

## Molecular phylogeny of *Utricularia* sections *Meionula* and *Nigrescentes* (Subg. *Bivalvaria*; Lentibulariaceae) with a new species for the mound springs of the Great Artesian Basin, Australia

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### Abstract

*Utricularia* subgenus *Bivalvaria* Kurz (Lentibulariaceae) is distributed across the Old and New World tropics. A recent molecular phylogeny that sampled across 13 sections of subg. *Bivalvaria* found sect. *Aranella* sister to two large clades of 1. *Oligocista*/*Benjaminia*-*Martinia*-*Enskide*/*Minutae*-*Stomoisia* sister to 2. *Nigrescentes*-*Phyllaria*-*Lloydia*-*Calpidisca*-*Australes*-*Meionula*. We present a molecular phylogeny of clade 2 using a matrix of the nuclear ITS and two chloroplast markers that includes 15 of the 36 recognised species sampled across the range of target species. The phylogenetic study sampled broadly within the closely allied sections *Nigrescentes* and *Meionula* (Raf.) P.Taylor from across each of their distributions. This study provides morphological and molecular evidence for recognition of a new species in sect. *Nigrescentes*, *Utricularia artesiana* R.W.Jobson & Baleeiro, from discharge mound spring habitats of western Queensland. Our description is based on the phylogenetic results and morphology. Morphological differences between closely related species are here discussed, and an identification key is provided. Distributions and habitat preferences of these species are discussed. We also provide molecular phylogenetic evidence for the presence of the Asian *U. geoffrayi* Pellegrin of sect. *Meionula* across northern Australia, and support for maintaining *U. nivea* Vahl as a synonym of *U. caerulea* L.

### Introduction

*Utricularia* subgenus *Bivalvaria* Kurz (Lentibulariaceae) is distributed across the Old and New World tropics. The subgenus is divided into 14 sections (Taylor 1989; Lowrie *et al.* 2008) that have been included in molecular phylogenies (Jobson *et al.* 2003, 2018). These studies observed paraphyly of some sections, and Jobson & Baleeiro (2023) proposed sinking sect. *Minutae* Lowrie, Cowie & Conran into sect. *Enskide* (Raf.) P.Taylor, and sect. *Benjaminia* P.Taylor into sect. *Oligocista* A.DC. The monotypic African sections *Oliveria* P.Taylor and *Candollea* P.Taylor, and the Asian sect. *Kamienskia* P.Taylor all fit best into subg. *Bivalvaria* morphologically but have not been included in any molecular phylogeny. The molecular phylogeny of Jobson *et al.* (2018) sampled across 13 of the subg. *Bivalvaria* sections finding sect. *Aranella* sister to two large clades of 1. *Oligocista*/*Benjaminia*-*Enskide*/*Minutae*-*Stomoisia* sister to 2. *Nigrescentes*-*Phyllaria*-*Lloydia*-*Calpidisca*-*Australes*-*Meionula*. The phylogeny of Clade 1 was expanded to include all Australian species with recognition of the new sect. *Oligocista* species *U. irwinica* R.W.Jobson & Baleeiro (Jobson & Baleeiro 2023).

Within Clade 2, Taylor (1989) recognised three species in sect. *Nigrescentes* including the southern tropical African *U. bracteata* R.Good, Chinese *U. warburgii* Goebel,

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and the highly morphologically variable Madagascan/Asian–Australasian *U. caerulea* L. Taylor's (1989) treatment of *U. caerulea* synonymised 31 taxa, with one of these, the Indian *U. roseopurpurea* Stapf ex Gamble, recently reinstated to species level based on morphological and molecular phylogenetic evidence (Krishnapriya *et al.* 2024). Krishnapriya *et al.* (2024) provided redescriptions of *U. caerulea* and *U. roseopurpurea*, and some evidence to maintain the synonymy of *U. nivea* Vahl under *U. caerulea*.

We present a molecular phylogeny of Clade 2 using a matrix of the nuclear ITS and two chloroplast markers that includes 15 of the 36 recognised species sampled across the range of target species. The phylogenetic study broadly sampled members of the closely allied sections *Nigrescentes* and *Meionula* (Raf.) P.Taylor from across each of their distributions. This study provides morphological and molecular evidence for recognition of a new species for sect. *Nigrescentes*, *Utricularia artesiana* R.W.Jobson & Baleeiro, from discharge mound spring habitats of the Great Artesian Basin (GAB) across western Queensland. This taxon was not seen by Taylor during his examination of *U. caerulea* specimens for his treatment of the genus (Taylor 1989). Our description is based on the phylogenetic results and morphology. Morphological differences between closely related species and distributions and habitat preferences of these species are discussed. We also provide molecular phylogenetic evidence for the presence of the Asian *U. geoffrayi* Pellegrin of sect. *Meionula* across northern Australia, and support for maintaining *U. nivea* as a synonym of *U. caerulea*.

## Methods

### Taxon sampling and DNA extraction

Newly sampled accessions for *rps16* ( $n = 51$ ), *trnD-T* ( $n = 43$ ), and ITS ( $n = 27$ ) were obtained from silica dried and herbarium sheet material and are listed in Table 1 of this study along with their relevant GenBank numbers for each sequenced marker. We expanded the ITS dataset to include ingroup sequences from sections *Nigrescentes* and *Meionula* with those previously published and those presented in table 1 of Krishnapriya *et al.* (2024) (Fig. 1; Table 1).

### Amplification and sequencing

Amplifications were performed as for Jobson *et al.* (2017) using two noncoding plastid (cpDNA) and nuclear ITS ribosomal gene marker (nuDNA). The cpDNA markers included the *rps16* intron and the *trnD-trnT* intron spacer (*trnD-T*). The nuclear ribosomal Internal Transcribed Spacer region, consisting of (ITS), was amplified using universal primers described in Stanford *et al.* (2000) and White *et al.* (1990). Forward and reverse sequences were assembled, edited and aligned as for Jobson *et al.* (2017).

### Phylogenetic analyses

Topologies obtained from individual *rps16* and *trnDT* analyses were congruent and were concatenated and analysed together. Separate phylogenetic analyses were performed on the combined *rps16/trnDT* (cpDNA) and nuclear ITS matrices and topologies were found to be congruent. We therefore analysed a concatenated cpDNA + ITS matrix (Fig. 1). For the Bayesian phylogenetic analyses, a suitable nucleotide substitution model

was chosen for each of the datasets using the Akaike information criterion (AIC) implemented in the program jMODELTEST, ver. 2.1.7 (Guindon & Gascuel 2003; Posada 2008). We found that the best fit model was GTR + I + G and GTR + G for each the cpDNA and ITS datasets respectively. All other analyses were performed under the same parameters as described in Jobson & Davies-Colley (2020).

## Results/Discussion

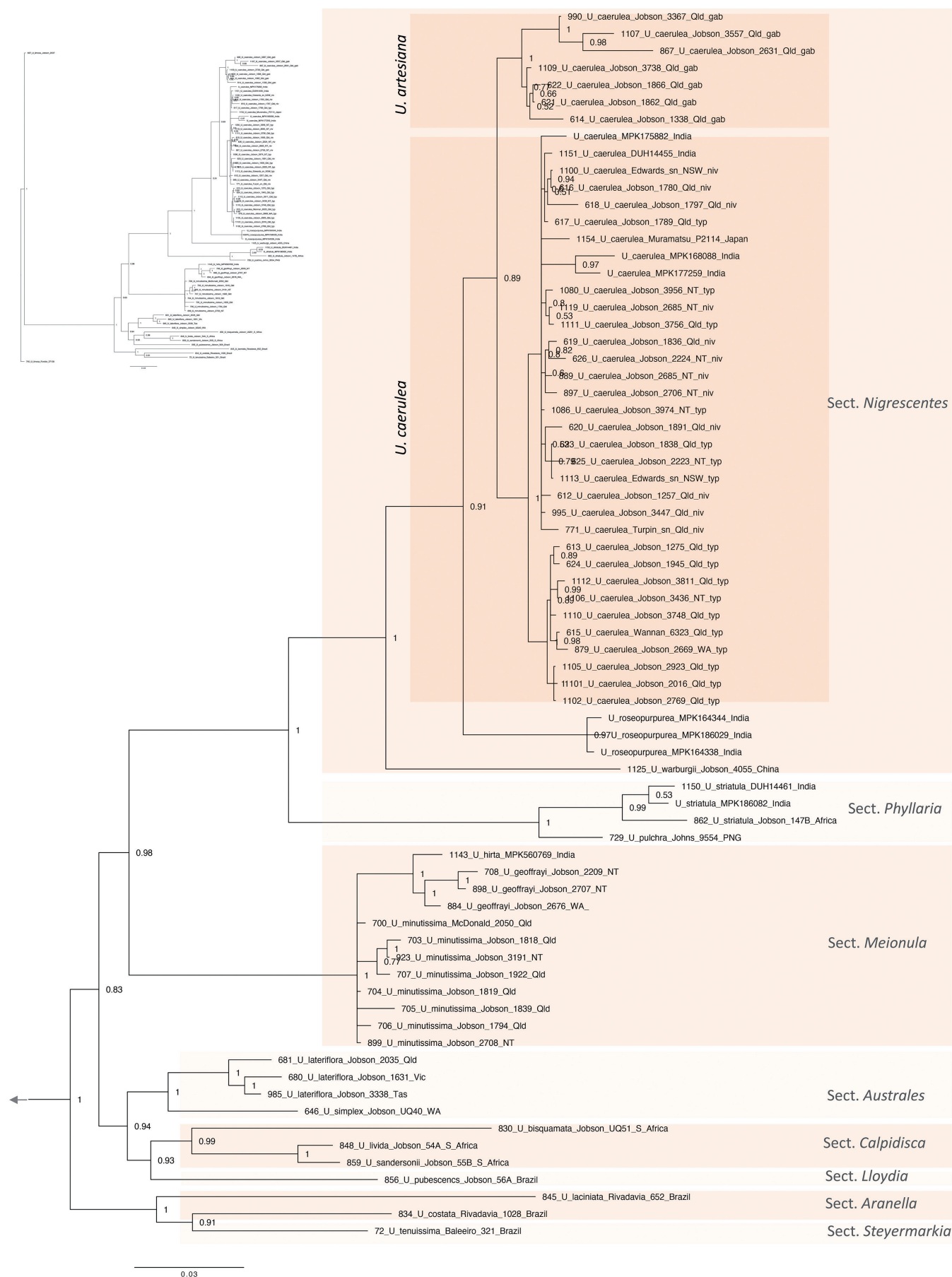
### Sequences and alignment

The *rps16* matrix was 1105 bp long of which 280 (25.3%) characters were parsimony informative, *trnDT* matrix was 936 long of which 129 (13.8%) characters were parsimony informative, and the ITS matrix was 925 bp long of which 230 (24.6%) characters were parsimony informative (tree not shown). The cpDNA and ITS datasets were analysed separately (not shown). An examination of the topologies showed the same branching order across both trees for all corresponding accessions allowing for concatenation. The combined (*rps16+trnDT+ITS*) dataset was 2966 bp long of which 689 (23.2%) were parsimony informative (Fig. 1).

In the Jobson *et al.* (2018) study the accession representing *U. tenuissima* Tutin was found to be a misidentified member of sect. *Oligocista*, hence its placement in that section. For the current study we provide a new sequence from new material (Baleeiro 321; Table 1) and we show the accession is placed with maximal support more logically in sect. *Aranella* (Barnhart) P.Taylor (Fig. 1). We here find that *U. tenuissima* of sect. *Martinia* P.Taylor is nested within the sect. *Aranella* clade near *U. costata* P.Taylor making the latter section paraphyletic (Fig. 1). This close relationship was noted by Taylor (1989) however he established the new monotypic section to accommodate *U. tenuissima* with its entire vs. fimbriate margins on the scales, bracts and calyx lobes of sect. *Aranella*, and its unique long, narrow capsule, and trap appendages (Taylor 1989). Based on this current result we here recommend the inclusion of *U. tenuissima* within sect. *Aranella* (Fig. 1).

Sister to sect. *Aranella*, are two weakly supported clades: the first includes the maximally supported Australian/New Zealand sect. *Australiales* that is sister to the likewise weakly supported and mostly African sects. *Calpidisca* and *Lloydia* P.Taylor (Fig. 1), the second clade contains sect. *Meionula* sister to sects. *Phyllaria/Nigrescentes* and all these relationships are maximally supported (Fig. 1). The sect. *Meionula* is represented by all three recognised species in an unresolved cluster of the SE Asian/Australasian *U. minutissima* (Fig. 2a), with a maximally supported grouping of the SE Asian *U. hirta* sister to maximally supported group of northern Australian accessions of *U. geoffrayi* (Fig. 2b). The Asian *U. geoffrayi* has not been included in previous phylogenetic studies and we now provide molecular evidence of its occurrence across northern Australia (Fig. 1, Fig. 2a–b).

Sister to sect. *Meionula*, two species of the diverse lithophytic African/Asian/Malesian sect. *Phyllaria* are represented in a the maximally supported clade that is sister to a maximally supported clade representing sect. *Nigrescentes*. In our study, sect. *Nigrescentes* includes three of the four recognised species; the Chinese *U. warburgii*, that is sister to a group including Indian *U. roseopurpurea* and *U. caerulea*. The latter species is broadly distributed from Madagascar throughout Asia to PNG/Australia (Krishnapriya *et al.* 2024; Fig. 1, 2 c–d, 3).



**Figure 1.** Phylogeny of *Utricularia* sections *Nigrescentes*, *Phyllaria*, *Lloydia*, *Calpidisca*, *Australes* and *Meionula*. 50% majority-rule Bayesian inference consensus tree for concatenated cpDNA/ITS data. Posterior probability (PP) support values are shown above branches. PP = 0.95–1.00: strong support; 0.84–0.94: weak support; <0.83: unsupported. Sections are shown in coloured boxes. *Utricularia caerulea* accessions labelled "typ" = matching the type; "niv" = matching '*U. nivea*'.

**Table 1.** New sequence accessions used in the ITS and cpDNA matrices. Secondary collectors are not included. Locality abbreviations: NSW, New South Wales; NT, Northern Territory; Qld, Queensland; Tas, Tasmania; Vic, Victoria; WA, Western Australia. GenBank accession numbers for each sequence are shown. NS indicates sequencing failed or not carried out.

Laboratory code	Section	Taxon	Collector	Coll. Date	Location	ITS	<i>rps16</i>	<i>trnD</i> T
680	Australes	<i>U. lateriflora</i> R.Br.	Jobson 1631 (NSW)	27/11/2012	Grampians, Vic	NS	OR141373	NS
681		<i>U. lateriflora</i> R.Br.	Jobson 2035 (NSW)	13/07/2013	Woodgate, Qld	NS	OR141374	OR141467
985		<i>U. lateriflora</i> R.Br.	Jobson 3338 (NSW)	30/03/2017	Recherche Bay, Tas	NS	OR141414	OR141492
708	Meionula	<i>U. geoffrayi</i> Pellegrin	Jobson 2209 (NSW)	19/04/2014	Jabiru, NT	NS	OR141382	OR141469
884		<i>U. geoffrayi</i> Pellegrin	Jobson 2676 (NSW)	16/04/2015	Mitchell Plateau, WA	NS	OR141394	OR141475
898		<i>U. geoffrayi</i> Pellegrin	Jobson 2707 (NSW)	19/04/2015	Humpty Doo, NT	NS	OR141399	OR141480
NA		<i>U. hirta</i> Klien ex Link	Chaudhary s.n. (DUH)	23/02/2019	Western Ghats, India	NS	MK560769	NS
700		<i>U. minutissima</i> Vahl	McDonald 2050 (BRI)	10/05/2004	Cook, Qld	NS	OR141376	NS
703		<i>U. minutissima</i> Vahl	Jobson 1818 (NSW)	22/04/2013	Laura, Qld	NS	OR141377	NS
704		<i>U. minutissima</i> Vahl	Jobson 1819 (NSW)	22/04/2013	Laura, Qld	NS	OR141378	NS
705		<i>U. minutissima</i> Vahl	Jobson 1839 (NSW)	24/04/2013	Mt Garnet, Qld	NS	OR141379	NS
706		<i>U. minutissima</i> Vahl	Jobson 1794 (NSW)	21/04/2013	Mt Tozer, Qld	NS	OR141380	NS
707		<i>U. minutissima</i> Vahl	Jobson 1922 (NSW)	6/07/2013	Cape Flattery, Qld	NS	OR141381	OR141468
899		<i>U. minutissima</i> Vahl	Jobson 2708 (NSW)	20/04/2015	Humpty Doo, NT	NS	OR141400	NS
923		<i>U. minutissima</i> Vahl	Jobson 3191 (NSW)	20/04/2016	Finnis River, NT	NS	OR141402	OR141481
614	Nigrescentes	<i>U. artesiana</i> R.W.Jobson & Baleeiro	Jobson 1338 (NSW)	1/12/2011	Edgbaston Station, Qld	NS	OR141346	OR141447
621		<i>U. artesiana</i> R.W.Jobson & Baleeiro	Jobson 1862 (NSW)	25/04/2013	Doongmabulla, Qld	NS	OR141353	OR141454
622		<i>U. artesiana</i> R.W.Jobson & Baleeiro	Jobson 1866 (NSW)	25/04/2013	Edgbaston Station, Qld	PQ340755	OR141354	OR141455
867		<i>U. artesiana</i> R.W.Jobson & Baleeiro	Jobson 2631 (NSW)	10/04/2015	Elizabeth Springs, Qld	NS	OR141391	OR141472
990		<i>U. artesiana</i> R.W.Jobson & Baleeiro	Jobson 3367 (NSW)	11/05/2017	Bundoona, Eulo, Qld	NS	OR141415	OR141493
1107		<i>U. artesiana</i> R.W.Jobson & Baleeiro	Jobson 3557 (NSW)	25/04/2019	Elizabeth Springs, Qld	PQ340756	OR141324	OR141425
1109		<i>U. artesiana</i> R.W.Jobson & Baleeiro	Jobson 3738 (NSW)	17/07/2019	Doongmabulla, Qld	NS	OR141325	OR141426
612		<i>U. caerulea</i> L.	Jobson 1257 (NSW)	20/05/2011	Mt Garnet, Qld	KY243543	OR141344	OR141445
771		<i>U. caerulea</i> L.	Turpin s.n. (BRI)	23/06/1995	Croydon, Qld	NS	OR141390	NS
1080		<i>U. caerulea</i> L.	Jobson 3956 (NSW)	19/03/2021	Berry Springs, NT	OR142134	OR141317	OR141418
1086		<i>U. caerulea</i> L.	Jobson 3974 (NSW)	22/03/2021	Finnis River, NT	OR142135	OR141318	OR141419



Laboratory code	Section	Taxon	Collector	Coll. Date	Location	ITS	<i>rps16</i>	<i>trnD</i> T
613		<i>U. caerulea</i> L.	Jobson 1275 (NSW)	7/06/2011	Musgrave, Qld	OR142153	OR141345	OR141446
615		<i>U. caerulea</i> L.	Wannan 6323 (NSW)	18/10/2012	Croydon, Qld	OR142154	OR141347	OR141448
616		<i>U. caerulea</i> L.	Jobson 1780 (NSW)	20/04/2013	Mt Tozer, Qld	OR142155	OR141348	OR141449
617		<i>U. caerulea</i> L.	Jobson 1789 (NSW)	21/04/2013	Mt Tozer, Qld	OR142156	OR141349	OR141450
618		<i>U. caerulea</i> L.	Jobson 1797 (NSW)	21/04/2013	Mt Tozer, Qld	OR142157	OR141350	OR141451
619		<i>U. caerulea</i> L.	Jobson 1836 (NSW)	24/04/2013	Irvinebank, Qld	OR142158	OR141351	OR141452
620		<i>U. caerulea</i> L.	Jobson 1891 (NSW)	4/07/2013	Caloundra, Qld	OR142159	OR141352	OR141453
623		<i>U. caerulea</i> L.	Jobson 1838 (NSW)	24/04/2013	Irvinebank, Qld	OR142160	OR141355	OR141456
624		<i>U. caerulea</i> L.	Jobson 1945 (NSW)	7/07/2013	Gamboola, Qld	OR142161	OR141356	OR141457
625		<i>U. caerulea</i> L.	Jobson 2223 (NSW)	20/04/2014	Flying Fox Ck, NT	OR142162	OR141357	OR141458
626		<i>U. caerulea</i> L.	Jobson 2224 (NSW)	20/04/2014	Flying Fox Ck, NT	OR142163	OR141358	OR141459
889		<i>U. caerulea</i> L.	Jobson 2685 (NSW)	17/04/2015	Pine Creek, NT	OR142169	OR141396	OR141477
897		<i>U. caerulea</i> L.	Jobson 2706 (NSW)	19/04/2015	Humpty Doo, Qld	OR142170	OR141398	OR141479
995		<i>U. caerulea</i> L.	Jobson 3447 (NSW)	21/05/2017	Nicholson, Qld	NS	NS	OR141495
1111		<i>U. caerulea</i> L.	Jobson 3756 (NSW)	20/07/2019	Bamaga, Qld	NS	OR141327	OR141428
1100		<i>U. caerulea</i> L.	Edwards s.n. (NSW)	19/05/2020	Coutts Crossing, NSW	OR142136	OR141319	OR141420
1101		<i>U. caerulea</i> L.	Jobson 2016 (NSW)	10/07/2013	Herbert River, Qld	OR142137	OR141320	OR141421
1102		<i>U. caerulea</i> L.	Jobson 2769 (NSW)	14/07/2015	Middle Spring, Qld	OR142138	OR141321	OR141422
1105		<i>U. caerulea</i> L.	Jobson 2923 (NSW)	23/07/2015	Kimba Plateau, Qld	OR142139	OR141322	OR141423
1106		<i>U. caerulea</i> L.	Jobson 3436 (NSW)	19/05/2017	Lorella Station, NT	OR142140	OR141323	OR141424
1110		<i>U. caerulea</i> L.	Jobson 3748 (NSW)	19/07/2019	Musgrave, Qld	OR142141	OR141326	OR141427
1112		<i>U. caerulea</i> L.	Jobson 3811 (NSW)	1/08/2019	Gamboola, Qld	OR142142	OR141328	OR141429
1113		<i>U. caerulea</i> L.	Edwards s.n. (NSW)	20/05/2020	Maclean, NSW	OR142143	OR141329	OR141430
1119		<i>U. caerulea</i> L.	Jobson 2685 (NSW)	8/05/2019	Pine Creek, NT	OR142144	OR141330	OR141431
879		<i>U. caerulea</i> L.	Jobson 2669 (NSW)	16/04/2015	Theda Station, WA	OR142167	OR141392	OR141473
NA		<i>U. caerulea</i> L.	Muramatsu P2114 (NICH)	10/08/2012	Japan	LC682653	NS	NS
NA		<i>U. caerulea</i> L.	Chaudhary 14455 (DUH)	23/02/2019	Western Ghats, India	NS	MK617625	NS
729	<i>Phyllaria</i>	<i>U. pulchra</i> P.Taylor	Johns 9554 (CANB)	1/06/1967	Papua New Guinea	NS	OR141384	NS
NA		<i>U. striatula</i> Sm.	Chaudhary 14461 (DUH)	23/02/2019	Western Ghats, India	NS	MK61762	NS
72	<i>Steyermarkia</i>	<i>U. tenuissima</i> Tutin	Baleeiro 321 (SPF)	10/07/2009	Gois, Brazil	NS	OR141385	NS

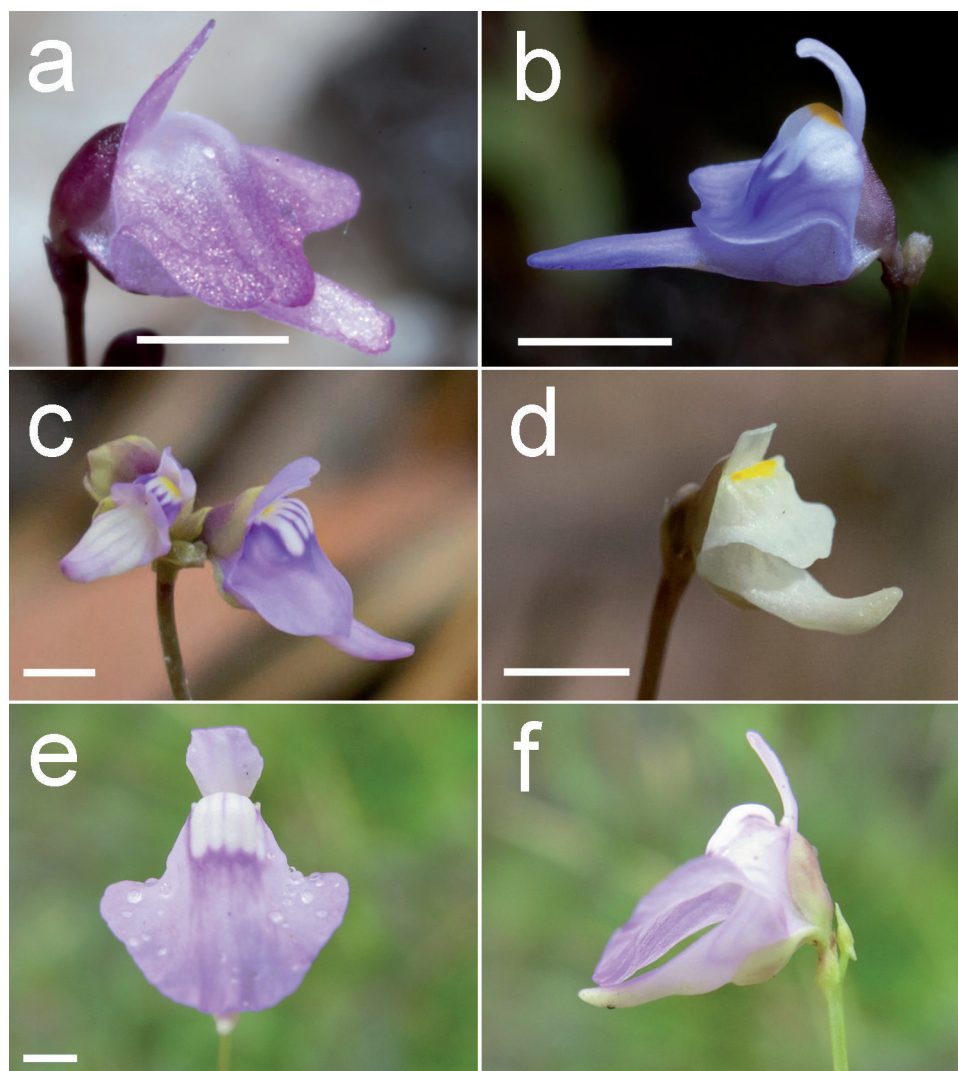
Our sampling of *U. caerulea* is from across the Australian distribution and one from Japan and four other accessions that were derived from collections from across India: in the north-east at Mawryngkneng (*Krishnapriya* 175882 (CALI)), near Western Ghats (*Chaudhary & Tandon* DUH14455), and two from the south-west near Mangaluru (*Krishnapriya* 168088, 177259 (CALI)) (Fig. 3). Although we didn't obtain a sequence from a Sri Lankan accession (type locality, *Hermann* s.n.), *Krishnapriya et al.* (2024) provides an extensive treatment using herbarium

material from across India/Sri Lanka to Australia, finding that the three above accessions fit material from the type locality (Fig. 3).

Within our sampling of *U. caerulea* (Fig. 1) we found that small stature, white flowered accessions fitting the description of synonym *U. nivea* (Kurz 1874; Fig. 2d) fall into multiple clades allied with accessions that fit the *U. caerulea* type specimen (Fig. 2c). In Australia, *U. nivea* was recognised at specific rank in the work of Lowrie (2013), and the informal phrase name

*U. sp. Small White* (M.O.Rankin 2450) NT Herbarium has been coined for some NT populations (Kerrigan & Albrecht 2007). Based on the results of our extensively sampled study we here

recommend following Taylor (1989) and Krishnapriya *et al.* (2024) in maintaining *U. nivea* as a synonym of *U. caerulea* (Taylor 1989).



**Figure 2.** *Utricularia minutissima* (a), *U. geoffrayi* (b), *U. caerulea* - typical form (c), *U. caerulea* - "*U. nivea*" form (d), *U. artesiana* (e, f): a–d & f, corolla lateral view; e, corolla frontal view. Scale bars: a–f = 2 mm (a–d are estimated). Images: a–d, with permission from Boaz Ng; e & f by R.W. Jobson (R.W. Jobson 3738 & P.C. Baleeiro).

Our topology supports that of Krishnapriya *et al.* (2024) with well supported (PP = 0.97) *U. roseopurpurea* as sister to the weakly supported (PP = 0.89) main clade of *U. caerulea* accessions (Fig. 1). The *U. caerulea* clade forms two maximally supported groupings with one of these involving *U. caerulea* accessions distributed in isolated discharge mound spring habitats of the GAB (Fig. 1), while the second contains all other accessions from across the Asian–Australian distribution (Fig. 1, 3). On close examination of the GAB accessions, it became clear that morphological characteristics differed when compared to those within the *U. caerulea* s.s. grouping (Fig. 2, 4). We here describe the entity as a new species for Queensland.

## Taxonomy

***Utricularia artesiana*** R.W.Jobson & Baleeiro, *sp. nov.*

**Diagnosis:** Similar to *U. caerulea* in having scales and bracts basiolute and base of corolla lower lip with four or five white vertical ridges, but differs in having upper and lower part of

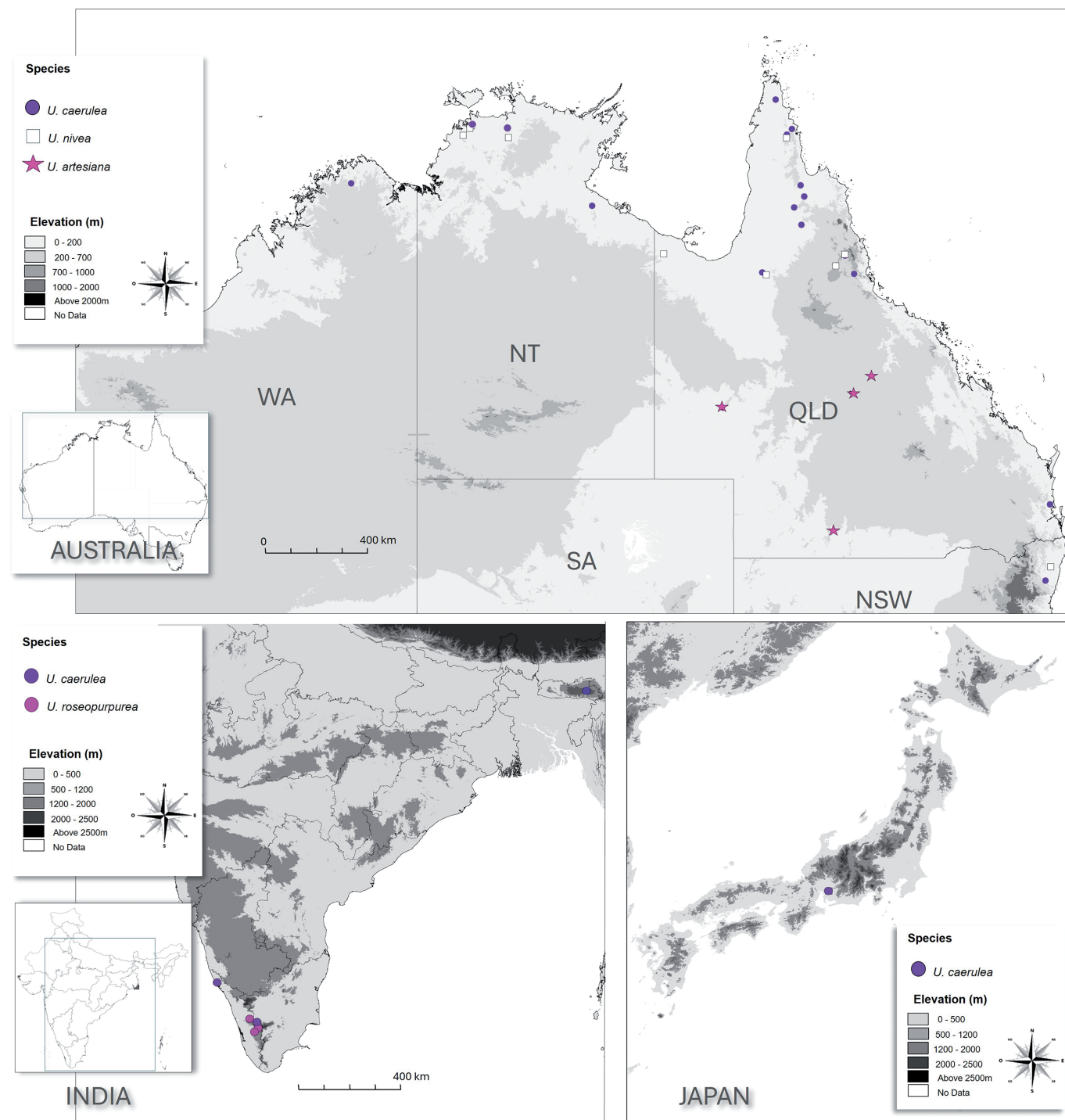
scales very short, broadly ovate and apically rounded/broadly acute in *U. artesiana* vs long, narrowly ovate/lanceolate and apically acute in *U. caerulea*. Restricted to inland mineral rich artesian spring habitats vs. mostly coastal creeks, swamps and savannah habitats.

**Type:** AUSTRALIA: QUEENSLAND: Gregory North District: Elizabeth Springs, Springvale Homestead, 10 April 2015, R.W. Jobson 2631 & W. Cherry (holo [prepared as two parts]: NSW 909509 (sheet), NSW 927123 (spirit); iso: BRI (spirit)).

Small, probably perennial, terrestrial. *Rhizoides* few, capillary, simple, up to 5 mm long, 0.2 mm thick. *Stolons* few, capillary, branched, 10–30 mm long, 0.45 mm thick, internodes c. 10 mm long. *Leaves* few, rosulate, single or in pairs at stolon nodes, petiolate, narrowly obovate with apex rounded, up to 4 mm long and 0.8–1.0 mm wide. *Traps* few on stolons and leaf margin, ovoid, 0.5–1.0 mm long, stalked 0.3–0.6 mm long, mouth lateral, dorsal appendage shorter than the body of the trap, beak-shaped, 0.4–0.7 mm long, few stipitate glands along margin.

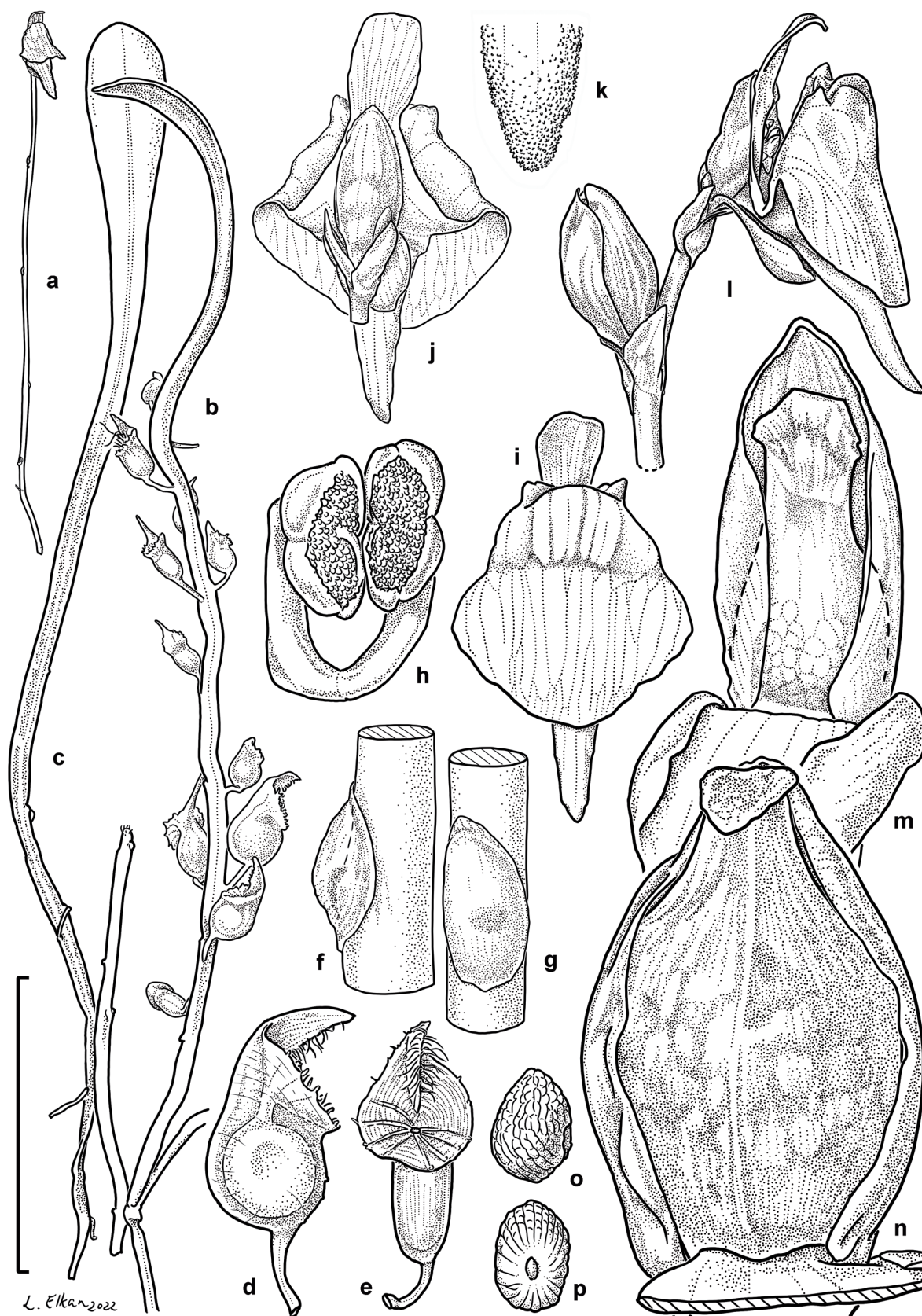
*Inflorescence* erect, simple, solitary 45–170 mm long; peduncle terete, 0.4–0.6 mm thick, glabrous. *Bracts* basisolute, 1.2–2 mm long, superior part narrowly ovate/lanceolate with apex acute, inferior part shorter, apex acute; *Bracteole* basisolute, 1.5–1.8 mm long, superior part narrowly ovate, apex acute, inferior part short, truncate. Scales few, basisolute, 1.0–1.9 mm long, broadly ovate, inferior and superior parts very short, apices rounded or broadly acute. *Flowers* 1–7, solitary or in a raceme; pedicel 5–10 mm long, c. 0.5 mm thick; *Calyx* lobes unequal, convex, 2.0–3.0 mm long, minutely papillose; upper lobe ovate, apex acute; lower lobe 2.0–2.5 mm long, apex broadly rounded, transversely elliptic. *Corolla* 5–8 mm long, pale or mid-violet, with 4–5 white,

slightly raised ridges at the base; *upper lip* limb, 3–3.5 mm long, constricted near the middle, superior part oblong to ovate with apex truncate; *lower lip* limb ovate, entire, apex rounded; palate transversely crested with a shortly raised horn either side; *spur* broadly conical, 5–6 mm long, minutely papillose, slightly curved and constricted near the acute apex, longer than the lower lip. *Filaments* curved, 0.7–1.0 mm long, anther thecae sub-distinct. *Ovary* globose; style short; stigma lower lip semicircular, upper lip shorter, deltoid. *Capsule* ellipsoid, 3.3–3.5 mm long, c. 2 mm wide, walls thin, dehiscing from an none-thickened longitudinal, ventral slit. *Seeds* obovoid, 0.26–0.31 mm long, surface rugulose. *Pollen* 3 colporate,  $31 \times 31 \mu\text{m}$ . **Figures 2e–f, 4, 5.**



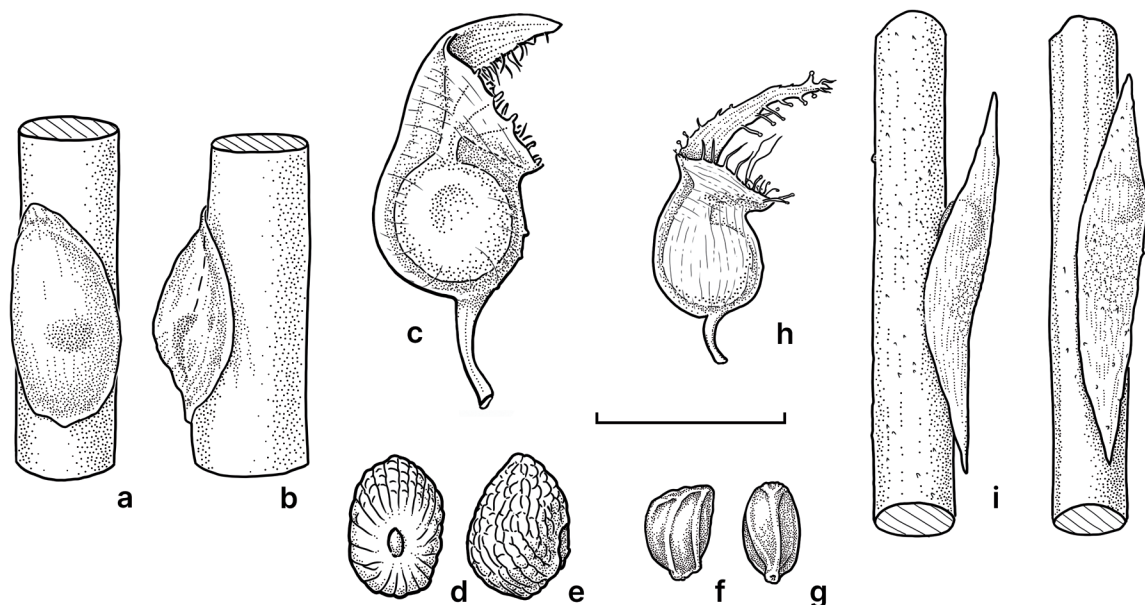
**Figure 3.** Distribution map showing accessions used in the molecular phylogeny of *Utricularia* sect. *Nigrescentes*. *U. caerulea* - typical form (purple circle), *U. caerulea* - "*U. nivea*" form (white squares), *U. roseopurpurea* (pink circles), *U. artesiana* (mauve stars). For accession details refer to Table 1 & table 1 in Krishnapriya et al. (2024).





**Figure 4.** *Utricularia artesiana*. a, habit; b, leaf with bladder-traps near the base; c, leaf adaxial surface; d, bladder-trap lateral view; e, bladder-trap dorsal view; f, peduncle scale in situ lateral view; g, peduncle scale in situ dorsal view; h, stamens frontal view; i, flower frontal view; j, flower rear view; k, corolla spur apex frontal view; l, flower and immature bud lateral view; m, immature fruit capsule in situ; n, mature fruit capsule in situ frontal view; o, seed lateral view; p, seed basal view. Scale bar: a = 33.33 mm; b & c = 5.0 mm; d–g, k, m & n = 2.0 mm; h = 1.67 mm; i, j & l = 7.0 mm; o & p = 1.0 mm. Material used: Jobson 3367 & Baleeiro (NSW934858 - spirit). Illustration by L. Elkan (RBG052572).





**Figure 5.** Comparison of *Utricularia artesiana* (a–e), *U. caerulea* (f–j), a & j peduncle scale dorsal view; b & i peduncle scale lateral view; c & h bladder-trap lateral view; d & g seed shape basal view; e & f seed shape lateral view. Scale bar: a, b, c, h, i & j = 1.0 mm; d, e, f, g = 0.5 mm. Material used: a–e = Jobson 3367 & Baleeiro (NSW934858 - spirit); f–j = Jobson 1836 & Cherry (NSW922718 - spirit). Illustration by L. Elkan (RBG052613).

**Additional specimens examined:** Queensland: Gregory North District: Elizabeth Springs, Springvale Homestead, 25 Apr 2019, R.W. Jobson 3557 & P.C. Baleeiro (NSW 1138283); Mitchell District: Edgbaston Station, 25 Apr 2013, R.W. Jobson 1866 (NSW 973312); Warrego District: Bundoona Spring, W of Eulo, 11 May 2017, R.W. Jobson 3367 (NSW 934858 – spirit); South Kennedy District: Doongmabulla, Moses Springs, 17 Jul 2019, R.W. Jobson & P.C. Baleeiro 3738 (NSW 1138285); Doongmabulla, Moses Springs, 12 Apr 2014, R.J. Fensham RJF6404 (BRI AQ0914065).

**Distribution and ecology:** Occurs in artesian mound spring habitats of western Qld. Known from Elizabeth Springs (type site), Bundoona Station near Eulo, Edgbaston Station NNE of Aramac, and Doongmabulla Station (Fig. 3). Grows in mineral rich clay-mud on artesian mound springs (Fig. 6).

**Phenology:** Collected in flower April–July.

**Conservation status:** This locally and regionally rare species is known from four GAB discharge mound spring sites across western Qld (Fig. 3). The taxon *U. caerulea*, under which *U. artesiana* was previously included, was not listed for protection under the Environment Protection and Biodiversity Conservation Act 1999 from 31 August 2023. (<http://www.environment.gov.au/biodiversity/threatened/communities/pubs/26-conservation-advice.pdf>). We recommend that *U. artesiana* be assessed for inclusion under the above act.

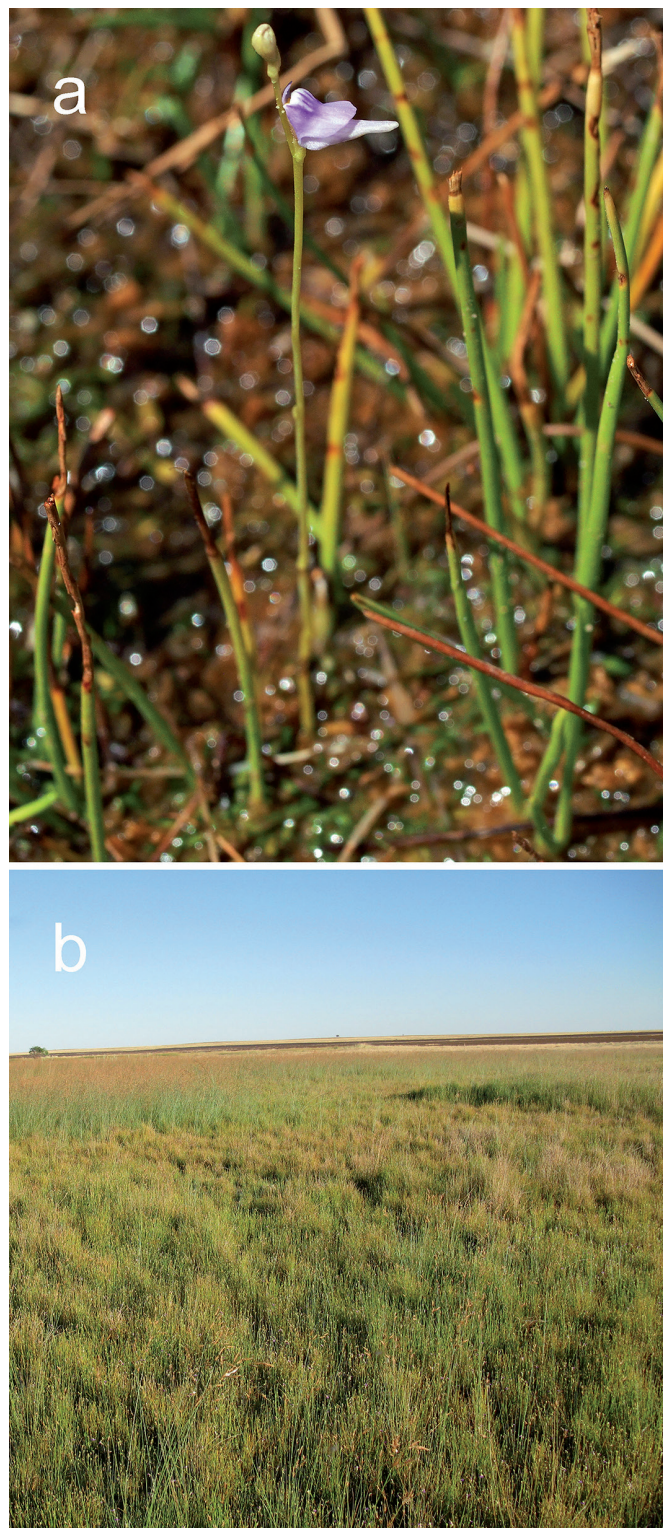
**Etymology:** The specific epithet *artesiana* refers to the artesian discharge spring habitat.

**Notes:** Specimens collected in the Cook District at Soda Springs near Gamboola, (Fensham 2545; Jobson 1945, 3811) fit the morphology of *U. caerulea* s.s. and in support of this observation we find our accessions in the phylogeny Jobson 1945, 3811 are nested within a subclade containing mainly coastal Qld *U. caerulea* s.s. (Fig. 1). This is unexpected because GAB springs are unusual wetlands because of their permanence and unusual chemistry relative to other wetlands (Fensham et al. 2011).

However, the *U. caerulea* s.s. occurs in seasonal wetlands only ~80 km to the south-east and ~90 km to the north of Gamboola. Collections of *U. caerulea* from GAB recharge springs near Taroom in the Leichhardt District of Qld (Fensham 2545, BRI AQ583000; Penay 130, BRI AQ769411) were also found to fit the morphology of *U. caerulea* s.s. An additional Leichhardt District GAB-spring specimen (Fensham 3801, BRI AQ491182) from Nogoia River, Salvator Rosa National Park, was not located for examination in this study. A collection from a non-GAB spring near Gilberton, Qld (Fensham 4479, BRI AQ498768) was examined and found to fit *U. caerulea* s.s.

A similar distributional pattern is found when comparing GAB species *U. fenshamii* R.W. Jobson and *U. dichotoma* ssp. *fontana* R.W. Jobson, both of sect. *Pleiochasia* (Jobson 2013; Jobson & Baleeiro 2020). Of these two closely related species, the former is almost exclusively found in GAB discharge springs, while the latter occupies GAB recharge springs across eastern Qld and extends to other non-GAB spring-like habitats along the coast and south into northern NSW (Jobson & Baleeiro 2020).

Corolla form has successfully provided useful characters for differentiation of species within the *U. amethystina* Salzmann ex A.St.Hil. & Girard complex (Baleeiro et al. 2015, 2019, 2022). Even so, these corolla characters can either vary heavily within a species such as *U. caerulea* (Taylor 1989; Krishnapriya et al. 2024) or maintain a general similarity leading to the lumping of cryptic taxa (Jobson & Baleeiro 2020). Features of the corolla may be strongly influenced by sexual selection pressures within a widespread taxon. For taxonomic differentiation these characters may not be as reliable as those less labile/plastic features of the inflorescence such as scales and bract/bracteole structures of the peduncle (Taylor 1989). Other morphological characters often used to differentiate species of *Utricularia* include seed shape, seed coat structure, and bladder-trap form (Taylor 1989). However, in line with the results of Krishnapriya et al. (2024) we find that these characters are quite plastic within *U. caerulea* s.s.



**Figure 6.** Typical erect habit (top) and habitat at Doongmabulla Springs (bottom) of *Utricularia artesiana*. Images by R. Jobson (R.W. Jobson 3738 & P.C Baleeiro).

In Jobson & Baleeiro (2020), molecular phylogeny supported morphological differences involving bract and bracteole shape. These inflorescence structures supported the division of *Utricularia dichotoma* s.l. into six additional taxa, with *U. dichotoma* s.s. assigned to seven subspecies based almost entirely of bract structure (Jobson 2013; Jobson & Baleeiro 2020). We find a similar cryptic situation in the comparison of corolla of *U. artesiana* and *U. caerulea* with its shape and colour not diverging from the variety observed across populations of the latter species (Fig. 2c–d vs. e–f; Taylor 1989; Krishnapriya

et al. 2024). Despite the above, the molecular phylogeny in the current study suggests divergence between *U. artesiana* and *U. caerulea* occurred prior to the dispersal of the latter taxon between Asia and Australia (Fig. 1).

There is great corolla colour variation across the widespread *U. caerulea* ranging from deep crimson to light purple, and white (Fig. 2c–d; Taylor 1989; Krishnapriya et al. 2024). Corolla shape is also very variable although the lower lip is always entire, and the length of the spur is always longer than the lower lip (fig. 43a–b in Taylor 1989; Krishnapriya et al. 2024). Corolla colour and shape also vary across the four populations of *U. artesiana* ranging from dark to light purple, with spur length ranging from longer than to almost equal to the length of the lower lip (Figs 2e–f, 4, 5). Characters that are very consistent across all observed forms of *U. caerulea* are peduncle scales that possess long superior and inferior parts with narrowly acute apices (Taylor 1989; Fig. 5). In contrast, we find that the very short superior and inferior parts of scales in *U. artesiana* are consistently broadly ovate and apically rounded/ broadly acute (Figs 4, 5).

### Key to species of *Utricularia* sects. *Australes*, *Meionula*, and *Nigrescentes* modified from Taylor (1989) & Krishnapriya et al. (2024)

(Abbreviations: As = Asia; Af = Africa; Au = Australia; NZ = New Zealand)

1. Scales, bracts and bracteole basifixed.....2
- 1: Scales, bracts and bracteole basisolute.....7
2. Corolla lower lip 3-lobed .....3
- 2: Corolla lower lip entire, emarginate .....5
3. Calyx covered in multicellular hairs (As).....*U. hirta*
- 3: Calyx glabrous .....4
4. Pedicel longer than the subtending bract (As/Au) .....*U. minutissima*
- 4: Pedicel shorter than the subtending bract (As/Au) .....*U. geoffrayi*
5. Inflorescence to 5 cm tall, 1-flowered; corolla upper lip wider than calyx (Au) .....*U. simplex*
- 5: Inflorescence 8–30 cm tall, 3–10-flowered; corolla upper lip narrower than calyx .....6
6. Raceme elongated; capsule dehiscing from ventral and dorsal sutures (Au).....*U. lateriflora*
- 6: Raceme congested; capsule dehiscing from ventral suture (NZ).....*U. delicatula*
7. Corolla pink to purple or white; bracteoles usually basisolute, attached (but sometimes very shortly) below the point of attachment.....8
- 7: Corolla yellow; bracteoles basifixed (Af).....*U. bracteata*
8. Palate of corolla with 2 hooked processes on its distal margin; dorsal appendages of traps narrowly oblong with rounded apex (As).....*U. warburgii*
- 8: Palate of corolla with or without hooked processes; dorsal appendages of traps narrowly deltoid with acute apex.....9
9. Spur shorter than or equal to the lower lip of corolla; seeds obovoid to obloid, periclinal wall of testa cells raised into cylindrical tubercles, surface finely verrucate (As) .....*U. roseopurpurea*
- 9: Spur longer than the lower lip of corolla; seeds obovoid to ellipsoid; periclinal wall of testa cells elongate with granulated surface .....10
10. Upper and lower part of scales very short, broadly ovate and apically rounded/broadly acute (Au).....*U. artesiana*
- 10: Upper and lower part of scales long, narrowly ovate/lanceolate and apically acute (Af/As/Au) .....*U. caerulea*



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