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# Revisiting *Utricularia* section *Nigrescentes* (Lentibulariaceae) in India and re-instating *Utricularia roseopurpurea*, integrating morphological and molecular data

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**Abstract**: *Utricularia* L. section *Nigrescentes* (Oliv.) Komiya (Lentibulariaceae), distributed in tropical Africa, Madagascar, Asia to Japan and Australia includes four species, *U. bracteata* R.D.Good, *U. caerulea* L., *U. roseopurpurea* Stapf ex Gamble and *U. warburgii* K.I.Goebel. *Utricularia caerulea* and *U. roseopurpurea* occur in India, and the latter species has long been treated as a synonym of the former. The identity of *U. roseopurpurea* has been confirmed using morphological, micromorphological, and molecular data and the species has been re-established. Multiple accessions of the species included in the phylogenetic study formed a sister clade to *U. caerulea* with strong branch support. The section *Nigrescentes* in India is revisited, and the distribution of both species is defined based on extensive field and herbarium surveys. The affinities between the two species are discussed. Full descriptions, notes on habitat requirements, nomenclature, assessment of the conservation status and photographs are provided for both species.

**Keywords**: Carnivorous plants, nrITS, Taxonomy, *Utricularia caerulea*, Western Ghats.

## Introduction

Lentibulariaceae comprise *c.* 350 species of carnivorous plants in three genera *viz.*, *Genlisea* A.St.-Hil., *Pinguicula* L. and *Utricularia* L. (Fleischmann & Roccia, 2018). *Utricularia* is one of the most intriguing and diverse genera with over 280 species (Baleeiro *et al.*, 2022; POWO, 2023) with a cosmopolitan distribution. Taylor (1989) recognized two subgenera, *Polypompholyx* (Lehm.) P.Taylor and *Utricularia* and the subgen. *Utricularia* includes 33 sections, and subgen. *Polypompholyx* two sections. But the molecular studies (Jobson & Albert, 2002; Jobson *et al.*, 2003; Müller & Borsch, 2005; Müller *et al.*, 2006; Reut & Jobson, 2010; Fleischmann, 2012; Rodrigues *et al.*, 2017; Silva *et al.*, 2018; Baleeiro *et al.*, 2019) had recognized three subgenera *viz.*, *Bivalvaria* (*c.* 10 sections), *Polypompholyx* (4 sections) and *Utricularia* (*c.* 19 sections).

Forty two species occur in India under two subgenera and seven sections, *viz.*, subgen. *Utricularia* (section *Utricularia*) and subgen. *Bivalvaria* (sections *Calpidisca, Meionula, Nigrescentes, Oligocista, Phyllaria,* and *Setiscapella*) (Taylor, 1989; Janarthanam & Henry, 1992; Biju *et al.*, 2020). Sect. *Nigrescentes* includes four species worldwide (*U. bracteata* R.D.Good, *U. caerulea* L., *U. warburgii* K.I.Goebel, and *U. roseopurpurea* Stapf ex Gamble, see discussion below). This section is easily distinguished by basisolute bracts and bracteoles (basifixed in *U. bracteata*), obovate-spathulate 1-nerved leaves, traps with lateral to latero-terminal mouth and oblique beak-like or funnel-shaped glandular hairy appendages. According to Taylor (*l.c.*), the section represents a single extremely variable species, *U. caerulea* in India. This species has a challenging circumscription with several synonyms and the nomenclatural confusions have persisted for decades (Oliver, 1858; Clarke, 1884; Cooke, 1905; Taylor, 1977, 1989; Bhattacharyya, 1976; 1986; Basak, 1979; Komiya & Shibata, 1980). *Utricularia roseopurpurea* has been treated as a synonym of *U. caerulea*, which resulted in an indiscriminate application of the two

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names. Subramanyam and Banerjee (1968) provided a detailed description and illustration of *U. roseopurpurea*, but Taylor (1989) stated, "This species is a minor variant of *U. caerulea* with flowers slightly larger than usual and with proportionately shorter spur". Taylor's delimitation, however, was not accepted by Janarthanam and Henry (1992) and they considered *U. roseopurpurea* distinct. Li (2007), Janarthanam *et al.* (2020), Narasimhan and Sheeba (2021) and POWO (2023), treated *U. roseopurpurea* as a synonym of *U. caerulea*. The present investigation is aimed to revise the section *Nigrescentes* in India and to determine the status of *U. roseopurpurea* based on morphological, micromorphological and molecular data.

## Materials and Methods

*Morphological analyses*: Specimens were obtained by field expeditions conducted throughout India. Herbarium specimens available in Indian herbaria (ASSAM, BSI, BSID, CAL, CALI, DD, KFRI, MH, RHT & SUK) and virtual herbaria (A, K, L, C, P, US, E, MICH; acronyms according to Thiers, updated continuously) were studied. Light microscopic analysis was carried out using a Stemi 508 stereo microscope equipped with an Axiocam colour camera (Zeiss, Jena, Germany). The terminology for describing the morphology followed Taylor (1989). Morphological observations of seeds, especially the testa ornamentation, were recorded. For the scanning electron microscopy (SEM) analysis, dried seeds (*Krishnapriya M.P. & Santhosh Nampy*, 164344 & 168088) were mounted on aluminium stubs, coated with 10–15 nm of gold with an SC7620 mini sputter coater (Emitech Quorum, PA, USA). Images were captured with a Gemini 300 field emission scanning electron microscope (Zeiss, Jena, Germany). A distribution map was built using the software QGIS v.3.28.0. (QGIS Development Team, 2022) from the coordinates taken in the field and from herbarium labels and data from GBIF (2023). The conservation status was assessed using IUCN Red List categories and criteria (IUCN, 2012, 2022) and the AOO and EOO were calculated with GeoCAT online (Bachman, 2011). Voucher specimens were deposited in CALI herbarium.

*DNA extraction and sequencing*: Total genomic DNA was extracted from fresh as well as silica dried plant material (inflorescence tips and flowers) using a modified protocol of Doyle and Doyle (1987). ITS 5P and ITS 8P (Moller & Cronk, 1997) were used for the amplification of nrITS forward and reverse respectively. The amplification reactions were performed in a Veriti® 96-well thermal cycler (Applied Biosystems, Waltham, USA) in a total of 25 µl reaction mix containing 1 µl of genomic DNA, 2.5 µl of 10× buffer with $MgCl_2$ (25 mM), 2 µl dNTPs (2.5 mM), 1.25 µl DMSO, 0.25 µl Taq polymerase (250 U) with TaKaRa Taq polymerase (TaKaRa Bio Inc., Shiga, Japan), 1.25 µl of each oligonucleotide primer (100 ng/ µl) and 15.5 µl of distilled water. PCR reactions started with 5 min initial denaturation at 95°C followed by 35 cycles of 45 sec at 95°C, 45 sec at 54°C and 1 min at 72°C, followed by a final extension at 72°C for 10 min, and terminated at 4°C. Amplified PCR products were purified using Nucleopore SureExtract Kit (Genetix, New Delhi, India) and the purified fragments were sequenced in BigDye™ Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems, Waltham, USA), following the manufacturers protocol. The sequences were amplified for forward and reverse strands and the contig sequences were assembled with Sequencher v.4.14. (Gene Codes Corporation, Ann Arbor, Michigan). The sequences were aligned and trimmed using MUSCLE (Edgar, 2004) embedded in MEGA v.11 (Tamura *et al.*, 2021), and the gaps were treated as missing data.

*Phylogenetic analyses*: Molecular analysis was carried out with 38 sequences, of which 20 sequences were newly generated, and 18 were retrieved from GenBank. The ingroup taxa included one sample from each of 18 species of *Utricularia* from four sections [sect. *Meionula* (*U. hirta* Klein ex Link, *U. minutissima* Vahl), sect. *Nigrescentes* (13 accessions of *U. caerulea* and three accessions of *U. roseopurpurea*), sect. *Oligocista* (*U. albocaerulea* Dalzell, *U. bifida* L., *U. cecilii* P.Taylor, *U. foveolata* Edgew., *U. graminifolia* Vahl, *U. polygaloides* Edgew., *U. purpurascens* J.Graham, *U. recta* P.Taylor, *U. reticulata* Sm., *U. sainthomia* P.Biju, Josekutty, Janarth. & Augustine, *U. uliginosa* Vahl) and sect. *Phyllaria* (*U. furcellata* Oliv., *U. kumaonensis* Oliv., *U. striatula* Sm.)]. Section *Utricularia* (*U. australis* R.Br., *U. minor* L., *U. stellaris* L.f.) was used as outgroup (Voucher information and GenBank

**Table 1.** Material of *Utricularia* and outgroups used in the present study, with voucher information and nrITS GenBank accession numbers

| Sl. No. | Species | Sections | Voucher details | GenBank accession number |
|---|---|---|---|---|
| 1 | *Utricularia minutissima* Vahl | *Meionula* | *Krishnapriya M.P. & Santhosh Nampy* 186039 (CALI) | OR257487 |
| 2 | *U. hirta* J.G.Klein ex Link | | *Krishnapriya M.P. & Santhosh Nampy* 186035 (CALI) | OR264666 |
| 3 | *U. caerulea* L. | *Nigrescentes* | *Krishnapriya M.P. & Santhosh Nampy* 175882 (CALI) | OR257486 |
| 4 | | | *Krishnapriya M.P. & Santhosh Nampy* 168088 (CALI) | OR257488 |
| 5 | | | *Krishnapriya M.P.* & *Santhosh Nampy* 177259 (CALI) | PP430640 |
| 6 | | | *Jobson* 1789 (NSW) | OR142156 |
| 7 | | | *Jobson* 1780 (NSW) | OR142155 |
| 8 | | | *Jobson* 1797 (NSW) | OR142157 |
| 9 | | | *Jobson* 1891 (NSW) | OR142159 |
| 10 | | | *Edwards s.n.* (NSW) | OR142143 |
| 11 | | | *Jobson* 2223 (NSW) | OR142162 |
| 12 | | | *Jobson* 1838 (NSW) | OR142160 |
| 13 | | | *Jobson* 3956 (NSW) | OR142134 |
| 14 | | | *Jobson* 3974 (NSW) | OR142135 |
| 15 | | | *Jobson* 2685 (NSW) | OR142144 |
| 16 | | | *Jobson* 2923 (NSW) | OR142139 |
| 17 | | | *Jobson* 2224 (NSW) | OR142163 |
| 18 | | | *Jobson* 1836 (NSW) | OR142158 |
| 19 | *U. roseopurpurea* Stapf ex Gamble | | *Krishnapriya M.P. & Santhosh Nampy* 164338 (CALI) | OR257831 |
| 20 | | | *Krishnapriya M.P. & Santhosh Nampy* 164344 (CALI) | OR257830 |
| 21 | | | *Krishnapriya M.P. & Santhosh Nampy* 186029 (CALI) | PP430639 |
| 22 | *U. albocaerulea* Dalzell | *Oligocista* | *Krishnapriya M.P.* & *Santhosh Nampy* 177281 (CALI) | OR264630 |
| 23 | *U. bifida* L. | | *Krishnapriya M.P. & Santhosh Nampy* 186040 (CALI) | OR264665 |
| 24 | *U. cecilii* P.Taylor | | *Krishnapriya M.P. & Santhosh Nampy* 168093 (CALI) | PP430641 |
| 25 | *U. foveolata* Edgew. | | *Jobson* 3566 (NSW) | OR142133 |
| 26 | *U. graminifolia* Vahl | | *Krishnapriya M.P. & Santhosh Nampy* 164391 (CALI) | PP430642 |
| 27 | *U. polygaloides* Edgew. | | *Krishnapriya M.P. & Santhosh Nampy* 186041 (CALI) | PP430644 |
| 28 | *U. purpurascens* J.Graham | | *Krishnapriya M.P. & Santhosh Nampy* 186072 (CALI) | PP430643 |
| 29 | *U. recta* P.Taylor | | *Krishnapriya M.P. & Santhosh Nampy* 177201 (CALI) | PP430645 |
| 30 | *U. reticulata* Sm. | | *Krishnapriya M.P. & Santhosh Nampy* 168084 (CALI) | PP531577 |
| 31 | *U. sainthomia* P.Biju Josekutty, Janarth. & Augustine | | *Krishnapriya M.P. & Santhosh Nampy* 168095 (CALI) | OR271835 |
| 32 | *U. uliginosa* Vahl | | *Jobson* 4196 (NSW) | OR142147 |
| 33 | *U. furcellata* Oliv. | *Phyllaria* | *Krishnapriya M.P. & Santhosh Nampy* 175454 (CALI) | OR264819 |
| 34 | *U. kumaonensis* Oliv. | | *Krishnapriya M.P. & Santhosh Nampy* 186009 (CALI) | OR338155 |
| 35 | *U. striatula* Sm. | | *Krishnapriya M.P. & Santhosh Nampy* 186082 (CALI) | PP430646 |
| 36 | *U. australis* R.Br. | *Utricularia* | *R.W. Jobson* 1391 (NSW) | MT248972 |
| 37 | *U. minor* L. | | *Volkova* 326275 | MT150760 |
| 38 | *U. stellaris* L.f. | | *Jobson* 1255 (NSW) | MT248969 |

accession numbers are provided in Table 1). Three accessions each of *U. caerulea* and *U. roseopurpurea* were newly generated, and 13 accessions of *U. caerulea* were retrieved from GenBank. Phylogenetic analyses were carried out using maximum likelihood (ML) and Bayesian inference (BI). Maximum likelihood analysis was performed using IQ-TREE online (Nguyen *et al.*, 2015) with 1000 ultrafast bootstrap replicates under TIM3e+I+G4 model. For the BI analysis, two independent Markov Chain Monte Carlo (MCMC) runs, with four chains were performed in GTR+I+G4 model in MrBayes v.3.2.7a x86_64 (Ronquist *et al.*, 2012). The best-fitting nucleotide substitution model for BI analysis was estimated using jModelTest 2.1.10 (Santorum *et al.*, 2014) under the Akaike Information Criterion (AIC). Trees were sampled every 1,000 generations and a total of 1,000,000 generations were performed until the standard deviation of splits frequencies reached a value below 0.01. The initial 25% of sampled trees were discarded as burn-in and the rest were used to calculate the posterior probability. The ML and BI trees were visualised and edited in FigTree v.1.4.3 (Rambaut, 2017).

## Results

## Taxonomic Treatment

**Utricularia** sect. **Nigrescentes** (Oliv.) Komiya, J. Jap. Bot. 48(5): 151. 1973; P.Taylor, Kew Bull. 41(1): 6. 1986, Gen. *Utricularia* 186. 1989. *Type*: *Utricularia caerulea* L.

Terrestrial, semi aquatic herbs. Rhizoids a few, simple or branched. Stolons many, branched. Leaves obovate to spathulate, 1-nerved. Traps numerous on stolons and leaf petiole, ovoid; mouth lateral, extends to an oblique funnel-shaped rim, glandular hairy towards margin; internal glands 2–4-armed. Scales and bracts basisolute; bracteoles basifixed or basisolute. Inflorescence simple or branched. Calyx lobes sub-equal, minutely papillate. Corolla blue–purple, white or yellow. Pollen 3 or 4-colporate, oblate, spherical or prolate. Capsule wall thickened, dehisce by a ventral slit. Seeds obovoid–oblongoid; testa cells slightly elongate, anticlinal wall concave, periclinal wall convex, surface verrucose or rugulose.

*Distribution*: Tropical Africa, Madagascar, Asia to Japan and Australia.

*Notes*: The name '*Nigrescentes*' was originally given by Oliver (1859) to a group of *Utricularia* species with shorter pedicels sub-equal to the length of bracts; medifixed scales and bracts with acute apices, minutely papillate calyx lobes and spur shorter or longer than the lower lip of the corolla. He segregated species of this group under two subsections: 1. *Corollae calcar labio inferior non longius* (short spurred*: U. rosea* Edgew.) 2. *Corollae calcar labium inferius excedens* (long spurred: *U. racemosa* Wall. ex Walp., *U. nivea* Vahl and *U. filicaulis* Wall.). Komiya (1973) raised 'Nigrescentes' into a formal section and included the species treated by Oliver under it. The section currently includes four species: *U. bracteata*, restricted to South Tropical Africa, *U. warburgii,* distributed in Southeast China, *U. caerulea* and *U. roseopurpurea* (*U. rosea, U. racemosa*, *U. nivea*, and *U. filicaulis* are presently considered as synonyms of *U. caerulea*).

**Utricularia roseopurpurea** Stapf ex Gamble, Fl. Madras 2: 983. 1924; Fyson, Fl. S. Ind. Hill Sta. 1: 438. 1932, as "*Utricularea rosa-purpurea* Staff"; Subr. & L.K.Banerjee, Bull. Bot. Surv. India 10(1): 103. 1968; V.Chandras. in A.N.Henry *et al.* (eds.), Fl. Tamil Nadu Ind., Ser. 1: Analysis 131. 1987; Janarth. & A.N.Henry, Taxon 38: 141. 1989, Bladderworts India 95. f. 28. 1992; Anil Kumar *et al.*, Fl. Pathanamthitta 368. 2005; Nayar *et al.*, Fl. Pl. W. Ghats India 587. 2014. *Lectotype* (designated by Janarthanam & Henry, 1989): INDIA, Anamalais, Paralai, 07.11.1901, *C.A. Barber* 3982 (MH [MH00002434!]).

*Utricularia racemosa sensu* Wight, Icon. Pl. Ind. Orient. f. 1. 4: 1584. 1850, *non* Wall. ex Walp., 1843.

*Utricularia rosea sensu* Oliv., J. Proc. Linn. Soc., Bot. 3: 184. 1858, *non* Edgew. 1847; C.B.Clarke in Hook.f., Fl. Brit. India 4: 333. 1884. **Figs. 1 & 2 (a–d)**

Terrestrial or lithophytic annual herbs. Rhizoids up to 35 mm long, *c.* 0.2 mm thick, capillary. Stolons *c.* 75 mm long, terete, glabrous, branches up to 40 mm long. Leaves usually 4–6 on peduncle base, rosulate, numerous on stolons; petioles up to 8 mm long; lamina oblanceolate to oblance-ovate, 6.35–8.8 × 1–1.5 mm, rounded at apex, 1-nerved,

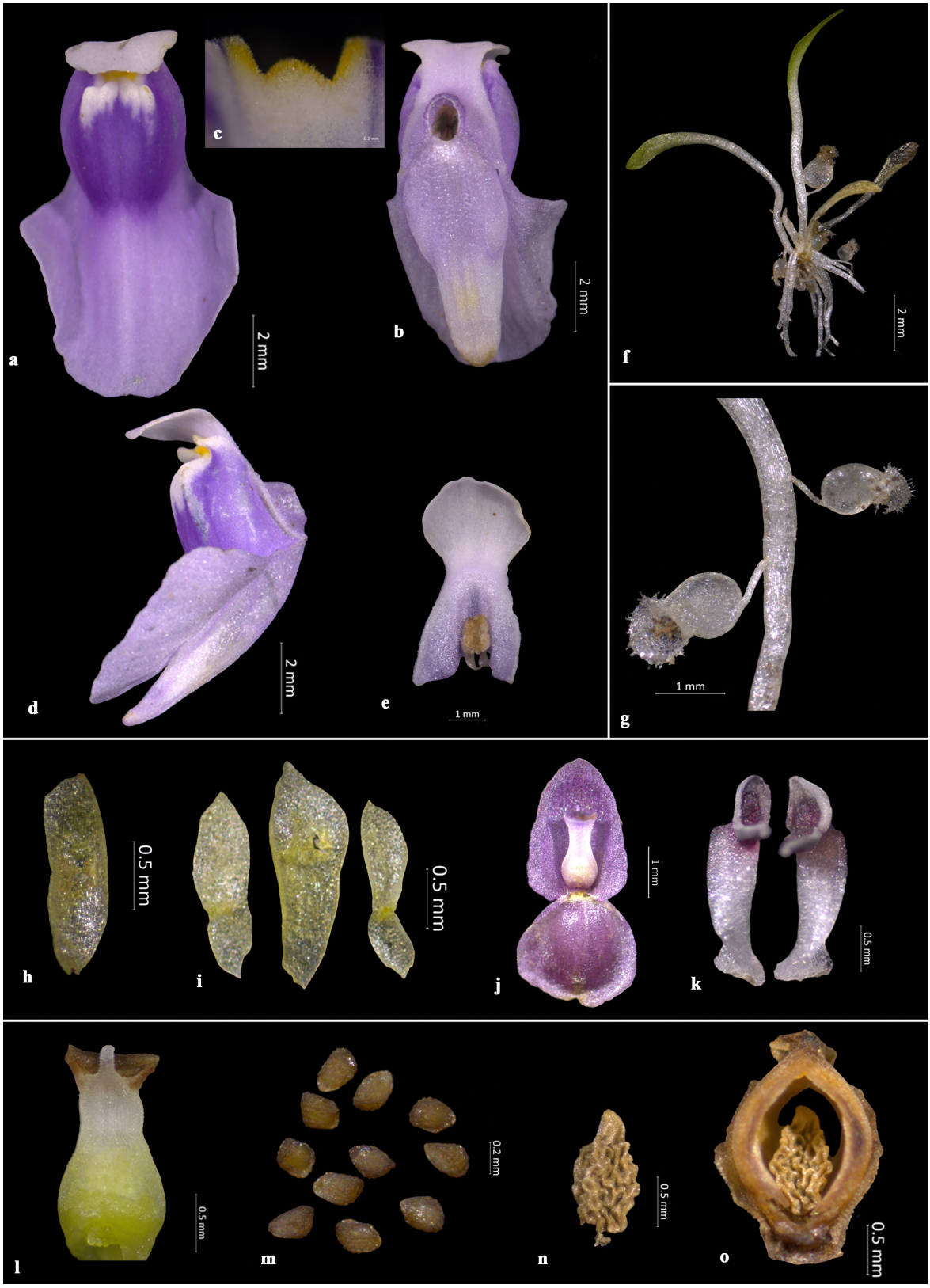


**Fig. 1**. *Utricularia roseopurpurea* Stapf ex Gamble: **a**. Corolla–adaxial view; **b**. Corolla–abaxial view; **c**. Enlarged view of corolla throat showing hairs and yellow colour; **d**. Corolla–lateral view; **e**. Upper lip of corolla with stamens–abaxial view; **f**. Peduncle base with leaves, stolons and traps; **g**. Stolon bearing traps (note the coiled appendages); **h**. Scale; **i**. Bract (middle) and bracteoles (lateral); **j**. Calyx lobes with pistil; **k**. Stamens; **l**. Pistil; **m**. Seeds; **n**. Placenta; **o**. Dehisced capsule (from *Krishnapriya M.P. & Santhosh Nampy* 164344; photos by Krishnapriya M.P.).

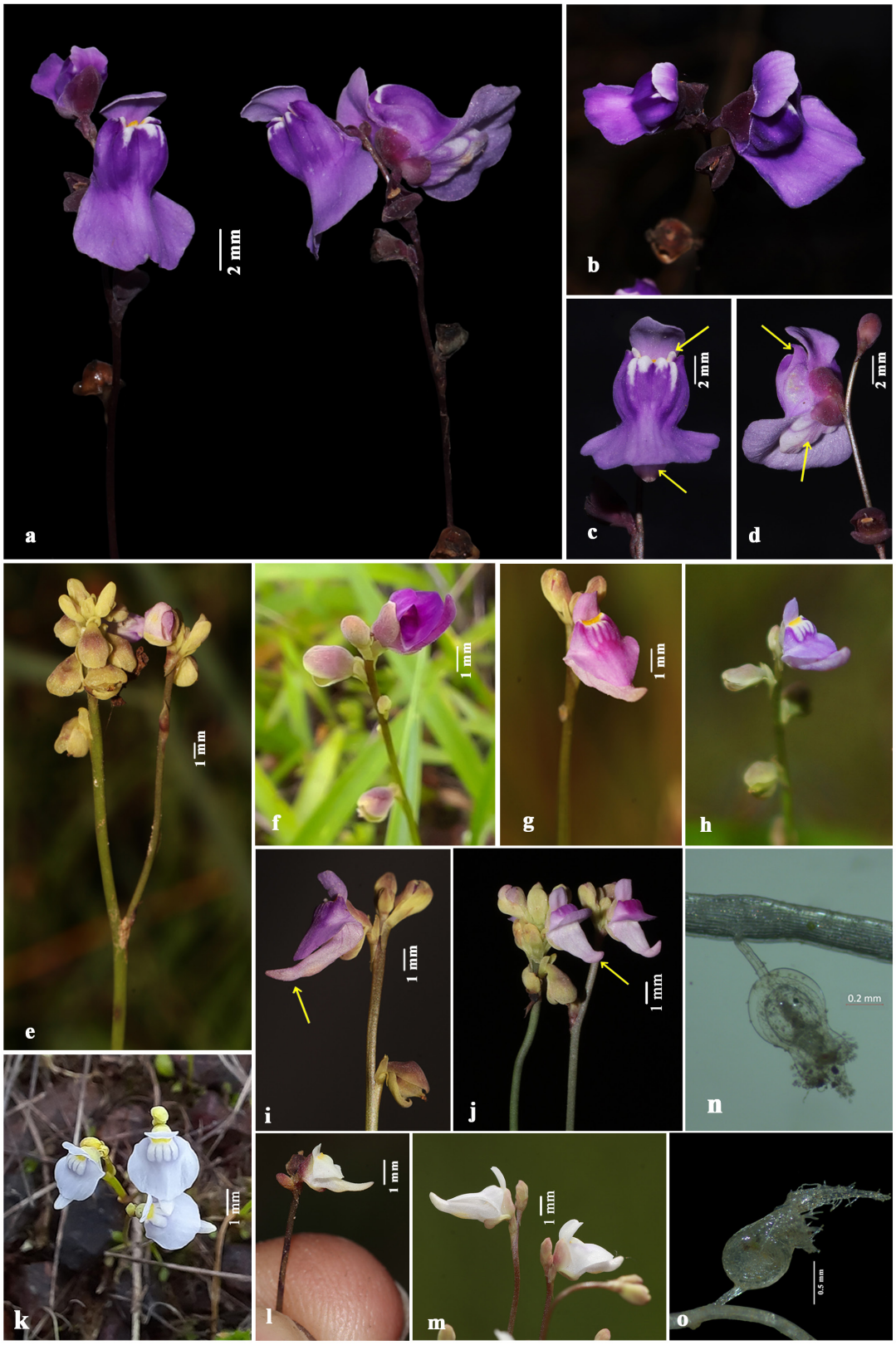


**Fig. 2**. **a–d**. *Utricularia roseopurpurea* Stapf ex Gamble: **a**. Inflorescences; **b**. Flowers–top view; **c** & **d**. Flowers–front (**c**.) and lateral (**d**.) Views (arrows indicate spurs which are shorter than lower lip and hook-like process of palate margin); **e–o**. *Utricularia caerulea* L.: **e**. Inflorescence; **f–m**. Variation in corolla colouration (l&m- see complete white morphotype; i&j- arrow indicates spur exceeding lower lip); **n** & **o**. Traps (note the beak-like extension of appendage) (photos by Krishnapriya M.P.).

nerves rarely branched. Traps more on stolons, few on petiole, oblique, globose, 1.08–1.3 mm across; stalk 0.3–1 mm long; mouth latero-terminal, body expanded into a circular, coiled or reflexed structure, with glandular hairs. Racemes erect, simple or rarely branched; peduncles terete, 45–180 mm long, 0.3–1.3 mm thick, purplish green, glabrous, 1–8-flowered. Scales attached obliquely below the middle, oblong, 1.6–2.3 × 0.6–0.85 mm, 1-nerved, acute at apex, bi-tridentate at lower part, minutely papillate. Bracts basisolute, attached just above the middle, rhombic, 1.25–2.4 × 0.4–0.9 mm, upper acute at apex, lower acute to bi-dentate at apex, minutely papillate; bracteoles basisolute, attached just below the middle, ovate to rhombic, 1.3–1.45 × 0.4–0.6 mm long, 1-nerved, acute at both ends, minutely papillate. Flowers 6–13 mm long; pedicels 0.8–1.2 mm long, erect, terete, slightly deflexed in fruit, papillate. Calyx lobes unequal, greenish-violet, or rarely yellowish green, convex, glabrous within, outer papillate; upper lip widely ovate, 2.7–4 × 3–4 mm, inflated at middle, acute-obtuse at apex; lower lip sub-orbicular, 1.5–2.6 × 2.2–2.7 mm, margins involute, obtuse-rounded at apex. Corolla pink to purple, or rarely greenish white to white; upper lip oblong, galeate, constricted at middle, 3–10 mm long, apical margin undulate, lower margins hairy, truncate-emarginate or rounded at apex; lower lip oblong, moderately flared towards tip, purple with a yellow patch at the palate, crested with two hook-like process at margins of throat with glandular hairs, palate extends into a prominent 4-lobed swelling with white patches, expands gradually into a sub-orbicular structure, margin undulate, 5.5–13 mm long, emarginate-rounded at apex; spur subulate, 5–8.5 mm long, shorter than or slightly equalling the lower lip of corolla, inner surface glandular, outer surface glabrous, obtuse-rounded at apex. Stamens 1.5–2 mm long; filaments flattened, strap-shaped, 1.2–1.6 × 0.3–0.55 mm, twisted at base; anther thecae distinct. Pistil *c.* 2.5 mm long; ovary ovoid-globose, 1.7–2.2 mm long, greenish purple; style *c.* 0.4 mm long, distinct, glandular hairy; stigma 2-lipped, lower lip sub-orbicular, curved inwards, upper lip tri-fid, obsolete, subulate, glandular hairy. Capsules ovoid, 2–3 mm long, wall prominently thickened, dehiscing by both dorsal and ventral longitudinal slits; placenta ovoid, 1–1.5 mm long. Seeds numerous, obovoid–oblongoid, 0.23–0.35 × 0.17–0.23 mm; hilum sub-terminal; testa cells irregularly shaped; surface rough, finely verrucate.

*Flowering & fruiting*: Flowering from early September till mid of January and fruiting from late September till the end of January.

*Habitat*: As small patches on mossy wet rocks, stream margins and marshy areas exposed to bright light, between 1000–2200 m elevation, along with *Utricularia nayarii* Janarth. & A.N.Henry, *Burmannia munnarensis* Dani & Nampy (Burmanniaceae), *Apocopsis mangalorensis* (Hochst. ex Steud.) Henrad, *Arundinella* sp., *Dimeria* sp., *Jansenella griffithiana* (Mull.Hal.) Bor (all Poaceae), *Cyanotis* sp. (Commelinaceae), *Drosera indica* L. (Droseraceae), *Eriocaulon brownianum* Mart., *E. nairii* Chandrab. & V.Chandras., *E. odoratum* Dalzell, *E. thwaitesii* Korn. (all Eriocaulaceae), *Fimbristylis* sp. (Cyperaceae), *Impatiens rakthakesara* M.Vishnu & Nampy (Balsaminaceae), *Laurembergia coccinea* Kanitz. (Haloragaceae), *Smithia racemosa* B.Heyne (Fabaceae) and some other grasses (Fig. 3a–d).

*Distribution*: Western Ghats and Sri Lanka (Fig. 4).

*Specimens examined*: INDIA, **Kerala,** Idukki district, Elaveezhapunchira, 29.10.2020, *Santhosh Nampy & M.P. Krishnapriya* 164389; Eravikulam National Park, 2100 m, 29.11.1979, *Nambiar* 1124 (KFRI); *Ibid.*, grassy slope, ±1722 m, 23.12.2019, *M.P. Krishnapriya & Santhosh Nampy* 164338; Kattadikadavu, 07.12.2018, *Santhosh Nampy & M.P. Krishnapriya* 168045 (CALI); Kulamavu, 03.10.1983, *C.N. Mohanan* 79967 (MH00126665); about 15 km from Idukki on the road to Kulamavu, 31.08.1973, *Cook, Rix & Schneller* 67 (P [P04425315 digital image]); Lockhart gap, Devikulam, 1675 m, 12.10.1963, *K.M. Sebastine* 17542 (MH [MH00126663, MH00126966]); Kumali road on dripping rocks, 13.12.1985, *M.K. Janarthanam* 82964 (MH [MH00126666, MH00126667]; BSID [BSID0012642]); Mathiketan Shola National Park, Vattachola grassland, 08.11.2018, *Syam Radh & M.P. Krishnapriya* 168033; *Ibid.*, 07.12.2018, *Syam Radh & M.P. Krishnapriya* 168044 (CALI); Munnar, 15.11.1961, *C. Saldanha* CS8045 (BLAT); Pettimudi grassland, ±1800 m, 10.12.2019, *M.P. Krishnapriya & Santhosh Nampy* 164335; *Ibid.*, ±1903 m, 29.12.2019,


**Fig. 3. a–d**. *Utricularia roseopurpurea* Stapf ex Gamble: **a**, **c**. Habitat (grassy soaks in rocky outcrops and shallow streams; also see purple and white morphotypes growing together; arrow indicating white morphotype); **b**. Purple morphotype; **d**. White morphotype; **e-g**. *Utricularia caerulea* L.: **e**. Habitat (lateritic plateaus of northern Kerala); **f**. Habit; **g**. White morphotype (photos by Krishnapriya M.P.).

*M.P. Krishnapriya & Dani Francis* 164341; Pettimudi Hilltop, way to Subran shed, ±2089 m, 30.12.2019, *M.P. Krishnapriya & Santhosh Nampy* 164344; Subran shed, near stream, 30.12.2019, *M.P. Krishnapriya* 164348; Upputhara, Vakavanam, 14.09.2019, *Dani Francis & M.P. Krishnapriya* 164308 (CALI); Palakkad district, Nelliyampathy, Kaarasoori, ±1130 m, 23.11.2022, *M.P. Krishnapriya* 186026; Nelliyampathy Hill top, ±1175 m, 24.11.2022, *M.P. Krishnapriya* 186028, 186029; Silent Valley National Park, Aruvampara, 12.11.2020, *M.P. Krishnapriya & Santhosh Nampy* 164396 (CALI); Pathanamthitta district, Kokkathode, 08.09.1989, *N. Anilkumar* 2024 (CAL); Thiruvananthapuram district, Agasthyamala, 21.12.2018, *M.P. Krishnapriya* 168053 (CALI); Western slopes of Agasthymala, 1400 m, 06.10.1973 *J. Joseph* 44629 (MH00126954); Ponmudi, opposite Indian Institute of Space Science complex, 02.11.2021, *M.P. Krishnapriya* 177227 (CALI). **Tamil Nadu**, Coimbatore district, Anamalai, around Attakatti, 25.01.1962, *J. Joseph* 13565 (MH [MH00126674]); *Ibid.*, Konalar, ± 1300 m, 13.12.2018, *Resmi S. & M.P. Krishnapriya* 168050; *Ibid.*, December 2019, *S. Resmi* 164329 (CALI); Grass hills above Iyerpadi, 10.01.1901, *C.A. Barber* 4025 (MH [MH00126676, MH00126677]); Poonachi, 10.10.1901, *C.A. Barber* 3716 (MH [MH00127006, MH00127007]); Dindigul district, Kodaikanal, new reservoir, 04.08.1985, *K.M. Matthew* 41687 (RHT [RHT044648]); swampy high ground near lake outflow, 20.05.1987, *Bourne* 16 (K [K000779503, K000779504 digital images]); Blackburn slopes facing Palamalai (Kavalamalai), 1400 m, 11.11.1987, *K.M. Matthew* 48220 (RHT [RHT044605]); Palni Hills, lake marsh by south, 08.09.1986, *K.M. Matthew & M. Charles* 46762 (RHT [RHT044602]); Peak north of Perumal Peak, 2100 m, 12.12.1986, *K.M. Matthew* 47915 (RHT [RHT044603]); Madurai district, Lake marsh, 10.05.1986, *s.col.*, 8675 (RHT [RHT044594]); Tirunelveli district, Agasthiar malai, 22.05.1901, *C.A. Barber* 2936 (MH [MH00126670]); way to Mahendragiri beyond Sengamal estate, 1025 m, 05.12.1969, *B.V. Shetty* 33050 (MH [MH00126671, MH00126672]); Muthukuzhivayal, ±1400 m, 29.09.1980, *A.N. Henry* 68866 (MH [MH00126668, MH00126669]); SRI LANKA, *s.loc., s.d., s.col.* CV277 (MH [MH00274881]); *s.loc.*, 1873, *R.H. Beddome s.n.* (MH [MH00126417]); *s.loc.*, 1847, *Gardner* 507 (K [K000779493, K000779502 digital images]); **Central Province**, Kandy district, 4 mi. directly SW of Maskeliya fishing hut area on the margin of the Moray Occurrence group tea estate, at the SE base of Adams Peak, 1400 m, 21.11.1974, *Gerrit Davidse & D.B. Sumithraarachchi* 8705 (US [US03216814 digital image]); Nuwara Eliya district, boggy ground along right side of route A-5 near pass going from Hakgala to Nuwara Eliya, 13.09.1969, *Robert W. Read & P.E. Desautels* 2276 (US [US03216859 digital image]).

*Conservation status*: It grows in a few localities in southern Western Ghats (Kerala and Tamil Nadu) and Sri Lanka in protected areas with an estimated Area of Occupancy (AOO) of 108 km$^2$ and an Extent of Occurrence (EOO) of 60011.492 km$^2$. It is prone to habitat alterations due to landslides and climate change. With the available data and considering the threats, the status is provisionally assessed as Endangered (EN) B2ab(ii,iii,iv,v)D) in the Indian context (IUCN 2012, 2022).

*Notes:* The name *Utricularia roseopurpurea* was originally based on a specimen by Stapf in the Kew herbarium (K), but we could not locate this specimen even after thorough search. Gamble (1924) validated this name in his *Flora of the Presidency of Madras*, and cited the locality as "*W. Ghats, Anamalais, Pulneys and hills of Travancore, to 7000 ft., in swamps*". Janarthanam and Henry (1989) designated a lectotype. Bhattacharyya (1976) treated *U. caerulea* (*U. racemosa* wall ex Walp.), *U. roseopurpurea*, and *U. nivea* under the *U. caerulea* complex, in which *U. nivea* was the white morphotype of the latter (see Abraham *et al.*, 1974). Taylor (1977, 1989) synonymized *U. roseopurpurea* under *U. caerulea*, and this was followed by others (Li, 2007; Janarthanam *et al.*, 2020; Narasimhan & Sheeba, 2021; POWO, 2023), except Janarthanam and Henry (1992), who considered *U. roseopurpurea* distinct. Poorly preserved or incomplete herbarium specimens, that lack sufficient floral detail, often result in misidentification of specimens (Baleeiro *et al.*, 2022) and this might be applicable to *U. roseopurpurea* (for further notes, see under discussion).

**Utricularia caerulea** L., Sp. Pl. 1. 18: 1753; Burm.f., Fl. Ind. 11. 1768; Vahl, Enum. Pl. I: 201. 1804; Wight, Hooker's J. Bot. Kew Gard. Misc. 1:

374. 1849, Icon. Pl. Ind. Orient. t. 1583. 1850; Fyson, Fl. S. Ind. Hill Stations 1: 438. 1932; Santapau, J. Bombay Nat. Hist. Soc. 49: 220. 1950; Ramaswamy & Razi, Fl. Bangalore Dist. 546. 1973; Gandhi in C.J.Saldanha & Nicolson (eds.), Fl. Hassan Dist. 564. 1978; N.Rani & K.M.Matthew in K.M.Matthew (ed.), Fl. Tamilnadu Carnatic I: f. 85c., 1112. 1983; D.M.Verma in D.M.Verma *et al.* (eds.), Fl. Raipur, Durg & Rajnandgaon 3: 26. 1985, *excl. syn. U. roseopurpurea*; N.R.Ugemuge, Fl. Nagpur Dist. 273. 1986; V.Chandras. in A.N.Henry *et al.* (eds.), Fl. Tamilnadu Ind., Ser: 1 Analysis 2: 129. 1987; Manilal, Fl. Silent Valley 199. 1988; B.G.Kulk., Fl. Sindhudurg 308. 1988; N.P.Singh, Fl. Eastern Karnataka 2: 473. 1988; Taylor, Gen. *Utricularia* 187. 1989 *p.p., excl. syn. U. roseopurpurea*; Vajr., Fl. Palghat Dist. 330. 1990; Kesh.Murthy & Yogan. Fl. Coorg Kranataka 317: 1990, *excl. syn. U. roseopurpurea*; Janarth. & A.N.Henry, Bladderworts India 42. f. 9. 1992; Kothari & Moorthy, Fl. Raigad Dist. 282. 1993; K.M.Matthew, Excurs. Fl. Centr. Tamilnadu 357. 1995; Sasidh. & Sivar., Fl. Pl. Thrissur For. 328. 1996; Naik & Associates, Fl. Marathwada 2: 638. 1998; M.R.Almeida, Fl. Maharashtra 3B: 431. 2001; Londhe in N.P.Singh *et al.* (eds.), FL. Maharashtra Dicot. 2: 564. 2001; L.K.Banerjee & T.A.Rao, Fl. Mahanadi Delta 227. 2001; Anil Kumar *et al.*, Fl. Pathanamthitta 367. 2002; N.Mohanan & Sivad., Fl. Agasthyamala 491. 2002; S.R.Yadav & Sardesai, Fl. Kolhapur Dist. 337. 2002; K.G.Bhat, Fl. Uduppi 455. 2003; Subba Rao & Kumari, Fl. Visakhapatnam Dist. 1: 599. 2003; Paria & Chattopadh., Fl. Hazaribagh Dist. 2: 797. 2005; Li in Wu *et al.* (eds.), Fl. China 19: 483. 2007 *excl. syn. U. roseopurpurea*; Sunil & Sivad., Fl. Alappuzha Dist. 516. 2009; G.P.Sinha in G.P.Sinha *et al.* (eds.), Fl. Mizoram 2: 194. 2012; Datar & Lakshmin., Fl. Bhagwan Mahavir Natl. Park 175. 2013; K.G.Bhatt, Fl. South Kanara 768. 2014; Nayar *et al.*, Fl. Pl. W. Ghats India I: 584. 2014; S.K.Mandal & Bhaumik in Lakshmin. *et al.* (eds.), Fl. West Bengal 4: 142. 2019; D.Naras. & Sheeba, Fl. Pl. Tamil Nadu 577. 2021 *excl. syn. U. roseopurpurea*. *Lectotype* (designated by Smith, 1805): **Ceylon**, Herb. Hermann 2: 13, No.23 (BM [BM000621547 digital image!]). **Fig. 2 (e–o)**

*Utricularia nivea* Vahl Enum. Pl. 1: 203. 1805; Wall. in Roxb., Fl. Ind. 1: 144. 1820; A.DC. in DC., Prodr. 8: 21. 1844; Wight, Hooker's J. Bot. Kew Gard. Misc. 1: 372. 1849, Icon. Pl. Ind. Orient. t. 1582. 1850; Oliv., J. Proc. Linn. Soc. Bot. 3: 186. 1858; Dalzell, Bombay Fl. 135. 1861; T.Cooke, Fl. Bombay 2: 319. 1905; N.P.Singh, Fl. E. Karnataka 2: 474. 1988. *Type*: Ceylon, *s.d., Koenig s.n.* (holo C [C10013896 digital image!]).

*Utricularia racemosa* Wall. ex Walp., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19 (Suppl. 1): 401. 1843; A.DC. in DC., Prodr. 8: 21. 1844; Wight, Hooker's J. Bot. Kew. Gard. Misc. 1: 374. 1849, Icon. Pl. Ind. Orient. t. 1584. f. 1. 1850; Oliv., J. Proc. Linn. Soc. Bot. 3: 186. 1858; Fyson, Fl. Nilgiri & Pulney Hill-Tops 1: 308. 1915. *Lectotype* (designated by Taylor, 1989): BANGLADESH, Silhet [Sylhet], *s.d., H. Bruce*, Wall. cat. no. 1496.1 (B, not located).

*Utricularia filicaulis* Wall. ex A.DC., Prodr. 8: 21. 1844; Oliv., J. Proc. Linn. Soc. Bot. 3: 186. 1858. *Utricularia racemosa* var. *filicaulis* (Wall. ex A.DC.) C.B.Clarke in Hook.f., Fl. Brit. India 4: 333. 1884. *Utricularia caerulea* var. *filicaulis* (Wall. ex A.DC.) Haines, Bot. Bihar & Orissa 645. 1922. *Lectotype* (designated by Taylor, 1989): Myanmar (Burma), Tanintharyi region (Tavoy), *s.d., Gomez s.n.* in Wallich 1501 (G, not located).

*Utricularia rosea* Edgew., Proc. Linn. Soc. London 1: 352. 1847; Oliv., J. Proc. Linn. Soc. Bot. 3: 184. 1858; C.B.Clarke in Hook.f., Fl. Brit. Ind. 4: 333. 1884. *Type*: Bengalia, Burdwan, *s.d., Edgeworth s.n.* (K, not located).

*Utricularia sampathii* Subr. & Yogan., J. Indian. Bot. Soc. 60. 123: 1981; M.Ahmed. & M.P.Nayar, Endem. Pl. Indian region 1: 155. 1986. *Type*: INDIA, **Karnataka**, Bangalore district, Dhyanashram, near Bannerghatta, 900 m, 03.11.1976, *K. Subramanyam & S.N. Yoganarasimhan* 123 (holo CAL [CAL00019121!]).

Terrestrial annual or sometimes perennial herbs. Rhizoids *c.* 20 mm long, simple, rarely branched, glabrous. Stolons up to 38 mm long, 0.1–0.2 mm thick, terete, glandular, simple or sparsely branched. Leaves usually 4 on peduncle base, rosulate, 1–4 per node on stolons; petioles 1.5–2.5 mm long; lamina narrowly obovate–spathulate, 3.5–8 × 1–1.5 mm, rounded–obtuse at apex, 1-nerved. Traps on petiole base and stolon node, oblique, ovoid, 1–2

mm wide; stalks 0.4–0.5 mm long; mouth latero-terminal, with a triangular, beaked upper lip bearing glandular hairs. Racemes erect, simple or branched; peduncles 15–300 mm long, 0.5–1 mm thick, terete, purplish green, glabrous, 1–12-flowered, flowers distantly arranged or congested towards apex. Scales attached below the middle, elliptic to rhombic, 2–2.5 mm long, 1-nerved, upper acuminate towards apex, lower 2–3-fid. Bracts basisolute, attached just above the middle, 1.5–3.5 mm long, elliptic to rhombic, 1-nerved, acute-acuminate at both apices; bracteoles basisolute, attached just below the middle, 1–2.5 mm long, minutely papillate, rhombic, upper acute at apex, lower 2–3-fid. Flowers 2–7 mm long; pedicels not so prominent, 0.2–0.6 × *c.* 0.4 mm, erect, terete, reflexed in fruit, papillate. Calyx lobes sub-equal, minutely papillose, margin hooded; upper lip widely ovate to orbicular, 2–2.5 × 1.5–2.5 mm, obtuse-rounded at apex; lower lip ovate or oblong, 2–2.5 × 1.5–2 mm, rounded at apex. Corolla white, pale pink to purple with a prominent yellow patch at throat; upper lip ovate to oblong, constricted at middle, 2–4 × 1.5–1.8 mm, ciliate along lower margins, truncate or emarginate at apex; lower lip semi-orbicular to widely ovate, hairy at throat; palate raised into 3 or 4 linear swellings, crested at middle, 2–6 × 2–4.5 mm, obtuse–rounded at apex; spur conical, straight or often curved forward up to 6.5 mm long, longer than lower lip of corolla, acute or notched at apex. Stamens *c.* 1.5 mm long; filaments strap-shaped, 0.15–0.2 × 0.7–1 mm, curved or twisted at base; anther thecae distinct, sparsely papillose. Pistil *c.* 1.75 mm long; ovary ovoid, 1–1.5 mm long, pale green-purplish green; style 0.3–0.4 mm long, thick, distinct; stigma 2-lipped, lower semi-orbicular and hairy, upper obscurely trifid, deltoid, glandular hairy. Capsules sub-globose to globose, 1.5–2 × 1.4–1.8 mm, wall uniformly thickened, dehiscing by a longitudinal ventral slit; placenta ovate–sub-globose, 0.8–1 × 0.7–0.9 mm, pitted. Seeds numerous, obovoid to ellipsoid, 0.2–0.3 × 0.1–0.18 mm; hilum sub-terminal testa cells elongate, surface rough, granulated.

*Flowering & fruiting*: Flowering from the end of May till December; fruiting from early June till January.

*Habitat*: Grows in seasonally waterlogged soil-filled depressions in rocky surfaces and margins of small seasonal pools on lateritic plateaus, in sandy soils and marshy areas, at an elevation of 10–1750 m, in association with *Utricularia bifida* L., *U. cecilii* P.Taylor, *U. hirta* Klein ex Link, *U. lazulina* P.Taylor, *U. malabarica* Janarth. & A.N.Henry, *U. minutissima* Vahl, *U. polygaloides* Edgew., *U. sainthomia* P.Biju, Josekutty, Janarth. & Augustine *Burmannia coelestis* D.Don (Burmanniaceae), *Drosera indica* L. (Droseraceae), *Eriocaulon* sp. (Eriocaulaceae), *Geissaspis cristata* Wight & Arn. (Fabaceae), *Isachne veldkampii* K.G.Bhat & Nagendran (Poaceae), *Cyperus* sp., *Fimbristylis* sp., *Fuirena ciliaris* (L.) Roxb. (all Cyperaceae), *Lindernia* sp. (Linderniaceae), *Murdannia semiteres* (Dalzell) Santapau, *M. crocea* subsp. *ochracea* (Dalzell) Faden. (both Commelinaceae), *Neanotis* sp. (Rubiaceae), *Ramphicarpa* sp., *Striga* sp. (both Orobanchaceae), *Rotala malabarica* Pradeep, K.T.Joseph & Sivar. (Lythraceae) and some other grasses (Fig. 3e-g).

*Distribution*: The native range is Tropical and Subtropical Asia, Japan, Madagascar, N. & E. Australia (POWO, 2023) (Fig. 4).

*Specimens examined*: INDIA, **Andhra Pradesh**, Chittoor district, Akkagarla Gudi, 800 m, 01.10.1974, *G.V. Subba Rao* 45935 (MH [MH00126950, MH00126951]); Thirumala, Narayanagiri, ±1100 m, 17.09.1987, *D. Ranga Charyulu* 1654 (MH [MH00126949]); Wadanapalli, 27.12.1921, *C.E.C. Fischer* 4710 (FRCH); Visakhapatnam district, way to Tanjavanam, 1075 m, *G.V. Subba Rao* 42621 (MH [MH00126948, MH00126947]). **Chhattisgarh**, Dantewada district, Bailadila, ± 915 m, 09.10.1940, *H.J. Mooney* 1519 (DD); Kanker, district, Raj bandha tank, 500 m, 17.11.1958, *K. Subramanyam* 7162 (CAL, MH [MH00126987, MH00126988]); Raigarh district, Dharamjaigarh, ±915 m, 19.03.1940, *H.F. Mooney* 1277 (DD). **Dadra and Nagar Haveli and Daman and Diu**; Dadra and Nagar Haveli district, Dadra, 29.09.1963, *M.Y. Ansari* 93837 (CAL, BSI). **Goa**, near Amaldem (Malem), 18.09.1970, *N.P. Singh & B.G. Kulkarni* 124356; Malem, 17.09.1970, *N.P. Singh & B.G. Kulkarni* (BSI). **Karanataka**, Kolar district, Chintamani road, 05.01.1976, *N.P. Singh* 142100 (BSI); Srinivaspur, Royalpal S.F., 04.01.1976, 825 m, *N.P. Singh* 142070 (BSI); Mysuru district, Hardur, river near Hardur Coffee Estate, 10.10.1961, *A.S. Rao* 75043 (CAL); Shivamogga district, Agumbe, Barakana, 16.10.1962, *R. Sundara Raghavan* 83273 (BSI);

Agumbe, near streams, 04.11.1960, *R. Sundara Raghavan* 68169 (BSI); Tumkur district, Gounbinur, Madhugiri road, 28.10.1975, *N.P. Singh* 141103 (BSI). **Kerala,** Idukki district**,** Valara waterfalls, near new dam construction site, 02.10.2021, *K.K. Jeomol & M.P. Krishnapriya* 177218 (CALI); Malappuram district, Adyanpara waterfalls, 03.09.2020, *M.P. Krishnapriya & Santhosh Nampy* 164372; Kodikuthimala, 08.10.2019, *M.P. Krishnapriya* 164317; Poonkavanam dam, 31.07.2019, *M.P. Krishnapriya* 168074; *Ibid.*, 14.09.2019, *M.P. Krishnapriya & Santhosh Nampy* 164306 (CALI); Kannur district, Blathoor, 22.08.2019, *M.P. Krishnapriya* 168092; Chooral, Aravanchal, 31.07.2022, *M.P. Krishnapriya* 177259; Madayippara, near Madayikkavu, 18.12.2010, *C. Pramod* 126618 (CALI); Kasaragod district, Cheemeni, near old Cyber park, 20.08.2019, *M.P. Krishnapriya & Santhosh Nampy* 168088; Cheemeni, 27.08.2021, *M.P. Krishnapriya* 175820; lateritic plateau opposite Central University, 26.08.2021, *M.P. Krishnapriya* 175806 (CALI); Kanhangad, Ramnagar, 20.08.1985, *M.K. Janarthanam* 82917 (MH [MH00126969, MH00126970]; BSID [BSID0012614]); Kappadampoyil, 27.08.2021, *M.P. Krishnapriya* 175822; Koyithatta lateritic plateau, 27.08.2021, *M.P. Krishnapriya* 175817 (CALI); Mulleria, 21.08.1985, *M.K. Janarthanam* 82923 (MH [MH00126967, MH00126968]; BSID [BSID0012615]); Periya, 20.08.1985, *M.K. Janarthanam* 82919 (MH [MH00126971, MH00126972]; BSID [BSID0012616]); Puthrakala, lateritic hillock, 26.08.2021, *M.P. Krishnapriya* 175812; *Ibid.*, ±180 m, 01.08.2022, *M.P. Krishnapriya* 177271 (CALI); Kozhikode district, near Iringal railway station, 25.08.1985, *M.K. Janarthanam* 82933 (MH [MH00126976, MH00126977]; BSID [BSID0012620]); Kakkayam, Ambalapara, 12.10.2019, *M.P. Krishnapriya & Santhosh Nampy* 164322; way to Urakuzhi waterfalls, 06.10.2022, *M.P. Krishnapriya* 186018; Ponkunnumala, 04.10.2019, *M.P. Krishnapriya & Santhosh Nampy* 164313 (CALI); Pathanamthitta district, Konni reserve forest, Perumala, 300 m, 18.11.1976, *M. Chandrabose* 49117 (MH [MH00126961, MH00126962]); Kozhenchery, 150 m, 07.12.1979, *C.N. Mohanan* 63705 (MH [MH00126957, MH00126958]); Ranni, 325 m, 27.07.1978, *C.N. Mohanan* 58340 (MH [MH00126959, MH00126960]); Palakkad district, Malampuzha water tank hillock,

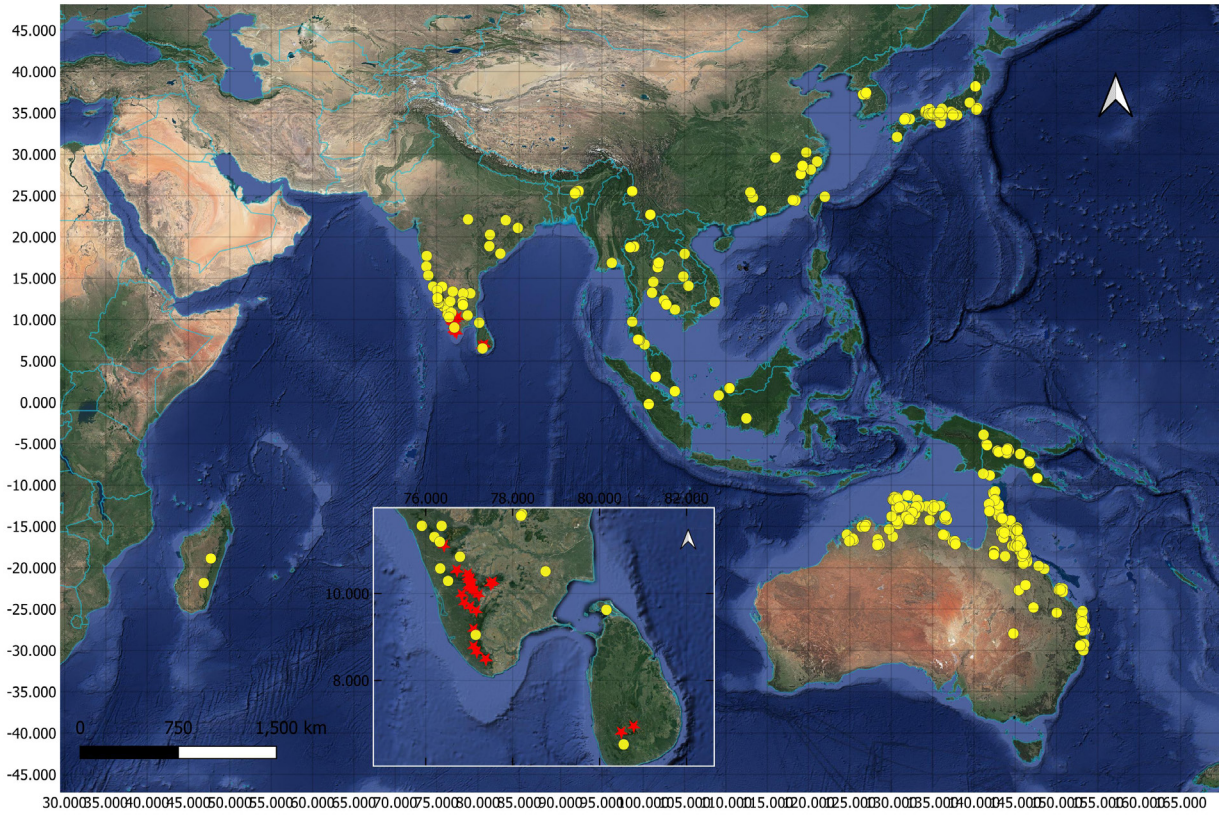


**Fig. 4**. Distribution map of *Utricularia roseopurpurea* Stapf ex Gamble (red stars) and *U. caerulea* L. (yellow dots). Map drawn with QGIS v.3.28.0 (2022).

15.09.1985, *M.K. Janarthanam* 82936 (MH [MH00126963, MH00126964]; BSID [BSID0012621]); Thiruvananthapuram district, Kottur R.F., 275 m, 27.09.1973, *J. Joseph* 44432 (MH [MH00126952, MH00126953]); Thrissur district, Athirapilly reserve, 150 m, 13.09.1976, *K. Ramamurthy* 48490 (MH [MH00126995, MH00126956]); Irunilamkode hill near temple, 07.09.2020 *M.P. Krishnapriya & Santhosh Nampy* 164378 (CALI); Kayampoovam, 06.09.2020, *M.P. Krishnapriya* 164376. **Malabar**, Concan, *s.d.*, *J.E. Stocks & J.S. Law s.n.* (MH [MH00126973]; GH [GH01977058 digital image]). **Madhya Pradesh**, Chhindwara district, way to Tamia, Seetha Downkei, ± 450 m, 11.11.2021, *M.P. Krishnapriya* 177239 (CALI); Satna district, Satna town, in paddy field, 400 m, 20.09.1959, *K.M. Sebastine* 8899 (MH [MH00126985, MH00126986]). **Maharashtra**, Nagpur district, Ambazari tank, 300 m, 18.11.1957, *K. Subramanyam* 4683A (MH [MH00126981]); Satara district, Kaas, September 1994, *M.P. Bachulkar Cholekar* 5976 (SUK). **Meghalaya**, East Khasi Hills district, Barapani, BSI Experimental Garden, ± 1000 m, 29.10.1986, *M.K. Janarthanam* 83031 (MH [MH00126991, MH00126992]; BSID [BSID0012665]); Cherrapunji, Mawsmai, 30.10.1986, *M.K. Janarthanam* (MH [MH00126989], BSID [BSID0012666]); way to Cherrapunji, ±1690 m, 17.09.2021, *M.P. Krishnapriya* 175829; *Ibid.*, ±1171 m, 17.09.2021, *M.P. Krishnapriya* 175834; way to Jowai from Shillong, ± 1340 m, 23.09.2021, *M.P. Krishnapriya & Santhosh Nampy* 175883 (CALI); around Leska, 26.09.2007, *M. Bhaumik* 116504 (ASSAM); Mawryngkneng, way to Kut village, 22.09.2021 *M.P. Krishnapriya & Santhosh Nampy* 175882 (CALI); Mount Khasia, Regio. trop., alt. 3–5000 ped, *s.d.*, *J.D. Hooker & T. Thomson s.n.* (GH [GH01977060 digital image]); Pynursla, 1370 m, 17.10.1945, *N.L. Bor s.n.* (DD); Shillong, September 1950, *G.K. Deka* 22985 (ASSAM); Jaintia Hills district, way to Jarain, ± 1360 m, 23.09.2021, *M.P. Krishnapriya* 175887; way from Jowai to Jarain, ± 1235 m, 23.09.2021, *M.P. Krishnapriya* 175889 (CALI); West Jaintia Hills district, Dawki, ± 833 m, 25.09.2021, *M.P. Krishnapriya* 175894; near Nartiang Durga temple, ±1158 m, 22.09.2021, *M.P. Krishnapriya & Santhosh Nampy* 175879 (CALI). **Odisha**, Purunakote section, 152 m, 06.09.2014, *K.C. Mohan* 005195 (BSID [BSID0010604]). **Tamil Nadu**, Dindigul district, Shenthetty kanal, 6-7000 feet, 20.09.1905, *C.A. Barber* 7531 (MH [MH00127002]); Kallakurichi district, Ulundurpettai, Pulloorkkadu forest Bunglow, 50 m, 30.12.1981, *K.M. Matthew, S.J. Britto & N. Rani* 28791 (RHT [RHT044624]); Chengalapattu district, Vandalur Zoological Park, 15.01.1986, *M.K. Janarthanam* 82975 (MH [MH00127006, MH00127007]; BSID [BSID0012668]); Thandarai, 06.01.2000, *K.T. Augustine* 61751 (RHT [RHT044625]); Krishnagiri district, Dharmapuri, Denkanikottai, Harur, Chitteri hills, Alangala malai slopes, 1000 m, 12.01.1976, *N. Venugopal* 20840 (RHT [RHT044618]); Denkanikotta Thally, Devarbetta, 900 m, 14.11.1979, *K.M. Matthew* 24572 (RHT [RHT044619]); Pudukottai district, Kulathur, Sathyamangalam, 150 m, 23.12.1978, *Fieldmen* 16087 (RHT); Narthamalai, 125 m, 23.09.1965, *K. Ramamurthy* 25944 (MH [MH00126993, MH0012694]); *Ibid.*, 150 m, 15.11.1975, *K.M. Matthew* 15064 (RHT [RHT044611]); *Ibid.*, 12.12.2022, *M.P. Krishnapriya* 186042 (CALI); *Ibid.*, Pommadimalai, 150 m, 16.12.1982, *K.M. Matthew & N. Rani* 29343 (RHT [RHT044614]); Siddannavasal, 02.02.1978, *K. Ramamurthy* 53737 (BSI); Salem district, Sittanavasal, 100 m, 02.02.1978, *K. Ramamurthy* 53737 (MH [MH00127000, MH00126444]); Yercaud, Brooklyn, ± 1260 m, 29.04.1966, *A.V.N. Rao* 27499 (MH [MH00126996, MH00126997]); Yercaud, Shevaroy, foot of the temple hill, 1400 m, 10.01.1980, *K.M. Matthew* 25639 (RHT [RHT044615]); *Ibid.*, slopes of temple, 1500 m, 25.02.1980, *K.M. Matthew* 26809 (RHT [RHT044616]); *Ibid.*, Temple hill half way up, 1550 m, 15.12.1980, *K.M. Matthew, J.B. Britto & N. Rani* 28032 (RHT [RHT044617]); Green hills, Shevaroys, January 1941, *E. Barnes. s.n* (DD); Sivaganga district, Sivaganga, Esani estate, 100 m, 16.12.1964, *K. Ramamurthy* 22732 (MH [MH00126998, MH001269999]); *Ibid.*, 16.12.1964, *K. Ramamurthy* 22733 (MH [MH00126445, MH00126446]); The Nilgiris district, Kinnacoorie, 23.01.1913, *C.E.C. Fischer* 3533; Attakatti, 27.12.1912, *C.E.C. Fischer* 3222 (FRC). **Orissa**, Angul district, Talcher state, Paifoal Dalki, 300 feet, December 1940, *H.J. Mooney* 1644 (DD); Ganjam district, Chatrapur, December 1889, *J.S. Gamble* 21560 (DD); Nuapada district, Khariar estate, Sonahera plateau, 2150 feet, 02.10.1949, *H.F. Mooney* 3689 (DD); Satkosia Tiger Reserve, Purunakote section, 125 m, 06.09.2014, *K.C.*

*Mohan* 5195 (BSID [BSID0010604]). AUSTRALIA, **Queensland**, Cape York Peninsula, Lockerbie, 10 miles WSW of Somerset, 20 m, 03.05.1948, *L.J. Brass* 18625 (A [A01977334 digital image]); Newcastle Bay, 2.5 miles S of Somerset, 5 m, 05.10.1948, *L.J. Brass* 18736 (CAL, A [A01977333 digital image]); Sanamere Lagoon, Jardine River, 10 m, 19.05.1948, *L.J. Brass* 18863 (A [A01977328 digital image]). BANGLADESH, Silhet, *Wall. Cat.* 1496 (K [K000779496], GH [GH01977061 digital images]). CHINA, **Yunnan**, Yunnan-sen district, 1902, *J. Cavalerie* 811 (E [E00265803 digital image]); Chengkang, Monkang, 1450 m, 31.08.1938, *T.T. Yu* 17533 (A [A01976888 digital image]). **Western Yunnan**, Tengchong Xian, Jietou Xiang, between Jietou and Datang, 1670 m, 27.10.1998, *Li Heng, Bruce Bartholomew & Dao Zhi-ling* 11059 (GH [GH01976863 digital image]). **Hong-Kong**, 1855, *M. Pabbe Furet s.n.* (P [P02981582 digital image]). INDONESIA, **New Guinea**, 1920 m, 11.04.1973, *J. Raynal* 17069 (L [L2829121, L3887064 digital images]). **West Papua province**, Anggi Gita Lake, Bivouac Noordpool, 1850 m, 09.01.1962, *Sleumer & Vink* BW14014 (L [L2827485 digital image]); E. foot of Pekeglabro, Kebo, Wissel lakes, 1760 m, 28.05.1960, *Vink & Schram* BW8976 (L [L2827285 digital image]); Logged *Dacrydium* forest near Keb, Wissel lakes, 1750 m, 27.05.1960, *Vink & Schram* BW8916 (L [L2827284 digital image]); Neentjapaki mountains, Kebar valley, ± 1100 m, 13.10.1958, *C. Kalkman* 6381 (L [L2827483 digital image]); Kebar valley, ± 810 m, 13.11.1958, *C. Koster* BW8037 (L [L2827282digital image]). **South Papua province**, Merauke Koerik Camp, *c.* 15 km NE of Koembe village on north bank of Koembe river, 07.09.1954, *P. van Royen* 4851 (L [L2827290 digital image]); Goenoeng Si Papan (in Concession Kaloebi: Typographic Sheet 41, southeast quarter), 7–14.04.1933, *Rahmat SI Toroes* 3760 (MICH [MICH1577903 digital image]); Langga Pajoeng (on the Soengei Kanan: Typographic Sheet 41, southeast quarter), 7–30.03.1933, *Rahmat SI Toroes* 3298 (MICH [MICH1577905 digital image]); *Ibid.*, 7–30.03.1933, *Rahmat SI Toroes* 3440 (MICH [MICH1577902 digital image]). PAPUA NEW GUINEA, Eastern Highlands district, Goroka subdistrict, near Miruma village, upper Asaro valley, 19.06.1956, *R.D. Hoogland & R. Pullen* 5395 (US [US03217131 digital image]); Morobe district, Wau subdistrict, Manki Trig, Bulolo, 5000 feet, 08.12.1967, *P. Apini & H. Streimann* NGF30948 (L [L2827457 digital image]); Mount Hagen subdistrict, Ogelbeng, 5600 feet, 12.09.1963, *A.N. Millar & L.A. Garay* 18721 (A [A01977252 digital image], L [L2827286 digital image]); road above Tomba, 8000 feet, 06.07.1957, *R.G. Robbins* 268 (L [L2827469 digital image]); bog West of Tomba, 2560 m, 27.05.1972, *P.F. Stevens & J.F. Veldkamp* LAE54925 (A [A01977256 digital image]); Sirunki beneath the village of Nanguris, 14.08.1962, *Walker* ANU 528 (A [A01977257 digital image]); Sepik district, Telefomin, 08.01.1965, *E.E. Henty* NGF20695 (L [L2827484 digital image]). JAPAN, Kyoto, Midorogaike, Kamigamo, Kita-ku, Kyoto-shi, 100 m, 11.09.2002, *S. Tsugaru, S. Mitsuta & T. Sawada* 31897 (A [A01976929]). **Shimotsuke**, Tochigi, Isokawa Hongoo-mura Kawachi-gun, 17.08.1959, *Miyoshi Furuse s.n.* (A [A01976932]). MYANMAR (Burma and Malay Peninsula), *s.d., Herb. Griffith* 4080 (A [A01977059]); Mergui, *Herb. Griffith* 4080 (K [K000779525]); Pegu plains, *s.d., S. Kurz* 288; Pegu, Irrawaddy and Sittang valley, Yangoon lake, December 1870, *S. Kurz* 2306 (CAL). **Kachin**, Bhamo district, Kantioe Sakan, Kaukkma valley, 120 m, 27.11.1916, *J.H. Lace* 6056 (CAL). MALAYSIA, Bako National Park, Lintang path, *c.* 100 m, 03.01.1964, *Paul Chai* S19711 (A [A01977224 digital image]); Kedah, Gunong Jerai (Kedah Peak), 3100–3200 feet, 15.01.1964, *H.M. Burkill* HMB3305 (A [A01977225 digital image]). SRI LANKA, **Sabaragamuwa**, Ratnapura district, Rajjuruwatta on Kalawana-Pedikanda Road, ± 250 m, 02.12.1976, *R.B. Faden & A.J. Faden* 76/441 (US [US03216805 digital image]). **Southern Province**, Galla district, Talgaswela, 20.02.197, *L.H. Cramer* 2853 (US [US03216804 digital image]). THAILAND, **Chiang Mai**, Bo Luang tableland, 18°45'N 98°25'E, *c.* 1000 m, 14.12.1969, *C.F. van Beusekom & C. Phengklai* 2509 (P [P00376754 digital image]); Doi Sootep, 720 m, 02.01.1910, *A.F.G. Kerr* 1910 (K [K000779758]); *Ibid.*, 518 m, 05.09.1909, *A.F.G. Kerr* 793 (K [K000779759 digital iamge]); Siam, *s.d., H. Garrett* 55; Siam, Chiangmai, 02.01.1910, *A.F.G. Kerr* 918 (CAL).

*Conservation status*: *Utricularia caerulea* is widely distributed in India, but many of its habitats are subject to threats such as land clearing, mining, residential and commercial developments etc. Based on its broad distribution and population size, *U. caerulea* is assessed as Least Concern (LC) (IUCN 2012, 2022).

*Notes*: *Utricularia caerulea* shows variation in plant size and nature of corolla (size, shape, and colour). Plants growing in lateritic areas at elevations of 10 to 1000 m reaches a height of up to 12 cm with flowers loosely arranged in simple peduncle, while those growing in swampy/ sandy soils at elevations of 1100 to 1750 m reaches 15–30 cm high with branched peduncles and dense flowers (Fig. 2e). Rather than the caerulean blue, the corolla colour varies from pure white to shades of pink and purple (Fig. 2f–m), and all these morphotypes are found in the same population.

## Key to the species of Utricularia sect. Nigrescentes

1. Corolla pink to purple or white; bracteoles usually basisolute, attached (but sometimes very shortly) below the point of attachment ..... 2

1. Corolla yellow; bracteoles basifixed ..... *U. bracteata*

2. Palate of corolla with 2 hooked processes on its distal margin; dorsal appendages of traps narrowly oblong with rounded apex ..... *U. warburgii*

2. Palate of corolla with or without hooked processes; dorsal appendages of traps narrowly deltoid with acute apex ..... 3

3. Spur longer than the lower lip of corolla; seeds obovoid to ellipsoid; periclinal wall of testa cells elongate with granulated surface ..... *U. caerulea*

3. Spur shorter than or equal to the lower lip of corolla; seeds obovoid to oblongoid, periclinal wall of testa cells raised into cylindrical tubercles, surface finely verrucate ..... *U. roseopurpurea*

## Seed micromorphology

*Utricularia roseopurpurea* Stapf ex Gamble: Seeds obovoid to oblongoid, 0.23–0.35 × 0.17–0.23 mm; hilum sub-terminal; testa cells irregularly shaped; folded and smaller near hilum; anticlinal wall concave, uneven, thick, scrobiculate; periclinal wall convex, raised into cylindrical tubercles, surface rough, finely verrucate (Fig. 5a–c).

*Utricularia caerulea* L.: Seeds obovoid to ellipsoid, 0.2–0.3 × 0.1–0.18 mm; hilum sub-terminal; testa cells elongate; smaller and congested around hilum; anticlinal wall concave straight, thick; periclinal wall convex, elongate, surface rough, granulated (Fig. 5d–f).

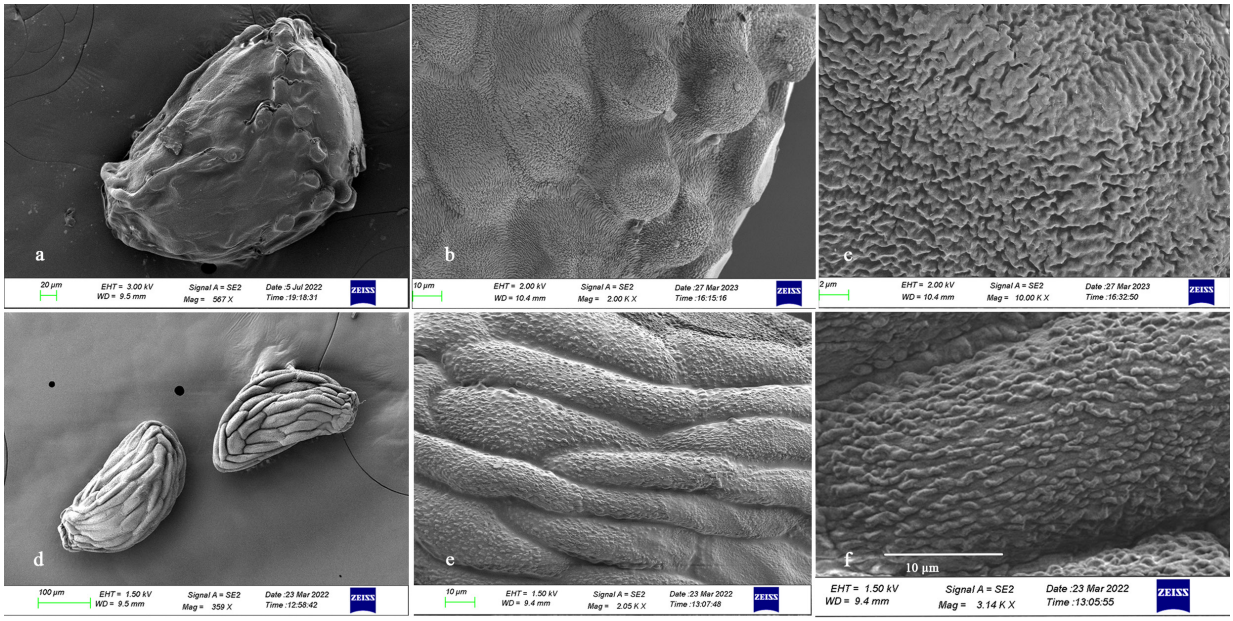


**Fig. 5**. Scanning electron microscopic images of seeds: **a–c**. *Utricularia roseopurpurea* Stapf ex Gamble; **a**. Seed; **b**. Testa cells; **c**. Magnified view of periclinal testa ornamentation; **d–f**. *Utricularia caerulea* L.; **d**. Seeds; **e**. Testa cells; **f**. Magnified view of periclinal testa ornamentation (a–c from *Krishnapriya M.P. & Santhosh Nampy* 164344; d–f from *Krishnapriya M.P. & Santhosh Nampy* 168088).

## Sequence data and phylogenetic tree

The nuclear ITS sequence alignment was 976 bp in length including gaps after removing ambiguous regions at the 5' and 3' ends, and had 363 constant sites, 428 parsimony informative sites, and 185 variable characters. The phylogenetic tree from the ML and BI analyses were congruent in general topology supported by moderate to high ML ultrafast bootstraps BS) and posterior probabilities (PPs) (Fig. 6). The tree is divided into two major clades with maximum bootstrap and posterior probability (PP=1 and BS=100%). Clade I (PP=0.72; BS=74%), represented by *U.* section *Meionula* (*U. hirta* and *U. minutissima*) and *U.* sect. *Oligocista* (*U. albocaerulea, U. bifida, U. cecilii, U. foveolata, U. graminifolia, U. polygaloides, U. recta, U. reticulata, U. sainthomia,* and *U. purpurascens*). Clade II (PP=0.70; BS=70%), bifurcated into two subclades. Subclade IIa represents *U.* section *Phyllaria* (*U. furcellata, U. kumaonensis* and *U. striatula*) with a branch support of PP=1.00 and BS=99%, Subclade IIb included *U. roseopurpurea* and *U. caerulea* of *U.* section *Nigrescentes*. Within the clade of *U.* section *Nigrescentes*, multiple accessions of *U. caerulea* and the samples of *U. roseopurpurea* formed sister pairs with high support (PP=1.00; BS=100%). The phylogenetic tree here shows a strong separation of the samples of *U. caerulea* from *U. roseopurpurea* supports the identity of the latter.

## Discussion

*Utricularia* sect. *Nigrescentes* is represented by four species, of which two, *U. caerulea* and *U. roseopurpurea*, are found in India. After careful examination of morphological, micromorphological and molecular data, the distinctiveness of *U. roseopurpurea* is


**Fig. 6**. Phylogenetic tree with the position of *Utricularia caerulea* L. and *Utricularia roseopurpurea* Stapf ex Gamble. Numbers along the branches are maximum likelihood bootstrap (BS, above) values and Bayesian posterior probabilities (PP, below).

confirmed. It can be easily segregated with the trap, seed and corolla characters. A variation in colour (white, pink-purple), size of inflorescence (1.5–30 cm long) arrangement of flowers (lax or clustered towards apex) can be seen in *U. caerulea*. *Utricularia roseopurpurea* presents white or purple flowers with 4.5–18 cm long inflorescences. There is considerable difference in the trap appendage structure between the *U. roseopurpurea* and *U. caerulea*: the traps are long, triangular, beak-like and glandular hairy in *U. caerulea* (Fig. 2n & o), while in *U. roseopurpurea* they are coiled or reflexed inwards forming a circular appendage (Fig. 1g). Further, the two species can be differentiated by the size and shape of flowers, length of the lower corolla lip and spur. The lower lip of the corolla is broad with a spur noticeably shorter than or equalling the length of the lower lip in *U. roseopurpurea* (Fig. 2c & d) *vs.* a narrow lower corolla lip with spur always exceeding the length of the lower lip in *U. caerulea* (Fig. 2i & j).

The seed micromorphology is also a strong character for separating both species. In *U. caerulea*, the seeds are obovoid to ellipsoid with convex periclinal wall with a rough and granulated testa surface (Fig. 5d–f), while, *U. roseopurpurea* possess obovoid to oblongoid seeds with a rough and convex periclinal cell wall extended into cylindrical tubercles (Fig. 5a–c). Both species have their own ecological preferences and distribution ranges. *Utricularia caerulea* has a widespread distribution (tropical to subtropical Asia to Japan, north and east Australia, Madagascar) within an altitudinal range of 10–1100 m (–1750 m), whereas *U. roseopurpurea* is restricted to higher altitude (1000–2200 m) cooler places in the Western Ghats (Kerala, Tamil Nadu) and Sri Lanka (Fig. 4).

Our research supports the differentiation between *U. caerulea* and *U. roseopurpurea* as distinct taxonomic entities, as evidenced by morphology and molecular phylogenetics. Despite our analysis being based on one nuclear marker, ITS, and being based on a reduced sample size of 21 out of approximately 280 recognized *Utricularia* species, representing a subset of the genus and specific sections like the Indian members of sect. *Nigrescentes*, it provides valuable insights. The phylogenetic tree separated *Utricularia caerulea* and *U. roseopurpurea* with high support (PP=1.0; BS=100). The dichotomy observed in *U. caerulea* terminals may due to various factors, but it is likely because the samples come from different populations that do not necessarily exhibit dichotomous diversification, but rather a network. Additionally, the low phylogenetic signal of nrITS may also contribute to the polytomy. Our phylogenetic analyses also support the sister relationship of the *U.* sect. *Nigrescentes* and *U.* sect. *Phyllaria* and is congruent with previous molecular studies (Jobson & Albert, 2002; Jobson *et al.*, 2003; Müller & Borsch, 2005; Müller *et al.*, 2006; Reut & Jobson, 2010; Silva *et al.*, 2018; 2023). The results corroborate conclusions by Taylor (1989) who noted the relationship between sections *Nigrescentes* and *Phyllaria* based on placenta morphology and the point of attachment of bracts. Our studies clarify the phylogenetic position, morphological and micromorphological features, habitat ecology and conservation assessment of the two species in detail.

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