

Bladderworts

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ABSTRACT

The aim of this review is to give a general idea of the current knowledge of the habitat, phylogeny, biogeography, reproduction, and carnivory of the genus *Utricularia*. These carnivorous species can be grouped according to into terrestrial, free-aquatic, affixed-aquatic, rheophytic, lithophytic and epiphytic habits, although many species have the capacity of inhabiting several different habitats. The terrestrial habit has been phylogenetically optimised as the ancestral condition, with the epiphytic and aquatic habits found to be mostly derived. The genus is cosmopolitan and phylogenetic optimizations of biogeographic area indicate a probable Neotropical origin. Some *Utricularia* species display almost complete sterility, and vegetative reproduction via turions, tubers and shoot fragments plays a dominant role in the establishment of these populations. There is controversy about the importance of insect pollination. *Utricularia* species do not face the pollinator-prey conflict, and the large flowered epiphytic species are probably derived, therefore, it seems likely that insect pollination may play an important role in the sexual reproduction of some *Utricularia* species. Bladders (utricles or traps) capture and digest prey, however strategies of chemo-attraction have not been determined. Finally, the benefit of carnivory is discussed in terms of the costs to photosynthetic rate and respiration associated with the production and maintenance of bladders.

Keywords: biogeography, carnivorous plant, habitat, physiology, phylogeny, reproduction

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INTRODUCTION

In the carnivorous plant family Lentibulariaceae, the bladderworts *Utricularia* is more species-rich, morphologically divergent and has a higher speciation rate than the other genera of the family, the lobster-pots *Genlisea*, and the butterworts *Pinguicula* (Jobson and Albert 2002; Müller *et al.* 2004). *Utricularia* is the most species-rich genus among carnivorous plants, containing 35% of all carnivorous plant species. This genus is diverse not only in terms of the number of species, but also in the spectrum of habitats in which it occurs and the extreme nutritional specialization, which mainly consists in the production of bladders that enable the capture of prey. These bladders rank among the most complex organs in the plant kingdom (Lloyd 1942; Juniper

et al. 1989).

In addition, this genus is important because of its worldwide distribution in aquatic and terrestrial environments (Taylor 1989), although it rarely dominates communities. This indicates tolerance for different environmental conditions, but with some restrictions that are probably associated with the cost of carnivory, which means that the genus only has the capacity to overwhelm other species under very specific environmental conditions of nutrient limitation.

Although the genus *Utricularia* has been studied since the early 19th century its taxonomy is still under discussion, and many important and surprising results are being continually revealed, indicating that the biology of this genus is still insufficiently understood. This review focuses on previous studies carried out so far about the characteristics such

as the habitat, phylogeny, biogeography, reproduction and, particularly, carnivory of *Utricularia* species.

HABITAT

The bladder-trap is a modified leaf structure that requires water for function and, therefore, a common characteristic of all *Utricularia* species is that they grow in aquatic habitats, or in habitats with more or less permanent or seasonally high humidity, even if sometimes the bladders are covered by a thin film of water (on rocks, tree trunks, etc.). This common requirement of all *Utricularia* species may be achieved in different habitats and, for a better understanding of the biology of this group, it is important to classify the species into different groups, according to their habitat. However, it is necessary to point out that the categorization of *Utricularia* species into different groups is still difficult, as the information about the habitat of many species is rather vague and, moreover, many species may be included in several groups. For instance, *U. humboldtii* that inhabits the water-filled leaf axils of Bromeliaceae can also be found on very wet soils in open savannah (Taylor 1989). Free-aquatic (e.g. *U. minor*) or affixed-aquatic species (e.g., *U. ochroleuca*) may inhabit an aquatic or terrestrial environment.

Taylor's classification (1989) identified six different groups: **terrestrial**, **free-aquatic**, **affixed-aquatic**, **rheophytic**, **lithophytic**, and **epiphytic** species. **Terrestrial** species are those that grow in wet soils (peat, sand, clay, open grassland, etc), that may be inundated during the wettest season because of proximity to swamps, shallow pools, streams, marshes, etc. Yet the plants may still experience periods when the soil is dry and, when waterlogged, the soils are partly (hypoxia) or entirely (anoxia) deprived of oxygen (Adamec 1997). **Free-aquatic** species are capable of growing and flowering in still or slowly flowing waters (pools, ponds, swamps, marshes, creeks, etc). **Affixed-aquatic** species are also able to exist as freely suspended aquatics in still or slowly flowing waters, but for better growth and flowering, they require to be anchored by specialized shoots in solid or slightly solid substrate. **Rheophytes** grow in more or less swiftly flowing water and, therefore, are equipped with special organs that anchor the plants to solid substrate (normally rocks). **Lithophytes** are species normally found on rocks. **Epiphytic** species are those that can grow on moss covered trees, mossy banks, etc, and in pools of water in the leaf axils of *Bromeliaceae* and occasionally of other families.

Around 220 *Utricularia* species have been formally described, although some still await confirmation. Most are terrestrial, and aquatic species (free, affixed and rheophytic species) constitute the second most numerous group (Fig. 1). At the opposite extreme are the epiphytes of bromeliads consisting of the three species (*U. reniformis*, *U. nelumbifolia* and *U. humboldtii*), although *U. reniformis* is usually terrestrial and *U. humboldtii* may be found on tree trunks and also on wet soils. In fact, many species may grow in different habitats. There are 11 species that can be categorized as terrestrial and/or sub-aquatic (e.g., *U. fulva*, *U. biloba*, *U. resupinata*), 5 species as terrestrial and affixed-aquatic (e.g., *U. arnhemica*, *U. smithiana*, *U. holtzei*), 9 species as terrestrial/lithophytes (e.g., *U. multicaulis*, *U. pulchra*, *U. geminiloba*) and 4 species as terrestrial/epiphytes (*U. asplundii*, *U. alpina*, *U. praetermissa* and *U. striatula*).

The capacity of some species to live in several different habitats may explain the high overlap of certain morphological characteristics among some species. A discriminant analysis showed that it is only possible to correctly classify approximately 67% of the species according to the maximum size of the rhizoids, leaves, stolons, seeds, corollas and inflorescences. The discriminant functions I and II, the maximum size of the leaf and that of the stolon, accounted for 63% and 32% of variance, respectively, and discriminated among species with larger leaves (epiphytic species) and among species with larger stolons (free-aquatic spe-

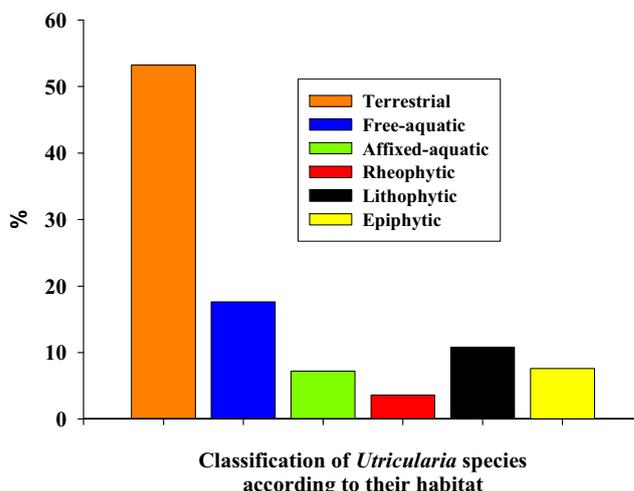


Fig. 1 *Utricularia* classification. Categorization of *Utricularia* species in different groups according to their habitat. The percentages have been calculated considering that the species may be in several groups.

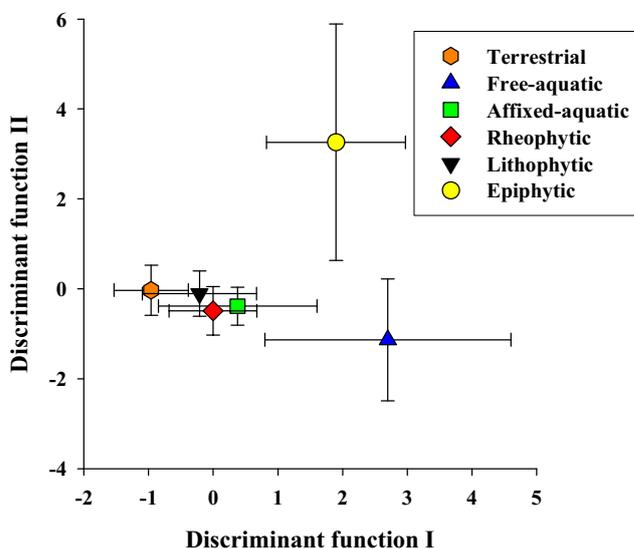


Fig. 2 Discriminant analysis. Plot of the first two functions, of the discriminant analysis performed to the morphological characteristics of the *Utricularia* species, showing the mean ± SD of the scores. Data taken from Taylor (1989).

Table 1 Results of a discriminant analysis showing the percent of groups of *Utricularia* correctly classified from the original data according to the maximum size of the rhizoids, leaves, stolons, seeds, corollas and inflorescences. Group abbreviations: terrestrial (Terr), free-aquatic (Free-A), affixed-aquatic (Aff-A), rheophytic (Rheo), lithophytic (Lith), and epiphytic (Epi) species.

True groups	Predicted groups					
	Terr	Free-A	Aff-A	Rheo	Lith	Epi
Terr	68.3	0.0	4.0	4.0	22.8	1.0
Free-A	3.7	63.0	14.8	3.7	11.1	3.7
Aff-A	11.1	0.0	66.7	0.0	22.2	0.0
Rheo	0.0	0.0	0.0	83.3	16.7	0.0
Lith	31.6	5.3	0.0	0.0	57.9	5.3
Epi	0.0	0.0	7.7	0.0	15.4	76.9

cies) (Fig. 2). In almost all groups, there was a high overlap with terrestrial species (Table 1), indicating that some species of each group have the typical morphological characteristics of terrestrial species and, thereby, concurring with the observed capacity of many species to be terrestrial and also to live in another habitat. However, it should be stressed that some characteristics, such as leathery leaves, storage organs and, particularly, bladder morphology, were

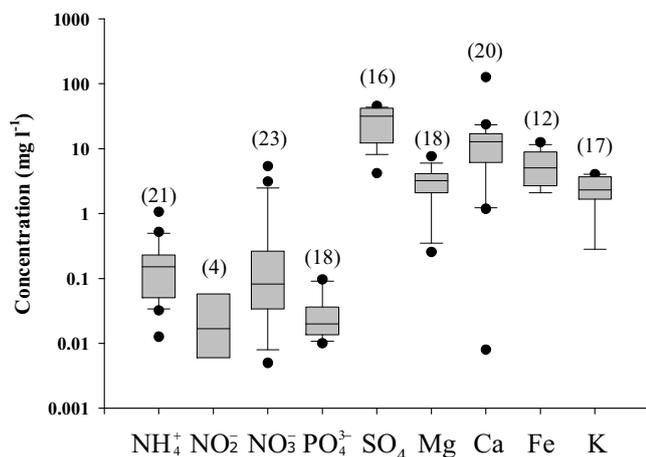


Fig. 3 Limnological characteristics of the habitat of aquatic *Utricularia* species. Concentration of some nutrients and elements obtained in the habitats occupied by some aquatic *Utricularia* species. Number in parentheses are the total number of observations (each observation is a unique species \times site combination). Sources: *U. vulgaris* (Roberts 1972; Kuczynska 2006), *U. australis* (Cirujano *et al.* 2000; Chicote *et al.* 2004; Navrátilová and Navrátil 2005a, 2005b; Navrátilová *et al.* 2006) *U. geminiscapa* (Roberts *et al.* 1985) *U. foliosa* (Guisande *et al.* 2004; Manjarrés-Hernández *et al.* 2006; Sanabria-Aranda *et al.* 2006), *U. purpurea* (Roberts *et al.* 1985), *U. aurea* (Jha *et al.* 1978), *U. resupinata* (Roberts *et al.* 1985), *U. gibba* (Roberts *et al.* 1985; Mazzeo *et al.* 2001), *U. intermedia* (Navrátilová and Navrátil 2005a, 2005b; Navrátilová *et al.* 2006; Adamec pers. comm.), *U. ochroleuca* and *U. minor* (Navrátilová and Navrátil 2005a, 2005b; Navrátilová *et al.* 2006), *U. obtusa* (Terneus 2002), *U. stygia* (Adamec pers. comm.).

not included and that they are specific for some groups, and might favour discrimination among the groups. Future research regarding estimations of growth and photosynthetic rates may also favour discrimination among these groups.

The information available for the environmental characteristics of the habitat occupied by *Utricularia* only relates to the aquatic species. Nevertheless, this information corroborates that *Utricularia* species, at least the aquatic ones, mainly live in habitats with a low concentration of nutrients (Fig. 3).

PHYLOGENY

The two phylogenetic studies of the family Lentibulariaceae (Lamiales) have both shown *Utricularia* to be sister to *Genlisea*, with these two genera forming a lineage sister to *Pinguicula* (Jobson and Albert. 2002; Jobson *et al.* 2003; Müller *et al.* 2004, 2005).

Of these studies Jobson and Albert (2002) used the predominantly non-coding plastid DNA regions comprising the *trnL-F* spacer and intron and *rps16* intron, while Müller and Borsch (2005) utilized the chloroplast DNA sequences of the *trnK* intron and *matK* gene. The number of substitutions per site between species pairs, originally shown in Fig. 10 of Müller and Borsch (2005), was used in a comparison with the number of substitutions per site between species pair of the tree shown in Fig. 1 of Jobson *et al.* (2002) and the number shown in Fig. 2 of Jobson *et al.* (2003).

It is clear that the number of substitutions per site between species pair in the tree of Müller and Borsch (2005) is similar to the one obtained in the tree of Jobson *et al.* (2002) (Fig. 4A) and Jobson *et al.* (2003) (Fig. 4B), with the sole exception of *U. olivacea* in both regressions (Figs. 4A and 4B). In the tree of Müller and Borsch (2005), *U. olivacea* is positioned within section *Utricularia*, in agreement with the classification of Taylor (1989), while the tree of Jobson and Albert (2002) and Jobson *et al.* (2003) *U. olivacea* is sister to section *Vesiculina*.

As each *Utricularia* species pair was not independent

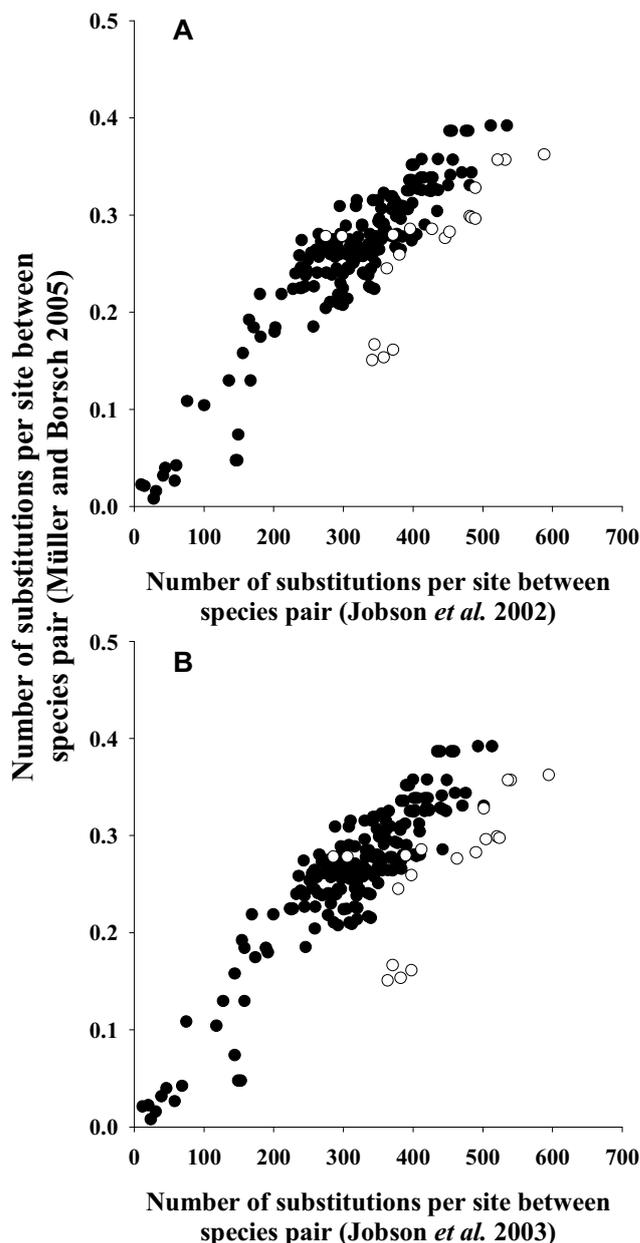


Fig. 4 Phylogenetic comparison. Relationship between the number of substitutions per site between species pair in the tree showed in Fig. 10 of Müller and Borsch (2005) and in (A) Fig. 1 of Jobson *et al.* (2002) and (B) Fig. 2 of (Jobson *et al.* 2003). White circles are the number of substitutions per site between *U. olivacea* and the other species and black circles are the rest of species.

from the other, a bootstrap method was used to evaluate the statistical significance of the relationships shown in Figure 4, excluding *U. olivacea* from both regressions. Each regression was recalculated 1000 times using a random series in which only 50% of the abundance data were used to calculate spatial niche overlap. In all cases, the slopes of both regressions were positive and significantly different from zero ($p < 0.001$). A better fit was obtained when comparing the tree of Müller and Borsch (2005) with that of Jobson *et al.* (2002) (Fig. 4A, $r^2 = 0.85$), than when comparing it with the tree shown in the study of Jobson *et al.* (2003) (Fig. 4B, $r^2 = 0.82$). Therefore, in this review the trees from Müller and Borsch (2005) and Jobson *et al.* (2002) were used to obtain a combined tree (Fig. 5), excluding the species *U. olivacea*. This combined tree was obtained by individually standardizing the number of substitutions per site obtained between species pairs for the trees from the two studies, to a scale range of between 0 and 1. The joining or tree clustering method, using a single linkage as the amalgamation rule and the Euclidean distance as the distance measure, was

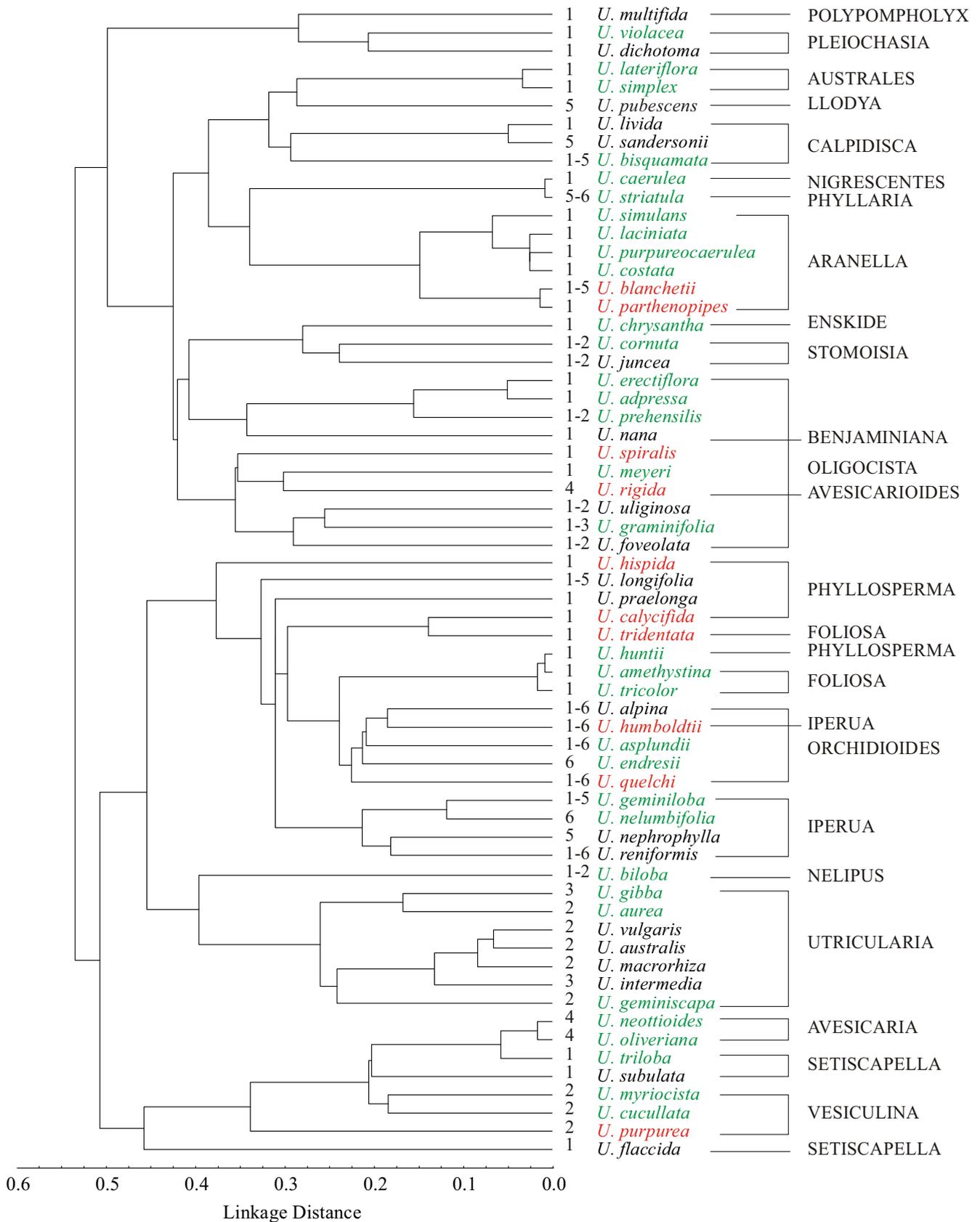


Fig. 5 Phylogeny of *Utricularia*. Tree as inferred with phylograms of Fig. 1 of Jobson and Albert (2002) and Fig. 10 of Müller and Borsch (2005). In red all the species that are only in the tree of Müller and Borsch (2005), in green those only present in the tree of Jobson and Albert (2002) and in black the sharing species between both trees. The numbers indicate the six different groups: terrestrial (1), free-aquatic (2), affixed-aquatic (3), rheophytic (4), lithophytic (5) and epiphytic species (6).

applied to these standardized data (Guisande *et al.* 2006). When the same species was included in both trees, the mean of the standardized data of both trees was calculated.

Although some sections are represented by completely different species in the trees of Jobson *et al.* (2002) and Müller and Borsch (2005), in general, the combined tree

obtained (**Fig. 5**) agrees with the classification of Taylor (1989), which was based on morphological characters and recognizes 35 sections. Most of the species that were classified into a certain section by Taylor (1989) are found in a well-supported group in the tree (**Fig. 5**). There are several exceptions. *Utricularia nana* is clearly in the section *Oligo-*

cista (Fig. 5), but Taylor (1989) included it in the monotypic section *Benjaminia*, even though in the same study the author mentioned that this section shares close affinity with section *Oligocista*. The differences between the sections *Phyllosperma* and *Foliosa* are not clear (Fig. 5), and the close affinity of sections *Phyllosperma* and *Foliosa* is also evident in the trees of Jobson and Albert (2002) and Müller and Borsch (2005). The rheophytic *U. rigida* was ascribed to the monophyletic section *Avesicarioides* (Taylor 1989), which is now nested within section *Oligocista* (Müller and Borsch 2005). Müller and Borsch 2005 also demonstrate that *U. humboldtii* is nested within section *Orchidioides* (Fig. 5), although Taylor included it in the section *Iperua*. Finally, there is a close affinity between the sections *Setiscapella*, *Vesiculina* and *Avesicaria* indicating that morphological differences between these sections are not clear (Fig. 5).

As already mentioned, the phylogenetic trees obtained by Jobson and Albert (2002) and Müller and Borsch (2005) are very similar (Fig. 4A), but in addition to the main discrepancy regarding *U. olivacea*, they also differ in the relationship among some clades. The clades that comprise the sections *Polypompholyx* and *Pleiochasia* form a monophyletic lineage sister to a clade containing all other *Utricularia* (Jobson and Albert 2002), but not in Müller and Borsch (2005). The combined tree (Fig. 5) supports the hypothesis of Jobson and Albert (2002) that both sections form a monophyletic group. The section *Aranella* is monophyletic in the study of Jobson and Albert (2002), but not in that of Müller and Borsch (2005).

Regarding the causal mechanism promoting the evolution of bladderworts, it has been shown that trap form (Jobson and Albert 2002) and habit (Jobson et al. 2003) are phylogenetically correlated and that, therefore, major groups within the bladderwort lineage are defined by distinct trap morphologies and habit as well as by phylogeny

(Jobson and Albert 2002; Jobson et al. 2003). As such variation in trap form across the genus may have permitted *Utricularia* to become a specialized carnivore, favouring the occupation of different habitats (Jobson and Albert 2002).

The sections *Polypompholyx* and *Pleiochasia* seem to be pleiomorphic regarding both morphological features and phylogenetic position (Fig. 5) and therefore may share a close relationship with the genus *Genlisea* (Jobson et al. 2003). Reifenrath et al. (2006) also suggest that there is a close relationship between the species of the genus *Genlisea* and the section *Polypompholyx*, based on the characteristics of the trap of *U. multifida*. They hypothesize that the trap of *U. multifida* may not function with a suction mechanism, but has tunnel-shaped entrances with an open door leading to a digesting chamber, similar to that seen in *Genlisea*. Despite the above study, Lloyd (1942) demonstrates a normal suction-trap mechanism for this species.

In the *Utricularia* lineage, the terrestrial habit has been phylogenetically optimised as ancestral (Jobson et al. 2003).

The fact that some species live in several habitats, the overlap in some morphological characteristics among species, and that some species occupying the same habitats are not close in the phylogenetic tree (Fig. 5), clearly questioned the usefulness of separating *Utricularia* into the six functional groups as described by Taylor (1989) and mentioned above. The close affinity among some of the sections described by Taylor (1989) also indicates that Taylor's classification based on morphological characters should be revised for some sections. However phylogenetic information for some sections is required to test the validity of all the sections described by Taylor (1989). Therefore, habitat classification and morphological groupings are not totally correct but, as the phylogenetic information is still not enough for grouping within all the genera, we decided to use the habitat classification as a way to show general patterns in *Utricularia*.

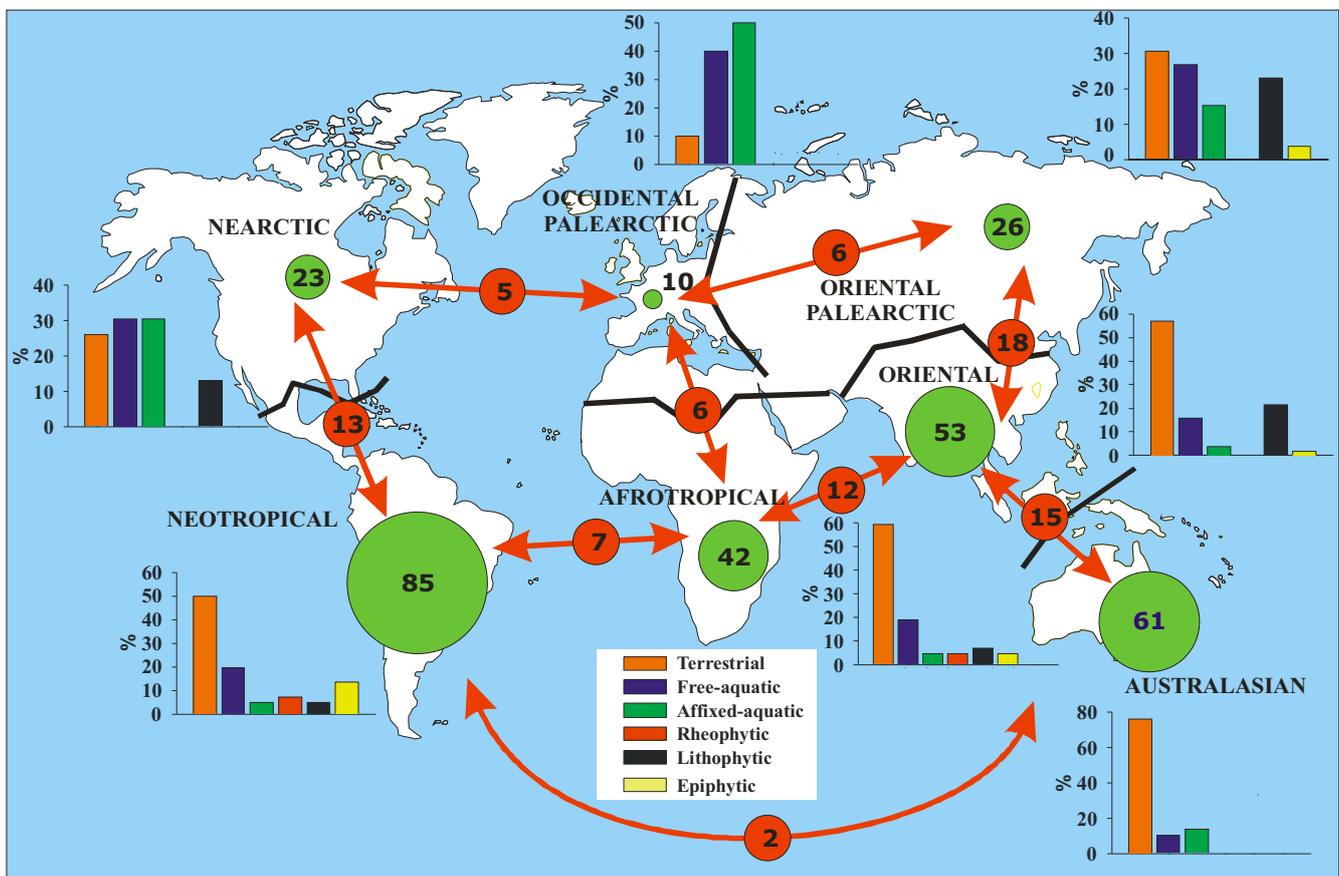


Fig. 6 Biogeography of *Utricularia*. The black lines represent the border of each biogeographic area. Number of *Utricularia* species in the different biogeographic areas (numbers inside green circles) and percentage of sharing species between neighbored areas (numbers inside red circles) are shown. The figures represent in each biogeographic area the percentage of species (which have been calculated considering that the species may be in several groups) for each of the groups categorized according to the habitat of the species.

BIOGEOGRAPHY

The genus *Utricularia* is cosmopolitan, but is absent at the poles and, in general, in arid regions and oceanic islands (Taylor 1989). Species richness is higher in the southern hemisphere (Fig. 6), maximum species diversity occurring in the Neotropical region. In the Afrotropical region, the proportion of the different groups is very similar to that of the Neotropical region, except for the endemism of bromeliad-tank epiphytes in the neotropics (Fig. 6), which is not surprising since Bromeliaceae is predominantly a Neotropical family.

Terrestrial species are the dominant group in the southern hemisphere and in the Oriental region. However, in the northern hemisphere the richness of aquatic species, particularly affixed and free aquatic species, is very similar to that of the terrestrial species and in the western Palearctic region the number of terrestrial species is lower, in comparison to that of aquatic species (Fig. 6).

It is important to point out that the number of neighbouring regions sharing species is very low, indicating that many are endemic. Only 2 species, *U. gibba* and *U. subulata* are found in many regions. The Oriental and the eastern Palearctic regions have the maximum number of shared species, just 15 (Fig. 6). In all non-neighbouring regions, the number of shared species is much lower. For example, the Neotropical and Australasian regions share only 2 species. The exception to this high number of endemic species is the western Palearctic region, where only *U. bremii* is endemic.

The geographical origin of *Utricularia* is not clear 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 Afrotropical and Australasian regions and, subsequently, to the rest of the regions. As previously mentioned, terrestrial habit has been inferred to be plesiomorphic, and the proportion of terrestrial species is clearly higher in the Neotropical region (Fig. 6), supporting this region as place of origin. In the northern hemisphere, there is a higher proportion of aquatic species, which corresponds with the probable evolutionary derived condition.

REPRODUCTION

Utricularia spp. reproduce sexually via seeds, by autogamy (self-pollination) or by xenogamy (cross-pollination), as well as by vegetative reproduction via turions, tubers and shoot fragments. A full description of the seeds is given by Taylor (1989).

Sexual reproduction

In sexual reproduction, *Utricularia* spp. may have cleistogamous and/or chasmogamous flowers. Chasmogamous flowers are those that show all the characteristics of insect-pollinated flowers (Fig. 7A). These flowers are adapted to cross-pollination, although Kondo (1972) mentioned that, in the sister taxa *U. cornuta* and *U. juncea*, chasmogamous flowers are also capable of self-pollination.

In carnivorous plants, the spatial and temporal coincidence between flowers and traps presents a potential conflict between the plant-pollinator and plant-prey systems (Zamora 1999). Probably for this reason, many carnivorous plants display considerable spatial separation between their chasmogamous flowers and traps (Juniper *et al.* 1989). *Utricularia* species have underground, aquatic or sub-aquatic traps and aerial chasmogamous flowers, ensuring that pollinators never get caught. However, although peduncle length plays no part in pollinator protection in *Utricularia* species, Anderson and Midgley (2001) showed that in terrestrial *Utricularia* peduncles are comparable in length to/or exceed those of *Drosera*. As *Utricularia* does not face the pollinator-prey conflict, long peduncles may be a response to improved pollinator attraction or seed dispersal.

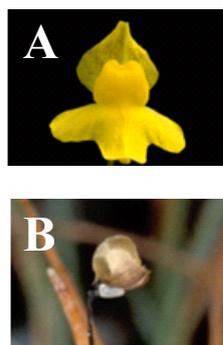


Fig. 7 Flowers of *Utricularia subulata*. Chasmogamous (A) and cleistogamous flower (B). Photos by Barry Rice.

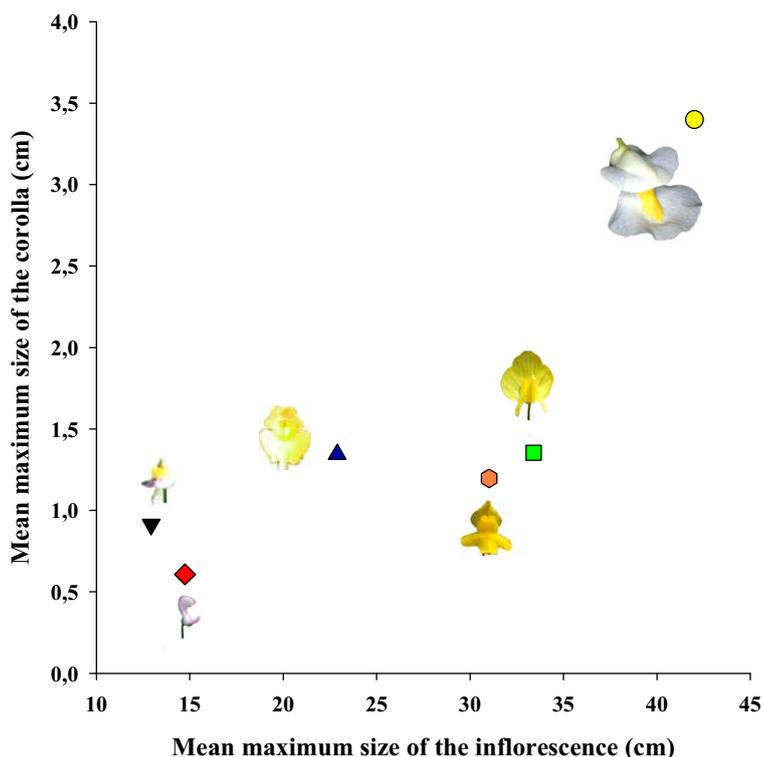


Fig. 8 Size of the inflorescence and corolla. Relationship between the maximum size of the inflorescence and the maximum size of the corolla of the different groups of *Utricularia* species categorized according to their habitat. Examples of terrestrial (*U. subulata*), free-aquatic (*U. foliosa*), affixed-aquatic (*U. gibba*), rheophytic (*U. resupinata*), lithophytic (*U. bisquamata*) and epiphytic species (*U. alpina*). Photos of Barry Rice with the exception of *U. foliosa*. Data taken from Taylor (1989).

Some authors have indicated that potential pollinators are scarce for *Utricularia* species (Kondo 1972; Raynal-Roques and Jérémie 2005), which might indicate that the large peduncle is mainly a strategy to enhance seed dispersal. However, other studies have shown that the flowers of *Utricularia* species are self- or cross-pollinated by aphids or small dipterous species (Yamamoto and Kanodo 1990). Hobbhahn *et al.* (2006) in a study carried out with terrestrial species (*U. albocaerulea*, *U. purpurascens* and *U. reticulata*) showed that in all three species the spatial arrangement of the reproductive organs makes an insect vector necessary for pollen transfer within and between flowers, and more than 50 species of pollinating insects were identified. Moreover, the significant relationship between the maximum size of the inflorescence and the maximum size of the corolla in *Utricularia* species (Fig. 8) ($r^2 = 0.67$, $p = 0.045$) suggests that insect pollination might be important, as large inflorescences are associated with large flowers, or it could be an ancestral reminder that insect pollination was important for their reproduction. The maximum size of the corolla is very similar in terrestrial, free-aquatic and affixed-aquatic, lower in rheophytic and lithophytic species, and higher in epiphytic species, particularly the epiphytes of bromeliads (Fig. 8). The phylogeny of Lentibulariaceae shows that the radiation of all lineages in this family started with the terrestrial habit, and both aquatic and epiphytic species represent derived conditions (Jobson *et al.* 2003; Müller *et al.* 2004). Therefore, it is probable that those species with a larger corolla, the epiphytic species, are derived, and therefore insect pollination may play an important role in the reproduction of some *Utricularia* species.

Cleistogamous flowers are not morphologically specialized to attract pollinators (Fig. 7B), although some attractive attributes of the flower are still present (Taylor 1989), which may signify that xenogamous reproduction is pleisomorphic (Raynal-Roques and Jérémie 2005). In these flowers, autogamy is probably the only method of reproduction. They also produce an abundance of seeds when cross-pollination is ineffective. As cleistogamous flowers are not designed for animal pollination, they are sometimes situated underground or submerged in the water column (Raynal-Roques and Jérémie 2005).

Vegetative reproduction

Some *Utricularia* species reproduce by vegetative reproduction via turions (mainly in aquatic species of the section *Utricularia*), tubers (mostly in epiphytic and lithophytic species) and shoot fragments. In some species, the vegetative reproductive structure is the leaf, e.g. *U. cornuta* and *U. juncea*. Leaves separate, float away after rain, and develop into new individuals (Kondo 1972).

Some *Utricularia* populations display almost complete sterility, e.g. *U. australis* (Kameyama *et al.* 2005) in Japan (although *U. australis* in Europe produces seeds), and vegetative reproduction by turions or shoot fragments plays a dominant role for the establishment of these populations (Araki and Kanodo 2003; Kameyama and Ohara 2006).

Turion and tuber production also permits a period of dormancy. This dormancy phase serves to tolerate periods of stress such as desiccation, low temperatures and/or nutrient deficiency (Winston and Gorham 1979; Taylor 1989; Adamec 1999). Day length, in some cases in combination with low temperature, serves as the environmental cue to initiate turion formation (Winston and Gorham 1979a). The turion undergoes no obvious morphological change during dormancy, but it does experience large physiological alterations. Winston and Gorham (1979a) suggested that *U. vulgaris* turions exhibit three states of dormancy: pre-, innate and imposed. The first is short and controlled by parental factors. The second lasts throughout the period when the growth conditions (water temperature, day length) are not too favourable. In *Utricularia* species, it has been observed that starch is the main storage carbohydrate during this phase (Compton 1909; Winston and Gorham 1979b), ac-

counting for up to 25% of dry weight in *U. vulgaris* (Winston and Gorham 1979a). In *U. vulgaris*, prior to turion formation and during the innate dormancy, abscisic acid-like and bound gibberellin-like levels were high, and free gibberellin-like and auxin-like levels were low. In contrast, during sprouting, there were low levels of abscisic acid-like and high levels of free gibberellin-like and auxin-like (Winston and Gorham 1979a). In some aquatic *Utricularia* species, in which turions are frost resistant organs, the turions are connected to the shoot and, when shoots die and decompose, they become denser than the water and drag the turions to the bottom. In early spring, when water temperature is increasing, the turions separate from the shoots and reach the water surface (Adamec 1999).

Reproductive investment

The biomass allocated to reproductive structures in terrestrial species ranges between approximately 86% and 92%, whereas in aquatic species it only ranges between approximately 10% and 17% (Brewer 1999; Porembski *et al.* 2006). It is possible that aquatic *Utricularia* species rely on vegetative fragments for reproduction and dispersal rather than on dispersal of seeds (Porembski *et al.* 2006). The information for epiphytic species is scarce, but it seems that they may be in an intermediate position, as Porembski *et al.* (2006) observed that the epiphytic species *U. quelchii* allocated 40.8% of its biomass to reproductive structures.

In some species, changes in the ratio of cleistogamous/chasmogamous flowers are probably a strategy to optimise reproductive investment. Cleistogamy probably uses less energy than chasmogamous flowers and, therefore, under unfavourable conditions (ephemeral pond, low temperature, etc.), in some species the ratio of cleistogamous/chasmogamous flowers is higher (Raynal-Roques and Jérémie 2005). Some aquatic species (*U. australis* and *U. ochroleuca*) are sterile but these plants invest in chasmogamous flowers.

CARNIVORY

Bladder architecture

The most detailed accounts of bladder-trap structure are those by Meierhofer (1902), Lloyd (1929; 1942), the review of Skutch (1928) and, more recently, the comparative study by Reifenrath *et al.* (2006) of the trap features of some *Utricularia* species adapted to different habitats. The bladders vary among species and, as mentioned above, major groups within the bladderwort lineage are well defined by distinct trap morphologies.

Traps are produced by phylloclades, shoots, stolons and rhizoids, and their positions vary among the *Utricularia* sections (Taylor 1989). The bladder is attached to the stem by a short stalk (Fig. 9). The wall of the trap usually consists of two cell-layers (Lloyd 1929), but in other species there are more than two layers (Lloyd 1942; Reifenrath *et al.* 2006).

The entrance of most traps is surrounded by hairs, described as trichomes, as the term trichome is used to describe all appendages arising from the epidermis without contributing to the structure for the subsequent cell layers (see Thurston and Seabury 1975). Meierhofer (1902) determined that all bladder hairs are of epidermal origin.

The utricle hairs or trichomes can be categorized by their location on, or within, the utricle (Fig. 9). In some species, in the dorsal position of the entrance, there is one pair of branched antennae (section *Utricularia*) (Fig. 9), whereas in other species there is one pair of non-branched wide appendages (section *Polypompholyx*), and in some others there are no appendages at this position, but merely a very small tissue elevation (section *Stomoisia*). In some species the trap entrance is surrounded by rows of appendages located in lips-like structures (section *Nigrescentes*) (Lloyd 1942; Reifenrath *et al.* 2006). Bristles are hairs that may appear on the outside of the door of some species (Fig.

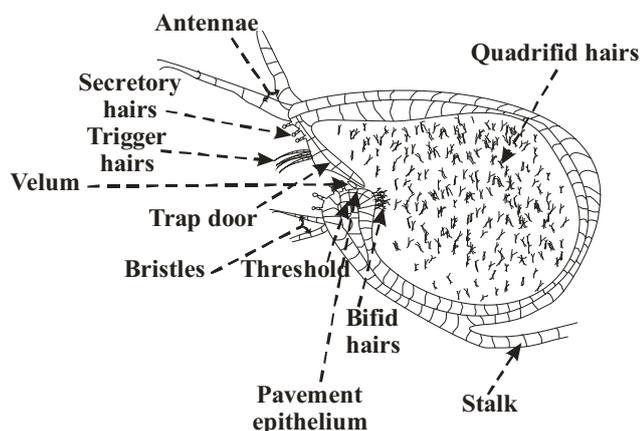


Fig. 9 Schematic representation of a bladder of *Utricularia*.

9). Antennae and bristles lead potential substratum-dwelling prey towards the valve where they can be captured, by offering the prey a favourable substratum that exploits their natural locomotor and feeding behaviour. Field results have demonstrated that a higher ratio of antenna size/bladder length enhances the capture efficiency of bladders (Sanabria-Aranda *et al.* 2006). This concurs with previous experimental work showing that the loss of any antenna or bristle causes a highly significant decrease in capture success (Meyers and Strickler 1979).

In most species, the closed trap door rests on the threshold (Fig. 9), and Reifenrath *et al.* (2006) distinguish between two types of thresholds, based on shape and cellular composition. The outer layer of the threshold is the pavement epithelium that appears to produce the velum and secretes mucilage. When closed, the end of the trap door is positioned on top of the pavement epithelium, and both the epithelium and the velum support the sealing of the door. The velum may function as a doorstop (Lloyd 1929).

In the central region outside the door, there are several trigger hairs in many species, which are touch-sensitive appendages, implying that a touch of the bristles releases the door from the velum (Fig. 9). The door opens inward when an animal touches the trigger hairs. However, in some species these trigger hairs are absent (Lloyd 1942; Taylor 1989; Reifenrath *et al.* 2006) and, therefore, trigger hairs may be nonessential for trap door function.

In the entrance-way of the bladders, there are also secretory (mucilage) hairs that vary in size (Fig. 9). They possess a stalk, neck cell and a capital or terminal cell (Thurston and Seabury 1975). In the pavement epithelium, there are many secretory hairs that may be responsible for secreting a mucilage-like substance that constitutes the velum.

Bifid and quadrifid (Fig. 9) hairs produce enzymes, which participate in the digestion of prey and the transport of water and ions (Fineran and Lee 1975; Plachno *et al.* 2006). Bifid hairs occur at the threshold, whereas the quadrifid hairs are within the utricle.

Mechanisms of attracting prey

Given their dependence on animal-derived nutrients, there are needs to be strong selection for carnivorous plants to evolve effective mechanisms for attracting prey (Ellison and Gotelli 2001). *Utricularia* spp. are no exception, given the potential importance of the prey's nutrient contribution to growth. Bladderworts capture prey non-randomly on a wide array of aquatic invertebrates (Harms 1999; Jobson and Morris 2001; Guisande *et al.* 2000, 2004), because the percentage of species captured by bladders is different from the percentage of species in the habitat. This may be because of the behaviour of some zooplankton and macroinvertebrates which swim close to the bladders looking for the food attached to them. However, to date, it has not been possible to show any kind of chemo-attraction strategy dis-

played by *Utricularia* species to lure prey (Guisande *et al.* 2000, 2004; Manjarrés-Hernández *et al.* 2006).

Cohen (1875, in Meyers 1982) was the first to propose that glandular structures of the valve and their associated mucilage constituted a source of prey attractant. However, a later study suggests that bladderworts lack attractants for prey (Meyers and Strickler 1979), which was corroborated by Sanabria-Aranda *et al.* (2006), who showed that carbohydrate production was not a strategy of *U. foliosa* to enhance the capture of prey, as the amount of carbohydrates in the bladder was positively related with the abundance of periphyton.

Another evolved mechanism for luring prey may be to enhance periphyton quality and/or quantity (Sanabria-Aranda *et al.* 2006). There is the possibility that aquatic plant hosts might use chemical control or merely texture to manipulate the composition of the periphyton community for their own advantage. In *U. foliosa* the amount of prey captured by bladders increases when the periphyton abundance and richness associated with bladders is higher. However, the abundance and richness of the periphyton associated with *U. foliosa* mainly depend on the amount of phosphorous and nitrogen in the water rather than on any facilitation mechanism displayed by the plant.

As already mentioned, the only strategy observed so far for luring prey is the presence of antennae and bristles, as these probably lead potential substratum-dwelling prey towards the valve for capture. It may be that the strategy of *Utricularia* prey capture is simply physical structures such as antennae and bristles, which clearly work for the plant (Sanabria-Aranda *et al.* 2006).

Bladder functioning

The main functions of the bladder are capture and digestion of prey. Little animals that touch trigger hairs near the entrance are sucked into the bladder through the trap door, because of the lower hydrostatic pressure created inside the trap. When the trap is set, the outer walls are concave and the chamber is under negative hydrostatic pressure. It is believed that setting the trap requires considerable energy in order to engage an active ion transport process, whereby water is pumped out through the thin bladder walls to create negative internal pressure. However, it seems that other species lack the trigger hairs (Reifenrath *et al.* 2006). According to these authors, the bladders in section *Polypompholyx* might not function with a low pressure-suction movement, but rather form channel traps with a permanent open door, similar to the traps of the sister genus *Genlisea*. However, Lloyd (1942) found normal function in this section, and close relative *U. westonii* has highly developed trigger hairs (Taylor 1989).

Enzymes may play an important role in the digestion of prey. Enzymes like protease, acid phosphatase and esterase, were found in both bifid and quadrifid hairs (Vinténjoux 1974; Sirová *et al.* 2003; Plachno *et al.* 2006), while phosphatase activity has also been observed in some pavement hairs (Plachno *et al.* 2006). It seems that stimulation by prey is not necessary for enzyme production (Plachno *et al.* 2006). For example, Sirová *et al.* (2003) found that enzymes from external aquatic environments might be accumulated in the bladders of some species. There are many species of living bacteria, fungi, algae, protozoa and rotifers (Jobson and Morris 2001; Richards 2001; Sirová *et al.* 2003; Plachno *et al.* 2006), that may also contribute to the enzymes found in the bladders and, hence, to the process of prey digestion.

Benefits of carnivory

Several features suggest that carnivory is important for *Utricularia* species: traps are the first structures to arise after the very minute cotyledons (Lloyd 1942); the relative contribution of nitrogen and phosphorous obtained from prey can be higher than 50% (Lollar *et al.* 1971; Friday and

Quarby 1994; Adamec 1997); carnivory enhances growth at low nutrient concentrations (Jobson *et al.* 2000); and investment in carnivory increases as nutrient concentration and zooplankton abundance diminish (Guisande *et al.* 2000, 2004; Kibriya and Jones 2007).

However, photosynthetic rates for leaves (between 1.9 and 32.5 nmol g⁻¹ s⁻¹ fresh weight) are approximately 2-7 times greater per unit biomass than bladders (between 1.4 and 4.1 nmol g⁻¹ s⁻¹ fresh weight) in *Utricularia* species (Knight 1992; Adamec 2006). Moreover, it seems that respiration of bladders is 1.7-3.3 higher per unit biomass than in leaves or photosynthetic shoots (Adamec 2006), although Knight (1992) did not find significant differences in respiration between bladders and leaves due to use of immature traps. Yet, even only in terms of the photosynthetic rate, bladders are a cost to the bladderworts, and the nutritional benefits of prey capture need to be very substantial to counteract the substantial costs of prey capture to *Utricularia* species.

According to one of the predictions of the cost-benefit model (Givnish *et al.* 1984), the primary energetic benefit of carnivorous behaviour would be either an increased rate of photosynthesis per unit leaf mass or an increase in the total leaf mass supported. Ellison (2006) questioned this prediction, because carnivorous plants have lower photosynthetic rates per unit leaf mass than non-carnivorous plants.

From data compiled by Ellison (2006), the photosynthetic rate per leaf biomass in carnivorous plants is clearly low compared to that of non-carnivorous plants (Fig. 10). The carnivorous plant section of this study only includes one species of *Utricularia*, *U. macrorhiza*, but the range obtained of photosynthetic rate for *U. macrorhiza* (Knight 1992), between 1.9 and 13.9 nmol g⁻¹ s⁻¹ (fresh weight) is similar to the mean shown by Ellison (2006) for carnivorous plants. Moreover, photosynthetic rates obtained by Adamec (2006) for six *Utricularia* species ranged between 11.1 and 32.5 nmol g⁻¹ s⁻¹ (fresh weight). Therefore, the mean value of photosynthetic rate for carnivorous plants shown by Ellison (2006) is a good indicator of the possible values that can be obtained for *Utricularia* species.

Knight (1992) observed variation in photosynthetic rate among sites in *U. macrorhiza* and, in agreement with the pattern observed in Fig. 10, a lower concentration of nitrogen leads to a lower photosynthetic rate. Therefore, it is possible that the low photosynthetic rates observed in *Utricularia* species could be due to the nutrient-poor environments they inhabit, leading to lower CO₂ uptake due to the limitation of nutrients and elements, and/or low affinity to nutrients and elements. It has been suggested that *Utricularia* species have a very high affinity for nutrient uptake from water (Adamec and Kovářová 2006) and, although most of the information is from aquatic species, it seems that *Utricularia* species are usually restricted to nutrient-poor environments (Fig. 3), which is the general pattern observed for other carnivorous plants.

In addition to photosynthetic rate, respiration can be another important aspect for understanding the benefits of carnivory in *Utricularia*. Bladders have been demonstrated to have a higher respiration rate than leafy structures (Adamec 2006) which may be associated with resetting of bladders; the plant must actively pump ions out of the bladder lumen to remove ~70% of the contained water. Jobson *et al.* (2004) and Lakkonen *et al.* (2006) suggest that adaptive amino acid changes in a mitochondrially encoded subunit of cytochrome *c* oxidase (COXI) (COX, a multi-subunit enzyme that catalyses the respiratory reduction of oxygen to water, generating a transmembrane electrochemical gradient that is used for the synthesis of adenosine triphosphate) as compared to other eukaryotes, may permit bladderworts to optimise power output (which equals energy times rate) during times of need, albeit with a 20% reduction in the overall energy efficiency of the respiratory chain. Hence, Laakkonen *et al.* (2006) suggests that the evolution of bladderwort carnivory should include respira-

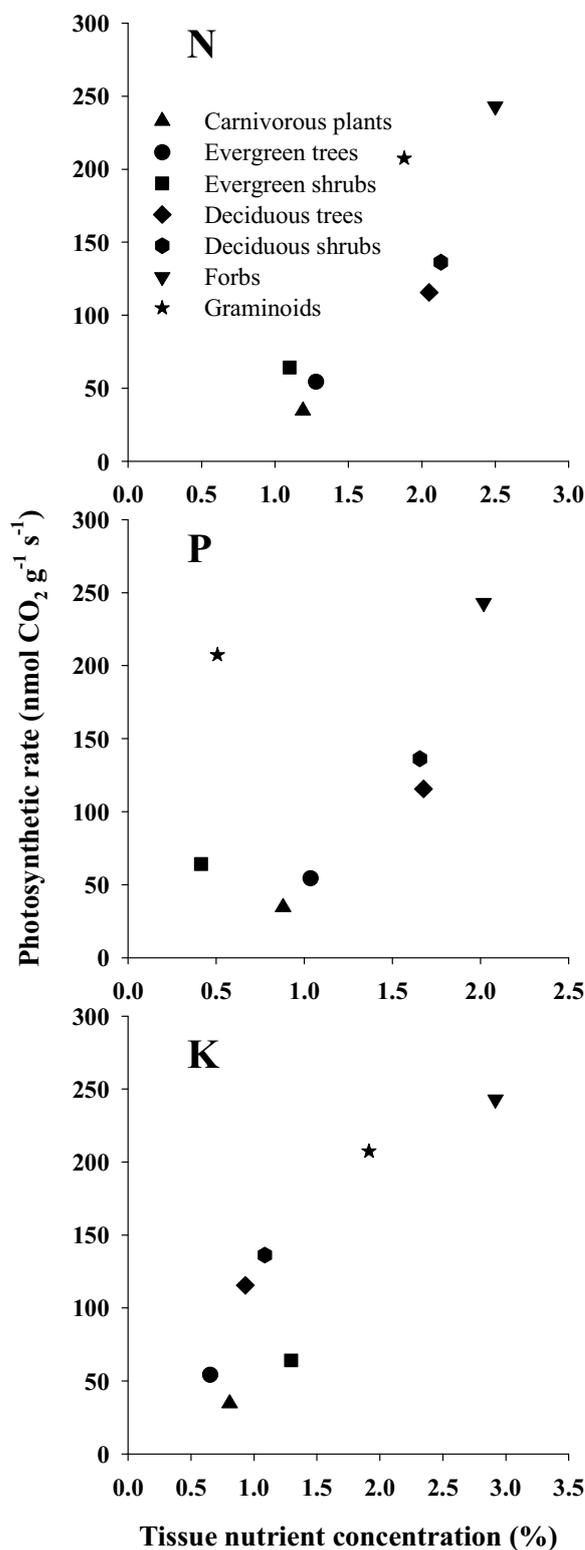


Fig. 10 Relationship between tissue concentration and photosynthetic activity. Relationship between the concentration of nitrogen, phosphorus and potassium and photosynthetic rate in leaves of carnivorous and non-carnivorous plants. Data taken from Figs. 2 and 3 of Ellison (2006).

tion, as an additional trade-off parameter, in addition to the photosynthetic rate. However, contrary to expectation, in *U. macrorhiza*, respiration rates did not differ significantly between bladders and leaves (Knight 1992), although the author noted that the bladders analysed were immature. In contrast, Adamec (2006) demonstrated in six *Utricularia* species that respiration of bladders was 1.7-3.3 times higher than in leaves or photosynthetic shoots and, furthermore, that the respiration of empty bladders in *U. ochroleuca* was the same as for bladders containing prey. It is clear that

future studies should be focused on this topic to determine whether these amino acid changes in COXI are in response to the increased energy demands of active pumping.

The apparent high costs associated to the production of bladders explain why aquatic *Utricularia* have the capacity to vary their investment in carnivory, according to zooplankton abundance (Guisande *et al.* 2000) and nutrient concentration availability (Knight and Frost 1991; Guisande *et al.* 2004; Kibriya and Jones 2007). The advantage of nutrients taken up from captured zooplankton probably decreases as the availability of inorganic nutrient increases.

CULTIVATION

The cultivation of some aquatic, terrestrial, affixed, and epiphytic *Utricularia* species has been well described (D'Amato 1998; Rice 2006). A standard growing technique for terrestrial species is to use a mixture of peat and sand in an eight cm pot. The pots are in trays with water, which fluctuate between just under the soil surface and letting the tray become completely dry. The light should be low, 4-5 standard fluorescent bulbs, and the plants should be about 40 cm from lights. The humidity in the terrarium should be around 50-60%, the temperature may vary between 21 and 30°C according to the species and the irrigation is by spraying. Some species require modifications to this standard method, which are mainly associated with changes in water level.

For the epiphytic species the substratum is moss of sphagnum or a mixture of long-fibre sphagnum and fine orchid bark (1:1). These plants are not growing in standing water, but are watered much like regular terrestrial species. The humidity should be around 75% and the irrigation by spraying should be more frequent than in terrestrial species. Temperature must be also slightly higher than for terrestrial species, between 25-30°C.

Finally, aquatic species require a completely different cultivation technique. These species may grow in small pools in the garden or in an aquarium with at least 50 litres. Rinsed sand, gravel, and peat moss may be used as substrates or nothing at all. The pH of the water must range between 4.5 and 7.5, with optimum values around 6. The optimal temperature varies according to the species and may range from 8 to 30°C. The aquarium or the pond must contain zooplankton as small cladocerans, copepods and rotifers, which are the prey of the plant, but no fish can be added to the system. The periphyton and bacteria attached to bladders and leaves of *Utricularia* are the food of these zooplankton species. As shown above aquatic species live in habitats with a low concentration of nutrients (Fig. 3), therefore, additional nutrients should not be added to the culture water (phosphate and nitrate), but in some places with low amount of iron in the water, a small amount of aquatic plant fertilizer containing iron may added to the water.

DIRECTIONS FOR FUTURE RESEARCH

The cost-benefit model in *Utricularia* should be evaluated by comparing carnivorous and non-carnivorous plants under the same nutrient limiting conditions, because differences in photosynthetic rates could simply be due to the amount of nutrients available. To test the validity of the cost-benefit model in *Utricularia* two questions should be addressed: 1) how much would the photosynthetic rate fall if bladderworts did not have the benefit of nutrients from prey capture? The cost benefit model predicts an increase in photosynthetic rate as a result of carnivory; 2) is the photosynthetic rate in *Utricularia* species higher than in non-carnivorous plants, given the same nutrient limiting conditions? The cost-benefit model predicts that carnivorous plants should have an energetic advantage in competing with non-carnivorous plants under nutrient limiting conditions.

There is some controversy regarding the role of the or-

ganisms that from associations with *Utricularia*, particularly bacteria and periphyton, as it has been shown that benefits can be obtained from mutualism (Wagner and Mshigeni 1986; Richards 2001; Sirová *et al.* 2003), even though some inhabitants may negatively affect the fitness of *Utricularia*, probably due to competition for nutrients (Jobson *et al.* 2000). Future studies should determine whether some *Utricularia* species can obtain benefits from the interaction with other organisms.

Although bladder functioning is probably one of the most important issues in the biology of *Utricularia*, it is also the one where information is most scarce. The details of the trapping mechanism are still not entirely understood in many species of the genus *Utricularia*, probably because it is a complex mechanism and many morphological and anatomical features of bladders vary among species, which might indicate different types of trapping mechanisms. Moreover, it is important to determine the mechanism of prey digestion, particularly the role of other organisms in this process, and the way nutrients are taken up by the plant. Special attention should be paid to the relationship between the morphology/physiology of the bladder-trap and correlated phylogenetic patterns.

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