

Molecular phylogenetic study of *Utricularia* section *Oligocista* in Australia and a new Cape York endemic species

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Abstract

Utricularia section *Oligocista* A.DC. (Lentibulariaceae) is distributed across the old and new world tropics. We present a molecular phylogeny using a matrix of the nuclear ITS and two chloroplast markers that includes 19 of the 37 recognised species sampled across the range of each species. The phylogenetic study also includes members of the closely allied sections *Enskide* (Raf.) P.Taylor (including section *Minutae* Lowrie, Cowie & Conran) and *Stomoisia* (Raf.) Kuntze from across each of their distributions. The phylogeny shows that Australia contains species from the two major clades of section *Oligocista*, with each involving ancestors with yellow and purple/mauve corolla colours. This study provides morphological and molecular evidence for recognition of a new species, *Utricularia irwinica* R.W.Jobson & Baleeiro, from Cape York Peninsula, Queensland. A lectotype is designated for the name *Utricularia cyanea* var. *alba* Benth. We also recommend changes to the taxonomy of sections *Enskide* and *Oligocista* based on the phylogenetic results and morphology.

Introduction

Utricularia section *Oligocista* A.DC. was circumscribed by Taylor (1989) containing 37 species distributed across the old and new world tropics with the majority found in Asia (14 spp.), followed by Africa and Madagascar (10 spp.), America (7 spp.) and Australia (5 spp.). Since Taylor (1989), six species have been described for Asia (Janarthanam & Henry 1989, 1990, 1992; Parnell 2005; Suksathan & Parnell 2010; Yadav et al. 2005), and one from the Neotropics (Souza & Bove 2011). The type for the section is *U. bifida* L., a small, yellow-flowered species from Asia and northern Australia/Papua New Guinea (Taylor 1989). The current study used plastid and nuclear markers to reconstruct the molecular phylogeny of sect. *Oligocista* to understand the biogeography of the Australian species. One of these species, *Utricularia uliginosa* Vahl, is morphologically variable and distributed across tropical and northern Asia, Malesia, and Australasia. Sampling included the known distribution of this species, the putatively allied white-flowered form known as *U. sp.* Steve Irwin Reserve (R.W.Jobson 4153) from western Cape York Peninsula, and the closely related *U. praeterita* P.Taylor that is endemic to India (Taylor 1989; Janarthanam & Henry 1992; Kolte et al. 2019). Comparisons with closely related species, *U. praeterita*, and Asian/Oceanian *U. uliginosa* are provided. Diagnostic features are illustrated, and distribution, habitat, and conservation status are discussed.

Methods

Taxon sampling and DNA extraction

Dried and alcohol-preserved material representing all available sect. *Oligocista* and related species were examined. These are held at the National Herbarium of New South Wales (NSW), Northern Territory Herbarium (DNA), Australian National Herbarium (CANB), Queensland Herbarium (BRI), Herbarium of IRD Nouméa (NOU), and Universidade de São Paulo (SPF).

We newly sequenced 48 accessions across sections *Oligocista/Enskide/Stomoisia* including a broad sampling of the widespread *U. uliginosa* (Table 1). Plant tissue was obtained from silica-dried and herbarium-sheet material. Based on the phylogeny of *Utricularia* by Jobson et al. (2003), five outgroup samples were selected from GenBank to represent the sister clade within the genus (Table 1). DNA isolation was performed as for Jobson et al. (2017). The final dataset contained 74 accessions of which 26 were previously published (Table 1).

Amplification and sequencing

Sequence amplifications used parameters for the nuclear ITS marker according to Jobson et al. (2022) and for the non-coding plastid markers (cpDNA) *rps16* intron and *trnD-trnT* intron spacer (*trnD-T*) according to Shaw et al. (2005). The nuclear ribosomal ITS region was amplified for several difficult samples using the forward primer ITS5A (Stanford et al. 2000) and the universal internal reverse primer ITS2, and reverse primer ITS4 and internal primer ITS3 (White et al. 1990). Polymerase chain reaction (PCR) conditions for ITS were performed as described in White et al. (1990).

Phylogenetic analyses

Phylogenetic analyses were performed on datasets for each of the three individual markers as well as a concatenated matrix from all three markers combined. The most suitable nucleotide substitution model for each of the three markers was assessed using the Akaike information criterion (AIC) implemented in jModelTest (ver.2.1.7, see <https://en.bio-soft.net/tree/MODELTEST.html>, accessed 20 April 2023; Guindon and Gascuel 2003; Posada 2008). The best fit was GTR+ I+G (*rps16*, *trnD-T*) and GTR+G (ITS) with a burn-in involving the first 25% of the sampled trees. We estimated Bayesian posterior probability with five independent runs of 20 million generations using four chains each sampling a tree every 1000 generations. All parameters were set as Dirichlet with a flat multinomial distribution. Stationarity was assessed by examining plots of the $-\ln L$ across generations in Tracer (ver. 1.7, Rambaut et al. (2018), see <http://beast.bio.ed.ac.uk/Trace>, accessed 20 April 2023). The effective sample size (ESS) was set to >1000, and the remaining trees were used to construct a 50% majority rule consensus tree that was visualised using FigTree (ver. 1.4.4, <http://tree.bio.ed.ac.uk/software/figtree>, accessed 25 April 2023).

Results

Sequences and alignment

The *rps16* matrix was 1108 bp long, of which 301 characters (27%) were parsimony informative, *trnD-T* matrix was 935 bp long, of which 181 characters (19%) were parsimony informative, and the ITS matrix was 786 bp long of which 230 characters (29%) were parsimony informative. The three datasets included accessions of *rps16* ($n = 66$), *trnD-T* ($n = 37$), ITS ($n = 33$) (Table 1). The concatenated three gene matrix contained 68 ingroup and six outgroup taxa and was 2829 bp long with 712 parsimony informative characters (25%).

Phylogenetic relationships

The *rps16*, *trnD-T* and ITS datasets were analysed separately and resulting trees were largely topologically congruent, particularly across clade C (Fig. 1; Table 1). The 50% consensus tree consisted of two major clades provided with strong posterior probability support (PP = 1).

Section *Enskide* and sect. *Minutae* together formed a strongly supported clade, but sect. *Enskide* was found to be paraphyletic due to inclusion of sect. *Minutae* (Fig. 1). Section *Stomoisia*, sect. *Enskide* and sect. *Minutae* together formed a clade sister to a strongly supported sect. *Oligocista*. Section *Oligocista* was found to be paraphyletic due to the inclusion of monotypic sect. *Benjaminia* (Fig. 1). To accommodate these new relationships, we provide recommendations for sectional recircumscription below.

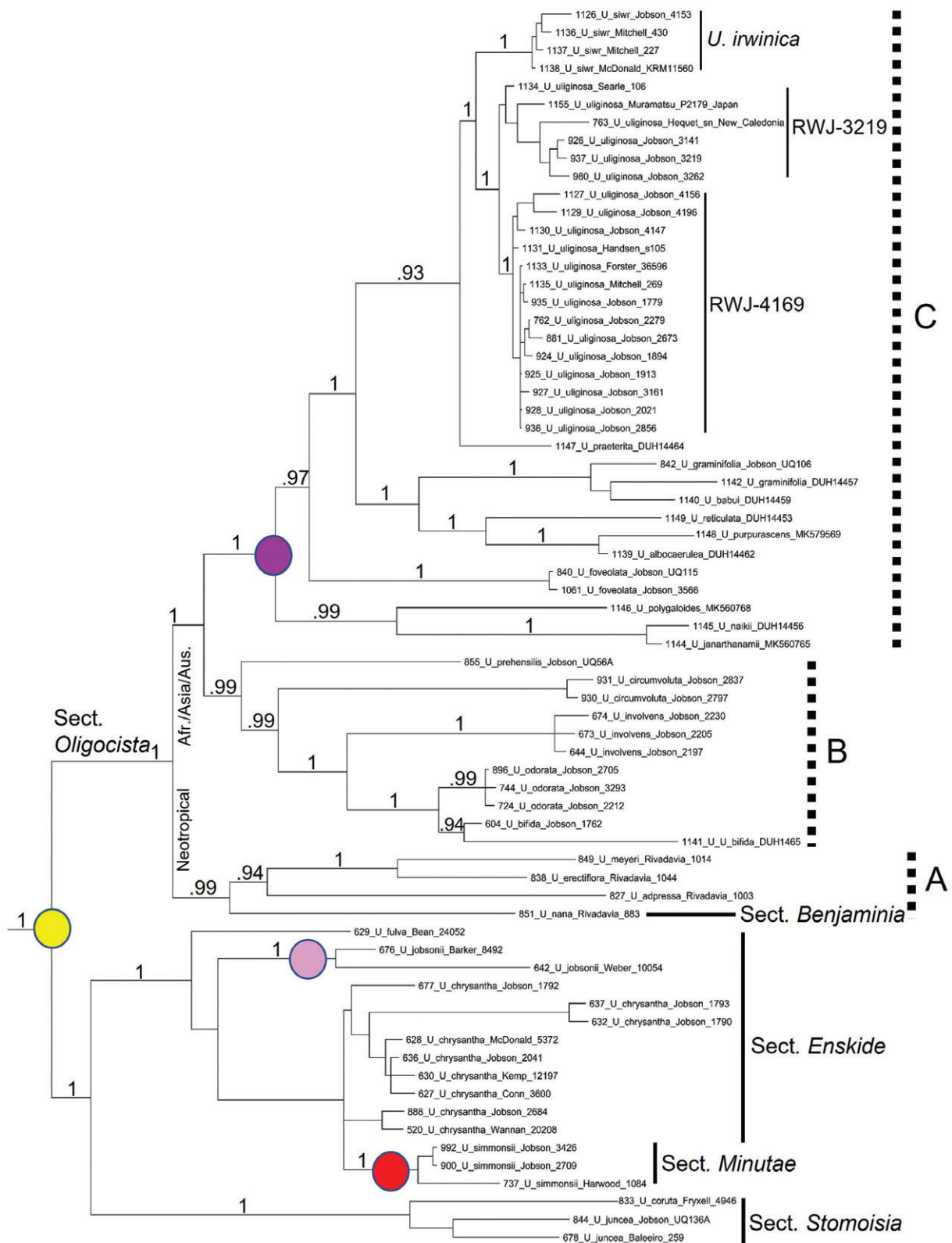


Fig. 1. 50% majority-rule Bayesian inference consensus tree for concatenated cpDNA/ITS data. Posterior probability (PP) support values are shown above important branches. PP = 0.95–1.00: strong support; 0.84–0.94: weak support (not shown); unsupported (not shown). Thin bars show two clades of *U. uliginosa* (RWJ-3219, RWJ-4196 – refer to Fig. 5) and the new species *U. irwinica*. Thick bars show sectional delimitations other than *Oligocista*. Three major clades of section *Oligocista* (A–C) shown behind broken lines. Character state transitions for corolla colour shown on relevant nodes (coloured circles).

Table 1. Accessions used in the nuclear (ITS) and cpDNA (rps16, trnDT) matrices. Secondary collectors are not included. Locality abbreviations: NSW, New South Wales; NT, Northern Territory; Qld, Queensland; WA, Western Australia. GenBank accession numbers for each sequence are shown. NS indicates sequencing failed or not carried out. GenBank numbers not preceded by "OR" are previously published. "Code" refers to specimen number.

CODE	Section	Taxon	Collector	Coll. Date	Location	ITS	RPS16	TRMDT
520	Enskide	<i>U. chrysantha</i> R.Br.	Wannan 20208 (DNA)	6/05/1987	Jabiru, NT	NS	NS	OR141444
627	Enskide	<i>U. chrysantha</i> R.Br.	Conn 3600 (NSW)	14/06/1995	Hope Vale, Qld	NS	OR141359	OR141460
628	Enskide	<i>U. chrysantha</i> R.Br.	McDonald 5372 (BRI)	24/06/2006	Starke National Park, Qld	NS	OR141360	OR141461
629	Enskide	<i>U. fulva</i> F.Muell.	Bean 24052 (BRI)	4/06/2005	Humpty Doo, NT	NS	OR141361	OR141462
630	Enskide	<i>U. chrysantha</i> R.Br.	Kemp 12197 (BRI)	8/06/1997	North Kennedy, Qld	NS	OR141362	NS
632	Enskide	<i>U. chrysantha</i> R.Br.	Jobson 1790 (NSW)	21/04/2013	Mt Tozer, Qld	NS	OR141363	OR141463
636	Enskide	<i>U. chrysantha</i> R.Br.	Jobson 2041 (NSW)	16/09/2013	Hope Vale, Qld	NS	OR141364	OR141464
637	Enskide	<i>U. chrysantha</i> R.Br.	Jobson 1793 (NSW)	21/04/2013	Lockhart River, Qld	NS	OR141365	OR141465
642	Enskide	<i>U. jobsonii</i> Lowrie	Weber 10054 (AD)	3/06/1988	Murgenella, NT	NS	OR141366	OR141466
676	Enskide	<i>U. jobsonii</i> Lowrie	Barker 8492 (AD)	26/05/2004	Timber Creek, NT	NS	OR141370	NS
677	Enskide	<i>U. chrysantha</i> R.Br.	Jobson 1792 (NSW)	21/04/2013	Mt Tozer, Qld	NS	OR141371	NS
888	Enskide	<i>U. chrysantha</i> R.Br.	Jobson 2684 (NSW)	17/04/2015	Pine Creek, NT	NS	OR141395	OR141476
900	Enskide	<i>U. simmonsii</i> Lowrie et al.	Jobson 2709 (NSW)	20/04/2015	Girraween, NT	NS	OR141401	NS
992	Enskide	<i>U. simmonsii</i> Lowrie et al.	Jobson 3426 (NSW)	17/05/2017	Lorrela Station, NT	NS	OR141416	OR141494
604	Oligocista	<i>U. bifida</i> L.	Jobson 1762 (NSW)	20/04/2013	Lockhart River, Qld	NS	OR141343	NS
644	Oligocista	<i>U. involvens</i> Ridley	Jobson 2197 (NSW)	18/04/2014	Pine Creek, NT	NS	OR141367	NS
673	Oligocista	<i>U. involvens</i> Ridley	Jobson 2205 (NSW)	18/04/2014	Kakadu Hwy, NT	OR142164	OR141368	NS
674	Oligocista	<i>U. involvens</i> Ridley	Jobson 2230 (NSW)	20/04/2014	South Alligator River, NT	NS	OR141369	NS
724	Oligocista	<i>U. odorata</i> Pellegrin	Jobson 2212 (NSW)	19/04/2014	Jabiru, NT	NS	OR141383	NS
744	Oligocista	<i>U. odorata</i> Pellegrin	Jobson 3293 (NSW)	2/05/2011	South Alligator River, NT	NS	OR141387	NS
762	Oligocista	<i>U. uliginosa</i> Vahl	Jobson 2279 (NSW)	26/04/2014	South Alligator River, NT	NS	OR141388	OR141470
763	Oligocista	<i>U. uliginosa</i> Vahl	Hequet sn (NOU)	1/07/2014	Mitchell Plateau, WA	OR142165	OR141388	OR141471
827	Oligocista	<i>U. adpressa</i> Saizm. ex A.St.Hil.	Rivadavia 1003 (SPF)	1/05/1999	Noumea, New Caledonia	OR142166	OR141389	OR141471
838	Oligocista	<i>U. erectiflora</i> A.St.Hil. & Girard	Rivadavia 1044 (SPF)	3/05/1999	de Goias, Brazil	AF482509	AF482555	NS
840	Oligocista	<i>U. foveolata</i> Edgew.	Jobson UQ115 (BRI)	12/03/1999	Goias, Brazil	NS	AF482568	NS
842	Oligocista	<i>U. graminifolia</i> Vahl	Jobson UQ106 (BRI)	26/09/1999	Merten Ck, WA	NS	AF482570	NS
849	Oligocista	<i>U. meyeri</i> Pilger	Rivadavia 1014 (SPF)	2/05/1999	India	NS	AF482573	NS
851	Oligocista	<i>U. nana</i> A.St.Hil. & Girard	Rivadavia 883 (SPF)	2/04/1999	Goias, Brazil	NS	AF482582	NS
855	Oligocista	<i>U. prehensilis</i> E.Meyer	Jobson UQ56A (BRI)	26/09/1999	Minas Gerais, Brazil	NS	AF482585	NS
881	Oligocista	<i>U. uliginosa</i> Vahl	Jobson 2673 (NSW)	16/04/2015	Zambia	NS	AF482592	NS
896	Oligocista	<i>U. odorata</i> Pellegrin	Jobson 2705 (NSW)	16/04/2015	Theda Station, WA	OR142168	OR141393	OR141474
924	Oligocista	<i>U. uliginosa</i> Vahl	Jobson 1894 (NSW)	19/04/2015	Humpty Doo, NT	NS	OR141397	OR141478
925	Oligocista	<i>U. uliginosa</i> Vahl	Jobson 1913 (NSW)	5/07/2013	Cardwell, Qld	OR142171	OR141403	OR141482
926	Oligocista	<i>U. uliginosa</i> Vahl	Jobson 3141 (NSW)	5/07/2013	Starke National Park, Qld	OR142172	OR141404	OR141483
927	Oligocista	<i>U. uliginosa</i> Vahl	Jobson 3161 (NSW)	13/04/2016	Morgans Landing, Qld	NS	OR141405	OR141484
				14/04/2016	Cape Flattery, Qld	OR142173	OR141406	OR141485

CODE	Section	Taxon	Collector	Coll. Date	Location	ITS	RPS16	TRNDT
928	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Jobson 2021 (NSW)	10/07/2013	Blencho Falls, Qld	OR142174	OR141407	OR141486
930	<i>Oligocista</i>	<i>U. circumvoluta</i> P.Taylor	Jobson 2797 (NSW)	16/07/2015	Laura, Qld	NS	OR141408	NS
931	<i>Oligocista</i>	<i>U. circumvoluta</i> P.Taylor	Jobson 2837 (NSW)	18/07/2015	Jungle Creek, Qld	OR142175	OR141409	OR141487
935	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Jobson 1779 (NSW)	20/04/2013	Portland Road, Qld	OR142176	OR141410	OR141488
936	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Jobson 2856 (NSW)	18/07/2015	Jungle Creek, NT	OR142177	OR141411	OR141489
937	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Jobson 3219 (NSW)	22/04/2016	Darke Forest, NSW	OR142178	OR141412	OR141490
980	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Jobson 3262 (NSW)	2/10/2016	Mimosa Creek, Qld	OR142179	OR141413	OR141491
1061	<i>Oligocista</i>	<i>U. foveolata</i> Edgew.	Jobson 3566 (NSW)	28/04/2019	Mitchell Plateau, WA	OR142133	NS	OR141417
1126	<i>Oligocista</i>	<i>U. irwinica</i> R.W.Jobson & Baleeiro	Jobson 4153 (NSW)	24/06/2022	Steve Irwin WR, Qld	OR142145	OR141332	OR141433
1127	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Jobson 4156 (NSW)	25/06/2022	Punsand Bay, Qld	OR142146	OR141333	OR141434
1129	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Jobson 4196 (NSW)	26/06/2022	Batavia Downs, Qld	OR142147	OR141334	OR141435
1130	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Jobson 4147 (NSW)	24/06/2022	Nimrod Creek, Qld	OR142148	OR141335	OR141436
1131	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Handsen s105 (BRI)	4/06/2017	NE of Aurukun, Qld	OR142149	OR141336	OR141437
1133	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Forster 36596 (BRI)	1/05/2010	Jack River, Qld	NS	OR141337	OR141438
1134	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Searle 106 (BRI)	9/05/2013	Twitheran Creek, Qld	OR142150	OR141338	OR141439
1135	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Mitchell 269 (BRI)	1/03/2009	Steve Irwin WR, Qld	NS	OR141339	OR141440
1136	<i>Oligocista</i>	<i>U. irwinica</i> R.W.Jobson & Baleeiro	Mitchell 430 (BRI)	3/03/2009	Steve Irwin WR, Qld	NS	OR141340	OR141441
1137	<i>Oligocista</i>	<i>U. irwinica</i> R.W.Jobson & Baleeiro	Mitchell 227 (BRI)	19/07/2010	Steve Irwin WR, Qld	OR142151	OR141341	OR141442
1138	<i>Oligocista</i>	<i>U. irwinica</i> R.W.Jobson & Baleeiro	McDonald 11560 (BRI)	13/06/2023	Steve Irwin WR, Qld	OR142152	OR141342	OR141443
1139	<i>Oligocista</i>	<i>U. albocaulis</i> Dalz.	Chaudhary DUH14462	13/06/2011	India	MK617624	MK531202	NS
1140	<i>Oligocista</i>	<i>U. babui</i> S.R.Yadav et al.	Chaudhary DUH14459	23/02/2019	India	MK617628	MK560772	NS
1141	<i>Oligocista</i>	<i>U. bifida</i> L.	Chaudhary DUH14465	23/02/2019	India	MK617620	MK560767	NS
1142	<i>Oligocista</i>	<i>U. graminifolia</i> Vahl	Chaudhary DUH14457	23/02/2019	India	NS	MK560774	NS
1144	<i>Oligocista</i>	<i>U. janarthanamii</i> S.R.Yadav et al.	Chaudhary sn (DUH)	23/02/2019	India	NS	MK560765	NS
1145	<i>Oligocista</i>	<i>U. naikii</i> S.R.Yadav et al.	Chaudhary DUH14456	23/02/2019	India	MK617621	MK560766	NS
1146	<i>Oligocista</i>	<i>U. polygaloides</i> Edgew.	Tandon sn (DUH)	23/02/2019	India	NS	MK560768	NS
1147	<i>Oligocista</i>	<i>U. praeterita</i> P.Taylor	Chaudhary DUH14464	23/02/2019	India	MK617626	MK560775	NS
1148	<i>Oligocista</i>	<i>U. purpurascens</i> Graham	Tandon sn (DUH)	23/02/2019	India	NS	MK579569	NS
1149	<i>Oligocista</i>	<i>U. reticulata</i> Sm.	Chaudhary DUH14453	23/02/2019	India	MK617622	MK531203	NS
1155	<i>Oligocista</i>	<i>U. uliginosa</i> Vahl	Muramatsu P2179	10/08/2012	Japan	LC682656	NS	NS
678	<i>Stomopsis</i>	<i>U. juncea</i> Vahl	Baleeiro 259 (NSW)	15/07/2009	Gois, Brazil	NS	OR141372	NS
833	<i>Stomopsis</i>	<i>U. coruta</i> Michx	Fryxell 4946 (NY)	1/04/1986	Texas, USA	NS	AF482564	NS
844	<i>Stomopsis</i>	<i>U. juncea</i> Vahl	Jobson UQ136A (BRI)	12/03/1999	Georgia, USA	NS	AF482576	NS
830	<i>Calpidisca</i> *	<i>U. bisquamata</i> Schrank	Jobson UQ51	12/03/1998	South Africa	NS	AF482562	NS
687	<i>Nelipus</i> *	<i>U. limosa</i> R.Br.	Jobson 2037 (NSW)	13/07/2013	Burrum Point, Qld	NS	OR141375	NS
1125	<i>Nigrescentes</i> *	<i>U. warburgii</i> Goebel	Jobson 4055	14/04/2022	China	NS	OR141331	OR141432
613	<i>Nigrescentes</i> *	<i>U. caerulea</i> L.	Jobson 1275	7/06/2011	Musgrave, Qld	OR142153	OR141345	OR141446
104	<i>Pleiochasia</i> *	<i>U. ameliae</i> R.W.Jobson	Jobson 2188 (NSW)	16/04/2014	E of Boulia, Qld	MK259674	KY243405	KY243695

Within sect. *Oligocista*, three well supported clades were found (Fig. 1). Clade A consisted of neotropical taxa and *U. nana* (sect. *Benjaminia*) and formed a sister clade to the African/Asian/Australasian (clades B and C, Fig. 1). In clade B the African species *U. prehensilis* E.Meyer is sister to four Australian species (Fig. 1) that all possess a yellow corolla. Clade C consisted mostly of species with corolla colour in varied shades of violet or blue (Fig. 1) and these are distributed in India, SE Asia and Australasia, with a single widespread species *U. foveolata* Edgew. extending from Australia into Africa. Within clade C, the *U. uliginosa* clade consisted of two subclades RWJ-3219 (lacking strong support) and RWJ-4169 (well supported), corresponding to two morphological forms (Fig. 1). Both of these forms are distributed across Cape York, the former distributed across northern Australia and extending into Asia while the latter broadly distributed across along the east coast of Australian and likewise extending into Asia (RWJ pers. observation). Our accessions of *U. uliginosa* are from across the entire Australian distribution with inclusion of a representative from New Caledonia (*Hequet s.n.*) and Japan (*Muramatsu P2179*) respectively (Table 1; Fig. 1). Sister to *U. uliginosa* is a strongly supported clade containing four accessions of *U. sp.* Steve Irwin Reserve (R.W.Jobson 4153) with both these clades together strongly supported and sister to the morphologically similar Indian species *U. praeterita* (Fig. 1).

The phylogeny resolved *U. uliginosa*, *U. sp.* Steve Irwin Reserve (R.W.Jobson 4153) and *U. praeterita* in an unsupported clade and revealed genetic divergence between all three entities that mirrors key morphological differences (refer to key). Taxonomic description and illustrations of this close relative of *U. uliginosa* is here described as *U. irwinica* R.W.Jobson & Baleeiro sp. nov. The morphological differences between *U. irwinica*, *U. uliginosa*, and *U. praeterita* are discussed, and an identification key is provided along with the distribution and habitat preference of the new species.

Taxonomy

Utricularia irwinica R.W.Jobson & Baleeiro, sp. nov.

Diagnosis: Similar to *U. praeterita* in having upper corolla lip longer than the upper calyx lobe and seeds ovoid but differs in having mostly cream-white vs deep blue lower corolla lip in *U. praeterita*, and spur upper half cream-white, apical half faint purple vs entirely bluish purple in *U. praeterita*.

Type: AUSTRALIA: QUEENSLAND: Cape York Peninsula: Steve Irwin Wildlife Reserve, upper tributary of Bertiehaugh Creek [precise location withheld], R. W. Jobson 4153 & P.C. Baleeiro, 24 June 2022, holo [prepared as two parts]: NSW1125309 (sheet), NSW963027 (spirit); iso: BRI (spirit).

Small, probably perennial, terrestrial or subaquatic herb. *Rhizoids* few, capillary, branched up to 20 mm long, 0.3 mm thick, from base of peduncle. *Stolons* numerous, capillary, 0.10–0.22 mm thick, branched, up to 50 mm long, internode length 5–10 mm long. *Leaves* numerous, one from stolon nodes, petiolate; lamina linear to lanceolate, 10–30 mm long, 0.3–5.0 mm wide, 3–7 nerved, apex rounded or acute, total length 35–55 mm. *Traps* few on rhizoids, one at internode of stolon, occasionally on leaves, globose, shortly stalked, mouth basal with two simple, subulate dorsal appendages, surface of stalk and appendages adorned with short glands. *Inflorescence* erect, solitary, 55–220 mm long; peduncle filiform, glabrous, solid, 0.2–0.3 mm thick. *Scales* few, basifixed, ovate apex subacute, 0.5–1.1 mm long, 0.3–0.5 mm wide. *Bracts* basifixed, ovate with apex acute, slightly swollen at base with scattered sessile glands, 1.0–1.3 mm long, 0.5–0.7 mm wide. *Bracteoles* linear, 0.6–0.7 mm long, 0.2–0.3 mm wide. *Flowers* (1–)2 or 3, raceme elongated; pedicels suberect, apically curved, slightly dorsiventrally flattened, 1.5–2.0 mm long. *Calyx* lobes unequal; upper lobe 2.8–3.0 mm long, 2.2–2.5 mm wide, ovate, slightly convex, apex acute; lower lobe 2.8–3.0 mm long, 1.8–2.2 mm wide, ovate, with apex bidentate; upper lobe margin minutely papillose at maturity. *Corolla* cream-white, 5.5–6.5 mm long with apical half of spur faint purple; upper lip erect or decurved, constricted near middle with superior part ovate, apex rounded, longer than the upper calyx lobe, inferior part oblong, galeate; lower lip limb circular, galeate, with prominent swelling near middle; palate with raised, distally pubescent rim; spur slightly conical at base, diverging at c. 90°, curved forward, longer than the lower lip, apex acute. *Staminal filaments* slightly curved, c. 0.1 mm long; anther thecae distinct. *Ovary* ovoid, c. 1 mm long; style c. 0.5 mm long; stigma with lower lip ovate, upper lip shorter, truncate. *Capsule* ovoid, c. 2.5 mm long; walls thin, membranous, dehiscent by a single, ventral, longitudinal, unthickened slit. *Seeds* ovoid 0.25–0.30 mm long, testa cells elongated with anticlinal walls raised. *Pollen* 3- or 4-colporate, 25 × 25 μm (R. W. Jobson 4153 & P. Baleeiro). Figs 2, 3, 4a, b, 5a, b.

Additional specimens examined. Queensland: Cook District: N of Weipa Airport, A. Mitchell 14-430 & B. Massey, 3 Mar 2009 (BRI); NE of Weipa, A. Mitchell 227 & E. Miller, 19 Jul 2010 (BRI); Steve Irwin Wildlife Reserve, N of Coolibah Ranger Station, K.R. McDonald KRM11560 & B.J. Lyon, 13 Jul 2011 (BRI).

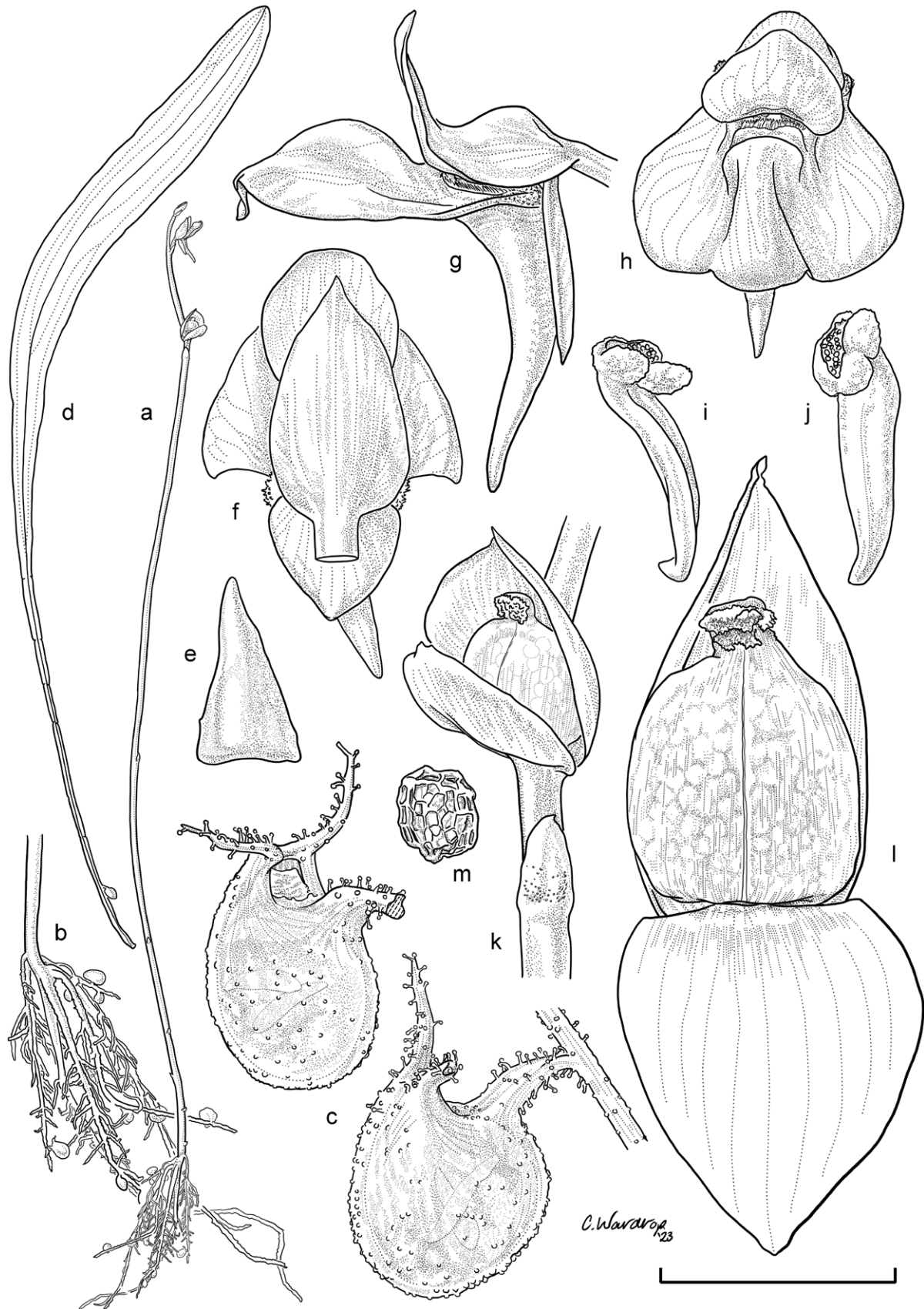


Fig. 2. *Utricularia irwinica*. a, habit; b, stolons with attached rhizoids from peduncle base in situ; c, bladder-trap lateral and $\frac{3}{4}$ view; d, leaf adaxial surface; e, bract; f, flower dorsal view; g, flower lateral view; h, flower frontal view; i, stamen lateral view; j, stamen frontal view; k, mature fruit capsule in situ; l, mature fruit capsule frontal view; m, seed. Scale bar: a = 32 mm; b & d = 10 mm; c, e, i & j = 1.25 mm; f–h & k = 3.2 mm; l = 2 mm; m = 0.8 mm. Material used: *Jobson 4153* & *Baleiro (NSW963027 - spirit)*. Illustration by C. Wardrop.

Distribution, Ecology & Phenology: Known only from four small spring-fed creek sites between the Wenlock and Ducie River catchments of western Cape York Peninsula (Fig. 6). All sites are within the Steve Irwin Wildlife Reserve. Grows in shallow water (1–5 cm depth) in a thin layer of mud over hard lateritic substrate (Fig. 3). Flowers observed March to July.

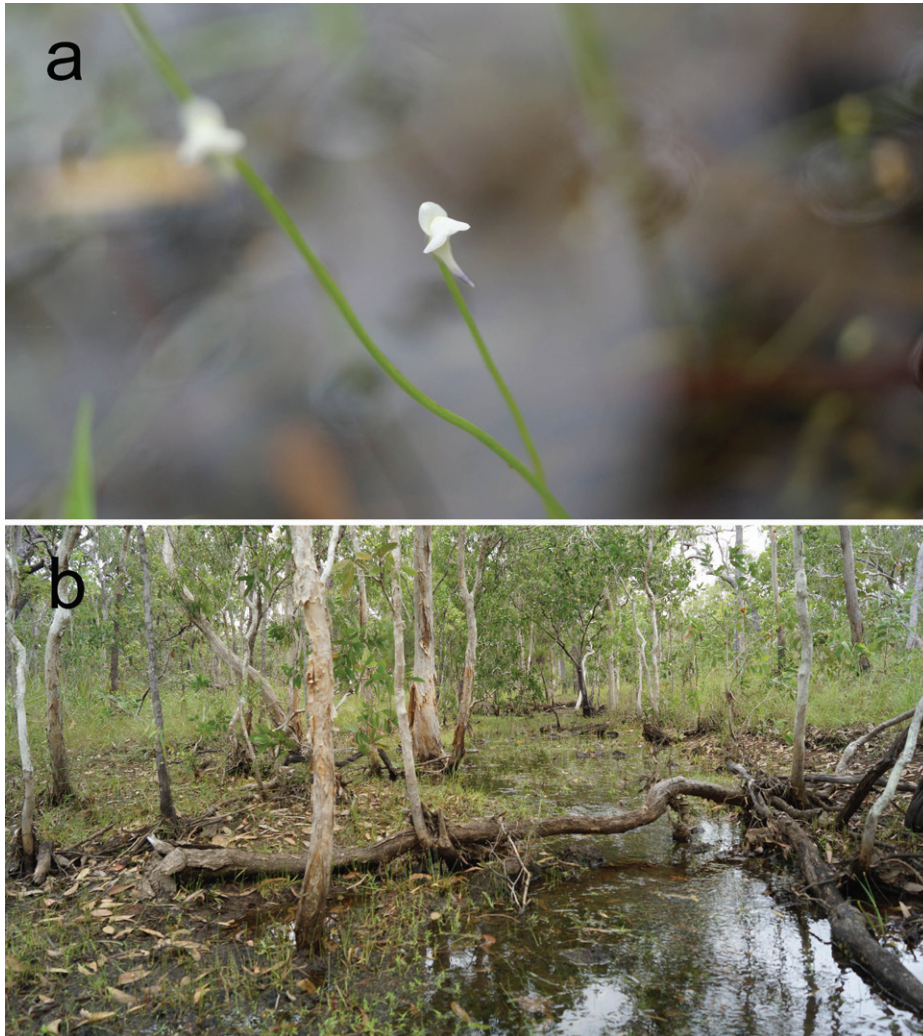


Fig. 3. Typical erect habit (a) and habitat (b) of *Utricularia irwinica*. Images = R. Jobson (R. W. Jobson 4153 & P.C Baleeiro)

Conservation status: This rarely collected species is known from four sites within the Steve Irwin Wildlife Reserve (Fig. 6). Although the reserve is conservation managed, wild pig damage was observed at the type location during the time of specimen collection. Perhaps the saving grace for these plants is the hard laterite substrate that seems to prevent pigs rooting through their microhabitat – unfortunately, the surrounding soft soil habitat was damaged. Despite broad surveys in the area, and the known threats, the known distribution is limited, but an assessment under IUCN equivalent Criteria for the Queensland Nature Conservation Act and the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) has not been performed.

Etymology: The specific epithet *irwinica* refers to the Steve Irwin Wildlife Reserve. Formerly known as Bertiehaugh Station, the reserve has been set aside as a tribute to the conservation work of Steve Irwin and is a place for scientific research and discovery.

Notes: We examined an image of the holotype of *U. uliginosa* Vahl, “India orientalis” Koenig s.n., 1804 (holo, C 10013933 - image), along with all available images of type specimens synonymised under *U. uliginosa* (Taylor 1989): *U. cyanea* R.Br., Grose River, NSW, Brown #2729, 1804 (holo, BM001041163 - image); *Utricularia brachypoda* Wight, “Peninsula Ind. orientalis”, Wight 2411, 1836 (iso, E00174037 - image); *Utricularia griffithii* Wight “peninsula Indiae orientalis”, Wight s.n., 1849 (holo, K 000450576 - image). From this examination we found that none of these specimens exhibited the characters that define *U. irwinica*, namely corolla upper lip and corolla spur exceeding the length of the upper calyx lobe and corolla lower lip, respectively (Fig. 4).

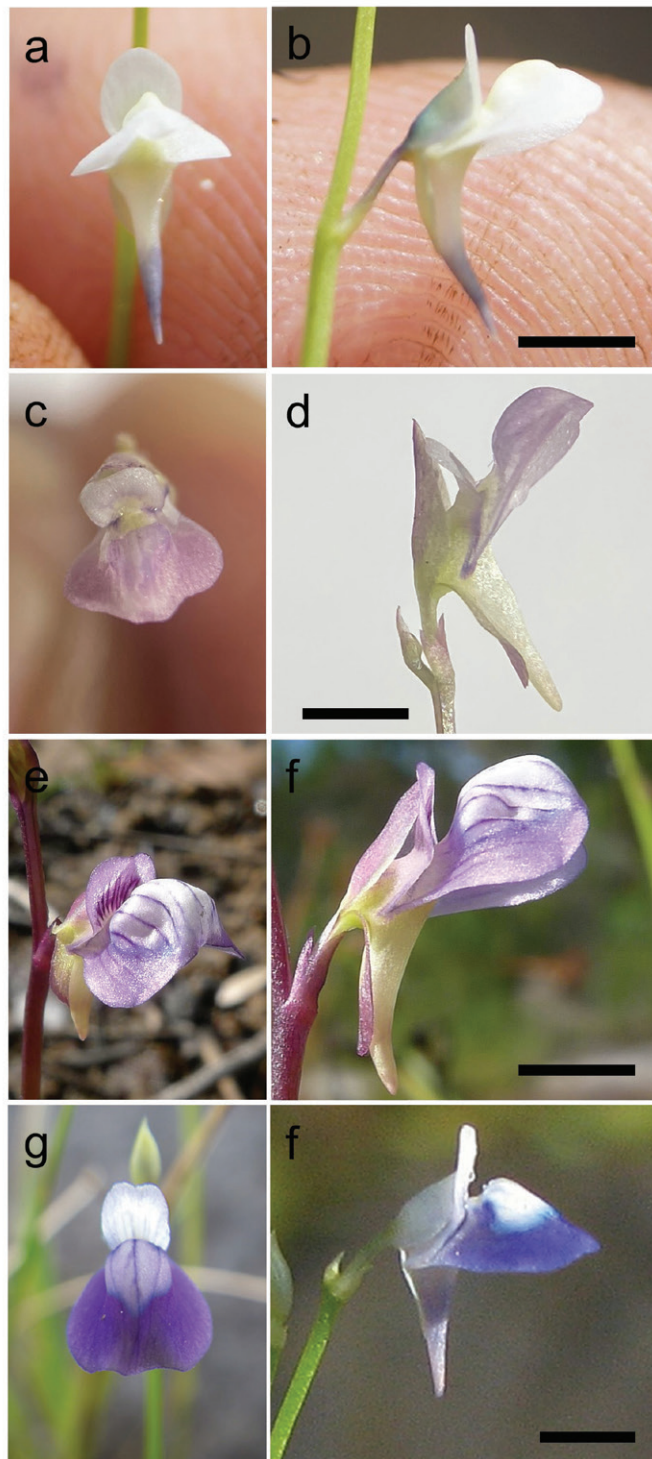


Fig. 4. *Utricularia irwinica* (a, b), *U. uliginosa* [RWJ-4169] (c, d), *U. uliginosa* [RWJ-3219] (e, f), *U. praeterita* (g, h); a, c, e, g corolla frontal view; b, d, f, h corolla lateral view. Scale bars: a–h = 3 mm (e–h are estimated). Images: a & b, by R.W. Jobson; c & d by A.P. Jobson; e & f and g & h with permission from John Tann and N. Sasidharan, respectively.

For other properly applied taxa listed by Taylor (1989) and Kew's POWO (2023) listed as synonyms of *U. uliginosa* we examined their protologues to determine whether they fit any of the major morphological characters of *U. irwinica*: the length of the spur relative to the lower calyx lip and the colour of the corolla (violet/blue/purple vs white). The synonyms described to have violet or purple flowers included *U. affinis* Wight (India: Hooker's *J. Bot. Kew Gard. Misc.* 1: 373, 1849), *U. decipiens* Dalzell (India; Hooker's *J. Bot. Kew Gard. Misc.* 3: 279, 1851), *U. intricata* Griff. ex Oliv. (Malaysia; *J. Proc. Linn. Soc., Bot.* 3: 179, 1859), and *U. lilacina* Griff. (Burma; *Not. Pl. Asiat.* 6(4): 168, 1854). Those that did not mention corolla colour but did describe a spur shorter or equal to the length of the lower calyx lip include *U. elachista* Goebel (India; *Ann. Jard. Bot. Buitenzorg* 9: 76, 1891) and *U. nayarii* Janarth. & A.N. Henry (India; Janarthanam & Henry 1992)).

Synonyms of which no type specimen or protologue could be located include *U. macrophylla* Masam. & Syozi (Taiwan), *U. uliginosa* f. *albida* (Makino) Komiya & C. Shibata (Japan; *Bull. Nippon Dental Univ.* 9: 179, 1980), and *U. yakusimensis* Masam. (Japan; *Mem. Fac. Sci. Taihoku Imp. Univ.* 11: 409, 1934). Given the distance between Japan and the type location it is unlikely these three synonyms represent *U. irwinica*.

The description for *U. cyanea* in Benth. (1868) includes designation of a white variety *U. cyanea* var. *alba* Benth., collected by *Dallachy s.n.* at Rockingham Bay, Qld, between 1863 and 1871. To check the identity of *Dallachy s.n.*, we obtained an image of the three sheets representing type specimens (MEL 0089867, MEL 0089868, MEL 0089869) and here designate MEL 0089869 as lectotype of *U. cyanea* var. *alba* Benth. We determined that Benth.'s white varietal form *U. cyanea* is not similar to *U. irwinica* because it corresponds with the morphology of *U. uliginosa*: the upper corolla lip is shorter than the upper calyx lip and the spur is only marginally longer than the lower calyx lip (Fig. 1; 4c, d; 5d–f). We also checked the short description of *U. uliginosa* var. *alba* F.L. Erickson, in Erickson (1968). Erickson (1968) noted that white forms of *U. uliginosa* are distributed from Bundaberg (Qld) to Botany Bay (NSW) and possess a slightly smaller calyx than those of the typical form. However, given our observations across these populations and that there is no mention of *U. irwinica* characteristics other than corolla colour across this distribution, we consider *U. uliginosa* var. *alba* a synonym of *U. uliginosa*.

Our phylogeny shows *U. praeterita* is sister to *U. uliginosa* and *U. irwinica* (Fig. 1) with all three species sharing a uniformly membranous fruit capsule (see above and Taylor 1989). In Australia, there are two morphological forms of *U. uliginosa* defined by two subclades (RWJ-3219 and RWJ-4169) in the phylogeny (Fig. 1). They are characterised by differing corolla coloration and patterning: usually pink vs blue or violet and, presence of four darker vertical stripes at the base of the upper lip limb vs up to 12, respectively.

A character for distinguishing *U. uliginosa* (both forms) is the minutely denticulate margin of the upper calyx lobe when mature, while in *U. praeterita* and *U. irwinica* the upper calyx lobe margin is instead minutely papillose (Fig. 5b, e, h; refer to fig. 87 in Taylor 1989 for *U. praeterita* illustration and description).

Taylor (1989) describes seed coat and shape as the most reliable character to differentiate *U. praeterita* and *U. uliginosa*. The seed of *U. irwinica* are ovoid with elongated testa cells and most similar to *U. praeterita*, although those of the latter are larger (0.2–0.3 vs c. 0.35 mm long in *U. irwinica*) (Fig. 5c). In comparison, in both forms of *U. uliginosa*, the seeds are globose with isodiametric testa cells (Fig. 5f, i).

In comparison to the short inflorescences of *U. praeterita* (2–15 cm tall), *U. irwinica* and *U. uliginosa* are taller, reaching 22 cm and 30(–40) cm tall, respectively (Taylor 1989). Although none of these species have previously been recorded as having a twining peduncle, a tall twining form of *U. uliginosa* (c. 40 cm tall) was recently collected at Cape Flattery on Cape York Peninsula (*R.W. Jobson 3141*); the representative specimen with this form nests within the RWJ-3219 clade of *U. uliginosa* (Fig. 1).

The upper corolla lip of *U. praeterita* and *U. irwinica* exceeds the length of the upper calyx lobe while that of *U. uliginosa* is always approximately the same length or shorter (Fig. 4; Taylor 1989; RWJ pers. observation). The corolla colour of each of the three species differs but is most similar between *U. praeterita* and both forms of *U. uliginosa* (Fig. 4). These two species share dark violet vertical stripes on upper and lower lip limbs with the number on the upper lip varying from four to 12 across the distribution of the latter species (Fig. 4; RWJ pers. observation).

Although Taylor (1989) mentions Australian populations with a white corolla in his *U. uliginosa* description, we have noticed that the typical corolla patterning in two such populations is faintly observable upon close examination (RWJ, pers. observation). Representatives of these white forms are included in the phylogeny (e.g., *Jobson 4147, 4196*; Fig. 1; Table 1) and are recovered within the *U. uliginosa* clade. In contrast, the corolla of *U. irwinica* can easily be distinguished from these forms because its corolla is a rich cream-white becoming purple towards the apex of the spur (Fig. 4a, b; RWJ, pers. observation). Spur length and shape differ between these two species. Spurs of *U. uliginosa* are usually shorter than the upper corolla lip and less curved than in *U. irwinica*, which has a spur that is longer than the upper lip and conspicuously curved forward (Fig. 4c–f; 5a, d, g).

Habitat similarities of *U. praeterita* and *U. irwinica* include shallow soil over a laterite (or other rocks in the former species) substrate in seasonal or spring-fed creeks (Fig. 3b). However, *U. uliginosa* occupies a much broader array of habitats in sandy silt of seepages, such as in creeks and swamps (Taylor 1989) as demonstrated by recent collections of *U. uliginosa* made in such habitats within the Steve Irwin Wildlife Reserve (e.g., *Jobson 4147, Mitchell 269*; Fig. 6).

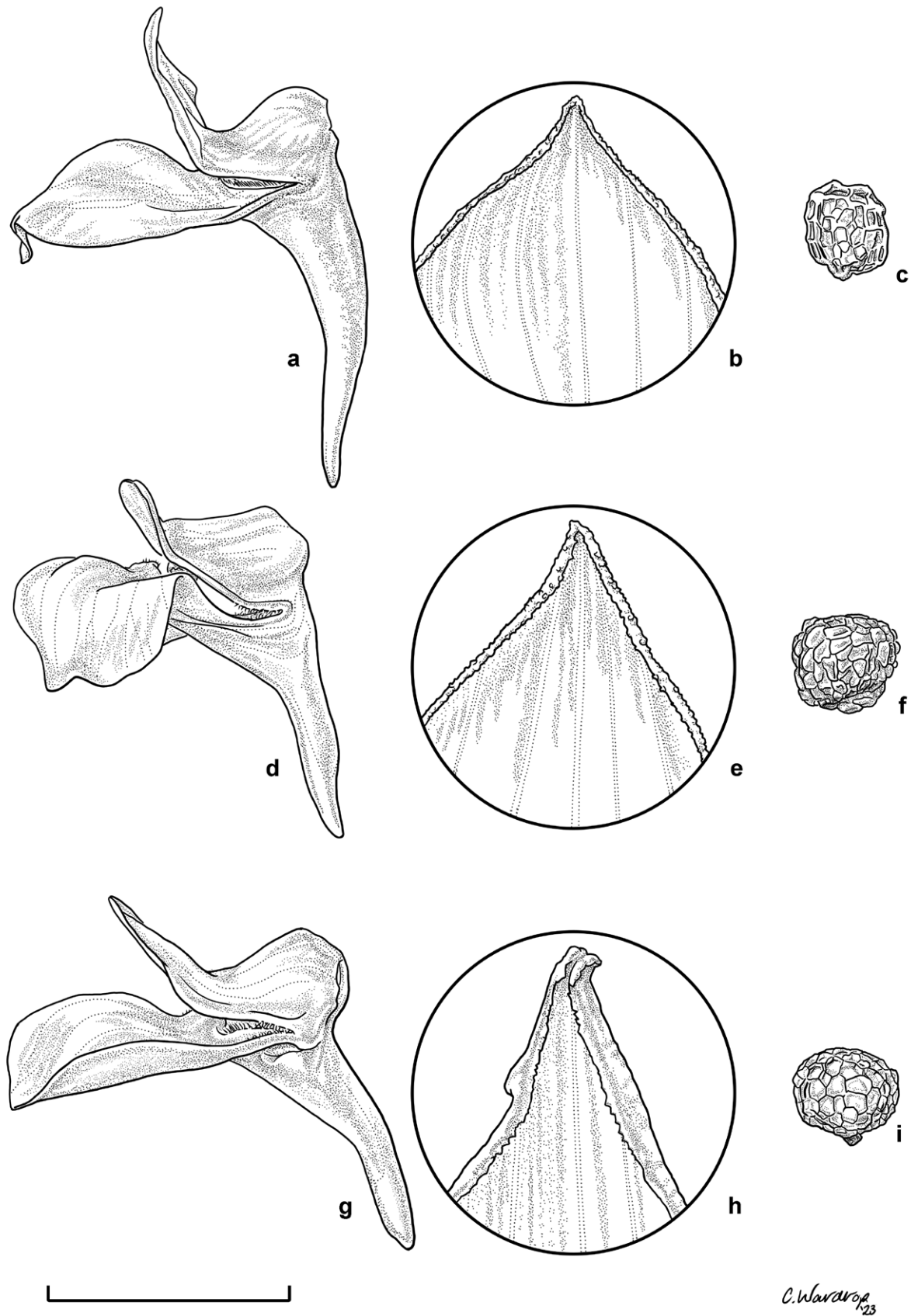


Fig. 5. Comparison of *Utricularia irwinica* (a–c), *U. uliginosa* (d–i); a, d & g, corolla shape lateral view; b, e & h adaxial surface of upper calyx showing incurved margin; c, f & i seed shape. Scale bar: a, d & g = 3.2 mm; b, e & h = 1.25 mm; c, f & i = 0.8 mm. Material used: a–c = Jobson 4153 & Baleeiro (NSW963027 - spirit); d–f = Jobson 4196 & Baleeiro (NSW963040 - spirit); g–i = Jobson 3219 & Baleeiro (NSW934787 - spirit).

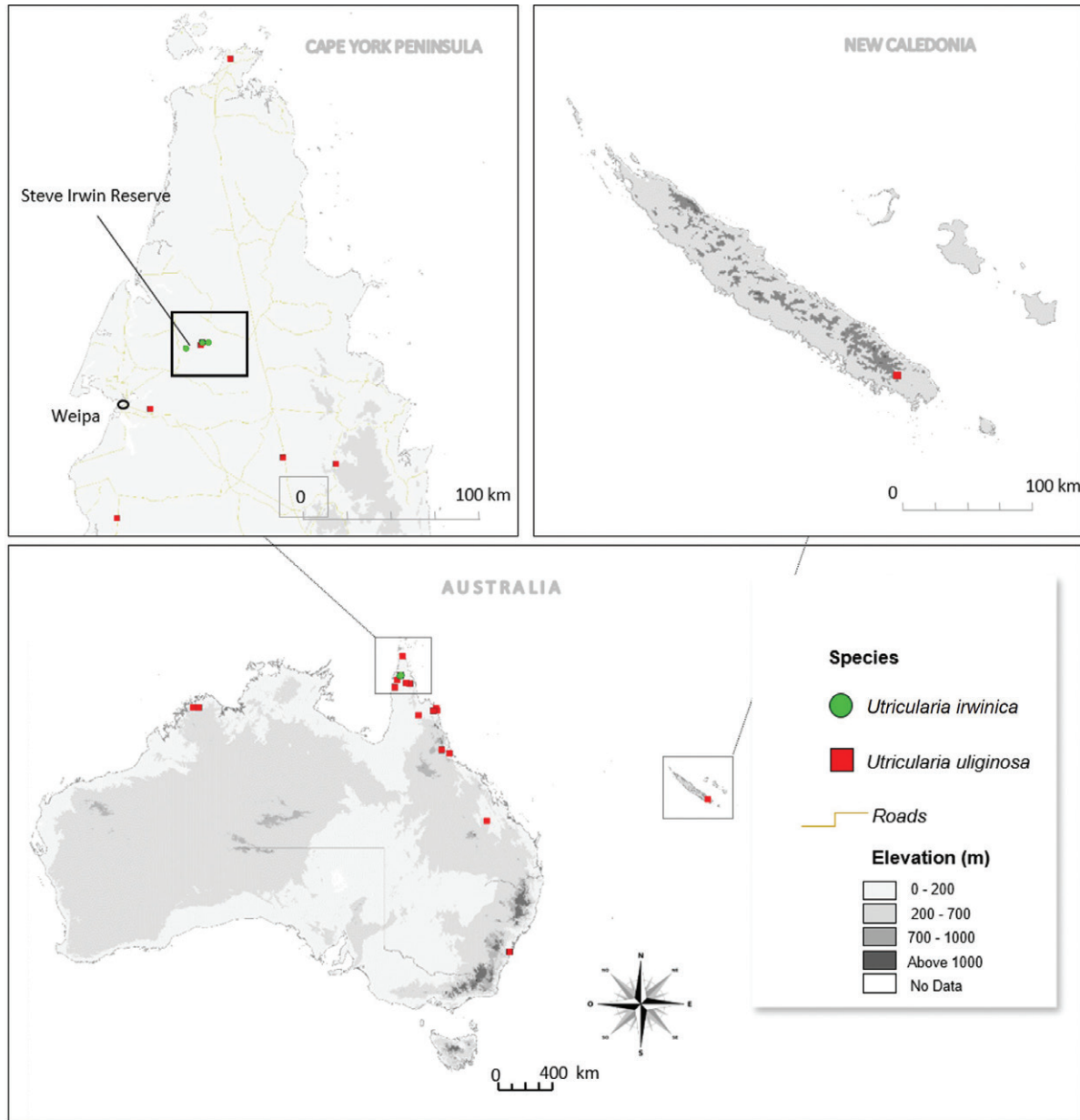


Fig. 6. Distribution map for Australia and New Caledonia showing accessions used in the molecular phylogeny of sect. *Oligocista*. *U. irwinica* (green circle), *U. uliginosa* (red square). For accession details refer to Table 1.

Key to Australian and relevant foreign species of section *Oligocista*

- 1a. Corolla with shades of violet, cream-white or white 2
- 1b. Corolla yellow 5
- 2a. Corolla 3–4 mm long, bladder-trap dorsal appendages branched *U. foveolata* (WA, NT, Qld)
- 2b. Corolla 5–8 mm long; bladder-trap dorsal appendages simple 3
- 3a. Corolla upper lip limb length shorter or equal to upper calyx lip *U. uliginosa* (WA, NT, Qld, NSW)
- 3b. Corolla upper lip limb longer than the upper calyx lip 4
- 4a. Corolla cream-white, spur violet towards the apex *U. irwinica* (Qld)
- 4a. Corolla violet, spur light violet, darker towards the apex *U. praeterita* (India)
- 5a. Peduncle weakly erect, always twining 6
- 5b. Peduncle erect, not twining 7

- 6a. Corolla ± 5 mm long..... *U. circumvoluta* (WA, NT, Qld)
 6b. Corolla 10–15 mm long..... *U. involvens* (NT)
 7a. Corolla 6–10 mm long; inflorescence 3–20 cm high..... *U. bifida* (WA, NT, Qld)
 7b. Corolla 10–15 mm long; inflorescence 25–55 cm high *U. odorata* (NT)

Revised sectional taxonomy

We recommend the following changes to sectional taxonomy based on the results shown in Fig. 1 and morphology. *Utricularia* L. sect. *Enskide* should be expanded to include the single species in *Utricularia* L. sect. *Minutae*. The three accessions from across the distribution (Table 1) form a clade nested within a strongly supported clade of all recognised members of sect. *Enskide* (Fig. 1). The molecular results are supported by morphology with similarity of bladder-traps and pollen structure (Taylor 1989; Cowie et al. 2008). *Utricularia* L. sect. *Oligocista* should be expanded to include the species in *Utricularia* L. sect. *Benjaminia*. *Utricularia nana* was nested within sect. *Oligocista* (Fig. 1). The molecular results are supported by morphology as outlined in Taylor (1989).

Utricularia L. sect. *Enskide* (Raf.) P.Taylor, *Kew Bull.* 41: 9 (1986)

Utricularia L. sect. *Minutae* Lowrie, Cowie & Conran, *Telopea* 12: 31–46 (2008), *syn. nov.* Type: *U. simmonsii* Lowrie, Cowie & Conran.

Utricularia L. sect. *Oligocista* A.DC. in DC., *Prodr.* 8: 12 (1844) *sensu* P. Taylor, *Kew Bull.* 41: 9 (1986)

Utricularia L. sect. *Benjaminia* P.Taylor, *Kew Bull.* 41: 8 (1986), *syn. nov.*

Type: *U. nana* A.St.-Hil. & Girard.

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