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Molecular phylogeny of the suspended aquatic *Utricularia* (sect. *Utricularia*) with a new hybrid species *U. × jacobsii* from northern Australia, a new section *Biovularia*, and confirmation of two species in New Zealand

Richard W. Jobson[A,C], Lesley F. Elkan[A] & Paulo C. Baleeiro[B]

[A]National Herbarium of New South Wales, Botanic Gardens of Sydney,
Locked Bag 6002, Mount Annan, New South Wales 2567, Australia
[B]Queensland Herbarium, Department of Environment, Science and Innovation,
Mount Coot-tha, Mt Coot-tha Road, Toowong Qld 4066, Australia
[C]Corresponding author. Email: richard.jobson@botanicgardens.nsw.gov.au

Abstract

Utricularia sect. *Utricularia* contains 36 recognised species world-wide, including the recently described *U. adamsii* from northern Australia. We here present a molecular phylogeny of subgenus *Utricularia* representing most Australian species based on sequences of two plastid markers and nuclear ITS. We provide molecular evidence for hybridization events between *U. aurea* and *U. muelleri* that have occurred sporadically across northern Australia. We found phylogenetic discordance between the plastid and nuclear sequences for two of the suspected hybrid specimens. The morphological differences between *U. muelleri*, *U. aurea* and the hybrid taxon are discussed with a formal description of the hybrid taxon presented as *Utricularia* × *jacobsii* R.W.Jobson & Baleeiro. We also provide molecular evidence for the introduction/naturalization of northeastern USA/Canada endemic *U. geminiscapa* into New Zealand (NZ) and confirm that a NZ accession of *U. australis* is most closely related to those *U. australis* populations distributed in south-eastern Australia. We expand the section *Avesicaria* to include the taxa in sections *Setiscapella* and *Steyermarkia*. Lastly, we recognise a new sectional name *Biovularia* (Kamieński) Baleeiro & R.W.Jobson for *U. olivacea* that was found to be excluded from sect. *Utricularia* and instead is supported as a close ally to sect. *Vesiculina*.

Introduction

Recent progress has been made in understanding phylogenetic relationships across the recognised species of *Utricularia* L. (Lentibulariaceae Rich.) occurring in Australia (Jobson *et al*. 2017; Jobson & Baleeiro 2020, 2022, 2023; Jobson & Davies-Colley 2020) resulting in an increase from the 57 Australian species recognised by Taylor (1989) to 86. Recent work in Europe has made progress in understand the relationships between Eurasian species (Astuti *et al*. 2020; Bobrov *et al*. 2022), and although phylogenetic studies are progressing in the United States and Asia, this is limited to just one or a few samples from each region (Krishnapriya *et al*. 2024; Tippery *et al*. 2024). There has been extensive work by Baleeiro *et al*. (2016, 2019, 2022) on the *U. amethystina* Salzm. ex A.St.Hil. complex where representative distributions were sampled from across Central and South America. However, apart from that significant work, the situation in the Neotropics and Africa has not progressed significantly since the early phylogenetic work on the genus (Jobson & Albert 2002; Jobson *et al*. 2003; Muller *et al*. 2004), with many of the recognised endemic species yet to be sampled for phylogenetic study.

Utricularia section *Utricularia* contains 34 species (Taylor 1989) with a world-wide distribution and is nested within subgenus *Utricularia* (Muller & Borsch 2005). Taylor

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(1989) recognised four species from the section in Australia with the recent description of the northern Australian species *U. corneliana* R.W.Jobson and *U. adamsii* R.W.Jobson & Davies-Colley increasing that number to six, and worldwide to 36 (Taylor 1989; Jobson 2013; Jobson & Davies-Colley 2020).

We present a molecular phylogeny for section *Utricularia* representing 25 of the 36 species, including most Australian taxa. We also include previously sampled representatives of sister clades including sections *Avesicaria* Kamieński, *Lecticula* (Barnhart) Komiya, *Nelipus* (Raf.) P.Taylor, *Setiscapella* (Barnhart) P.Taylor, *Steyermarkia* P.Taylor, and *Vesiculina* (Raf.) P.Taylor. Topological comparison of the plastid non-coding and nuclear ribosomal ITS trees provided molecular evidence of phylogenetic discordance between the sequences representing two suspected hybrid specimens. The two suspected hybridization events occurred between *U. aurea* and *U. muelleri* in northern Australia (as suspected by Taylor 1989). The morphological similarities between *U. muelleri*, *U. aurea* and the hybrid taxon are discussed. We also provide a formal description of *U.* x *jacobsii* R.W.Jobson & Baleeiro to allay confusion in the field and aid in biodiversity management. We provide molecular evidence for the introduction/naturalization of USA endemic *U. geminiscapa* Benj. into New Zealand (NZ) (Salmon 2001; Heenan *et al*. 2004; Champion & Hofstra 2024). We also provide molecular evidence of the presence of *U. australis* on the north island of NZ (Taylor 1989) and find it is most closely related to those populations distributed in south-eastern Australia.

As observed in Jobson *et al*. (2003) we find that *U.* sect. *Setiscapella* is paraphyletic and expand *U.* sect. *Avesicaria* Kamieński ex Prantl to accommodate the species from *U.* sect. *Setiscapella* (Barnhart) P.Taylor and *U.* sect. *Steyermarkia* P.Taylor. Lastly, our data supports two previous phylogenetic studies that each used different *U. olivacea* C.Wright ex Griseb. samples and found it is excluded from sect. *Utricularia* and is supported as a close ally to sect. *Vesiculina* (Jobson *et al*. 2003; Silva *et al*. 2023). To accommodate these results, we recognise the new section *Biovularia* (Kamieński) Baleeiro & R.W.Jobson for *U. olivacea*.

Methods and Materials

Taxon sampling and DNA extraction

DNA isolations were performed as for Jobson *et al.* (2017) with all ingroup and outgroup samples shown in table 1 of Jobson & Davies-Colley (2020) used in the current study. We obtained previously published sequences from GenBank that were published in Jobson & Albert (2002) and where samples were sourced from other studies, the GenBank number was included in the accession label (Figs 1, 2). Newly sampled accessions for *rps16* (n = 26), *trnD-T* (n=19), and ITS (n=19) 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 plastid *rps16*/*trnD-T* (cpDNA) dataset to include ingroup sequences from sections *Avesicaria*, *Nelipus*, *Setiscapella*, and *Vesiculina* with most of these being previously published and presented in table 1 of Jobson & Albert (2002) (Fig. 1). The nuclear ITS dataset was restricted to ingroup accessions representing sect. *Utricularia* with most previously published in table 1 of Jobson & Davies-Colley (2020) (Table 1; Fig. 2).

Amplification and sequencing

Amplifications were performed as for Jobson *et al.* (2020) using two noncoding plastid (cpDNA) and nuclear ribosomal Internal Transcribed Spacer (ITS) region (nuDNA). The cpDNA markers included the *rps*16 intron amplified according to the program described in Oxelman *et al.* (1997), while the *trnD-trnT* intron spacer (*trnD-T*) (Demesure *et al.* 1995) was amplified using parameters described in Shaw *et al.* (2005). The ITS region was amplified using universal primers described in White *et al.* (1990) and Stanford *et al*. (2000). Forward and reverse sequences were assembled, edited and aligned as for Jobson *et al.* (2017).

Phylogenetic analyses

Topologies obtained from individual *rps16* and *trnD-T* analyses were congruent and were concatenated and analysed together. Separate phylogenetic analyses were performed on the combined *rps16/trnD-T* (cpDNA) and nuclear ITS matrices. 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

Sequences and alignment

The *rps16* matrix was 1012 bp long of which 297 (29.3%) characters were parsimony informative, *trnD-T* matrix was 1422 long of which 250 (17.5%) characters were parsimony informative (Fig. 1), and the ITS matrix was 947 bp long of which 345 (36.4%) characters were parsimony informative (Fig. 2). An examination of the topologies showed the same branching order across both trees for all corresponding accession except those found to be of hybrid origin. Due this known incongruence (see also Jobson & Davies-Colley 2020), the cpDNA and nuDNA datasets were analysed separately (Figs 1, 2).

Phylogenetic relationships

The cpDNA tree (Fig. 1) corresponds with that of Jobson *et al.* (2003) with accessions representing section *Nelipus* maximally supported (posterior probability (PP) = 1.00) as sister to a clade containing sections *Avesicaria*, a paraphyletic *Setiscapella*, and *Steyermarkia*. Together the clade is sister to a maximally supported clade containing sect. *Vesiculina* which is sister to two accessions of *U. olivacea* of sect. *Utricularia* (Fig. 1). Sister to the above clade, sect. *Lecticula* is sister to a weakly supported sect. *Utricularia* that is supported here to be polyphyletic given the above-mentioned position of *U. olivacea* (Fig. 1). Within sect. *Utricularia* both the cpDNA and ITS trees show a similar branching order with a maximally supported monophyletic clade of *U. gibba* sister to *U. striata* and *U. floridana* (Figs 1, 2). Neither cpDNA nor ITS analyses were able to fully resolve relationships among the two major groups sister to the *U. gibba* clade. The first group involves the African accessions of *U. reflexa* and *U. benjaminiana* (also in the Neotropics) sister to a clade of Afrotropical/Asian and Australasia *U. inflexa*/*U. stellaris* that together were sister to a maximally supported Asian/Australasia group including *U. aurea*

+ *U. muelleri*/*U. adamsii* (Figs 1, 2). All members of the group except *U. reflexa* possess inflorescence flotation organs (Taylor 1989). We observed incongruence between the cpDNA and ITS topologies (Figs 1, 2) with two accessions *Jobson 2784*, and *Jobson 3588*, placed within the *U. aurea* and *U. muelleri* clades respectively in the cpDNA tree, while the opposite was the case in the nuclear tree, suggesting different sexual parents for each of these two hybrids (compare Figs 1, 2).

Table 1. Accessions used in the cpDNA and ITS matrices. Secondary collectors are not included. Locality abbreviations: NSW, New South Wales; NT, Northern Territory; Qld, Queensland; SA, South Australia; WA, Western Australia. GenBank accession numbers for each sequence are shown. NS indicates a sequence that either failed or was not included in the study. Information for previously published sequences provided in Jobson & Albert (2002), and Jobson & Davies-Colley (2020).

Section	Taxon	Collector	Location	ITS	*RPS16*	*trnDT*
Utricularia	*U. australis* R.Br.	R.W. Jobson 1369 (NSW)	Trebon, Czech Republic (ex. L. Adamec)	PQ130292	PQ129439	PQ129465
	U. australis R.Br.	R.W. Jobson 1617 (NSW)	Nangwarry, SA	PQ130293	PQ129440	NS
	U. australis R.Br.	R.W. Jobson 1591 (NSW)	Cape Le Grand National Park, WA	PQ130294	PQ129441	NS
	U. australis R.Br.	R.W. Jobson 1580 (NSW)	Cape Le Grand National Park, WA	PQ130295	NS	NS
	U. australis R.Br.	P.B. Heenan s.n. (CHR)	North Island, NZ	PQ130296	NS	NS
	U. australis R.Br.	R.W. Jobson 2270 (NSW)	Mitchell Falls, Kimberley, WA	PQ130297	NS	NS
	U. australis R.Br.	R.W. Jobson UQ184B (NSW)	Trebon, Czech Republic (ex. L. Adamec)	PQ130298	PQ129442	NS
	U. australis R.Br.	R.W. Jobson 3348 (NSW)	Apsley River, Tas.	PQ130303	NS	NS
	U. australis R.Br.	R.W. Jobson 1064 (NSW)	Sale, Vic.	PQ130286	NS	NS
	U. australis R.Br.	R.W. Jobson 1106 (NSW)	Myall Lakes, NSW	PQ130287	NS	NS
	U. australis R.Br.	R.W. Jobson 1168 (NSW)	Corduroy, NSW	PQ130288	NS	NS
	U. australis R.Br.	R.W. Jobson 1233 (NSW)	Richmond, NSW	PQ130289	NS	NS
	U. bremii Heer ex Kölliker	R.W. Jobson 1418 (NSW)	Trebon, Czech Republic (ex. L. Adamec)	NS	PQ129443	PQ129466
	U. breviscapa Wright ex Griseb.	R.W. Jobson 1420 (NSW)	Brazil (ex. L. Adamec)	NS	PQ129444	PQ129467
	U. floridana Nash	R.W. Jobson 1368 (NSW)	USA (ex. L. Adamec)	NS	PQ129445	PQ129468
	U. foliosa L.	R.W. Jobson 1421 (NSW)	Cuba (ex. L. Adamec)	NS	PQ129446	PQ129469
	U. geminiscapa Benj.	P. Champion 125 (CHR)	Westland District, NZ	PQ130290	NS	PQ129482
	U. gibba L.	R.W. Jobson 1362 (NSW)	Bundeena, NSW	NS	PQ129447	PQ129470
	U. gibba L.	R.W. Jobson 1380 (NSW)	Mt Garnet, Qld	NS	NS	PQ129471
	U. gibba L.	R.W. Jobson 2250 (NSW)	Humpty Doo, NT	NS	NS	PQ129472
	U. gibba L.	R.W. Jobson 2321 (NSW)	Dampier Penninsula, WA	NS	NS	PQ129473
	U. gibba L.	F. Rivadavia 974 (SPF)	Minas Gerais, Brazil	NS	PQ129448	NS
	U. gibba L.	R.W. Jobson 1373 (NSW)	Florida, USA (ex. L. Adamec)	NS	PQ129458	PQ129477
	U. gibba L.	R.W. Jobson 2632 (NSW)	Elizabeth Springs, Qld	NS	NS	PQ129481
	U. hydrocarpa Vahl	R.W. Jobson 1424 (NSW)	Brazil (ex. L. Adamec)	PQ130299	PQ129449	PQ129474
	U. hydrocarpa Vahl	P.C. Baleeiro 329 (SPF)	Rio De Janeiro, Brazil	NS	PQ129450	NS
	U. hydrocarpa Vahl	F. Rivadavia 1029 (SPF)	Goias, Brazil	NS	PQ129451	NS
	U. inflata Walter	R. Haynes 10211 (UNA)	Autauga Co., Alabama, USA	PQ130300	PQ129452	NS
	U. intermedia Hayne	R.W. Jobson UQ185 (NSW)	Trebon, Czech Republic (ex. L. Adamec)	NS	PQ129453	NS
	U. macrorhiza LeConte	J. Ricketson 4425 (NY)	Coconino Co., Arizona, USA	NS	PQ129454	PQ129475
	U. minor L.	R.W. Jobson 1419 (NSW)	Trebon, Czech Republic (ex. L. Adamec)	NS	PQ129455	PQ129476
	U. muelleri Kaminénski	R.W. Jobson 4020 (NSW)	Jabiru, NT	PQ130291	PQ129464	PQ129483
	U. ochroleuca R.Hartm.	R.W. Jobson 1371 (NSW)	Trebon, Czech Republic (ex. L. Adamec)	NS	PQ129456	NS
	U. ochroleuca R.Hartm.	R.W. Jobson UQ186 (NSW)	Trebon, Czech Republic (ex. L. Adamec)	NS	PQ129457	NS
	U. radiata Small	B. Hellquist 17370 (MCLA)	USA (ex. B. Hellquist)	PQ130301	NS	PQ129478
	U. reflexa Oliver	R.W. Jobson 1423 (NSW)	Zambia (ex. L. Adamec)	PQ130302	PQ129459	PQ129479
	U. warmingii Kaminénski	P. Cardoza 131 (SPF)	Pantanel, Brazil	NS	PQ129462	PQ129480
	U. stygia Thor	R.W. Jobson 1422 (NSW)	Trebon, Czech Republic (ex. L. Adamec)	NS	PQ129460	NS
Setiscapella	*U. subulata* L.	D. Murfet 6118 (DNA)	Sanamere Lagoon, Qld	NS	PQ129463	NS
Steyermarkia	*U. steyermarkii* P.Taylor	P.C. Baleeiro 333 (NSW)	Mato Grosso, Brazil	NS	PQ129461	NS

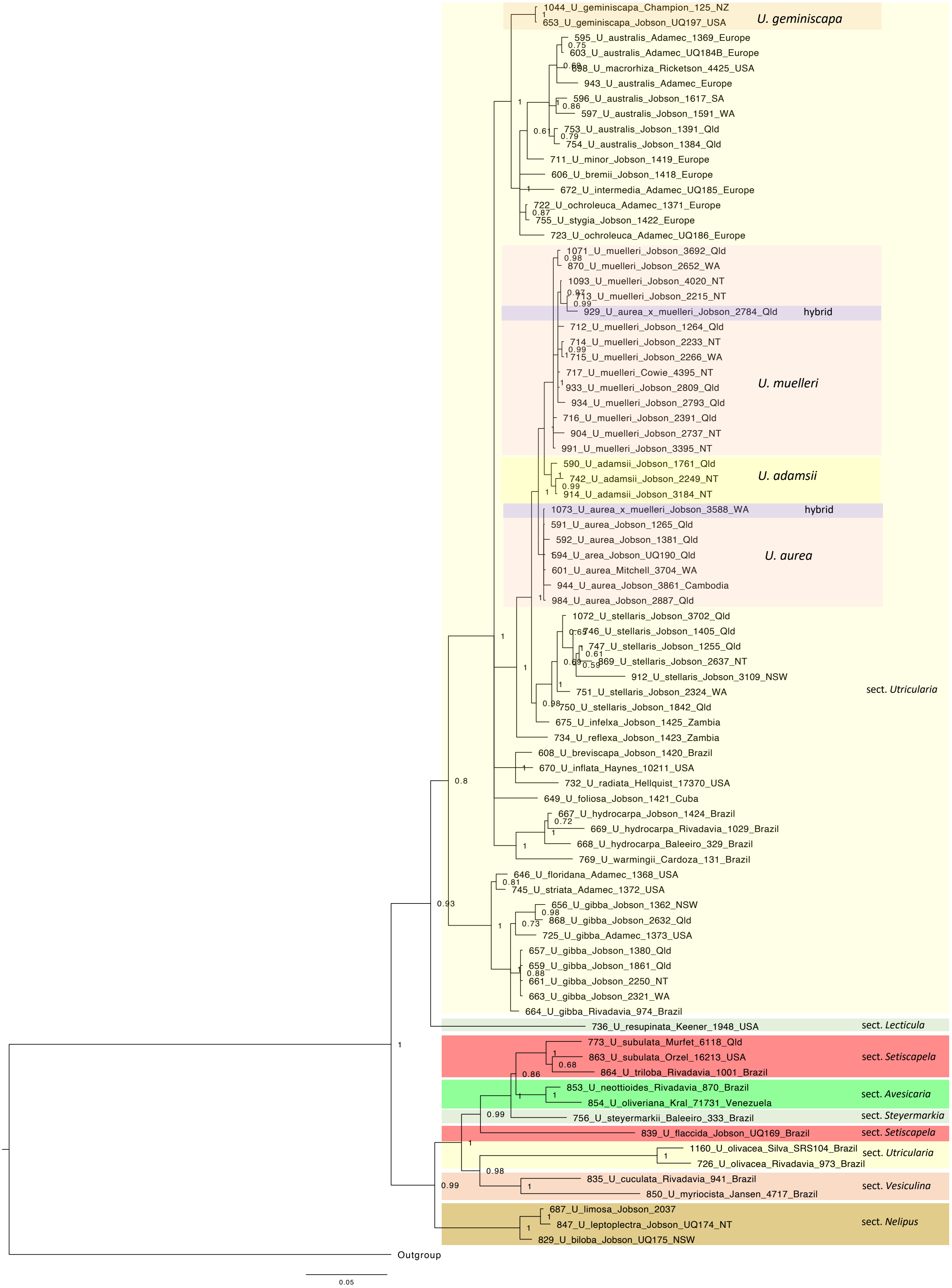

Figure 1. 50% majority-rule Bayesian inference consensus tree for concatenated cpDNA data set; Posterior probability (PP) support values are shown above branches. PP = 1.0–0.95: strong support; 0.94–0.84: weak support; <0.84: not supported. Shaded boxes coloured according to section. Hybrid accessions indicated by purple shading, Accessions of *U. geminiscapa* shown with orange shading.

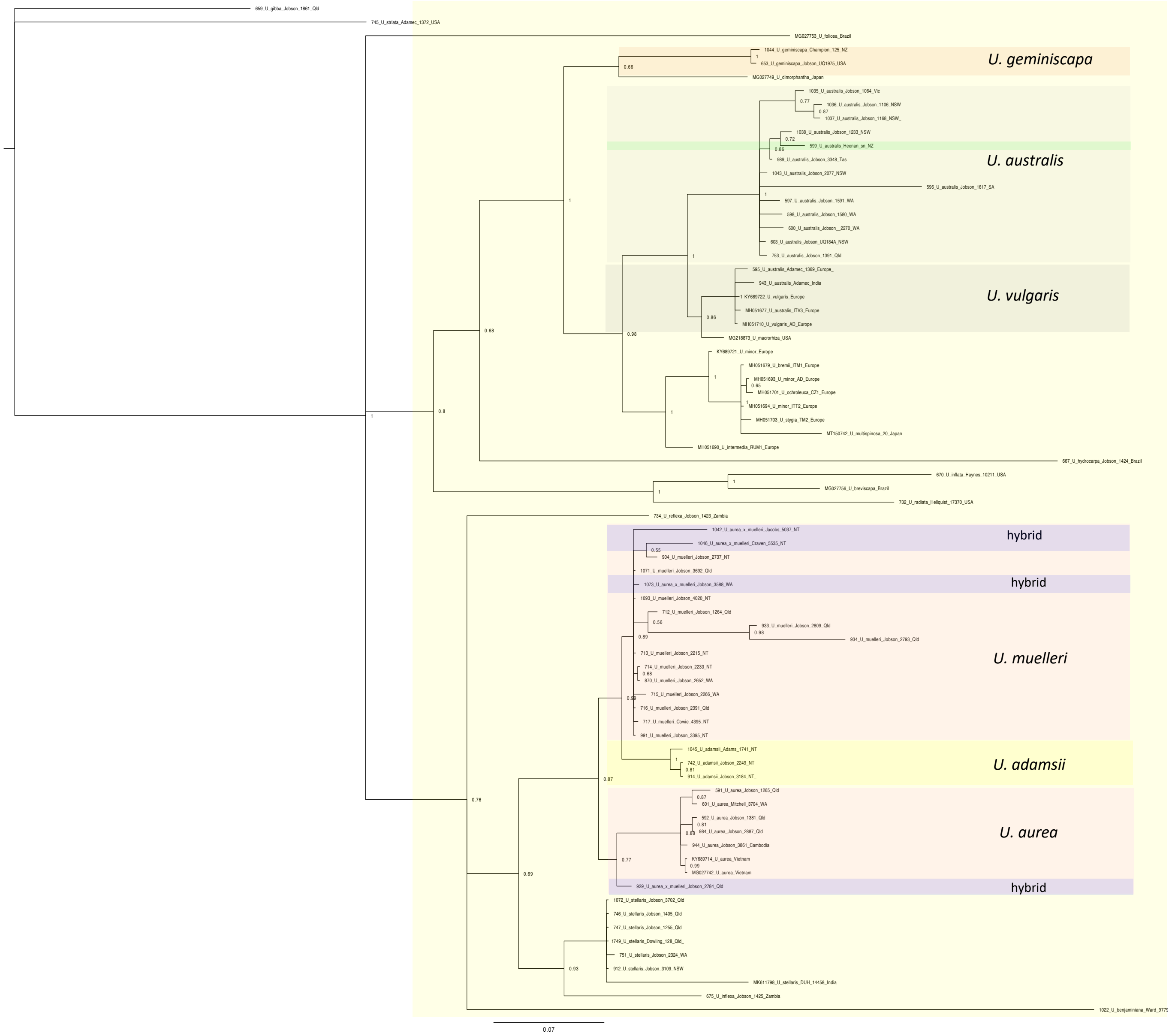

Figure 2. 50% majority-rule Bayesian inference consensus tree for ITS data set; Posterior probability (PP) support values are shown above branches. PP = 1.0–0.95: strong support; 0.94–0.84: weak support; <0.84: not supported. Shaded boxes coloured according to section. Hybrid accession indicated by purple shading, New Zealand accession of *U. australis* and *U. geminiscapa* shown with green and orange shading respectively.

A single representative of the Afrotropical/Neotropical and morphologically distinct *U. foliosa* is unresolved in both cpDNA and ITS trees and may form a third clade along with other currently unsampled species (Figs 1, 2). The second major grouping involves mainly Palaearctic/Nearctic species with *U. breviscapa* and *U. hydrocarpa* extending into the Neotropics, and *U. australis* into most realms except the Afro-tropic/Neotropics, although this group is mostly unresolved in the cpDNA tree (Fig. 1).

The ITS tree provides maximally supported resolution showing the three species possessing inflorescence floats namely *U. breviscapa*/*U. inflata*/*U. radiata* (Fig. 2) sister to a maximally supported clade of mainly Palaearctic/Nearctic species with *U. australis* extending to Afro-tropics/Asia/ Australasia (Fig. 2). Both trees show the North American *U. geminiscapa* is sister to the *U. australis* group including *U. intermedia*/*U. bremii*-*U. vulgaris*-*U. macrorhiza*-*U. minor*-*U. ochroleuca*.

The ITS tree shows the Neotropical *U. hydrocarpa* sister to *U. geminiscapa*/*U. australis* + allies with the Japanese *U. dimorphantha* sister to *U. geminiscapa* (Fig. 2). Both trees show the New Zealand accession of *U. geminiscapa* is sister to an accession of that species from its natural North American range. In addition, a *U. australis* accession from the north Island of New Zealand is nested within a grouping of that species from south-eastern Australia (Fig. 2).

Discussion

Hybridization between U. aurea *and* U. muelleri

Two suspected hybrids of *Utricularia aurea* and *U. muelleri* were identified by Taylor (1989) under his description of *U. muelleri* involving collections by *Craven 5535* (CANB) and *Jacobs 1862* (NSW). These specimens appear to be sterile with no fruit development observed and possess an intermediate morphology with a suite of characters; similar floral features to *U. aurea*, while peduncle floats resembled those of *U. muelleri* (Figs 3, 4).

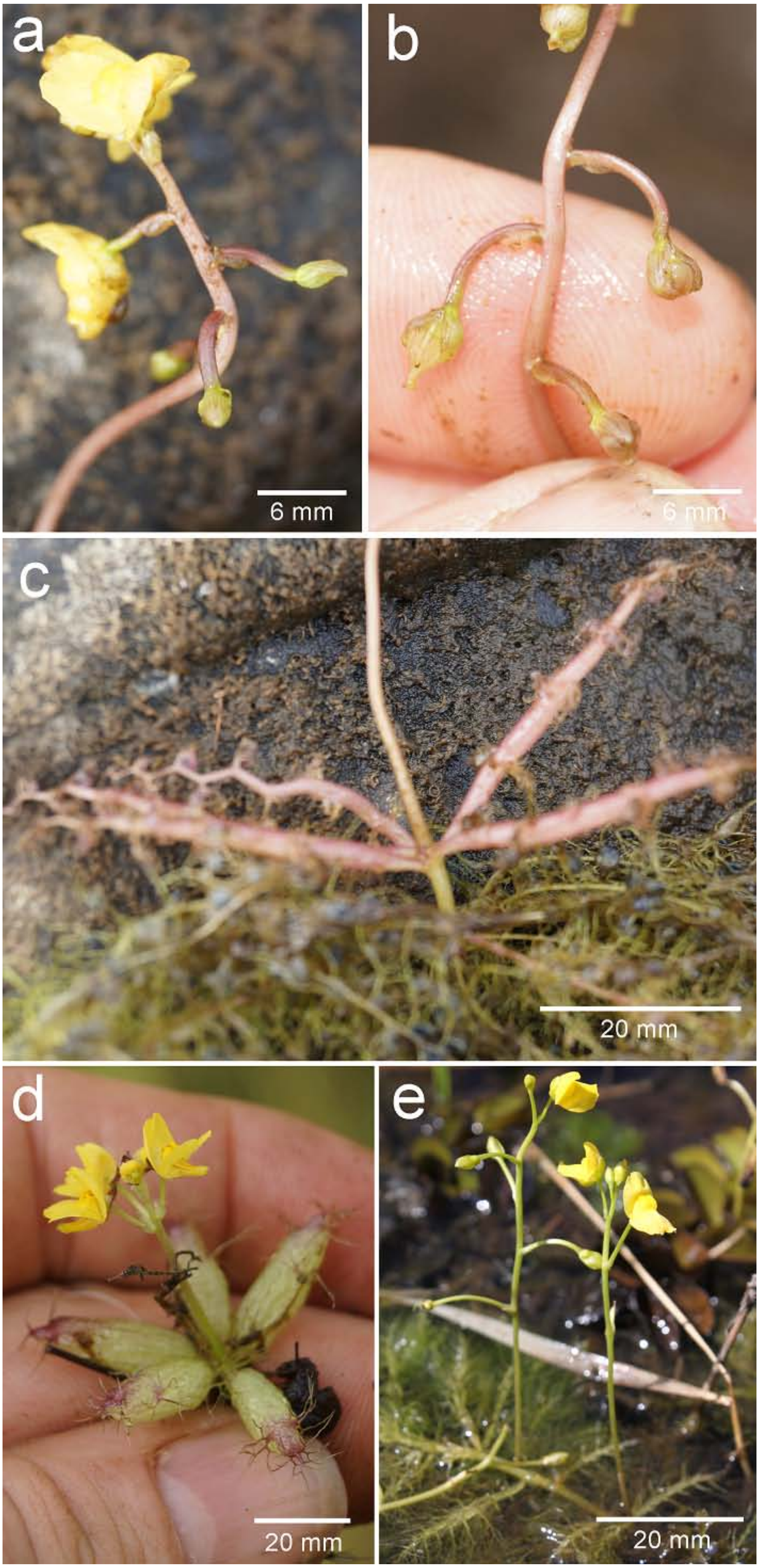

Figure 3. *Utricularia × jacobsii*: **a**, Inflorescence with flowers; **b**, immature seed capsules; **c**, habit showing floating organs towards the base of peduncle; **d**, *U. muelleri* showing inflorescence and attached floating organs; **e**, *U. aurea* habit showing primary stolon axis with erect inflorescences. Scale bars: a–c = 4 mm; c–e = 10 mm. Images: a–c = *Jobson 3588 & Baleeiro* (NSW 945185); d *Jobson 4157 & Baleeiro* (NSW 963030); & e = Glenn Leiper.

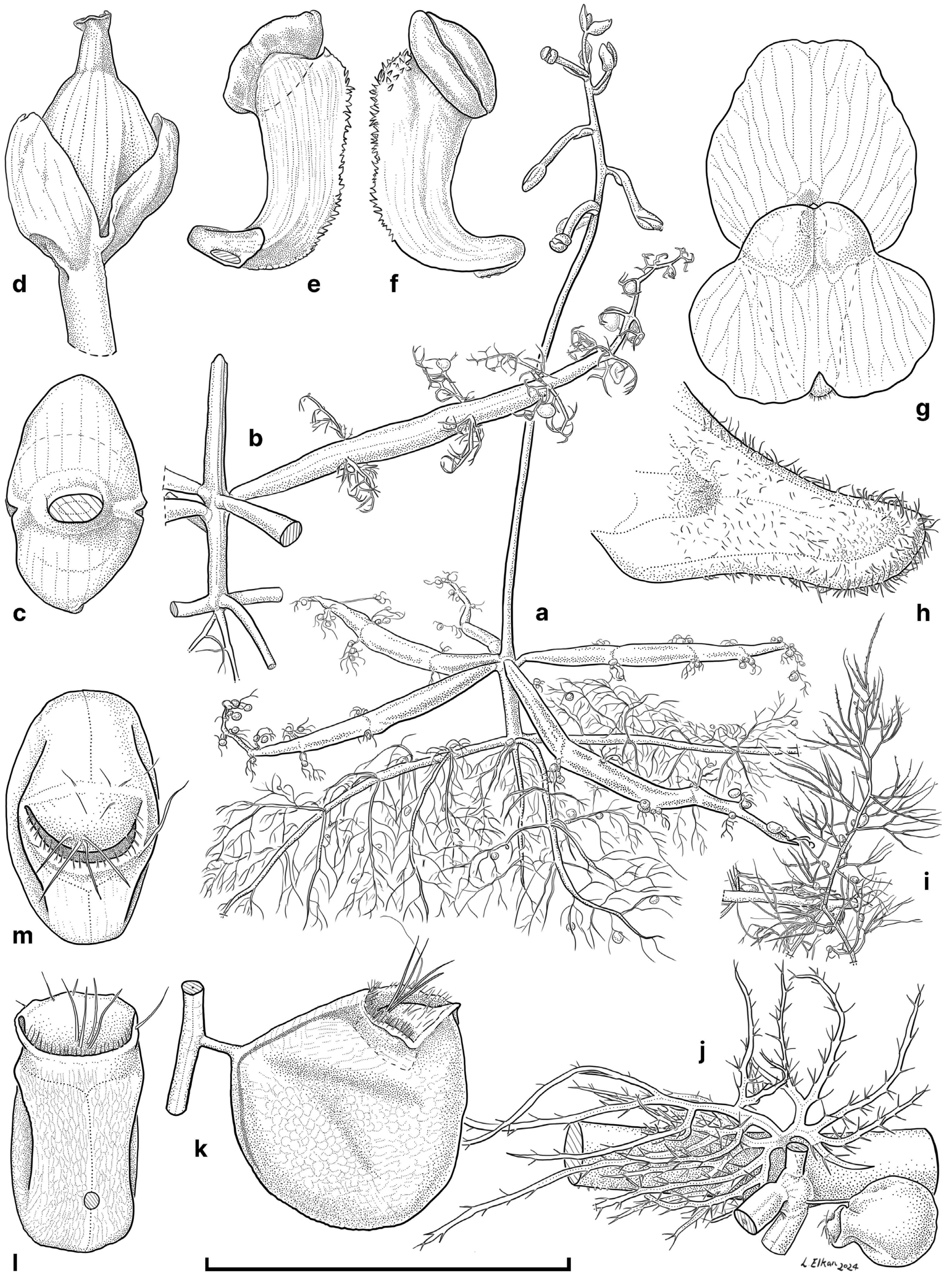

Figure 4. *Utricularia × jacobsii*. a. habit; b, peduncle float in situ; c, calyx dorsal view; d, immature capsule in situ; e, stamen dorsal view; f, stamen frontal view; g, corolla frontal view; h, corolla spur lateral view; i, leaf secondary segment; j, stolon node with leaf and bladder-trap in situ; k, bladder-trap lateral view; l, bladder-trap dorsal view; m, bladder-trap frontal view. Scale bar: a & i = 40 mm; c & d = 7.5 mm; e & f = 2.5 mm; h = 12 mm; j = 6 mm; k = 3 mm; l & m = 4 mm. Material used: *Jobson 3588 & Baleeiro* (NSW945185 - spirit). Illustration by L. Elkan.

Two more recent peduncle-float bearing collections of *U. aurea* from Cape York (*Jobson 2784*) and the Kimberley, WA (*Jobson 3588*) were used in this study to determine topological position in plastid and nuclear ITS trees (Figs 1, 2). We found that *Jobson 2784* was nested in *U. aurea* in the ITS phylogeny, while in the plastid phylogeny it is placed within the *U. muelleri* clade (compare Figs 1, 2). In the case of *Jobson 3588* we find the opposite situation where it was nested in *U. muelleri* in the ITS phylogeny, while nested with *U. muelleri* in the plastid tree (compare Figs 1, 2). This comparison was not possible for the *Craven (5535)* and *Jacobs (1862)* accessions due to the age and condition of the preserved specimens preventing amplification of usable chloroplast fragments for sequence assembly. However, the ITS sequences place both accessions within the *U. muelleri* clade (Fig. 2).

In comparison to *Craven 5535* and *Jacobs 1862*, *Jobson 2784* and *Jobson 3588* looked to be fertile, possessing several mature seed capsules. However, seed were found to be prismatic in shape like those of *U. aurea*, but otherwise malformed with no obvious testa cells (RWJ, pers. obs.). Likewise, pollen was found to be clumped with no obvious external structure (RWJ, pers. obs.). From these observations it is likely that hybrids form sporadically across northern Australia and the maternal taxon can involve either of the parent species.

Taxonomy

Utricularia × jacobsii R.W.Jobson & Baleeiro sp. nov.

Diagnosis: Inflorescence similar to *U. aurea* in possessing calyx lobes half as long as the capsule, and *U. muelleri* having floats positioned mid-way along the peduncle but differs from *U. muelleri* in the shape of its floats and the ad hoc positioning of floats in the whorl.

Type: Australia: Northern Territory: Darwin and Gulf: Near Jim Jim Creek, 6.5 km south-east of Cooinda. *L.A. Craven 5535*, 17 May 1980 (holo: DNA D0019326 – sheet!; iso: CANB 316054.1 – sheet!; CANB 316054.2 – spirit!).

Medium-sized perennial, suspended aquatic herb. *Rhizoids* few from base of peduncle, 10–15 mm long bearing short papillose branches. *Stolons* filiform, terete, 50–60 mm long, 0.9–1.2 mm thick, unbranched, hairy, internodes 6–11 mm long. *Leaves* numerous, 2 or 3 primary segments at each node, 25–35 mm long, slightly flattened, divided near the base into 2 or 3 primary segments, with few further dichotomously divided segments, laterally and apically setulose. *Traps* inserted along segments, shortly stalked, ovoid 2.0–3.1 mm long, mouth lateral with dorsal antennae absent or, two small setiform appendages c. 0.2 mm long. Internal glands 4-armed, each cylindrical arm ~same length, up to 130 μ long. *Inflorescence* erect, simple, emergent; peduncle filiform 50–150 mm long, 0.8–1.2 mm thick, terete, glabrous, with a ± whorl of 4 spongy floats, position near the middle of the peduncle, each float 30–40 mm long, c. 0.5 mm thick, sessile, cylindrical, zig-zag shaped towards the apex, bearing short leaf segments along the margin. *Scales* absent. *Bracts* basifixed, ovate when flattened, convex, 2.0–2.5 mm long, 1.2–1.5 mm wide, apex acute. *Bracteoles* absent. *Flowers* 5–10 on an elongated raceme axis; pedicels terete, thickening toward the apex, glabrous, erect or deflexed, 6.0–8.0 mm long, 0.5–0.7 mm thick. *Calyx* lobes subequal, gapping or adnate to ovary, each slightly glandular towards the apex, upper lobe broadly ovate slightly longer, 2.8–3.1 mm long, 0.9–1.1 mm wide, apex acute; lower lobe broadly ovate, 2.8–3.1 mm long, 0.6–1.1 mm in diam 2.6–2.8 mm long, 0.9–1.0 mm wide, apex rounded or emarginate. *Corolla* bright yellow, 9–10 mm long, with few very faint brownish-red nerves near the base of the upper lip; upper lip limb broadly ovate with apex rounded or truncate 6–7 mm long, 5.0–5.5 mm wide; lower lip limb transversely elliptic, 5.0–5.5 mm long, c. 6 mm wide, lower surface sparsely glandular, bilobed, with a prominent swelling at the base; spur glandular near apex, 4.0–4.2 mm long, c. 2 mm wide, equal length of lower lip, conical with rounded apex. *Filaments* curved c. 1.4 mm long, theca sub-distinct. *Ovary* globose. Immature capsules c. 3.1 mm long, c. 3.0 mm in diameter, walls fleshy, dehiscence unknown. *Seeds*, where produced (e.g., *Jobson 2784*) are prismatic but deformed – shaped unlike either parent. *Pollen* 14–17 colporate, 15 × 15 μ, often deformed (*Jobson 3588*), or all observed grains deformed (*Craven 5535* & *Jacobs 1862* sensu Taylor (1989)). **Figure 3a–c, 4**.

Additional probable hybrid specimens examined: AUSTRALIA: Northern Territory: Goomadeer Station, Goomadeer River, *S. Jacobs 1862*, 5 Jun 1974 (NSW 681749); East Alligator River crossing. *D.H. Benson 977*, 14 Jul 1974 (NSW 681750); Jabiluka billabong, Magela Ck. *S. Jacobs 5037, G. Sainty & K.L. Wilson*, 17 May 1987 (NSW 833516). Queensland: Cook: Crosbie Creek near Homestead, *R.W. Jobson 2784*, 15 July 2015 (NSW 922658). Western Australia: North Kimberley: Little Mertens Falls, *R.W. Jobson 3588 & P.C. Baleeiro*, 29 Apr 2019 (NSW 945185)

Etymology: The specific epithet honours the late Dr. Surrey Wilfrid Laurance Jacobs (1946–2009) who in June 1974 collected the first known specimen of *U. aurea × muelleri*. Surrey Jacobs worked as a systematic botanist at the National Herbarium of NSW at the Royal Botanic Gardens, Sydney. His major research efforts focussed on the systematics of water plants, grasses, chenopods, and weeds.

Distribution and ecology: Although this hybrid is only known from five collections (Fig. 5), it has been observed in several other locations where both parents *U. aurea* and *U. muelleri* occur (RWJ, pers. obs.). The collections were made on Cape York, Qld in a small lagoon (*Jobson 2784*), with *U. muelleri* and *Najas malesiana*. In the NT, one site was in a river system near Gunn Point east of Darwin (*Jacobs 1862*), and three sites in the region around Jabiru (*Jacobs 5037, Benson 977, Craven 5535*). A single collection was made from WA in a small pool above Little Mertens Falls, North Kimberley (*Jobson 3588*) growing with *U. australis*, *U. muelleri* and *Nymphaea violacea*.

Phenology: Flowers April–July. Functionally sterile.

Conservation status: Although *U. × jacobsii* is known from a wide distribution on Cape York, Qld, Top End, NT, and Kimberley region, WA, (Fig. 5) its density within any particular area is mostly unknown. From the few collections since *Jacobs 1862* (1974) it seems that its occurrence is rare. Future surveys are required to determine conservation status, and based on the available data, this species should be considered data deficient. As an apparently sterile hybrid, its presence in the landscape may be most reliant on repeated hybridisation events, though vegetative reproduction is entirely possible.

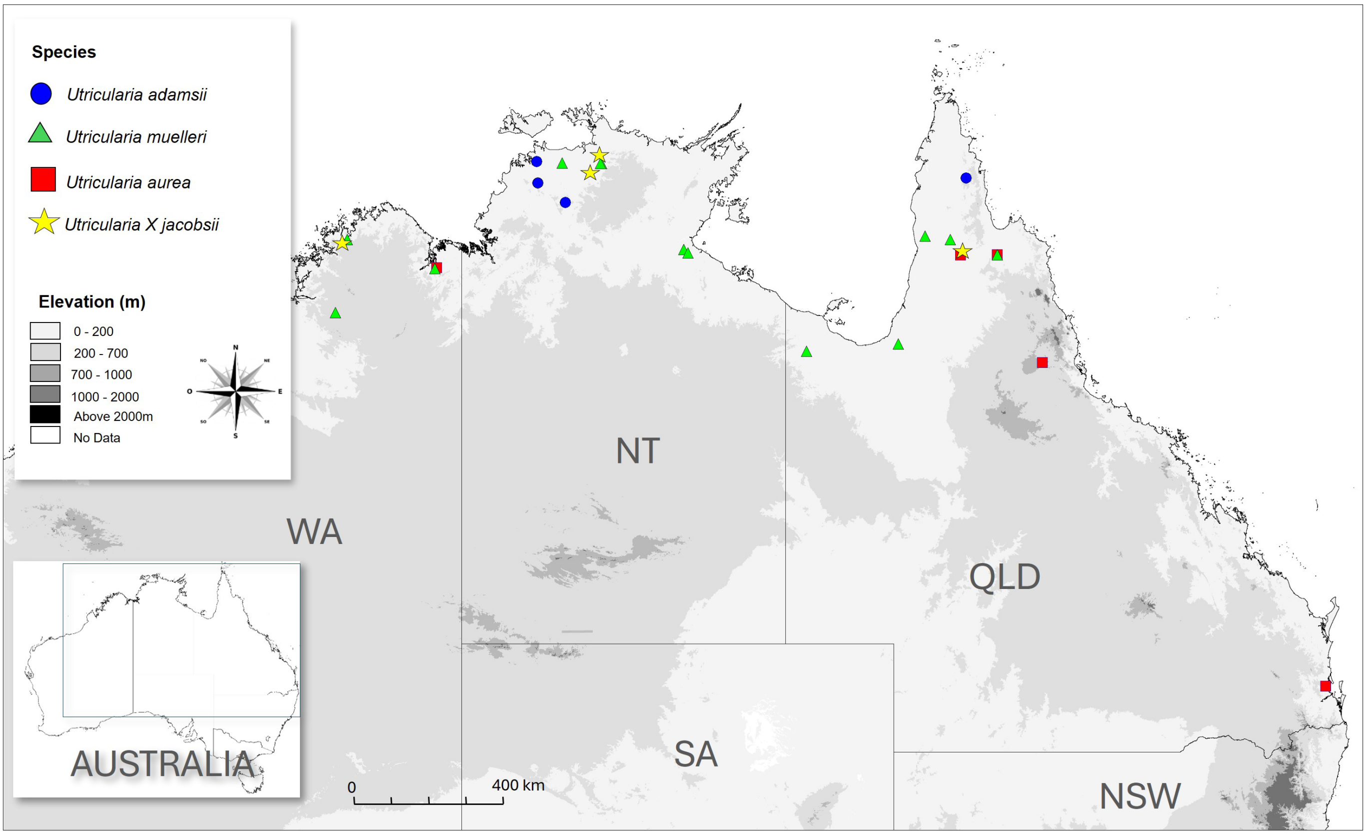

Figure 5. Distribution map showing accessions of *Utricularia muelleri* and allied species used in the current study: *Utricularia adamsii* (blue circle), *U. aurea* (red square), *U. muelleri* (green triangle), *U. × jacobsii* (yellow star).

Molecular evidence for the naturalisation of *U. geminiscapa* Benj., and presence of *U. australis* R.Br., in New Zealand

Utricularia geminiscapa is a perennial, suspended aquatic herb with a natural distribution across northeastern USA and Canada (Taylor 1989). The first collection of this species on the west coast of South Island, New Zealand (NZ) was in February 1975 (*Moar N.T & Mason R. 13126*; CHR 357934). On the North Island of NZ, the Eurasian/Australian *Utricularia australis* (syn = *U. protrusa*) occurs as a rare native species that is superficially morphologically similar and this name was originally applied to the NZ *U. geminiscapa* plants (Salmon 2001). Webb & Sykes (1997) examined the dorsiventrally compressed and rounded seed from the collection and found similarity to those of *U. geminiscapa* Benj. but not to those of the NZ populations of *U. australis*. Based on this evidence and in agreement with Moar & Mason (1975), Webb & Sykes (1997) re-instated *U. protrusa* Hook.f suggesting that the collection matched the type specimen. Salmon (2001) was first to realise that the *Moar N.T & Mason R. 13126* collection was not *U. protrusa* but instead was a cleistogamous form of *U. geminiscapa* that was likely introduced to NZ. Based on comparison of morphological characters such as internal bladder-trap glands, Heenan *et al.* (2004) provided a formal description of the *Moar N.T & Mason R. 13126* collection, along with several subsequent gatherings from the region, as *U. geminiscapa*, concluding that it is most likely recently naturalised.

Our study included an accession of a suspended aquatic taxon that was collected from a pool feeding into Dismal Creek near Waiatoto on the west coast of the South Island, New Zealand (*Champion 125*; CHR 608055A). This is one of several other gatherings of what appears to be the same taxon further north-west along the coast at Hokitika (225 km), and Westpoint (340 km). Our plastid phylogeny places *Champion 125* as sister to a previously sequenced collection from Bass River, New Jersey, USA (*R.W. Jobson 197*; BRI). The cpDNA representing *Champion 125* (used in this study Fig. 1), and an additional *trnL-F* sequence (not shown) were identical to those of the USA collection. Our ITS data includes an accession of the Japanese endemic species *U. dimorphantha* Makino of which the two *U. geminiscapa* accession are sister (Fig. 2). These results suggest the populations represented by *Champion 125* are likely very recent introductions to NZ. Further population genetic data may provide clues to timing and gene flow within and between NZ populations. Our ITS data also included a NZ sample of *U. australis* (*Heenan s.n.*, Table 1) and our analyses resolved it as sister to the south-eastern Australian accessions of that species, that together are sister to two monophyletic clades containing USA *U. macrorhiza* and European accessions of *U. australis*-*U. vulgaris* respectively (Fig. 2).

Proposal for changes to sectional circumscriptions

Following the results of Jobson *et al.* (2003) and those in Fig. 1, showing *U.* sect. *Setiscapella* (Barnhart) P.Taylor in Kew Bull. 41:15 (1986) as paraphyletic we propose that *Utricularia* sect. *Avesicaria* Kamieński ex Prantl in Nat. Pflanzenfam. 4(3b): 121 (1891) should be expanded to include the species in *U.* sect. *Setiscapella* and *U.* sect. *Steyermarkia* P.Taylor in Kew Bull., Addit. Ser. 14: 517–518 (1989). Our results show sect. *Setiscapella* paraphyletic with *U. flaccida* sister to a clade that includes taxa from sections *Setiscapella*, *Steyermarkia* and *Avesicaria* (Fig. 1).

Proposal for new section

Based on the polyphyletic position of sect. *Utricularia* relative to *U. olivacea* (Fig. 1) the latter has been assigned to the new section *Biovularia* (see below). A Brazilian accession of *U. olivacea* (*R.F. Rivadavia 937*, SPF) was fully supported as sister to sect. *Vesiculina* using plastid *rps16* and *trnL-F* (Jobson & Albert 2002; Jobson *et al*. 2003, 2018). Although another study using the plastid *matK* marker (Muller *et al*. 2004) placed the leafless *U. olivacea* near *U. gibba* (sect. *Utricularia*), the material used in that study was found to be a small-leaved form of *U. gibba* from southern USA (= *Adamec 1373*, this study; L. Adamec, pers. comm.; Jobson *et al*. 2018). In support of the Jobson *et al*. (2003) result, Silva *et al*. (2023) included a different Brazilian accession of *U. olivacea* (= *Silva SRS104* this study) in their full chloroplast *and* mitochondrial analysis and placed the accession sister to a single accession representing sect. *Vesiculina*. In this study, we have used the *rps16* and *trnD-T* introns (*Silva* SRS104) extracted from the plastid genome assembly used in the Silva *et al*. (2023) study in addition to those used previously representing *R.F. Rivadavia 937* (Jobson & Albert 2002; Jobson *et al*. 2003, 2018). A future study that includes accessions of the morphologically similar species *U. naviculata* and *U. biovularioides* will help further resolve relationships within this unusual group.

Figure 6. Lectotype of *U. olivacea* showing gathering of *Wright 2891* (GOET005729).

In the terrestrial/subaquatic sections *Nelipus* and *Setiscapella*, and suspended aquatic section *Vesiculina*, dehiscence is mostly from a single ventral longitudinal slit (Taylor 1989). Seeds are generally ovoid to globose in shape with varying forms of testa ornamentation, including multicellular outgrowths (Taylor 1989). In contrast, the seed capsule in the three species *U. biovularioides, U. naviculata* and *U. olivacea* is indehiscent; a situation where the seed/s are released upon breakdown of the capsule walls (Robins & Subramanyam 1980; Taylor 1989). These three species also share a lack of free-ending leaf segments (Beal & Quay 1968; Taylor 1989) and they differ from all other members of subgen. *Utricularia* in producing two to several ovules, and producing a single, 3–4 or 7 seed/s (Taylor 1989). A difference within the group is that *U. biovularioides* and *U. olivacea* have unwinged smooth-coated seeds while in *U. naviculata* the seeds have a marginal wing (Taylor 1989).

Utricularia section ***Biovularia*** (Kamieński) Baleeiro & R.W.Jobson, sect. et. stat. nov.

Basionym: *Biovularia* Kamieński, Zap. Novorossiisk. Obshch. Estestvoisp. 15: 205 (1890).

Type species: *Utricularia olivacea* C.Wright ex Griseb., here designated.

Illustration: Taylor (1989), fig. 211.

Herba aquatica, minuta. Folia alterna, capillariter partita, ascidiifera. Ascidia birostrata. Scapus esquamatus, bracteatus, 1–3-florus; bractea infirma ad caulem proxima; bracteae basifixae; bracteolae nullae. Calyx 2-lobatus; lobi subaequales. Corolla xanthica, hyalina, valde 2-labiata; labia integra; palatum tantum convexitas; calar saccatum. Antherae subglobosae. Ovarium 2-ovulatum. Capsula (achenium) globosa, 1-seminata, indehiscens.

Minute, suspended aquatic. Rhizoids and leaves absent. Stolon capillary bearing numerous traps. Traps ovoid with lateral mouth; long stalk and two long setiform appendages. Scales absent, bracts basifixed, bracteoles absent. Inflorescence bearing 2–5 flowers, apparently reduced or no peduncle. Sepals subequal, rounded, inferior slightly larger. Diminutive corolla creamy-white or white. Ovary ovoid with two ovules and producing one seed, indehiscent.

We here designate a lectotype for the type species of the section: *Utricularia olivacea* C.Wright ex Griseb., Cat. Pl. Cub. [Grisebach] 161 (1866). Lectotype (here designated): *Wright 2891*, (lecto: GH [GOET005729; Fig. 6]; isolecto: BM, G, K, LE, N, P, S, US, W, YU).

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References

Astuti G, Petroni G, Adamec L, Miranda VFO, Peruzzi L (2020) DNA barcoding approach fails to discriminate Central European bladderworts (*Utricularia*, Lentibulariaceae), but provides insights concerning their evolution. *Plant Biosystems* 154: 326–336. DOI

Baleeiro P, Jobson RW, Sano P (2016) Morphometric approach to address taxonomic problems: The case of *Utricularia* sect. *Foliosa* (Lentibulariaceae). *Journal of Systematics & Evolution* 54: 175–186. DOI

Baleeiro P, Sano P, Jobson RW (2019) Molecular phylogeny of the *Utricularia amethystina* complex (Sect. *Foliosa*) addressed using plastid and nuclear sequences data. *Systematic Botany* 2: 398–404. DOI

Baleeiro PC, Sano P, Gonella P, Jobson RW (2022) Unveiling the true colours of *Utricularia amethystina*: a taxonomic revision of *U.* sect. *Foliosa*, Lentibulariaceae. *Phytotaxa* 576: 29–54. DOI

Barnhart JH (1915) Segregation of genera in the Lentibulariaceae. *Memoirs of the New York Botanical Garden* 6: 39–64

Beal EO, Quay TL (1968) A review of *Utricularia olivacea* Wright ex Grisebach (Lentibulariaceae). *Journal of the Elisha Mitchell Scientific Society* 84: 462–466.

Bobrov AA, Volkova PA, Kopylov-Guskov YO, Mochalova OA, Kravchuk AE, Nekrasova DM (2022) Unknown sides of *Utricularia* (Lentibulariaceae) diversity in East Europe and North Asia or how hybridization explained old taxonomical puzzles. *Perspectives in Plant Ecology, Evolution and Systematics* 54: 1–19. DOI

Champion P, Hofstra D (20242). *Utricularia geminiscapa*. NIWA publication. URL

Guindon S, Gascuel O (2003) A simple, fast and accurate method to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52: 696–704. DOI

Heenan PB, de Lange PJ, Knightsbridge PI (2004) *Utricularia geminiscapa* (Lentibulariaceae), a naturalised aquatic bladderwort in the South Island, New Zealand. *New Zealand Journal of Botany* 24: 247–251. DOI

Jobson RW (2012) *Utricularia corneliana* R.W.Jobson (Lentibulariaceae), a new species from the North Kennedy district of Queensland. *Austrobaileya* 8: 601–607. DOI

Jobson RW, Albert VA (2002) Molecular rates parallel diversification contrasts in carnivorous plant sister lineages. *Cladistics* 18: 127–136. DOI

Jobson RW, Baleeiro PC (2020) Radiations of fairy-aprons (*Utricularia dichotoma*, Lentibulariacceae) across eastern Australia: molecular evidence for new species and proposal for new subspecies. *Australian Systematic Botany* 33: 278–310. DOI

Jobson RW, Baleeiro PC (2022) Rescircumscription of *Utricularia leptorhyncha* and *U. lasiocaulis* and three related new species for northern Australia. *Telopea* 25: 363–383. DOI

Jobson RW, Baleeiro PC (2023). Molecular phylogenetic study of *Utricularia* section *Oligocista* in Australia and a new Cape York endemic species. *Telopea* 26: 145–158 DOI

Jobson RW, Baleeiro PC, Guisande C (2018) Systematics and evolution of Lentibulariaceae: III. *Utricularia*, Pg. 89–104, In Ellison A, Adamec L (Eds) *Carnivorous plants: physiology, ecology, and evolution*. Oxford University Press: Oxford.

Jobson RW, Baleeiro P, Reut M. (2017) Molecular phylogeny of subgenus *Polypompholyx* (*Utricularia*; Lentibulariaceae) based on three plastid markers: diversification and proposal for a new section. *Australian Systematic Botany* 30: 259–278. DOI

Jobson RW, Davies-Colley T (2020) Redescription of the suspended aquatic *Utricularia aurea* Lour. (sect. *Utricularia*) and a new species *U. adamsii* for northern Australia. *Telopea* 23: 21–33. DOI

Jobson RW, Playford J, Cameron KM, Albert VA (2003) Molecular phylogenetics of Lentibulariaceae inferred from plastid *rps*16 intron and *trn*L–F DNA sequences: implications for character evolution and biogeography. *Systematic Botany* 28: 157–171. DOI

Moar NT, Mason R (1975) Discovery of *Utricularia protrusa* Hook.f. near Westport, South Island, New Zealand. *New Zealand Journal of Botany* 13: 803–805. DOI

Müller K, Borsch T (2005) Phylogenetics of *Utricularia* (Lentibulariaceae) and molecular evolution of the *trnK* intron in a lineage with high substitutional rates. *Plant Systematics and Evolution* 250: 39–67. DOI

Oxelman B, Lidén M, Berglund D (1997) Chloroplast *rps*16 intron phylogeny of the tribe Sileneae (Caryophyllaceae). *Plant Systematics and Evolution* 206: 393–410. DOI

Posada D (2008) jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution* 25: 1253–1256. DOI

Robins RJ, Subramanyam K (1980) Scanning electron microscope study of the seed surface morphology of some *Utricularia* (Lentibulariaceae) species from India. *Proceedings of the Indian National Science Academy* 46B: 310–324.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, and Huelsenbeck JP (2012) MRBAYES 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. *Systematic Biology* 61: 539–542. DOI

Salmon B (2001) *Carnivorous plants of New Zealand*. Auckland, Ecosphere Publications.

Shaw J, Shafer HL, Leonard OR, Kovach MJ, Schorr M, Morris AB (2005) The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *American Journal of Botany* 92: 142–166. DOI

Silva SR, Miranda VF, Michael TP, Płachno BJ, Matos RG, Adamec L, Pond SL, Lucaci AG, Pinheiro DG, Varani AM (2023) The phylogenomics and evolutionary dynamics of the organellar genomes in carnivorous *Utricularia* and *Genlisea* species (Lentibulariaceae). *Molecular Phylogenetics and Evolution* 181, 107711. DOI

Stanford AM, Harden R, Parks CR (2000) Phylogeny and biogeography of *Juglans* (Juglandaceae) based on matK and ITS sequence data. *American Journal of Botany* 87: 872–882. DOI

White TJ, Bruns T, Lee S, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In *PCR protocols: A guide to methods and applications*. (Eds MA Innis, DH Gelfand, JJ Sninsky, TJ White) pp. 315–322. Academic Press, Inc.: New York, NY, USA.

Taylor P (1989) The genus *Utricularia*. *Kew Bulletin Additional Series* 14. Royal Botanic Gardens: Kew.