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CHAPTER

8   Systematics and evolution of Lentibulariaceae: III. *Utricularia* 🔓

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Abstract

Utricularia is a morphologically and ecologically diverse genus currently comprising more than 230 species divided into three subgenera—*Polypompholyx*, *Utricularia*, and *Bivalvaria*—and 35 sections. The genus is distributed worldwide except on the poles and most oceanic islands. The Neotropics has the highest species diversity, followed by Australia. Compared to its sister genera, *Utricularia* has undergone greater rates of speciation, which are linked to its extreme morphological flexibility that has resulted in the evolution of habitat-specific forms: terrestrial, rheophytic, aquatic, lithophytic, and epiphytic. Molecular phylogenetic studies have resolved relationships for 44% of the species across 80% of the sections. Scant data are available for phylogeography or population-level processes such as gene flow, hybridization, or pollination. Because nearly 90% of the species are endemics, data are urgently needed to determine how to protect vulnerable species and their habitats.

Keywords: Biogeography, bladderworts, character evolution, conservation, Lentibulariaceae, phylogeny, phylogeography, taxonomy, Utricularia

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8.1 Introduction

Utricularia (bladderworts) currently comprises >230 species (Taylor 1989, Rutishauser 2016), divided into three subgenera (*Polypompholyx, Utricularia*, and *Bivalvaria*) and 35 sections (Taylor 1989, Müller and Borsch 2005, Lowrie et al. 2008, Jobson et al. 2017; Appendix). The genus is distributed worldwide with the exception of both poles and most oceanic islands (Taylor 1989). The Neotropics has the highest species diversity, followed by Australia (Taylor 1989, Guisande et al. 2007). *Utricularia* has diversified more rapidly than its sister genera *Pinguicula* (Chapter 6) and *Genlisea* (Chapter 7), a pattern that has been linked to its extreme morphological flexibility (Jobson and Albert 2002, Rutishauser 2016) and that is apparent in its many forms and habitats (Jobson et al. 2003, Müller and Borsch 2005). The evolution of its highly modified Bauplan, including its suction bladder trap, has long attracted researchers (e.g., Darwin 1875, Lloyd 1942).

8.2 Phylogeny and taxonomy

8.2.1 Early classification and delimitation

Linneaus (1753) collated the seven known species of *Utricularia* and typified the suspended aquatic *U. vulgaris*. Each of these seven species were described as having two stamens, a single pistil, a two-parted calyx, a gamopetalous corolla, a one-celled ovary and capsule, and a free-central placenta. By 1895, at least 13 genera of bladderworts had been recognized; Kamieński (1895) placed all, except for some species in *Biovularia* and *Polypompholyx*, into *Utricularia*. Barnhart (1916) recognized and reassigned the aforementioned 13 bladderwort genera based almost entirely on the position and shape of inflorescence bracts and bracteoles.

Taylor (1989) united all previously recognized bladderwort genera into *Utricularia*, separating them into two subgenera— *Polypompholyx* (three species) and *Utricularia* (211 species)—that were delimited based entirely on the presence of a four- versus two-parted calyx respectively. Taylor (1989) further synonymized many of the then ≈900 recognized species, and proposed and described novel taxa based on biogeography and morphology. The end result was 35 sections—*U.* sects. *Polypompholyx* and *Tridentaria* in *U.* subg. *Polypompholyx* and 33 others in *U.* subg. *Utricularia*—representing 214 species (Taylor 1989; Figure 8.1).

Figure 8.1 Molecular phylogeny of *Utricularia* representing 80% of all sections and 44% of all described species; modified from Jobson et al. (2003) and Jobson and Baleeiro (*unpublished data*) with monophyletic sections collapsed. This maximum credibility tree is derived from Bayesian inference analysis based on sequences of *rps16* and *trnLF*. Sections assigned by Taylor (1989) and those assigned since 1989 are shown with thin bars; subgenera assigned by Taylor (1989) and subsequent changes by Müller and Borsch (2005) are shown with thick bars. Clades discussed in the text (*U.* sect. *Pleiochasia sensu* Taylor) are labeled A–F. Asterisks above branches indicate weak jackknife support (60–75%). All other branches are well supported (76–100%).

8.2.2 Contemporary phylogenies

Relationships among subgenera.

The majority of Taylor's (1989) sections were well supported as monophyletic groupings by molecular phylogenies using the plastid markers *rps16* and *trnL-F* (Jobson et al. 2003) and the plastid *trnK* intron (Müller et al. 2004). However, these two studies were inconsistent in their support for the relationship between *U.* subg. *Polypompholyx* and *U.* subg. *Utricularia*. The *rps16/trnL-F* results of Jobson et al. (2003) showed strong branch support for a sister relationship between *U.* subg. *Polypompholyx* and *Utricularia* sensu

Taylor (1989), whereas the *trnK* ↳ ↳ results placed *U.* subg. *Polypompholyx* within *U.* subg. *Utricularia* (Müller et al. 2004). Jobson's finding of a sister relationship between the two subgenera was supported further by Müller et al. (2006), who used a supertree approach in which branch support values from each phylogenetic hypothesis are statistically weighted, with branching order assembled according to overall support.

In both Jobson et al. (2003) and Müller et al. (2004, 2006), *U.* subg. *Utricularia* was paraphyletic: *U.* sect. *Pleiochasia* was revealed as sister to *U. multifida* of *U.* sect. *Polypompholyx* (*U.* subg. *Polypompholyx*). Jobson et al. (2003) recommended, and Müller and Borsch (2005) formally proposed, including *U.* sect. *Pleiochasia* within *U.* subg. *Polypompholyx* (Figure 8.1). Reut and Jobson (2010) supported this sister relationship in a study of the *rps16* plastid gene sampled from 23 species of *U.* subg. *Polypompholyx sensu* Müller and Borsch (2005). Jobson et al. (2017) used *rps16, trnL-F*, and *trnDT* sampled from all recognized species to further support the sister relationship between *U.* subg. *Polypompholyx sensu* Müller and Borsch (2005) and *U.* subg. *Utricularia sensu* Taylor (1989), and also supported Taylor's (1989) placement of *U.* sect. *Tridentaria* within *U.* subg. *Polypompholyx*. Müller and Borsch (2005) also proposed dividing *U.* subg. *Utricularia* into two subgenera—*Utricularia* and *Bivalvaria*—based on clearly recognizable monophyletic groups. *Bivalvaria* resurrected a previously synonymized subgenus (Taylor 1989) and now includes all sections contained within clade U2–U4 of Jobson et al. (2003) (Figure 8.1).

Resolving sections.

Molecular studies also revealed a handful of Taylor's (1989) sections within *U.* subg. *Utricularia* to be polyphyletic or paraphyletic (Jobson et al. 2003, Müller et al. 2004). Both groups found *U.* sect. *Psyllosperma* to be paraphyletic. Jobson et al. (2003) included in *U.* sect. *Psyllosperma* the species *U. amethystina, U. tricolor* (both in *U.* sect. *Foliosa*), and an additional sequence attributed to a specimen identified as *U. huntii* (*U.* sect. *Psyllosperma*). However, this *U. huntii* accession subsequently was determined to have been a misidentified member of the *U.* sect. *Foliosa* complex (Baleeiro et al. 2016). Thus, the results of Jobson et al. (2003) should be interpreted as *U.* sect. *Foliosa* forming a clade sister to a clade containing members of *U.* sect. *Psyllosperma*. Müller et al. (2004) included in *Psyllosperma* a single species of *U.* sect. *Foliosa* (*U. tridentata*) and four from *U.* sect. *Psyllosperma*, but *U. calycifida* (*U.* sect. *Psyllosperma*) was sister with *U. tridentata*. Work is currently underway (Baleeiro et al. *unpublished data*) to determine whether these sections are monophyletic (Figure 8.1).

Baleeiro et al. (2016, *unpublished data*) combined morphometric and molecular data in an attempt to disentangle the high levels of morphological variation observed within the Neotropical *U.* sect. *Foliosa sensu* Taylor (1989). The work focused on the diverse species complex *U. amethystina*, into which Taylor (1989) had synonymized 31 previously recognized species. Baleeiro et al. (2016) used inflorescence characters to identify eight distinct entities within this species complex. Using nuclear ITS and three plastid genes (*rps16, trnL-F*, and *trnDT*), Baleeiro et al. (*unpublished data*) resolved the *U. amethystina* type as sister to *U. tricolor*, while the eight entities identified by Baleeiro et al. (2016) formed independent clades outside this type clade. From this work Baleeiro et al. (*unpublished data*) propose the resurrection of four previously synonymized taxa, and identify two new species.

Jobson et al. (2003) resolved *U.* sects. *Iperua* and *Orchidioides* as monophyletic, whereas Müller et al. (2004) included *U. humboldtii* (*U.* sect. *Iperua*) in their sequencing and found that it was a member of *U.* sect. *Orchidioides*; Müller and Borsch (2005) then proposed that *U.* sect. *Iperua* should be lumped within *U.* sect. *Orchidioides*. Gomes Rodriques et al. (2017) provide further support for this proposal using both chloroplast and nuclear markers (Figure 8.1). Jobson et al. (2003) found *U. nana*, the only species within the South American *U.* sect. *Benjaminia*, to be derived within *U.* sect. *Oligocista*, and sister to the other South American taxa included in their study. Müller et al. (2004) included an African and Asian species from *U.* sect. *Oligocista* and found

that *U. nana* was a sister to *U.* sects. *Oligocista* + *Avesicarioides* (Figure 8.1). Although this result may be a result of a lack of South American *U.* sect. *Oligocista* species in the study, further work is required to clarify the sister relationships within this section.

Last, Jobson et al. (2003) revealed *U.* sect. *Utricularia* to be polyphyletic because their South American accession of *U. olivacea* (*U.* sect. *Utricularia*) is sister to section *Vesiculina*. In contrast, Müller and Borsch (2005) placed their United States accession of *U. olivacea* within *U.* sect. *Utricularia*. Recent re-sampling and sequencing of an additional *U. olivacea* accession confirmed the position sister to *U.* sect. *Vesiculina* (Silva et al. 2016; Figure 8.1). A future study that includes related species *U. naviculata* and *U. biovularioides* will help resolve relationships within this unusual group, possibly requiring formation of a new section.

New sections proposed for *Utricularia*.

Since Taylor (1989) there have been two proposals for new sectional classification. The first is *U.* sect. *Minutae* to include *U. simmonsii* (Lowrie et al. 2008), which has the smallest known flowers in the genus and bladder traps that resemble those found in *U.* sect. *Enskide*. Reut and Jobson (2010) included *U. simmonsii* in a re-analysis of the sequence matrix of Jobson et al. (2003) and found it to be sister to *U. chrysantha* (*U.* sect. *Enskide*). More recently the two other members of *U.* sect. *Enskide, U. fulva* and *U. jobsonii*, have been included in an analysis demonstrating that *U.* sect. *Enskide* forms a clade sister to *U.* sect. *Minutae* (Jobson and Baleeiro *unpublished data*; Figure 8.1).

The second involves *U.* sect. *Pleiochasia*, in which Reut and Jobson (2010) identified two major clades (1 and 2). The first includes species distributed in both tropical northern and temperate southern Australia, whereas the second includes mostly tropical northern species. Jobson et al. (2017), including all recognized species of *U.* subg. *Polypompholyx*, resolved the same two strongly supported clades as A–C and D–F respectively (Figure 8.1). With the type species of *U.* sect. *Pleiochasia* (*U. dichotoma*) contained within the former clade, Jobson et al. (2017) propose that clades D–F should represent a new section: *Lasiocaules* (Figure 8.1).

8.3 Evolution of life histories and morphology

8.3.1 Habitats and life history

The mapping of habit across the genus indicates that the ancestral state of *Utricularia* was terrestrial (Jobson et al. 2003, Müller and Borsch 2005), with subsequent evolution of forms possessing affixed aquatic, affixed subaquatic, suspended aquatic, epiphytic, lithophytic, and rheophytic habits (Figure 8.2). Shifts to the lithophytic habit have occurred independently, within *U.* sects. *Iperua* (*U.* subg. *Utricularia*), *Phyllaria*, and *Lloydia* (*U.* subg. *Bivalvaria*) (Jobson et al. 2003), and in *U. wannanii* from northern Australia (*U.* subg. *Polypompholyx*) (Jobson and Baleeiro 2015). Jobson et al. (2003) found that the epiphytic habit evolved from the terrestrial habit independently at least twice in the Afrotropical-Indomalayan-Australasia section *Phyllaria* (*U.* subg. *Bivalvaria*) and within the Neotropical sections *Iperua* and *Orchidioides* (*U.* subg. *Utricularia*) (Figures 8.1, 8.2). These species are specialized for the epiphytic habit by having water-storage tubers, with two members of section *Iperua* specialized for growth in the tanks of epiphytic bromeliads (Taylor 1989).
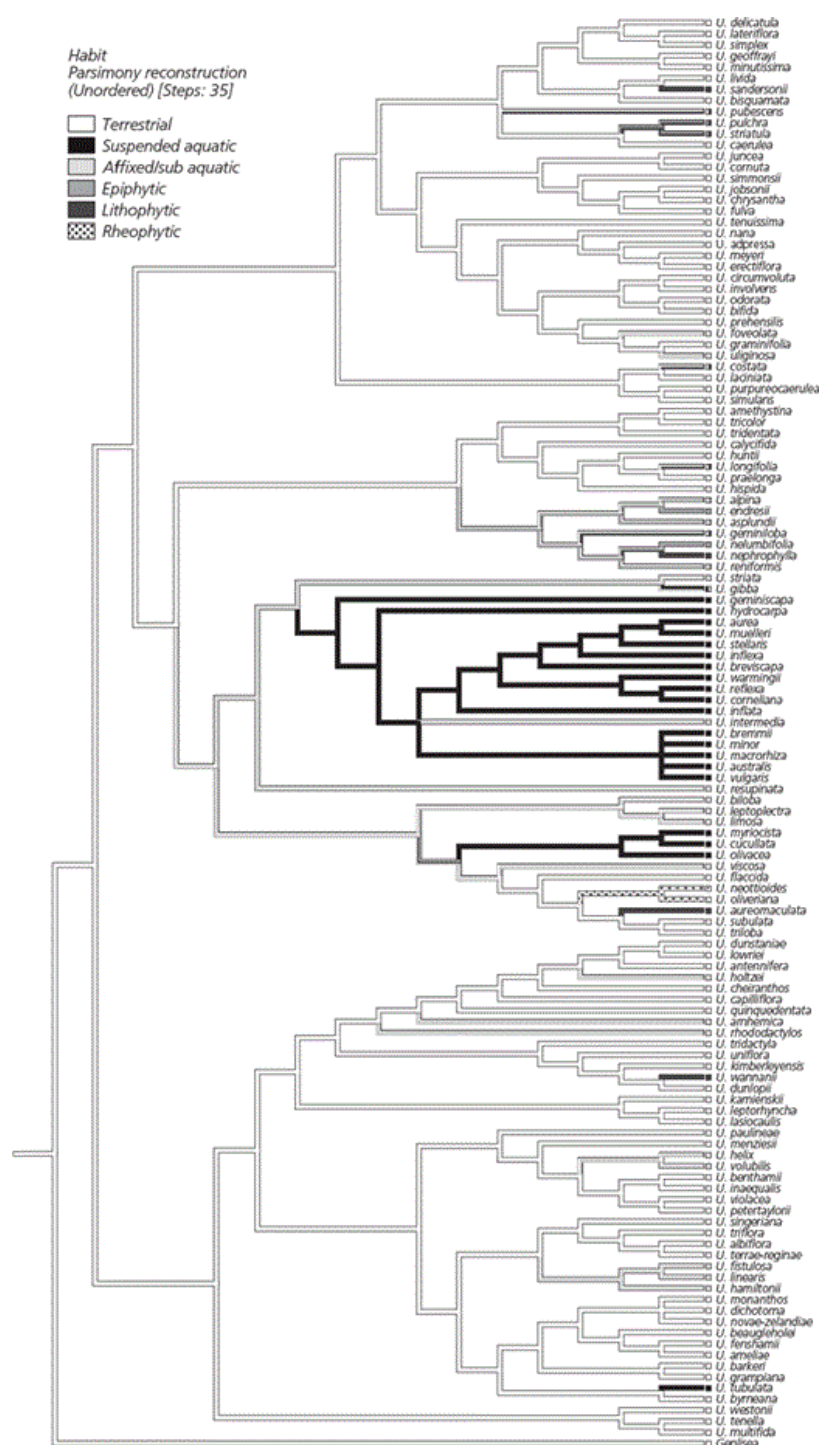
Figure 8.2 Cladogram of the strict consensus tree showing parsimoniously optimized analyses based on habitat and life form. Equivocal branches indicate parsimoniously optimized plesiomorphic characters

(modified from Jobson et al. 2003)

Shifts from terrestrial *Utricularia* into aquatic habitats have occurred at least twice with the rheophytic habit, as well as with suspension in the water column (Jobson et al. 2003, Müller et al. 2004) (Figure 8.2). Rheophytic *Utricularia* are specialized for growth in fast-flowing waters (Taylor 1989), with ventrally papillate, claw-like rhizoids for adherence to rock surfaces and reduced or pinnate leaves (Taylor 1989). The African *U.* sect. *Avesicarioides* is sister to *U.* sect. *Oligocista* in *U.* subg. *Bivalvaria* (Müller et al. 2004), whereas the rheophytic section *Avesicaria* (*U. neottioides, U. oliveriana*) is derived within the mainly terrestrial *U.* sect. *Setiscapella* (*U.* subg. *Utricularia*; Figure 8.1). The affixed aquatic habit has arisen multiple times across all three subgenera (Jobson

et al. 2003, 2017, Reut and Jobson 2010). Overall, the diversification in habitat and life history by *Utricularia* has led to a great deal of morphological evolution.

8.3.2 Stolons, rhizoids, and leaves

All species of *U.* sects. *Polypompholyx, Tridentaria*, and several species within clade A (Figure 8.1) of *U.* sect. *Pleiochasia* lack

stolons and form stemmed rosettes similar to those of the sister genus *Genlisea* (Taylor 1989, Fleischmann et al. 2010). Most species

of *Pleiochasia* possess stolons, and Taylor (1989) postulated that presence of stolons in most species is a derived feature, and that the rosette-forming species are ancestral. However, Jobson et al. (2017) have shown that the lack of stolons in members of *U.* subg. *Polypompholyx* is just as likely to be a reversal to a more ancestral state.

Rhizoids resemble true roots but they lack typical root structure and appear to function only to anchor the plants in wet substrates. Although true functional roots are present in all *Pinguicula* species, they are aborted during early embryogenesis in all *Genlisea* and *Utricularia* species (Lloyd 1942, Juniper et al. 1989). Rhizoids are produced from the base of the peduncle or nodes of the stolons, but they are reduced in *U.* sects. *Vesiculina* and *Utricularia*. They are usually capillary, simple or branched, and, in members of *U.* sect. *Pleiochasia*, helically twisted. In a few lithophytic and rheophytic species, the undersurface of the rhizoid possesses trichomes modified for adhering to surfaces (Taylor 1989).

Leaves range from small (≈0.5 mm), linear, elliptic, obovate, and cordate, to the reniform, rounded blades of *U.* sect. *Orchidioides/Iperua* that can reach 65 cm in length (*U. reniformis*) or 10 cm in diameter (*U. nelumbifolia*). In contrast, the bladeless aquatic and rheophytic species possess dichotomous ramifications that resemble the nerves of normal leaves, whereas the suspended aquatic *U. olivacea* and *U. biovularioides* possess leafless stolons. Further, water storage tubers that develop from stolons have evolved multiple times across the genus (Taylor 1989). Gomes Rodriques et al. (2017) found that these important adaptations for water storage have evolved at least twice within the epiphytic/terrestrial *U.* sect. *Orchidioides/Iperua*.

The general lack of distinction between leaves, leaf-like organs, and stolons in *Utricularia* has been discussed in two ways. Taylor (1989) considered leaf structures, stolons, and rhizoids to be independent homologous organs to lend clarity to his taxonomic revision of the genus based on morphology. However, he clearly recognized that this suggestion was inadequate to provide a developmental explanation for observed morphological patterns in the genus. Alternatively, Sattler and Rutishauser (1990), Rutishauser and Isler (2001), and Rutishauser (2016) proposed a continuum ("fuzzy") morphology model, in which organs are considered morphological transformations derived from developmental program amalgamation, rhizoids and stolons are considered stem homologs (Troll and Dietz 1954), and leaf-like organs are considered leaf homologs (Goebel 1891b, Kumazawa 1967). Genomic analysis of *Utricularia* (Chapter 11) will enable future investigation into the evolution of genetic programs involved in the developmental pathways that have led to its unusual morphologies (Ibarra-Laclette et al. 2013).

8.3.3 Bladder-trap morphology

All *Utricularia* species have modified leaves that form bladder traps that must be submerged in or surrounded by water to capture prey (Lloyd 1942, Juniper et al. 1989; Chapters 14, 19). The traps actively pump internal fluid to the exterior when the trap is reset (Juniper et al. 1989, Płachno et al. 2015a; Chapters 13, 14). The traps themselves are hollow, ovoid, or globose modified leaves that are 0.2–12 mm in length and develop in a diverse range of positions on, and attached by a stalk to, the plant (Figure 8.3). The trap entrance ("mouth") is described as basal when positioned adjacent to the stalk, terminal when the mouth is opposite the stalk, and lateral when intermediate on the ventral side of the trap (Taylor 1989).
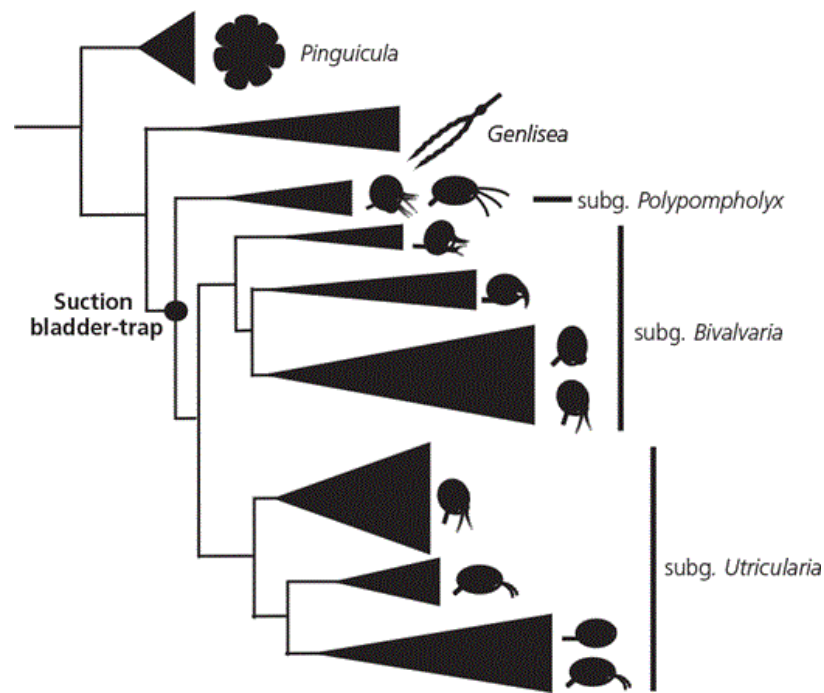
Figure 8.3 Diagram representing the Lentibulariaceae phylogeny (modified from Albert et al. 2010), with schematics of trap types per clade showing rosettes of sticky leaves for *Pinguicula*, passive corkscrew traps of *Genlisea*, and active suction bladder traps of *Utricularia*. Trap forms across *Utricularia* generally are lineage-specific. Branch lengths inferred from nucleotide substitutions are ± relative to one another; collapsed clade sizes represent the taxonomic sampling of Jobson and Albert (2002).

The homologous traps of both *Utricularia* and *Genlisea* develop from an inward-rolling of the adaxial leaf surface with subsequent marginal fusion ("epiascidiate" leaves). In *Genlisea*, traps form from cylindrical primordia with an invaginated tip, whereas in *Utricularia* a spherical invagination forms the primordial trap (Lloyd 1942, Juniper et al. 1989, Albert et al. 1992, Reut 1993). The large variation found in its external morphology (Meierhofer 1902, Lloyd 1942, Taylor 1989) is generally monophyletic among sections in all three subgenera (Jobson and Albert 2002, Albert et al. 2010; Figure 8.3).

In *U.* subg. *Polypompholyx*, traps arise only from the base of the peduncle in all species of *U.* sects. *Polypompholyx, Tridentaria*, and some members of *Pleiochasia*. In other members of *U.* sect. *Pleiochasia* they also arise from stolon nodes, occasionally ↳ at internodes, and only from whorl nodes in suspended aquatic *U. tubulata*. Traps are positioned only terminally on leaves in affixed aquatic sister species *U. volubilis* and *U. helix*, both of which have dimorphic trap appendage forms specialized either for substrate or water-column positions (Taylor 1989, Jobson et al. 2017).

Trap structures in *U.* subg. *Polypompholyx* are diverse, but in general consist of a usually simple, bifid, or trifid dorsal appendage (rostrum), two lateral setiform or wing-like appendages on either side of the mouth, and a pair of ventral lamella-like wings. Any or all of these may be polymorphic, reduced, or absent, depending on species (Taylor 1989; Figure 8.3). Taylor (1989) differentiated *U.* sect. *Polypompholyx* from *U.* sect. *Tridentaria* based on the presence of a bifid or trifid dorsal rostrum, respectively. Appendage types have arisen multiple times across *U.* subg. *Polypompholyx* and generally correspond with aquatic or terrestrial habits. Reut and Jobson (2010) found that the evolution of filiform antennae appendages around the mouth was associated with the shift from the terrestrial to affixed aquatic habit.

In the epiphytic sections of *U.* subg. *Utricularia* (*U.* sects. *Orchidioides, Iperua*) and *U.* subg. *Bivalvaria* (*U.* sect. *Phyllaria*) with well-developed aerial leaves, traps develop on stolons, rhizoids, and the base of the peduncle, but not on leaves, probably because leaves are rarely submerged in water. In the remaining terrestrial, lithophytic, and epiphytic species, traps can develop not only on stolons, rhizoids, and at the base of the peduncle, but also laterally on the leaf lamina (Taylor 1989). Appendage types include a single dorsal rostrum in *U.* sect. *Calpidisca, Nigrescentes, Meionula, Phyllaria*, and some species in *U.* sect. *Aranella*. In *U.* sects.

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Candollea, Martinia, and several species of *Calpidisca*, an additional appendage is a bifid or gland-covered ventral rostrum (Taylor 1989; Figure 8.3).

In several species of *U.* sect. *Oligocista*, the ventral rostrum is reduced to a bulge-like protrusion. In the closely related *U.* sects. *Enskide, Minutae*, and *Stomoisia*, and in the monotypic *U.* sects. *Benjaminia* and *Sprucea*, traps are mostly naked with a slight dorsal bulge. Members of *U.* sects. *Oligocista, Orchidioides, Iperua, Foliosa, Psyllosperma, Chelidon, Kamienskia*, and *Oliveria* bear two, often simple, sometimes gland-covered dorsal appendages (Taylor 1989)—a character found to be polyphyletic (Jobson and Albert 2002). In the mostly affixed aquatic *U.* sects. *Nelipus, Lecticula, Setiscapella*, and *Steyermarkia*, the ↳ two dorsal appendages are beset with setae, while in the suspended aquatic *U.* sect. *Utricularia* these appendages are often branched setiform antennae. In the suspended aquatic section *Vesiculina*, traps are borne terminally on whorled leaves, with a single ventral appendage or completely naked (Taylor 1989, Jobson and Albert 2002; Figure 8.3). In three species placed within *U.* sect. *Utricularia* (Taylor 1989), traps resemble those of other members of the section but they are attached to leafless stolons (e.g., *U. olivacea*; Figure 8.3).

The internal surfaces of the bladder trap are adorned with two main internal gland types; two-armed trichomes usually located near the threshold at the entranceway, and four-armed quadrifid trichomes scattered on most of the inner wall surface. Both gland types are highly variable between sections and also vary in shape and length of arms between species. Although Taylor (1989) does not use these structures as strong differentiating characters, he does provide a description for most species in the genus. The structures rarely have been used for taxonomy, with the exception of Thor (1988 and previous work cited therein) and Płachno and Adamec (2007), who have used the length and shape of quadrifid arms as a character in combination with others to differentiate between two or more species. Future work is needed to assess the utility of these trichomes for taxonomic characterization across the genus.

8.3.4 Bladder-trap evolution

Most species have well developed trigger hairs on the outer surface of the trapdoor that act to release the door during firing (Juniper et al. 1989, Reifenrath et al. 2006, Płachno et al. 2015a; Chapter 14). The traps of species within *U.* sect. *Polypompholyx* often are considered ancestral because of their inflated stalk and the structure of the shortly bifid dorsal appendage that folds over the trap mouth forming a funnel-like entrance-way (Taylor 1989, Reifenrath et al. 2006). Their traps also are thickened with four-layered walls, and the trigger hairs either are highly reduced (Taylor 1989) or not present (Reifenrath et al. 2006). This suggests that there should be a corresponding absence of "active" bladder-trap function in these species and that their traps should function more like the passive eel traps of species in the sister genus *Genlisea* (Chapters 7, 15). However, Lloyd (1942) found that these bladders functioned actively, like others in the genus. The "passive" hypothesis is further belied by the lack of a funnel-like entrance-way and presence of highly developed trigger hairs in the sister species *U. westonii* (*U.* sect. *Tridentaria*). This scenario suggests that seemingly ancestral traps of *U.* sect. *Polypompholyx* may be derived within the lineage (Jobson et al. 2017). Traps within *U.* sect. *Pleiochasia* also are active; studies of *U. monanthos* report typical suction action (Sydenham and Findlay 1973, Juniper et al. 1989). Finally, Płachno et al. (2015a) found that the number of cell-wall layers, which varies from two to five across *U.* subg. *Polypompholyx*, and from two to four layers within the same species complex, has no obvious relationship with efficiency of trap firing.

Jobson et al. (2004) hypothesized that the metabolically expensive bladders led to adaptive innovations during radiation of the genus. For example, hypothesized adaptive advantages of different trap appendage forms include: exclusion of soil particles from around the mouth by overhanging wings (mainly in terrestrial species; Lloyd 1942, Taylor 1989); support for functionally vital surface films of water at the trap mouth by thickly set dorsal wings in some epiphytic species (Taylor 1989); and formation of funnels that may guide potential prey organisms to the trap door (in suspended aquatic taxa; Darwin 1875, Lloyd 1942, Meyers and Strickler 1979, Juniper et al. 1989, Taylor 1989). Appendage variation across the genus may have permitted specialization on particular prey by different *Utricularia* species in both aquatic and terrestrial habitats (Harms 1999, Jobson and Morris 2001, Guisande et al. 2004; Chapter 21). Finally, positive selection for molecular changes in the mitochondrial subunit 1 of cytochrome *c* oxidase have been implicated in the altered energetics of trap resetting (Jobson et al. 2004, Laakkonen et al. 2006, Albert et al. 2010; Chapters 11, 14),

8.3.5 Inflorescences, flowers, and pollen

Lentibulariaceae have zygomorphic flowers with persistent calyces that form an upper and lower lip, a sympetalous corolla tube, a basally spurred or saccate lower lip, two anthers, four sporangia ↳ and one or two confluent thecae, two fused carpels, and a unilocular ovary (Casper 1966, Fromm-Trinta 1981, Taylor 1989; Chapters 6, 7). *Pinguicula* have single-flowered scapes, but *Genlisea* and *Utricularia* have synapomorphic racemes of few to many flowers (Casper 1966, Fromm-Trinta 1981, Taylor 1989, Jobson et al. 2003). Within *Utricularia U.* subg. *Polypompholyx*, shifts in habitat and life-form tend to correspond with shifts in inflorescence size and corolla color: five independent shifts from terrestrial to affixed and suspended aquatic life-forms that correspond with shifts from small to medium/large inflorescences. Two of these shifts also correspond with a shift from purple to white corolla color, while for the only suspended aquatic species in the subgenus (*U. tubulata*) the shift is to a pale pink corolla.

Inflorescences.

Along with racemes has come an array of different arrangements of bracts, bracteoles, and scales (sterile bracts) upon the peduncle (Taylor 1989). Bracts are present in all species of *Utricularia*, and adjacent bracteoles are present in all sections excepting *U.* sects. *Sprucea, Avesicaria, Mirabiles, Steyermarkia, Lecticula, Setiscapella, Nelipus, Utricularia*, and *Vesiculina* (Taylor 1989). Scales are present in all species except those circumscribed to *U.* subg. *Polypompholyx*, to *U.* sects. *Minutae, Vesiculina* (including *U. olivacea*), and to several species of *U.* sects. *Utricularia* and *Lecticula* (*U. resupinata, U. aurea, U. geminiscapa*, and *U. inflata*) (Taylor 1989). Several suspended aquatic species within *U.* sect. *Utricularia* possess whorled flotation organs at various positions on the peduncle that maintain the aerial position of the inflorescence (Taylor 1989). The floats seem to have evolved only once, with reversal to non-float-bearing peduncles in at least two species (Jobson and Baleeiro, *unpublished data*).

Flower structure.

The calyx of *U.* sect. *Polypompholyx* and *Tridentaria* has four sepals, whereas that of *U.* subg. *Utricularia* has two sepals. Taylor (1989) hypothesized that the four-parted calyx of *U.* subg./*U.* sect. *Polypompholyx* may be evolutionarily intermediate between *Genlisea* and *U.* subg. *Utricularia*. However, an optimization showing the earliest node as having two sepals (Jobson et al. 2003), and the lateral sepals forming an epicalyx in *U.* sect. *Polypompholyx* and thus not being homologous to those of *Genlisea*/*Pinguicula*, suggest that the four-parted calyx is an independent apomorphy. During the initial developmental stages of the floral bud of *U.* subg. *Utricularia* and *Bivalvaria*, five sepals are evident; the anterior part has two sepals and the posterior has three. These sets each fuse, forming two sepals later in development (Lang 1901).

Floral color in subgenus *Polypompholyx*.

Jobson et al. (2017) used a parsimony-based ancestral state reconstruction to examine shifts in habit that correspond with the evolution of corolla lower lip color and inflorescence size. The earliest node shows a split between pink flowers in *U.* sects. *Polypompholyx* + *Tridentaria*, and a combined character state containing various shades of purple as ancestral for *U.* sect. *Pleiochasia*. Within *U.* sect. *Pleiochasia*, Jobson et al. (2017) found that a red corolla has arisen once (in *U. menziesii*) from a violet ancestor, a trait that is accompanied by a corolla spur 2–3× longer that the lower lip (Taylor 1989), whereas a pink corolla has arisen twice independently within *U.* sect. *Pleiochasia* and *Lasiocaules* from purple ancestors. A white corolla has arisen six times mainly from purple ancestral nodes, whereas the cream-colored corolla in *U. holtzei* and the pink of its sister species *U. cheiranthos* evolved from an apricot ancestor. Also from a purple ancestor, a white corolla evolved in the lithophytic *U. wannanii* and an apricot-colored corolla evolved in its terrestrial sister species, *U. dunlopii* (Reut and Jobson 2010, Jobson et al. 2017). Along with a shift to an apricot-colored corolla and from very small to minute inflorescences, Reut and Jobson (2010) also showed that filiform corolla appendages evolved independently three times: twice from the upper lip lobe and once from the lower lip lobe.

Pollen.

Lobreau-Callen et al. (1999) described nine pollen types for *Utricularia* mainly based on aperture number and features of the exine and that, with few exceptions, is associated more with the phylogeny than habitat specialization. Morphological variation of pollen within *Utricularia* is complex, although the exines of most species within the genus are generally smooth or rugose. An exception is the rheophytic *U.* sect. *Avesicaria* (*U. neottioides, U. oliveriana*), that have an exine covered with ↳ micro-spines (Sohma 1975, Taylor 1989, Lobreau-Callen et al. 1999). A general trend in lower aperture number, between three and eight, is seen in the mostly terrestrial *U.* subg. *Polypompholyx* and *Bivalvaria*. In contrast, aperture number ranges from 8 to 23 within *U.* subg. *Utricularia*, except for *U.* sect. *Orchidioides* with 3–4 (Thanikaimoni 1966, Huynh 1968, Sohma 1975, Taylor 1989, Lobreau-Callen et al. 1999). Aperture number also appears to vary widely within a species (e.g., 8–15 in the *U. amethystina* complex), but this may reflect cryptic taxonomic diversity rather than intraspecific variation (Baleeiro et al. *unpublished data*).

8.3.6 Cytology

Chromosome numbers have been determined for 28 species. Values do not follow any clear pattern apart from the prevalence of low, seemingly aneuploid counts of $n = 5, 7, 9, 10, 11$, or 14 within *U.* subg. *Polypompholyx* and *Bivalvaria*, excepting the terrestrial *U. livida* ($n = 18$) and *U. caerulea* ($n = 18/20$). Counts for the suspended aquatic *U.* sect. *Utricularia* are usually greater (e.g., $n = 9$ to 22; Taylor 1989), and although it is evident that polyploidy has occurred during the evolution of the genus it has been hypothesized that extant species rarely hybridize (Kondo 1972a, Jérémie and Jeune 1985, Taylor 1989, Raynal-Roques and Jérémie 2005). However, at least some temperate species in *U.* sect. *Utricularia* (*U. australis, U. bremii, U. ochroleuca, U. stygia*) are evidently (Kameyama and Ohara 2006) or probably (Taylor 1989) derived from hybrid origins.

8.3.7 Fruits and seeds: structure and dispersal

The range of capsule dehiscence and seed types appear to correspond with both habit and phylogeny (Jobson et al. 2003). Fruits from the earliest node of the *Utricularia* clade dehisce from a single ventral longitudinal suture that varies in length and thickness (Jobson et al. 2003). Dehiscence types involving both dorsal and ventral slits occur in the terrestrial *U.* sects. *Tridentaria* and *Australes*, and several species in *U.* sect. *Oligocista* (Taylor 1989). A deviation from the dorsi-ventral orientation of the suture occurs in *U.* sect. *Foliosa sensu* Taylor (1989) where the entire capsule is dorsi-ventrally bivalvate (Taylor 1989, Jobson et al. 2003).

Most species with this ancestral dehiscence type are terrestrial (Figure 8.2), and it may be that all other *Utricularia* dehiscence types are derived from it (Jobson et al. 2003). Considering that fruits of both *Pinguicula* and *Genlisea* have more complex, laterally bivalvate or multi-sutured dehiscence (Casper 1966, Taylor 1989), respectively, it seems that dehiscence in *Utricularia* has become simplified. The earliest node of the *Utricularia* clade has seeds that are globose/ovoid in shape, mostly with reticulated testa and raised anticlinal walls (Jobson et al. 2003). Such a surface is similar to those found in *Genlisea* (Robins and Subramanyam 1980, Taylor 1989) and may allow seeds to remain afloat. This flotation may aid dispersal via water birds (Taylor 1989).

Although seed morphology varies across the genus, in most sections they are small or very small (0.2–1 mm long), ovoid to cylindrical, and subglobose with reticulated testa (Taylor 1989). Members of *U.* sects. *Phyllaria* and *Iperua* have seed coats with multicellular outgrowths that may be a specialization for host attachment, whereas those of *U.* sect. *Orchidioides* are cylindrical or fusiform in shape with smooth coats that may be associated with wind dispersal (Robins and Subramanyam 1980, Taylor 1989). Dehiscence types, seed shapes, and seed surfaces are similar in *U.* sects. *Avesicaria* and *Avesicarioides*, which have seeds covered in mucilage that presumably aids dispersal in fast-flowing streams (Robins and Subramanyam 1980, Taylor 1989). Similar seeds are found among other Neotropical rheophytes in *U.* sects. *Choristothecae* and *Mirabiles*. The affinity of these two sections with *U.* sects. *Avesicaria* and *Setiscapella* currently is unknown, so it is uncertain whether or not the habit and seed type has evolved twice or more.

In the mostly suspended aquatic clades of *U.* sect. *Utricularia* (Figure 8.1), equatorially circumscissile dehiscence predominates (Jobson et al. 2003); the few exceptions (e.g., *U. gibba*) have laterally bivalvate dehiscence (Taylor 1989, Jobson et al. 2003). In

p. 99   circumscissile dehiscence, the equatorial plane of the capsule is separated, presumably giving greater space for dispersal of the large and usually winged prismatic, lenticular seeds; seeds of several species ↳ also have surface appendages (Taylor 1989). The seeds of *U.* sect. *Utricularia* have a diverse array of shapes ranging from globose/ovoid, prismatic/conical, to discoid/lenticular, with many species having multicellular outgrowths such as wings (e.g. *U. gibba*) (Robins and Subramanyam 1980, Taylor 1989).

In contrast, the sister of *U.* sect. *Utricularia*, the subaquatic *U.* sect. *Lecticula*, dehisces via a longitudinal slit that is similar to that of *U.* sects. *Nelipus* and *Setiscapella*; the seeds in these sections range in shape from prismatic and globose to ellipsoid (Taylor 1989, Jobson et al. 2003). In the terrestrial/subaquatic sections *Nelipus* and *Setiscapella* and suspended aquatic section *Vesiculina* (Figures 8.1, 8.2), dehiscence is mostly from a single ventral longitudinal slit (Taylor 1989), and seeds are generally ovoid to globose in shape with varying forms of testa ornamentation, including multicellular outgrowths (Taylor 1989).

Indehiscence, a situation in which the seeds are released upon breakdown of the capsule walls, is found in suspended aquatic species circumscribed to *U.* sect. *Utricularia* (*U. biovularioides, U. olivacea*, and *U. naviculata*) that produce a single or few ovoid and smooth seeds that are adnate to the capsule wall (Robins and Subramanyam 1980, Taylor 1989). Indehiscence is also found in *U. tubulata* (*U.* sect. *Pleiochasia*) and involves release of a few seeds with elongated papilla-like testa cells (Taylor 1989).

8.4 Population dynamics

8.4.1 Population genetics

Population genetic studies are scant, and are so far restricted to suspended/affixed aquatic species. In a Japanese form of *U. australis* pollinators have not been observed, and the stigmatic surface and anthers are adjacent to each other at dehiscence, possibly promoting self-fertilization (Yamamoto and Kadono 1990, Khosla et al. 1998, Araki and Kadono 2003). However, the virtually complete absence of outcrossing, and to a lesser extent inbreeding, is a barrier to gene flow (Yamamoto and Kadono 1990). In different populations of the same species, Araki and Kadono (2003) found that clonal dominance predominated and seed contributed little to population genetic structure. Using isozymes, Kameyama and Ohara (2006) found no within-population genetic variability and they hypothesized that sterility may have resulted from a prior hybridization event.

8.4.2 Pollination

Lineages within derived clades have evolved highly specialized floral structures such as functional nectar discs, probable vector-specific spurs, and floral sizes and shapes that tend to correlate with vector-specific color and scent (Taylor 1989, Hobbhahn et al. 2006). Taylor (1989) noted visits by various insects and hummingbirds to *Utricularia* flowers. Visitation by insects was observed for three Indian species of *U.* sect. *Oligocista* (Hobbhahn et al. 2006) and the Neotropical terrestrial/epiphytic species *U. reniformis* (*U.* sect. *Iperua*; Clivati et al. 2014). Highly modified corolla lobes have evolved multiple times in *U.* sect. *Pleiochasia* that likely were driven by pollinator specialization (Reut and Jobson 2010, Płachno et al. 2015b). In addition, Gloßner (1992) described ultraviolet patterns presumed to guide vectors in the flowers of at least one species of *Utricularia*.

In a study of the sympatric terrestrial sister species *U. cornuta* and *U. juncea* (*U.* sect. *Stomoisia*), Kondo (1972a) observed a reduction in floral size in *U. juncea* that may have led to a high incidence of cleistogamy. This was hypothesized to have resulted from a lack of selective pressure on floral form because of the absence of pollinators and predominance of autogamy among populations (Kondo 1972a). Although Clivati et al. (2014) did show evidence of pollinator interaction and possession of a sensitive stigma to avoid self-pollination, frequency of visitation was low, which may affect gene flow and lead to a loss of genetic diversity. This result supports the observations of Jérémie and Jeune (1985) who used morphometric analyses and observations on pollination vectors within populations of the Neotropical terrestrial/epiphytic *U. alpina* (*U.* sect. *Orchidioides*). They found little evidence of insect pollination and strong variation between plants occupying terrestrial versus epiphytic microhabitats and they hypothesized that sympatric isolation was occurring between these subpopulations. Given the highly specialized floral structures across the lineage,

p. 100   autogamy within populations of most ↳ studied *Utricularia* species is probably a relatively recent evolutionary development (Jobson and Albert 2002). It also seems likely that the wide variation in corolla color, size, and shape (§8.3.5), the majority of which

is phylogenetically independent, indicates strong pollinator selection pressure across the lineage. Further work is required to understand more fully pollination systems across the genus (Guisande et al. 2007; Chapter 22).

8.4.3 Clonal growth

Many of the aquatic *Utricularia* species readily reproduce asexually via excised vegetative segments and turions that could become highly mobile in the varied aquatic habitats, possibly transported to new sites by water birds (Taylor 1989). From the scant data on gene flow it appears that *Utricularia* fits an "island" model in which little migration occurs. When it does, it consists mostly of migration of asexual (vegetative) clones that likely have little effect on gene frequencies in already established populations (Ellison et al. 2003).

8.5 Contemporary biogeography and phylogeography

8.5.1 Global patterns of diversity

The genus *Utricularia* has a circumglobal distribution (Figure 8.4), although no species grow at the poles (Taylor 1989), on most oceanic islands, or in all arid regions with exception of the mound spring habitats of Australia's Great Artesian Basin (Jobson 2013). Species richness is higher in the southern hemisphere, with maximum species and sectional diversity occurring in the Neotropical realm (Figure 8.4).
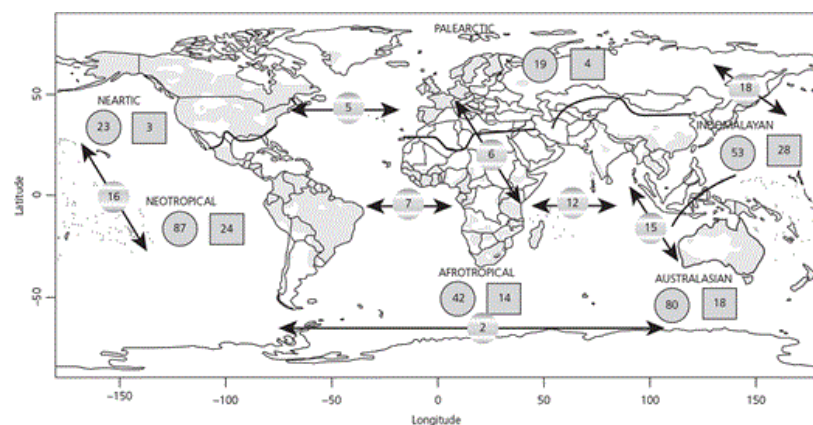
Figure 8.4 Global distribution of *Utricularia*. Black lines represent the border of each biogeographic realm. Number of species for each biogeographic realm are inside circles, number of endemic species (extent restricted < 10,000 km^2) are inside squares, and number of species shared between neighboring areas are inside shaded circles with arrows. The grey pattern shows the distribution around the world estimated by applying kernel distribution to a dataset of 28,773 records obtained from different sources (Guisande et al. 2004, ALA 2016, GBIF 2016).

The number of neighboring realms sharing species is very low, indicating that many are endemic (range size <10,000 km^2; Figure 8.4). The percentage of endemic species is highest in the Indomalayan realm (52.8%), followed by the Afrotropics (33.3%) and Neotropics (26.8%). Only a few species have wide distributions: *U. australis* (Palaearctic, Indomalaya, Australasia, Afrotropics), and *U. minor* (Palaearctic, Indomalaya, Australasia, and Nearctic realms) are present in four realms, whereas ↳ *U. subulata* and *U. gibba* are found in at least five realms. In all non-neighboring realms, the number of shared species is low. For example, the Neotropical and Australasian realms share only the two sub-cosmopolitan species (Figure 8.4).

Terrestrial species are the dominant group in the southern hemisphere and in the Indomalayan realm (Guisande et al. 2007). However, in the northern hemisphere the richness of affixed and suspended aquatic species is very similar to that of the terrestrial species, and in the western Palaearctic there are fewer terrestrial than aquatic species (Guisande et al. 2007). In the Afrotropics and

Neotropics, the proportion of the different groups is similar except for the Neotropical endemic bromeliad-tank epiphytes (Guisande et al. 2007).

8.5.2 Phylogeography

The geographical origin of *Utricularia* is unknown, but morphological and phylogenetic studies indicate a probable Neotropical origin of the genus (Taylor 1989, Jobson et al. 2003, Müller and Borsch 2005), with further dispersion, initially to the Afrotropics and Australasia (Figures 8.4, 8.5). The terrestrial habit has been inferred to be plesiomorphic (§8.3.1), and the proportion of terrestrial species is clearly higher in the Neotropics (Guisande et al. 2007), supporting this hypothesized place of origin. In the northern hemisphere, there is a higher proportion of aquatic species, which corresponds with the probable evolutionarily derived condition (Guisande et al. 2007).
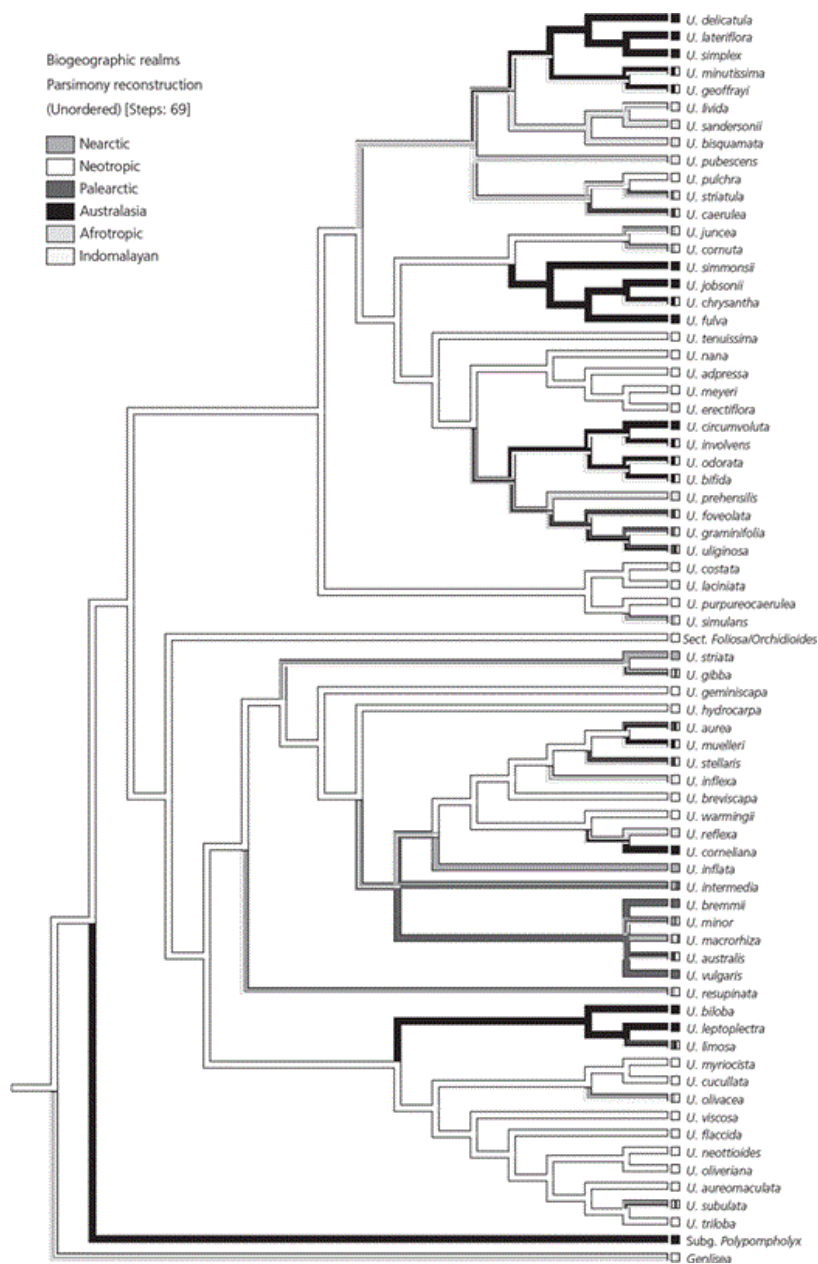
Figure 8.5 Cladograms of the strict consensus tree showing parsimoniously optimized analyses of biogeographic area. Equivocal branches indicate parsimoniously optimized plesiomorphic areas

(modified from Jobson et al. 2003).

In the Neotropics, sequences of nuclear rDNA (ITS region) revealed that haplotypes of five populations of the pantropical affixed aquatic species *U. gibba* were shared between Northern Brazil and Cuba, suggesting a recent dispersal from South to Central America (Marulanda et al. *unpublished data*). Jobson et al. (*unpublished data*) used nuclear and plastid markers across 270 populations of the morphologically variable *U. dichotoma* complex to study its phylogeographic patterns across Australia (all states except Northern Territory) and the New Zealand distribution. Independent clades representing five species (Gassin 1993, Jobson 2013) were resolved for what previously had been thought to be habitat-specific variants of *U. dichotoma* occupying deep coastal wallum swamps, shallow ephemeral pans, arid discharge and recharge mound springs, montane hanging swamps, alpine meadows, wet heathlands, and high elevation soakages (Reut and Fineran 2000).

Future population genetic and phylogeographic studies are now made more tractable by the recent development of broad spectrum microsatellite primers applicable to *Utricularia* (Clivati et al. 2012), and the sequencing of the full chloroplast genomes of *U. foliosa* and *U. reniformis* (Silva et al. 2016, 2017). In addition, the nuclear genome of *U. gibba* could provide a framework for high-throughput genome-wide genotyping in other species (Chapter 11).

8.5.3 Diversification and molecular rate acceleration

The *Utricularia*/*Genlisea* clade is substantially more species-rich and morphologically divergent than its sister group, *Pinguicula* (Chapter 6). Sampling across major clades using genes from all three genomic compartments, Jobson and Albert (2002) found that *Utricularia*/*Genlisea* genomes evolve significantly faster than those of *Pinguicula* (Figure 8.3). In an attempt to explain this heterogeneity in rates of genome evolution, Jobson and Albert (2002) first tested a generation time effect, hypothesizing that diversification rates were associated with life-history differences (annual vs. perennial). They found no significant association between life history and diversification rate, and instead suggested that the data could be explained better by the "speciation rate hypothesis," which postulates a relationship between increased nucleotide substitution rate and increased cladogenesis (Jobson and Albert 2002). They further suggested that flexible vegetative development in *Utricularia* could have been a key innovation that reduced selection pressure, enabling the invasion of underutilized nutrient-poor niches.

Using a broader taxonomic comparison across 292 angiosperm genera, including representative sequences from most other carnivorous plant lineages, Müller et al. (2004) found molecular rates in the chloroplast *matK/trnK* gene to be highest for the *Utricularia/Genlisea* lineage. Müller et al. (2004) postulated that this was caused by a positive feedback between more abundantly

p. 102   available prey-derived ↳

p. 103   ↳

biosynthetic building blocks and morphological evolution, recently termed the "predictable prey capture hypothesis" (Ellison and Gotelli 2009; Chapter 11).

8.5.4 Diversification time and biogeographic shift in subgenus *Polypompholyx*

Although there is a lack of reliable fossil data for Lentibulariaceae, recent molecular divergence dating by Bell et al. (2010), based on fossil calibration points from across angiosperms, provides an estimated divergence time for most families. Using these data, Jobson et al. (2017) estimated that the split between *U.* subg. *Polypompholyx* and *Bivalvaria* + *Utricularia* occurred ≈31 million years ago (Mya), with the subsequent split between *U.* sect. *Polypompholyx* and *U.* sects. *Pleiochasia* + *Lasiocaules* occurring ≈15 Mya. This suggests that the *U.* subg. *Polypompholyx* ancestral lineage was present in Australia for ≈15 Mya prior to the mid-Miocene when its warm and wet inland regions began a process of aridification (Byrne et al. 2011).

The molecular dating and vicariance-dispersal analyses of Jobson et al. (2017) reveal that *U.* subg. *Polypompholyx* underwent a major vicariance event ≈15 Mya between southwest Western Australia (SW) and northwest Western Australia/Northern Territory (NW) coincident with aridification of drainages across the intermediate linkage Pilbara-Gascoyne (GP) and North Western Plateau (NWP) regions (Figure 8.6). At around this same time, a coastal incursion of the far western edge of GP + NWP also occurred, with subsequent drying of the surrounding region (Byrne et al. 2011).
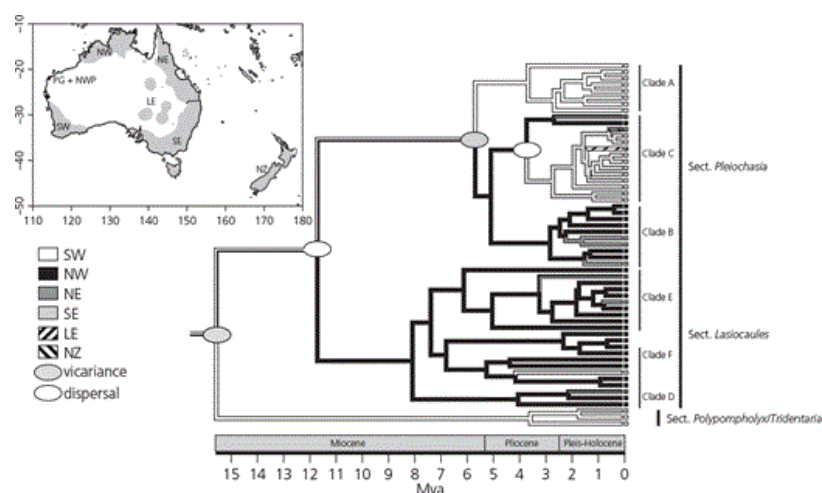
Figure 8.6 Ancestral state reconstruction for six biogeographic areas of the subgenus *Polypompholyx* distribution. Regions optimized to nodes shown on Australian/New Zealand map (southwest = SW, northwest = NW, northeast = NE, southeast = SE, Lake Eyre basin = LE, New Zealand = NZ). Clades A–F are shown behind thin lines and sections are behind thick lines. Ovals at key nodes indicate vicariance (gray) or dispersal (white) events as predicted from S-DIVA analysis, with geological epoch at base of tree.

Modified from Jobson et al. (2017) with permission.

The incursion was a likely dispersal barrier until it receded to the current coastline ≈10 Mya, after which time it may have provided suitable oligotrophic swampy habitats until the GP + NWP drainages dried up ≈6 Mya (Byrne et al. 2011). This process of loss (15–11 Mya), gain (11–6 Mya), and ↳ loss (6 Mya–present) of linkage habitats between SW and NW corresponds with the first vicariance event at the establishment of the two major clades (*U.* sects. *Polypompholyx + Tridentaria* and *Pleiochasia + Lasiocaules*), a subsequent dispersal event NW to SW at ≈11 Mya, and a second major vicariance event (*U.* sects. *Pleiochasia* and *Lasiocaules*) between SW and NW at ≈6 Mya that led to the diversification of a second SW clade within *U.* sect. *Pleiochasia* (clade A of Figures 8.1, 8.6).

Jobson et al. (2017) also found that between six and one Mya, several subsequent dispersal events occurred from either the NW or northeast (NE) regions to the southeast (SE) region. They show that dispersal of species from the SW region to the SE, and SE to the mound spring habitats of the Lake Eyre Basin (LE) and New Zealand occurred 4–1 Mya. Each of the two SW clades contain a species with disjunct distributions in SE (*U. violacea* and *U. tenella*), predicted to have dispersed across the Nullarbor Plain (NP) from SW to SE ≈2 Mya (Figure 8.6). This pattern corresponds with the geological history of the NP with a reversion to wet climates during the mid-Pliocene ≈3.5 Mya. At this time there possibly were suitable oligotrophic swampy habitats that persisted until a period of extreme cooling and drying during the Pleistocene 2–1 Mya (Byrne et al. 2011), resulting in the isolation of populations either side of the region (Figure 8.6).

8.6 Conservation issues

From the estimated > 230 species of *Utricularia*, there is information only for 29 species in the IUCN Red List (IUCN 2016); almost all of them are categorized as "unknown." Despite the restrictive criterion used for considering endemic species—only those species restricted to a particular region and whose range size <10,000 km^2—there are 69 species (≈30%) of *Utricularia* that are considered endemic. This percentage of endemic species is very high relative to other plant groups (Joppa et al. 2013). Endemic species could tend to have lower reproductive effort and dispersal capacity and be more vulnerable to disturbances or habitat changes than more widespread species (Brook et al. 2008, Pelayo-Villamil et al. 2015). As small geographical range sizes also increase extinction probabilities (Gaston 1994), the high proportion of endemic species in *Utricularia* potentially means a high proportion of vulnerable species in this genus.

8.7 Future research

Although much progress has been made in resolving phylogenetic relationships within *Utricularia*, the inclusion and phylogenetic resolution of species representing sections that are currently missing or poorly sampled are needed. These mostly involve taxa from the Neotropics, Afrotropics, and Indomalaya. Ideally, these and other new examinations of phylogenetic relationships and phylogeographic patterns should focus on fast evolving genes and take advantage of next-generation sequencing techniques. As full genomes and transcriptomes become available, future investigations into the genetic programs involved in the development, function, and energetics of bladder traps; nutrient uptake and use; and distinctions between leaves and shoots should become possible.

Studies of macroecology, conservation, and biogeography will require a detailed analysis of the taxonomic limits and of the quality of specimen records. These data could help identify the main factors affecting the diversity and distribution of *Utricularia* and the abiotic and biotic factors contributing to its speciation rate. Finally, population-level studies, including population genetics, breeding systems, pollination, and basic population dynamics should focus on narrow endemics and threatened species with an eye toward developing conservation measures for rare *Utricularia*.