 0.25–0.5 mm apart, developed as acute low ridges 0.2–0.25 mm high, outer edge revolute, entire, inner edge with teeth 0.2 mm long and broad, visible only at the base of the column, the inner edge otherwise folded inwards; lid narrowly ovate, 1.8–2.8 by 0.8–1.2 mm, apex acutely rounded, base truncate and shortly and abruptly cordate, upper surface with indumentum as the outer pitcher surface, lower surface with both a basal and apical appendage arising from the midline ridge, basal appendage inconspicuous, laterally flattened, inequilaterally triangular, c. 1.5 mm long, c. 0.8 mm high with nectar glands sparse, apical appendage filiform-cylindrical (1–)2.8–4 by 0.25 mm, arising 0.4–0.5 mm before the lid apex, with 3–7 nectar glands concentrated at the apex, nectar glands absent from the midline of the lid (except the midline in the distal part often with 1–2 longitudinally elliptic nectar glands up to 0.7 by 0.3 mm, Fig. 1k) and from the marginal 0.2–0.3 mm numerous, mostly ± monomorphic and uniformly dense, c. 12 per mm^2, orbicular, 0.15–0.25(–0.3) mm diam, bordered, the borders covering 30–50 % of the surface area, the peripheral nectar glands at the smaller end of the size range, and sparser, sessile depressed-globose or 8-rayed glands scattered over the entire surface, c. 0.05 mm diam, marginal 0.1–0.2 mm of lid with dense bushy hairs 0.05–0.1 mm long; spur filiform, simple, inserted 3–4 mm below the lid, 6 mm long, indumentum of short patent, black hairs with 100 % cover. *Female inflorescence* (male unknown) erect 21.2–33 by 3 cm, indumentum a mixture of randomly orientated appressed white hairs 0.1–0.4 mm long and red depressed-globose glands 0.06 mm diam extending from peduncle to lower surface of tepals, peduncle 7.2–16 cm long, by 0.2 cm diam, glabrescent; rhachis 13–17 cm long, 50–80 % covered in indumentum; partial-peduncles 20–27, each 1-flowered, bracts absent, pedicels 0.3–0.6 cm long, about 50 % covered in indumentum. *Female flowers* with tepals (4–)5–6, narrowly oblong-elliptic 2.3–2.6 by 0.8–0.9 mm, apex rounded, upper surface with 15–20 longitudinally elliptic nectar glands, lower surface about 20 % covered in hairs; ovary bottle-shaped, 3.5 by 1.1 mm, 100 % covered in white appressed hairs 0.2–0.3 mm long; stigmas four, bifurcate, basally united, forming a head 1 mm diam, drying glossy black. *Fruit* valves 4, 9.5 by 1.5 mm, with dense appressed hairs. *Seeds* filiform-fusiform, 4.4 by 0.11 mm, pale yellow, central portion smooth.

Distribution & Ecology — Indonesia, Sulawesi Tengah. Open grassland with *Imperata, Arundina* and *Spathoglottis* species; substrate grey-yellow clay; altitude 1000–1700 m. Unlike the majority of species in the genus this species flowers precociously in cultivation both in size and age, and this may well be an adaptation to frequent fires in its native habitat.

Vernacular name — Kantong semar (*Ramadhanil et al. 280*).

Additional specimens. Indonesia, Sulawesi, Sulteng Prov., Lake Poso area, 1000 m, seed collected in 1985 by John Turnbull, cultivated at Royal Botanic Gardens, Kew in the Tropical Nursery, specimen made Jan. 2016 *Cheek 18271* (K).

Conservation — The records of Turnbull (preserved as *Cheek 18271*) and of *Ramadhanil et al. 280* give two locations in close proximity for *N. minima,* but give no indication of the numbers of individuals seen. McPherson's excellent notes (2009, cited above) on this species imply that he saw several plants in more than one place since he twice remarks that he observed 'populations'. He also refers to the populations reported to him by Ch'ien Lee, another notable observer of *Nepenthes*. Since McPherson gives an altitudinal range of 1400–1700 m, above the range in which fall the specimens cited in this paper, it is reasonable to conclude that he and Ch'ien Lee each saw plants at two to four locations giving a total probable number of locations of between six and ten. Threats to the species do not appear to be high, but in several grassland plains, new areas of settlement and cultivation seem to have appeared in recent years which will pose a danger if the species is not protected. The known sites for *N. minima* do not fall in a protected area. *Nepenthes minima* is here assessed as Vulnerable, VU B2a, b(iii) under the criteria of IUCN (2012), since ten or less locations are known with an Area of Occupancy of 40 km^2 at most, using IUCN preferred 2 by 2 km gridcells.

Note — *Nepenthes minima* appears to have high potential as an indoor plant given its small size, rapid growth, and ability to withstand both waterlogging and drying-out. It has colourful, elegantly-shaped pitchers which are freely produced. All these features lend the species to employment as an ornamental windowsill plant in temperate zones of the world, possibly in terraria or other enclosed cases if humidity is low.

The Highland Grasslands of Central Sulawesi

About 20 % of Sulawesi lies above 1000 m, most of which occurs in the central portion, Sulawesi Tengah. Searching on Google Earth reveals amongst the prevailing forest cover about 10–12 large grassland areas occurring in the 1000–2000 m range. Many of these are more or less flat plains drained by meandering rivers. In area they mainly fall in the range 7 by 10 km, or, as at S1°42'37.85" E120°13'24.98", to 12 by 28 km (the type locality).

Some of these grasslands contain large lakes (danau), such as Lake Lindu, and others none. The high altitude grasslands of Central Sulawesi have generally been regarded as being man-made. "None of the grasslands or savannas of Sulawesi are natural, but are instead the result of human activities" (Whitten et al. 1987).

A recent study of vegetation history using pollen cores at one such grassland area, the Lore Lindu Biosphere Reserve and National Park confirms this view. Grass pollen shows a massive increase beginning c. 2000 years Before Present which appears to be correlated with the arrival of humans. Before this date levels of grass pollen were very low and overshadowed by pollen of forest trees, suggesting that grassland at this location is not natural (Kirleis et al. 2011).

However, elsewhere Whitten et al. (1987: 454) have written that grasses and reeds probably form the natural vegetation on some types of terrain that are subject to frequent flooding. Henley (2005) supports this statement by citing sources (Riedel 1870, Frohwein 1933) from the colonial period which describe

periodically inundated grasslands around certain lakes and whole valley plains flooding. He concludes that this factor may have led to the maintenance of grasslands around the Tondano, Lindu and Poso Lakes, and in the Palu valley.

The fact that *N. minima* is adapted, and apparently restricted to high altitude grasslands in Sulawesi suggests that these habitats predate the influence of the humans that arrived 2000–3000 BP. This is because it seems most unlikely that the species evolved within this time span from its presumed forest ancestor, *N. maxima,* which it so closely resembles in miniature, apart from the characters in Table 1. However, to test this hypothesis a reliably dated molecular phylogenetic tree of sect. *Regiae*, incorporating all three Sulawesi species, is required, and to date no such investigation has been accomplished in the genus. That *N. minima* arose from a forest ancestor seems highly plausible, since its placement in sect. *Regiae* is clear on morphological grounds, and since all other species of the section in Sulawesi and neighbouring areas of Wallacea and Borneo are forest species.

The existence of *N. minima* suggests that, while humans may have greatly expanded the area of grassland in the mountains of Central Sulawesi, some grassland may predate that period. A detailed study of the species composition of these grasslands might yield additional narrowly endemic species that would further support this hypothesis.

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