Recent Progress in Understanding the Evolution of Carnivorous Lentibulariaceae (Lamiales)

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Abstract: Carnivorous plants have emerged as model systems for addressing many ecological and evolutionary questions, and since Lentibulariaceae comprise more than half of all known carnivorous species (325 spp.), they are of particular interest. Studies using various molecular markers have established that Lentibulariaceae and their three genera are monophyletic with *Pinguicula* being sister to a *Genlisea-Utricularia*-clade, while the closest relatives of the family remain uncertain. Character states of the carnivorous syndrome in related proto-carnivorous lamialean families apparently emerged independently. In *Utricularia,* the terrestrial habit has been reconstructed as plesiomorphic, and an extension of subgenus *Polypompholyx* is warranted. In the protozoan-attracting *Genlisea,* subgenus *Tayloria* is revealed as basal lineage. In *Pinguicula,* the six major lineages found reflect radiations in clearly defined geographic regions, whereas most previously recognized subgeneric taxa are non-monophyletic. *Genlisea* and *Utricularia* exhibit substitutional rates that rank among the highest in angiosperms for the molecular markers analyzed. One possible explanation for this lies in selective constraints on a wide range of genomic regions that may have been lowered due to the use of an alternative mode of acquiring nutrients.

Key words: Carnivorous plants, Lentibulariaceae, *Utricularia, Genlisea, Pinguicula,* phylogeny, substitutional rates, molecular evolution.

Introduction

The Lentibulariaceae (bladderwort family) comprise approximate 325 species according to most recent diversity estimates (e.g., Barthlott et al., 2004; Fischer et al., 2004), with about 85 species currently distinguished in *Pinguicula,* 21 species of *Genlisea,* and an estimated 220 species in the largest carnivorous plant genus, *Utricularia.*

Of all genera in Lentibulariaceae, *Pinguicula* (the butterworts) arguably exhibits the most primitive trapping system, basically consisting of mucilage-covered leaves borne in a basal rosette, the margins of which can be rolled inwards (Fig. **1A**). The most elaborate treatment of *Pinguicula* is the monograph of Casper (1966), while a number of later-described species were reviewed by Legendre (2000). A detailed phylogenetic treatment, however, was not available until very recently (Cieslack et al., 2005).

Genlisea (the corkscrew plants) is the smallest genus and has Y-shaped, twisted subterrestrial eel traps used to attract and trap soil protozoa (Barthlott et al., 1998) (Fig. **1B**). Systematic treatments for the African (Fischer et al., 2000) and South American species (Fromm-Trinta, 1977, 1978, 1979, 1981; Fromm-Trinta and Taylor, 1985; Taylor and Fromm-Trinta, 1983) are available, but there has not been a more extensive phylogenetic treatment.

The largest genus, *Utricularia* (the bladderworts), exhibits the most complex trapping device, among the most complicated leaf modifications known in the plant kingdom. The bladder traps of *Utricularia* are either submerged (Fig. **1C**) or subterrestrial and work by means of low pressure, and at least some of the terrestrial species have also been shown to trap protozoa or algae (Seine et al., 2002).

Here, we attempt to summarize recent studies that have addressed the evolution of Lentibulariaceae from a molecular phylogenetic perspective. We briefly discuss the state of knowledge on the closest relatives of the Lentibulariaceae among Lamiales, and argue that considerable work remains to be done before a convincing picture emerges. We further illustrate the current hypotheses on organismal phylogenies of each of the three genera, and point out inconsistencies between gene trees or where a more extensive sampling will be required to obtain further insights. Finally, we extend our considerations to the molecular evolutionary level by discussing alternative hypotheses put forward to explain remarkably increased DNA substitution rates in *Utricularia* and *Genlisea.*

Phylogenetic Relationships in Lamiales and the Closest Relatives of Lentibulariaceae

All phylogenetic studies hitherto conducted in Lamiales that sampled more than one representative of Lentibulariaceae have identified the family as monophyletic (Albach et al., 2001; Albert et al., 1992; Bremer et al., 2002; Jobson et al., 2003; Müller et al., 2004; Olmstead et al., 2001; Olmstead

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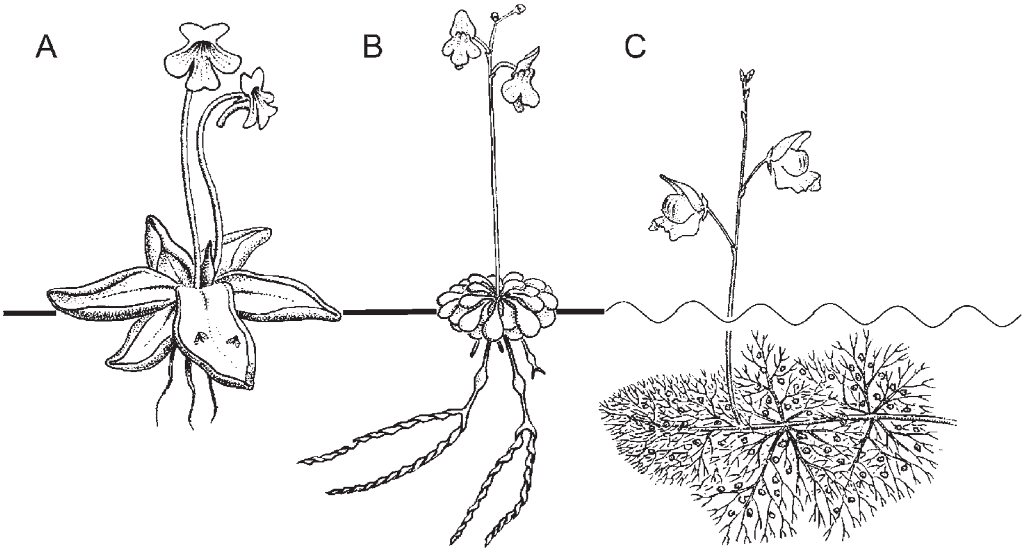

Fig. 1 Sketches showing the principal morphology of the three genera of Lentibulariaceae. (**A**) *Pinguicula*, with a basal rosette of leaves that function as flypaper traps. (**B**) *Genlisea*, showing the Y-shaped, twisted subterrestrial eel traps. (**C**) *Utricularia*, an example of a freely suspended aquatic with small bladder traps.

and Reeves, 1995; Rahmanzadeh et al., 2005; Reeves and Olmstead, 1998). Only Jobson et al. (2003) and Müller et al. (2004), however, sampled enough species of Lentibulariaceae to conduct a thorough test of monophyly.

Various hypotheses have been put forward on the closest relatives of Lentibulariaceae in Lamiales, but none have received significant statistical support. The close proximity of protocarnivorous genera in Lamiales *(Byblis, Ibicella)* was considered the most parsimonious scenario, requiring only one single emergence of adaptations that are key to later expression of the full carnivorous syndrome (pre-adaptations). *Byblis* was reconstructed as closest relative in an early analysis of *rbc*L (Albert et al., 1992), though statistical support was lacking. Other studies using more comprehensive sampling of the order Lamiales arrived at different candidates from within Lamiales, e.g., Hédren et al. (1995) and Oxelman et al. (1999). Such studies highlighted the effects of taxon sampling and hypotheses based upon differing inference methods (Bignoniaceae vs. Lamiaceae, Müller et al., 2004; Rahmanzadeh et al., 2005) (Fig. **2**). *Byblis* was seen as closest relative in most studies (Albert et al., 1992; Bremer et al., 2002; Jobson et al., 2003), a fact that may have led to its inclusion in the Lentibulariaceae in recent APG classifications (APG2, 2003). However, there is general agreement that the phylogenetic "backbone" of the order Lamiales is still far from being understood, and the interrelationships of most of the formerly accepted families in the order continue to be unclear (Albach et al., 2005; Ghebrehiwet et al., 2000; Hoggard et al., 2003; Olmstead et al., 2001; Oyama and Baum, 2004; Wolfe et al., 2002).

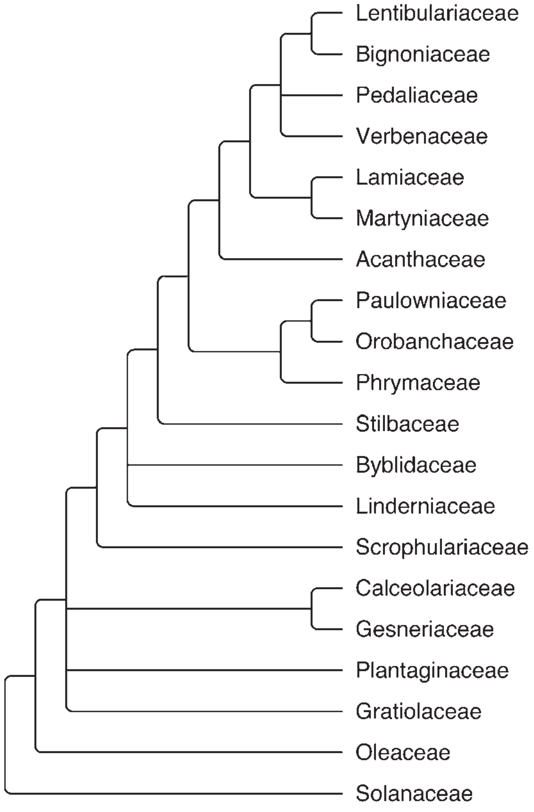

Fig. 2 Strongly simplified phylogenetic relationships in Lamiales based on chloroplast *trn*K (incl. *mat*K) sequences. Only nodes with Bayesian posterior probabilities > 0.5 are shown. Modified after Rahmanzadeh et al., 2005.

A recent analysis of *mat*K could not establish the closest relatives with confidence and, using topological tests, rejected the scenario of proto-carnivorous genera in Lamiales *(Byblis* or *Ibicella)* being closest relatives. In consequence, the scenario of a single evolutionary gain of key components of the carnivorous syndrome in the order was rejected, and a parallel acquisition of pre-adaptations to carnivory was favoured by the data (Müller et al., 2004). Differences in gland morphology support parallel acquisition of carnivorous traits in *Byblis* (Byblidaceae), *Ibicella* (Martyniaceae), and Lentibulariaceae. Digestive glands in all three genera of Lentibulariaceae are attached to vessels, unlike secretory glands of Byblidaceae and Martyniaceae that rest on at least two epidermal cells.

Accordingly, much work remains to be done before a satisfactory identification of the closest relatives of Lentibulariaceae in Lamiales is possible. A series of studies recently identified new lineages in the order and invalidated original/old taxonomic concepts. First, the traditional circumscription of the family Scrophulariaceae had to be abandoned (Olmstead et al., 2001; Olmstead and Reeves, 1995; Oxelman et al., 2005; Reeves and Olmstead, 1998). Later, a new circumscription for Plantaginaceae emerged (Albach et al., 2005; Bello et al., 2002; Hoggard et al., 2003; Rønsted et al., 2002) and morphology and DNA data allowed the delimitation of new families such as Linderniaceae (Rahmanzadeh et al., 2005), whereas former tribes of Scrophulariaceae continue to be elucidated (Albach et al., 2004; Ghebrehiwet et al., 2000; Wolfe et al., 2002). While Lamiales have long been known to be notoriously difficult to resolve with common DNA markers (Albach et al., 2001; Olmstead et al., 1992, 2000, 2001; Olmstead and Reeves, 1995), non-coding markers have proved to have particularly promising properties (Borsch et al., 2005; Müller et al., 2006; Olmstead et al., 1998) for resolving lineages in the order, and first analyses of rapidly evolving chloroplast DNA markers have already improved resolution in parts of the Lamiales tree (Bremer et al., 2002; Rahmanzadeh et al., 2005). Further work in that direction is underway.

Relationships Among Genera and Evolution of Carnivory in the Family

All studies conducted so far concur in that the three genera are clearly monophyletic and that *Pinguicula* branches first as sister to a clade consisting of *Utricularia* and *Genlisea* (Cieslack et al., 2005; Jobson et al., 2003; Müller and Borsch, 2005; Müller et al., 2000, 2004).

After screening the morphology of the various gland types in Lentibulariaceae and other families of Lamiales, it appears that one of the key inventions of the most recent common ancestor (MRCA) of Lentibulariaceae was absorptive glands attached to tracheid elements, consisting of one epidermal cell supporting an endodermoid cell and glandular head cells occurring in multiples of two (Müller et al., 2004). By means of digestive enzymes, the glands can absorb organic substances such as amino acids and nucleotides that are released during the decomposition of insects and other organic matter (Dixon et al., 1980; Lüttge, 1983), thus supplementing the energetically expensive reduction of nitrogen oxides by direct uptake of N-containing organic molecules (e.g., amino acids) and ammonium from prey. Such compounds were previously unavailable through the roots since free macromolecules are first consumed by microorganisms in the natural environment and since roots cannot secrete proteinases to allow direct uptake (Marschner, 1995). Such a supply is likely to have increased the fitness of a plant growing in low-nutrient habitats, and may be regarded as a crucial factor during the evolution of true carnivory in Lamiales.

The MRCA of Lentibulariaceae most likely was a terrestrial plant, since both *Genlisea* and *Pinguicula* are terrestrial and character optimization on *Utricularia* phylogenies clearly inferred the terrestrial habit as ancestral in *Utricularia* (Jobson et al., 2003; Müller and Borsch, 2005; Müller et al., 2004). Aquatic, lithophytic, and epiphytic life forms in *Utricularia* are derived. This MRCA was further reconstructed and shown to have possessed a basal rosette composed of flat leaves and a primary root, reduced soon after germination (Müller et al., 2004). A rosette was later lost with the adaptation to aquatic habitats in a terminal lineage of *Utricularia*. While in the *Pinguicula* lineage adventitious roots were maintained, root functions were taken over by the leaves or shoots in *Utricularia* and *Genlisea*, and roots were lost in both genera (Brugger and Rutishauser, 1989; Lloyd, 1942; Taylor, 1989).

The MRCA of *Utricularia* and *Genlisea* developed inverse tropism and epiascidiate leaves, with abaxially closed leaf margins. Indeed, traps in extant *Utricularia* and *Genlisea* are morphologically regarded as highly modified epiascidiate leaves (Lloyd, 1942; Rutishauser and Sattler, 1989). Also, mutants with epiascidiate pitchers instead of flat leaves are known from various angiosperms, including *Plantago* and *Pinguicula* (Barthlott et al., 2004; Juniper, 1986), suggesting a narrow genetic basis for this mutation. Similarly, inverse tropism is not uncommon in plants, as exemplified by pendent epiphytic life forms. In Lentibulariaceae, it has been suggested that the selection pressure to reverse tropism may be sought in the rich and probably more regular nutrient supply encountered in the soil (Müller et al., 2004), with an abundance of protists and other microscopic organisms (Barthlott et al., 1998; Seine et al., 2002).

In *Genlisea,* traps evolved with two helically twisted arms that increase the surface area exposed to water, while *Utricularia* evolved highly complex traps with a door and a doorstep for tight closure and a trigger system to open on demand; both genera apparently actively attract prey chemically (Barthlott et al., 1998; Seine et al., 2002).

Highly enhanced substitutional rates in all genomes found in *Utricularia* and *Genlisea* are likely to have played a major role in the evolution of this lineage (Jobson and Albert, 2002; Müller et al., 2004; see below).

Biogeography Correlates Well with Major Clades in *Pinguicula*

Pinguicula is the second most diverse genus of the Lentibulariaceae, with 85 currently accepted species (Legendre, 2000). Here, insects are caught and digested by sessile and short-stalked mucilage-producing glands on the upper side of rosette leaves forming so-called “flypaper traps”. The common name “butterworts” is derived from the shiny leaf surface caused by these glands.

Phylogenetic relationships in *Pinguicula* were recently elucidated by Cieslack et al. (2005). Fig. **3** strongly simplifies the results of this study based on 43 species of *Pinguicula*. Most previously recognized subgenera and sections of the genus (Casper, 1966; reviewed and supplemented by Legendre, 2000) were shown to be para- or polyphyletic. A notable exception is section *Pinguicula,* which is monophyletic. However, the identified lineages largely reflect radiations in clearly defined geographic regions.

All Central American, Mexican, and Caribbean species (clade 1 in Fig. **3**) were resolved in a clade sister to the Eurasian *Pinguicula alpina*. This surprising relationship was also supported by indels, but no morphological synapomorphy is currently

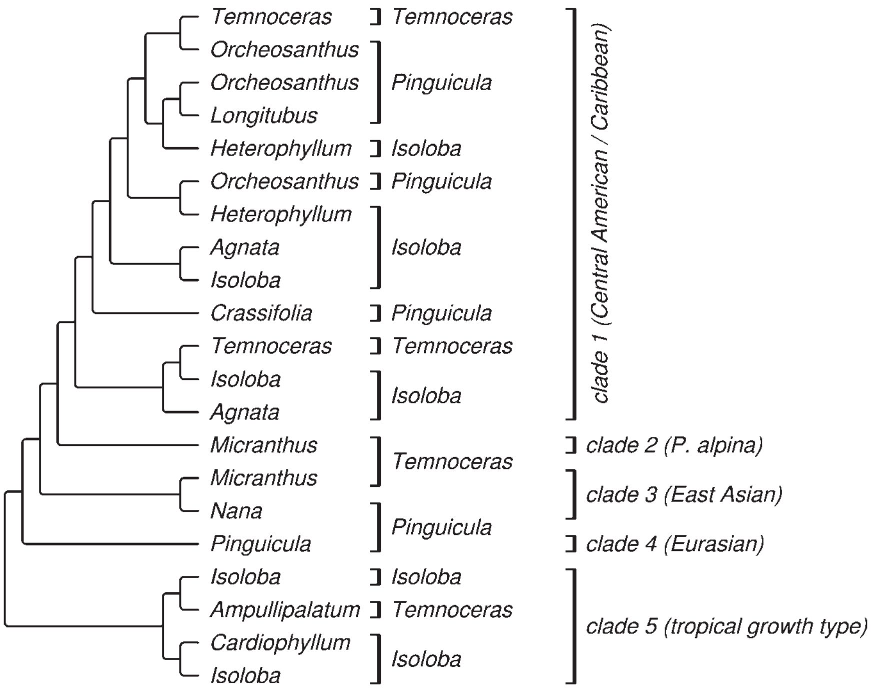

Fig. 3 Major clades found in *Pinguicula* and phylogenetic relationships between sections (according to Casper, 1966) in *Pinguicula,* based on chloroplast *trn*K (incl. *mat*K) sequences, strongly modified from Cieslack et al. (2005). To the right, subgenera according to Casper are annotated, as well as the clade names provided in Cieslack et al. (far right).

known for these two clades. Clade I disagrees with most previous infrageneric classifications, with the exception of De Candolle's (1844) concept of section *Orcheosanthus*.

An East Asian clade was identified as successive sister to this clade of Central American, Mexican, and Caribbean species. A morphological synapomorphy for these East Asian species is peduncles that are densely covered by mucilage glands. All three clades together are characterized by the production of flower buds on winter-resting plants, a specific corolla hair structure, and a very large corolla lower central lobe.

Another diverse clade is composed of species with primarily European distribution, including the widespread type species *Pinguicula vulgaris*. For this clade, vegetative reproduction during dormancy is synapomorphic.

Species native to SE North America and the South American Andes and a group of Mediterranean and NE Atlantic coast species together appear in another well-supported clade that is characterized by a particular growth type. It is the only clade that has reached temperate zones of the southern hemisphere.

Among the more obvious taxonomic changes that are suggested by the results of the study of Cieslack et al. is that *Pinguicula moranensis,* currently in section *Orcheosanthus* (Casper, 1966), should be included in section *Longitubus* together with *Pinguicula laueana,* with which it shares a conspicuously long spur.

The evolution of morphological traits will be discussed in more detail in another paper of this issue.

Classification and Preliminary Phylogenetic Insights in *Genlisea*

Like *Utricularia* (see below), *Genlisea* lacks roots, which have been replaced by rhizophylls that are derivatives of leaves and epiascidiate in ontogeny (Juniper, 1986; Juniper et al., 1989). These achlorophyllous rhizophylls are Y-shaped, ending in two helically twisted arms (Fig. **1 B**), and have long been considered to be traps for catching small invertebrates (e.g., Darwin, 1875; Juniper et al., 1989; Lloyd, 1942). However, they have recently been demonstrated to chemotactically attract and digest protozoa in the soil (Barthlott et al., 1998). The trapping of prey is facilitated by rows of inward-pointing hairs that make the hollow arms a one-way road for any organism that enters the trap (Fig. **1 C**). A second, non-modified leaf type is epiterrestrial, usually spathulate, contains chlorophyll and forms a more or less dense rosette (Fig. **1 A**).

Since the description of the genus by Saint-Hilaire in 1833 for five neotropical species, 16 more species have been described, including 10 from Africa (Chevalier, 1912; Fischer et al., 2000; Good, 1924; Oliver, 1865; Porembski et al., 1996; Stapf, 1906). Several regional taxonomic treatments have been published on the genus for South America (Fromm-Trinta, 1978, 1979, 1981; Taylor, 1967) as well as Africa (Taylor, 1955, 1967, 1972, 1973, 1988), but a monograph has been unavailable. However, a key and checklist for the species distinguished until 1991 was compiled by Taylor (1991). Also, a more detailed treatment of the neotropical species exists (Fromm-Trinta, 1978), as well as a recent revision of the African species (Fischer et al., 2000).

The current widely accepted classification of *Genlisea* is that of Fischer et al. (2000), who propose a subgeneric rank for the two sections in *Genlisea* that had been described earlier by Fromm-Trinta (1977). These two subgenera are based upon the differences in capsule dehiscence found between their members. While in subgenus *Tayloria* capsules open septicidally, subgenus *Genlisea* displays a unique circumscissile dehiscence type, with capsules sometimes opening spirally (illustrated in Stopp, 1958). In addition, Fischer et al. (2000) suggest three groups for the African species. These groups were distinguished based on floral characters and indumentum characteristics and were not assigned a taxonomic rank.

The first phylogenetic studies including at least a few species of *Genlisea* were those of Müller et al. (2004, six spp.) and Jobson et al. (2003, five spp.). These studies infer two clades reflecting subgenera *Tayloria* and *Genlisea,* respectively. The tree in Müller et al. (2004) also incorporated a representative of each of the three distinguished African groups, and points towards the non-monophyly of these African species, with the Madagascan and East African *G. margaretae* showing affinities to the neotropical species.

Extending the taxon sampling of Müller et al. (2004) with additional sequences of *G. pygmaea, G. repens,* and *G. guianensis* (Worberg et al., unpublished data; data matrix available upon request) provides the preliminary picture provided in Fig. **4**. More sequences from additional taxa are currently being compiled and a detailed study, including a morphological survey of trap morphology using scanning electron microscopy, is underway and will be published elsewhere.

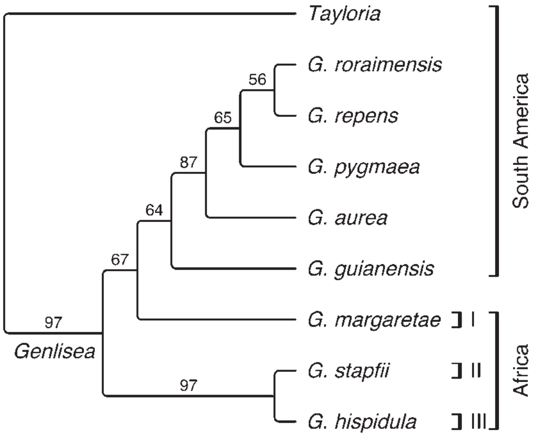

Fig. 4 Preliminary phylogenetic tree of *Genlisea,* based on chloroplast *trn*K (incl. *mat*K) sequences (Müller et al., 2004; Müller, Worberg, Borsch, Barthlott, unpublished data) and *rbc*L sequences (Worberg, Müller, Borsch, unpublished data). Roman numbers indicate groups distinguished for African taxa by Fischer et al. (2000). Two sister clades reflecting subgenera *Tayloria* and *Genlisea* were also found with plastid *rps16* intron and *trn*L-F sequences (Jobson et al., 2003).

Phylogeny of *Utricularia*

Among carnivorous plants, the bladderwort *Utricularia* stands out for a variety of reasons. There are conspicuous modifications in vegetative morphology, with a body plan that exhibits greatly relaxed developmental and positional constraints, strongly deviating from the bauplan found in most other flowering plants. *Utricularia* possibly represents the most striking example of homeosis and heterotopy in plants (Brugger and Rutishauser, 1989; Rutishauser, 1999; Rutishauser and Isler, 2001; Rutishauser and Sattler, 1989). Moreover, the trapping devices of the genus, the so-called bladder traps, rank among the most complex leaf structures known in the plant kingdom (Juniper et al., 1989; Lloyd, 1942). They represent a type of suction trap, working by means of low pressure and absorbing small organisms from the surrounding water or soil (Juniper et al., 1989; Lloyd, 1942). In spite of numerous treatments (Darwin, 1875; Le Strat-Broussaud, 2000; Meyers and Strickler, 1979; Richards, 2001; Sirova et al., 2003; Vintejoux and Shoar-Ghafari, 1997), the details of the trapping mechanism are still not entirely understood. In addition, with about 220 currently accepted species (Taylor, 1989), *Utricularia* is the most diverse genus of all carnivorous plants. Compared to the sundew genus *Drosera* (110 species; Droseraceae [Rivadavia et al., 2003; Seine and Barthlott, 1994; Williams et al., 1994]) and the pitcher plant *Nepenthes* (approximately 80 species; Nepenthaceae; Meimberg et al., 2001), it exhibits more than twice the species diversity. *Utricularia* is also diverse in ecological terms, having populated a wide spectrum of habitats in all continents, the only exceptions being very arid regions and some oceanic islands (Dörrstock et al., 1996; Taylor, 1989).

Until now, two studies have attempted to identify major lineages within *Utricularia* and test taxonomic concepts proposed for the genus by Taylor (1989). Jobson et al. (2003) used the chloroplast *rps16* intron and *trn*L-F, with a total of 2096 characters. Müller and Borsch (2005) sequenced the chloroplast *trn*K intron including the gene *mat*K, which resulted in 2713 characters. Jobson et al. (2003) included more species, but some of the species covered by Müller and Borsch (2005) were not included. The latter study also explored effects of using different phylogenetic inference methods and utilizing information from length mutational events. The phylogenetic trees recovered for *Utricularia* in both studies are largely congruent. Indeed, basic conclusions such as the monophyly of the vast majority of sections determined by Taylor, and a likely neotropical origin of the genus with terrestrial species at the beginning of its diversification, are identical. Nevertheless, in some parts conflicts still persist. Although a complementary taxon sampling and combination of markers is desirable, in the current absence of such data we will try to summarize the picture emerging from these studies, thereby indicating where conflicting issues remain to be resolved.

To summarize the phylogenetic hypotheses as a supertree, a matrix representation with parsimony (MRP, Baum, 1992; Ragan, 1992) was used here. Binary matrices reflecting the nodes present in trees from either study, with characters weighted by the statistical support of each node, were constructed with help of r8s (Sanderson, 2003), following recommendations in Bininda-Emonds and Sanderson (2001) and Salamin et al. (2002). Tree topologies and jackknife proportions were exported from TGF files to r8s-readable Newick format using TreeGraph (Müller and Müller, 2004). The MRP analysis resulted in two most parsimonious trees, the strict consensus tree of which is given in Fig. **5C**. In a separate analysis, weights were not taken into account. This analysis resulted in four most parsimonious trees, the consensus tree of which only differed from the first by collapsing the branch uniting sections *Bivalvaria* and *Utricularia.* The significance of differences of bootstrap (Felsenstein, 1985) or jackknife (Farris et al., 1996) proportions was assessed using SeqState (Müller, 2005 a), based on binomial variances (Hedges, 1992; Müller, 2005 b).

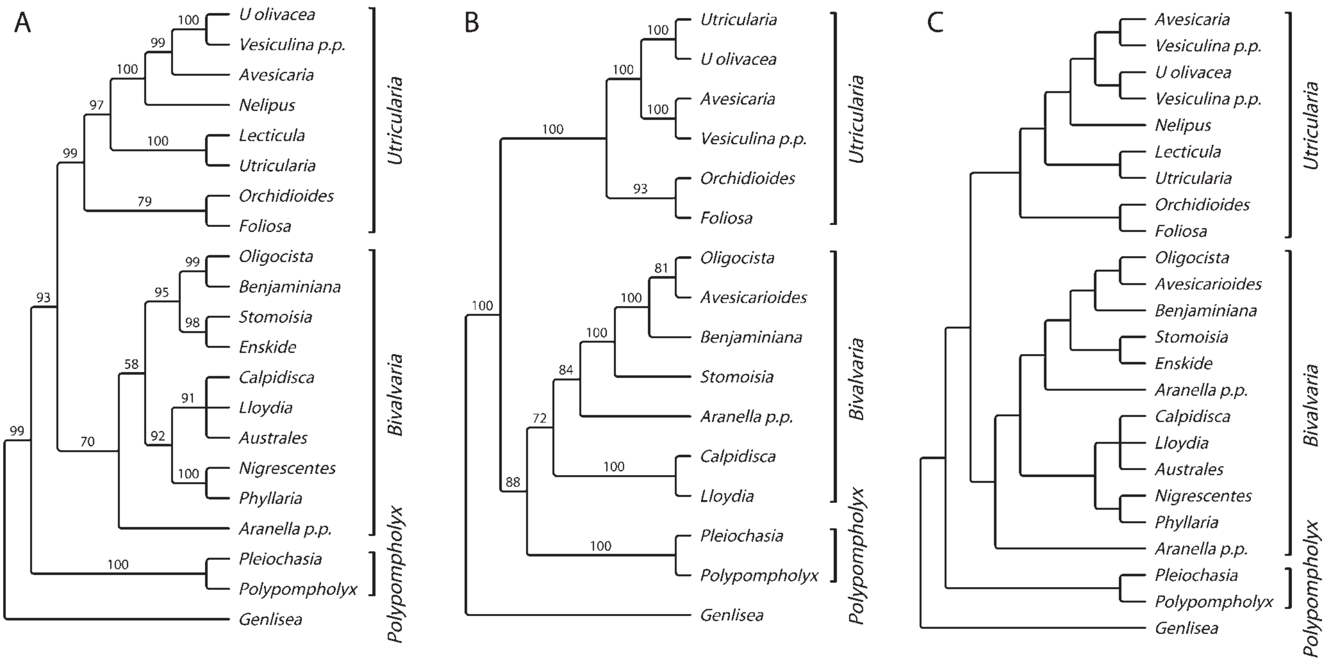

Fig. 5 (**A**) Simplified phylogenetic relationships of *Utricularia* based on chloroplast *trn*LF/*rps16* sequences (Jobson et al., 2003), showing only sectional names according to Taylor (1989). (**B**) Phylogenetic relationships of *Utricularia* based on chloroplast *trn*K data (Müller et al., 2004), otherwise as in **A**. (**C**) Supertree representation of phylogenetic relationships of *Utricularia*, summarizing the results of both studies, using a matrix representation approach with characters weighted by the statistical support of each node.

All current evidence suggests that subgenus *Utricularia* is paraphyletic. This is because section *Pleiochasia* is resolved as closest relative of subgenus *Polypompholyx*. The classification by Taylor into two subgenera *Utricularia* and *Polypompholyx* was therefore suggested to be modified to better reflect phylogenetic relationships (Müller and Borsch, 2005). Subgenus *Polypompholyx* was redefined to also include section *Pleiochasia*. Subgenus *Utricularia* was proposed to be narrowed down to include most of the aquatic and epiphytic sections (Fig. **5**). The old subgeneric name *Bivalvaria* has been proposed to be restored to circumscribe all remaining taxa (Fig. **5**). The respective clade, however, receives less than the average node support in the *Utricularia* tree (72% with *trn*K, 70% with *trn*LF/*rps16*). The relationship between the three subgenera remains largely unresolved. While *Polypompholyx* is sister to *Bivalvaria* based on *trn*K (88% support), it is sister to the remainder of *Utricularia* using *trn*LF/*rps16* (93%). Taking 95% confidence intervals into account, given the number of replicates used in both studies, the support for the conflicting node found with *trn*LF/*rps16* is significantly higher (though close to insignificance at alpha = 0.05). Enhanced taxon sampling and use and combination of more data will help to resolve the remaining conflict with respect to the *Utricularia* "backbone" topology.

The vast majority of the 34 sections distinguished by Taylor (1989) are monophyletic, with the following notable exceptions. Müller and Borsch (2005) established the paraphyly of section *Iperua* P. Taylor, since *Utricularia humboldtii* Schomb. is unequivocally supported as member of a clade comprising species of section *Orchidioides* ADC. The resulting enhanced section *Orchidioides* is remarkable for its representatives with relatively large, orchid-like flowers (hence the name). According to both studies, section *Setiscapella* is paraphyletic to *Vesiculina,* and *Psyllosperma* is paraphyletic to *Foliosa,* which led Müller and Borsch (2005) to a new circumscription of the section with the older names, namely *Vesiculina* and *Foliosa*.

Jobson et al. (2003) revealed the non-monophyly of sections *Oligocista* (with *U. nana* of section *Benjaminiana* nested within *Oligocista*) and *Utricularia* (with *U. olivacea* showing affinities to section Vesiculina). These relationships could not be confirmed by *trn*K, most likely due to differences in taxon sampling. With inclusion of other representatives of *Vesiculina,* the latter section shows affinities to *Setiscapella* rather than *Utricularia. Setiscapella* itself appears clearly paraphyletic to *Avesicaria* in the *trn*L-F/*rps16* tree, so *Avesiaria* is used in Fig. **5**.

The situation remains unresolved so far with respect to section *Aranella*. Both studies incorporated a mutually exclusive set of representatives of this section, and both found that the species clustered together, but in different parts of the *Bivalvaria* clade. In the *trn*LF/*rps16* tree, *Aranella* appears as sister to the remainder of *Bivalvaria,* though only supported with 58% JK. In the analysis of *trn*K/*mat*K, it branches next in a series after *Lloydia* and *Calpidisca*. Complementary inclusion of the missing *Aranella* species in the *trn*L-F/*rps16* and *mat*K datasets is likely to reveal that this section is also polyphyletic.

All current evidence suggests that the ancestral life form of *Utricularia* was terrestrial. Epiphytes and lithophytes are derived within the genus, and independently occurred in sections *Orchidioides* and *Phyllaria* (Jobson et al., 2003; Müller and Borsch, 2005).

Also, aquatics occupy derived positions within the *Utricularia* phylogeny. It appears that a parallel evolution of suspended plants (in sect. *Vesiculina* and independently *Utricularia*) took place, and that affixed aquatics can be considered intermediates in a transgression from terrestrials to free-floating, suspended aquatics (Jobson et al., 2003; Müller and Borsch, 2005). Interestingly, there also appears to be a parallel evolution of rheophytes (plants living in waterfalls or swiftly floating water) from terrestrials, once in section *Avesicarioides* (palaeotropical; Müller and Borsch, 2005), and independently in the neotropical section *Avesicaria* (Jobson et al., 2003).

Current estimates concur in identifying South America as the geographic origin of *Utricularia,* taking the highly likely neotropical origin of the sister genus *Genlisea* into account (Jobson et al., 2003; Müller and Borsch, 2005).

High Evolutionary Rates in *Utricularia* and *Genlisea*

DNA substitution rates were found to be significantly higher in *Genlisea* and *Utricularia* compared to *Pinguicula,* based on a variety of relative rate test variants (using step distributions, distance-based and likelihood ratio tests) and several loci representing all three genomic compartments (Jobson and Albert, 2002; Müller et al., 2004). Moreover, comparing rates in chloroplast *trn*K sequences across 375 angiosperm genera, rates in the rootless, protozoa-trapping *Utricularia-Genlisea* lineage rank among the highest in angiosperms (Müller et al., 2004; Müller et al., submitted), slightly exceeded only by the similarly rootless, morphologically highly aberrant aquatic Podostemaceae. A parallel data matrix of *rbc*L sequences shows the same trend, though less statistical significance in view of lower overall rates in this genomic region (Müller et al., submitted).

A positive correlation of species diversity and branch lengths has been reported for angiosperms (Barraclough and Savolainen, 1996, 2001; Savolainen and Goudet, 1998) and was also used to explain longer branches found in the species-rich genus *Utricularia* versus *Pinguicula,* which contains less species (Jobson and Albert, 2002). In these studies, cladogenesis or diversification contrasts were assumed whenever one lineage comprised more species than the other. However, stochastic differences in initial rates can lead to a much higher diversity in one of the lineages (Slowinski and Guyer, 1989). We applied the standard null model test (Slowinski and Guyer, 1993) to assess the significance of species diversity contrasts. This test highly significantly rejects ($p = 0.528$; $p \gg 0.05$) amplified diversification in *Utricularia* (220 spp.) and *Genlisea* (21 spp.) as compared to the sister group *Pinguicula* (86 spp., Barthlott et al., 2004; Cieslack et al., 2005). Additional analyses, using for example tree imbalance (Kirkpatrick and Slatkin, 1993) or more sensitive three-taxon tests (Sanderson and Donoghue, 1994, 1996), are unlikely to change the basic conclusion of insignificant differences in diversification rates. Note that even in the most species-rich angiosperm genus, *Astragalus,* comprising five to ten times the number of species in all hypothesized sister groups, no higher diversification rates were found using three different analytic approaches (p always > 0.3, Sanderson and Wojciechowski, 1996).

On the other hand, the currently available data indicate a trend towards high rates in lineages where the normal uptake of inorganic nutrients via roots is accompanied or replaced by some other mode of acquiring nutrients. It can be hypothesized that organic molecules, such as amino acids, play a substantial role in the nutrition of *Genlisea* and *Utricularia* and can be used directly in various metabolic pathways, resulting in a decreased need for nitrate reduction or transamination (Müller et al., 2004). As a consequence, selective constraints on a wide range of genomic regions could have been lowered. This does not preclude overlapping effects of differences in polymerase fidelity or repair systems, which so far have not been investigated (Müller et al., submitted).

Instead of relaxed constraints, positive selection may underlie lineage-specific changes in substitutional rates, such as in the highly interesting case of *coxI,* where rate shifts have been related to adaptive evolution of cytochrome c oxidase that may have been key to the successful radiation of *Utricularia* (Jobson et al., 2004).

According to these insights, a highly unconventional molecular evolutionary mode is evident in bladderworts and corkscrew plants. Interestingly, this is further underlined by the finding of extremely low genome sizes in these plants (see Greilhuber et al., 2006).

Conclusions

As yet, our understanding of the evolution of Lentibulariaceae is still incomplete. Although relationships between the genera are clearly unambiguous, and those within *Pinguicula* and *Utricularia* appear to be largely resolved, the closest relatives of the family still require substantiation. The same is true for the relationships within *Genlisea* and those of certain crucial, “difficult-to-sample” representatives of the other two genera. However, the data collected so far and the hypotheses put forward testify to the strong potential of extremely specialized lineages of organisms to provide insights into more fundamental mechanisms involved in molecular and character evolution. Interestingly, and in support of this statement, fundamental biological mechanisms have previously first been unravelled by investigation of carnivorous plants, such as the function of the Golgi apparatus (Schnepf, 1960, 1961). Further studies on rather extreme model systems like Lentibulariaceae, with amazing alterations in biochemical or morphological characters, will be an invaluable complement to the in-depth analysis of the few model organisms.

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References

Albach, D. C., Soltis, P. S., Soltis, D. E., and Olmstead, R. G. (2001) Phylogenetic analysis of asterids based on sequences of four genes. Annals of the Missouri Botanical Garden 88, 163 – 212.

Albach, D. C., Martinez-Ortega, M. M., Fischer, M. A., and Chase, M. W. (2004) A new classification of the tribe Veroniceae – problems and a possible solution. Taxon 53, 429 – 452.

Albach, D. C., Meudt, H. M., and Oxelman, B. (2005) Piecing together the “new” Plantaginaceae. American Journal of Botany 92, 297 – 315.

Albert, V. A., Williams, S. E., and Chase, M. W. (1992) Carnivorous plants: phylogeny and structural evolution. Science 257, 1491 – 1495.

APG2 (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Botanical Journal of the Linnean Society 141, 399 – 436.

Barraclough, T. G. and Savolainen, V. (1996) Rate of *rbc*L gene sequence evolution and species diversification in flowering plants (angiosperms). Proceedings of the Royal Society B, Biological Sciences 263, 589 – 591.

Barraclough, T. G. and Savolainen, V. (2001) Evolutionary rates and species diversity in flowering plants. Evolution 55, 677 – 683.

Barthlott, W., Porembski, S., Fischer, E., and Gemmel, B. (1998) First protozoa-trapping plant found. Nature 392, 447.

Barthlott, W., Porembski, S., Seine, R., and Theisen, I. (2004) Karnivoren. Biologie und Kultur fleischfressender Pflanzen. Stuttgart: Ulmer.

Baum, D. A. (1992) Combining trees as a way of combining datasets for phlylogenetic inference, and the desirability of combining gene trees. Taxon 41, 3 – 10.

Bello, M. A., Chase, M. W., Olmstead, R. G., Rønsted, N., and Albach, D. C. (2002) The pàramo endemic *Aragoa* is the sister genus of *Plantago* (Plantaginaceae, Lamiales): evidence from plastid *rbc*L and nuclear ribosomal ITS sequence data. Kew Bulletin 57, 585 – 597.

Bininda-Emonds, O. R. P. and Sanderson, M. J. (2001) Assessment of the accuracy of matrix representation with parsimony analyses. Systematic Biology 47, 497 – 508.

Borsch, T., Löhne, C., Müller, K., Hilu, K. W., Wanke, S., Worberg, A., Barthlott, W., Neinhuis, C., and Quandt, D. (2005) Towards understanding basal angiosperm diversification: recent insights using rapidly evolving genomic regions. Nova Acta Leopoldina NF 342, 85 – 110.

Bremer, B., Bremer, K., Heidari, N., Erixon, P., and Olmstead, R. G. (2002) Phylogenetics of asterids based on 3 coding and 3 non-coding chloroplast DNA markers and the utility of non-coding DNA at higher taxonomic levels. Molecular Phylogenetics and Evolution 24, 274 – 301.

Brugger, J. and Rutishauser, R. (1989) Bau und Entwicklung landbewohnender *Utricularia*-Arten. Botanica Helvetica 99, 91 – 146.

Casper, S. J. (1966) Monographie der Gattung *Pinguicula* L. Bibliotheca Botanica 127/128, 1 – 209.

Chevalier, A. (1912) Novitates Florae Africanae. Lentibulariaceae. Mémoire de la Societé Botanique France 8, 186 – 188.

Cieslack, T., Polepalli, J. S., White, A., Müller, K., Borsch, T., Barthlott, W., Steiger, J., Marchand, A., and Legendre, L. (2005) Phylogenetic analysis of *Pinguicula* (Lentibulariaceae): chloroplast DNA sequences and morphology support several geographically distinct radiations. American Journal of Botany 92, 1723 – 1736.

Darwin, C. (1875) Insectivorous Plants. London: Murray.

De Candolle, A. P. (1844) Prodromus Systematis Naturalis Regni Vegetabilis VIII. Paris: S. G. Mason.

Dixon, K. W., Pate, J. S., and Bailey, W. J. (1980) Nitrogen nutrition of the tuberous sundew *Drosera erythrorhiza* Lindl. With special reference to catch of arthropod fauna by its glandular leaves. Australian Journal of Botany 28, 283 – 297.

Dörrstock, S., Seine, R., Porembski, S., and Barthlott, W. (1996) First record of the American *Utricularia juncea* (Lentibulariaceae) from Africa. Kew Bulletin 579 – 583.

Farris, J. S., Albert, V. A., Källersjö, M., Lipscomb, D., and Kluge, A. G. (1996) Parsimony jackknifing outperforms neighbor-joining. Cladistics 12, 99 – 124.

Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39, 783 – 791.

Fischer, E., Porembski, S., and Barthlott, W. (2000) Revision of the genus *Genlisea* (Lentibulariaceae) in Africa and Madagascar with notes on ecology and phytogeography. Nordic Journal of Botany 20, 291 – 318.

Fischer, E., Barthlott, W., Seine, R., and Theisen, I. (2004) Lentibulariaceae. In The Families and Genera of Vascular Plants (Kubitzki, K., ed.), Berlin: Springer.

Fromm-Trinta, E. (1977) *Tayloria* Fromm-Trinta – nova seca do genere *Genlisea* St.-Hil. Boletim do Museu Nacional Rio de Janeiro. Botanica 44, 1 – 4.

Fromm-Trinta, E. (1978) Revisao das especies do genero *Genlisea* St.-Hil das regioes sudeste e sul do Brasil. In Dissertacao de Mestrado apresentada a Coordenacao do Curso de Pos-Graduacao em Botanica da UFRJ.

Fromm-Trinta, E. (1979) Revisao do genero *Genlisea* St.-Hil. das regioes sudeste e sul do Brasil. Rodriguésia 31, 17 – 139.

Fromm-Trinta, E. (1981) Revisao do genero *Genlisea* St.-Hil. do Brasil. Boletim do Museu Nacional Rio de Janeiro. Botanica 61, 1 – 21.

Fromm-Trinta, E. and Taylor, P. (1985) *Genlisea pallida* Fromm-Trinta and Taylor, P. – una nova especie para o genero *Genlisea* St.-Hil. Bradea 4, 176 – 179.

Ghebrehiwet, M., Bremer, B., and Thulin, M. (2000) Phylogeny of the tribe Antirrhineae (Scrophulariaceae) based on morphological and *ndh*F sequence data. Plant Systematics and Evolution 220, 223 – 239.

Good, R. (1924) New tropical African Lentibulariaceae. Journal of Botany 62, 165.

Greilhuber, J., Borsch, T., Müller, K., Worberg, A., Porembski, S., and Barthlott, W. (2006) Smallest angiosperm genomes found in Lentibulariaceae, with chromosomes of bacterial size. Plant Biology 8, 770 – 777.

Hedges, S. B. (1992) The number of replications needed for accurate estimation of the bootstrap *p* value in phylogenetic studies. Molecular Biology and Evolution 9, 366 – 369.

Hédren, M., Chase, M. W., and Olmstead, R. G. (1995) Relationships in the Acanthaceae and related families as suggested by cladistic analysis of *rbc*L nucleotide sequences. Plant Systematics and Evolution 194, 93 – 109.

Hoggard, R. K., Kores, P. J., Molvray, M., Hoggard, G. D., and Broughton, D. A. (2003) Molecular systematics and biogeography of the amphibious genus *Littorella* (Plantaginaceae). American Journal of Botany 90, 429 – 435.

Jobson, R. W. and Albert, V. A. (2002) Molecular rates parallel diversification contrasts between carnivorous plant lineages. Cladistics 18, 127 – 136.

Jobson, R. W., Playford, J., Cameron, K. M., and Albert, V. A. (2003) Molecular phylogenetics of Lentibulariaceae inferred from plastid *rps16* intron and *trn*L-F DNA sequences: implications for character evolution and biogeography. Systematic Botany 28, 157 – 171.

Jobson, R. W., Nielsen, R., Laakonen, L., Wikström, N., and Albert, V. A. (2004) Adaptive evolution of cytochrome c oxidase: infrastructure for a carnivorous plant radiation. Proceedings of the National Academy of Sciences of the USA 101, 18064 – 18068.

Juniper, B. E. (1986) The path to plant carnivory. In Insects and the Plant Surface (Juniper, B. E. and Southwood, R., eds.), London: Echvard Annald.

Juniper, B. E., Robins, R. J., and Joel, D. M. (1989) The Carnivorous Plants. London: Academic Press.

Kirkpatrick, M. and Slatkin, M. (1993) Searching for evolutionary patterns in the shape of a phylogenetic tree. Evolution 47, 1171 – 1181.

Le Strat-Broussaud, F. (2000) Organization and specificities of *Utricularia* traps. Acta Botanica Gallica 147, 29 – 36.

Legendre, L. (2000) The genus *Pinguicula* L. (Lentibulariaceae): an overview. Acta Botanica Gallica 147, 77 – 95.

Lloyd, F. E. (1942) Carnivorous plants. In Chronica Botanica Co. Massachusetts: Waltham.

Lüttge, U. (1983) Ecophysiology of carnivorous plants. In Physiological Plant Ecology, Vol. III (Lange, O. L. et al., eds.), Berlin, Heidelberg: Springer.

Marschner, H. (1995) Mineral Nutrition of Higher Plants. London: Academic Press.

Meimberg, H., Wistuba, A., Dittrich, P., and Heubl, G. (2001) Molecular phylogeny of Nepenthaceae based on cladistic analysis of plastid *trn*K intron sequence data. Plant Biology 3, 164 – 175.

Meyers, D. G. and Strickler, R. J. (1979) Capture enhancement in a carnivorous aquatic plant: function of antennae and bristles in *Utricularia vulgaris*. Science 203, 1022 – 1025.

Müller, J. and Müller, K. (2004) TreeGraph: automated drawing of complex tree figures using an extensible tree description format. Molecular Ecology Notes 4, 786 – 788.

Müller, K., Borsch, T., Legendre, L., Porembski, S., and Barthlott, W. (2000) A phylogeny of Lentibulariaceae based on sequences of *mat*K and adjacent non-coding regions. American Journal of Botany 87, S145 – S146.

Müller, K., Borsch, T., Legendre, L., Porembski, S., Theisen, I., and Barthlott, W. (2004) Evolution of carnivory in Lentibulariaceae and the Lamiales. Plant Biology 6, 477 – 490.

Müller, K. (2005 a) SeqState-primer design and sequence statistics for phylogenetic DNA data sets. Applied Bioinformatics 4, 65 – 69.

Müller, K. (2005 b) The efficiency of different search strategies in estimating parsimony jackknife, bootstrap, and Bremer support. BMC Evolutionary Biology 5, 58.

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

Müller, K., Hilu, K. W., and Borsch, T. (2006) Phylogenetic utility of rapidly evolving DNA on high taxonomical levels: comparing three cpDNA datasets of basal angiosperms. Molecular Phylogenetics and Evolution 41, 99 – 117.

Oliver, D. (1865) On the Lentibulariaceae collected in Angola by Dr. Welwitsch, with an enumeration of the African species. Journal of the Linnean Society, Botany 9, 145 – 146.

Olmstead, R. G., Michaels, H. J., Scott, K. M., and Palmer, J. D. (1992) Monophyly of the asteridae and identification of their major lineages inferred from DNA sequences of *rbc*L. Annals of the Missouri Botanical Garden 79, 249 – 265.

Olmstead, R. G. and Reeves, P. A. (1995) Evidence for the polyphyly of the Scrophulariaceae based on chloroplast *rbc*L and *ndh*F sequences. Annals of the Missouri Botanical Garden 82, 176 – 193.

Olmstead, R. G., Reeves, G., and Yen, A. C. (1998) Patterns of sequence evolution and implications for parsimony analysis of chloroplast DNA. In Molecular Systematics of Plants II : DNA Sequencing (Soltis, D. E. et al., eds.), Boston: Kluwer Academic Publishers.

Olmstead, R. G., Kim, K.-J., Jansen, R. K., and Wagstaff, S. J. (2000) The phylogeny of asteridae sensu lato based on chloroplast *ndh*F gene sequences. Molecular Phylogenetics and Evolution 16, 96 – 112.

Olmstead, R. G., DePamphilis, C. W., Wolfe, A. D., Young, N. D., Elisons, W. J., and Reeves, P. A. (2001) Disintegration of the Scrophulariaceae. American Journal of Botany 88, 348 – 361.

Oxelman, B., Backlund, M., and Bremer, B. (1999) Relationships of the Buddlejaceae s. l. investigated using parsimony jackknife and branch support analysis of chloroplast *ndh*F and *rbc*L sequence data. Systematic Botany 24, 164 – 182.

Oxelman, B., Kornhall, P., Olmstead, R. G., and Bremer, B. (2005) Further disintegration of the Scrophulariaceae. Taxon 54, 411 – 425.

Oyama, R. K. and Baum, D. A. (2004) Phylogenetic relationships of North American Antirrhinum (Veronicaceae). American Journal of Botany 91, 918 – 925.

Porembski, S., Fischer, E., and Gemmel, B. (1996) *Genlisea barthlottii* (Lentibulariaceae) – a new species from Guinean inselbergs. Adansonia 18, 151 – 154.

Ragan, M. A. (1992) Phylogenetic inference based on matrix representation of trees. Molecular Phylogenetics and Evolution 1, 53 – 58.

Rahmanzadeh, R., Müller, K., Fischer, E., Bartels, D., and Borsch, T. (2005) Linderniaceae and Gratiolaceae (Lamiales) are further lineages distinct from Scrophulariaceae. Plant Biology 7, 67 – 78.

Reeves, P. A. and Olmstead, R. G. (1998) Evolution of novel morphological and reproductive traits in a clade containing *Antirrhinum majus* (Scrophulariaceae). American Journal of Botany 85, 1047 – 1056.

Richards, J. H. (2001) Bladder function in *Utricularia purpurea* (Lentibulariaceae): is carnivory important? American Journal of Botany 88, 170 – 176.

Rivadavia, F., Kondo, K., Kato, M., and Hasebe, M. (2003) Phylogeny of the sundews, *Drosera* (Droseraceae), based on chloroplast *rbc*L and nuclear 18S ribosomal DNA sequences. American Journal of Botany 90, 123 – 130.

Rønsted, N., Chase, M., Albach, D. C., and Bello, M. A. (2002) Phylogenetic relationships within *Plantago* (Plantaginaceae): evidence from nuclear ribosomal ITS and plastid *trn*L-F sequence data. Botanical Journal of the Linnean Society 139, 323 – 338.

Rutishauser, R. and Sattler, R. (1989) Complementary and heuristic value of contrasting models in structural botany. III. Case study on shoot-like "leaves" and leave-like "shoots" in *Utricularia macrorhiza* and *U. purpurea* (Lentibulariaceae). Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 111, 121 – 137.

Rutishauser, R. (1999) Polymerous leaf whorls in vascular plants: developmental morphology and fuzziness of organ identities. International Journal of Plant Science 160, S81 – S103.

Rutishauser, R. and Isler, B. (2001) Developmental genetics and morphological evolution of flowering plants, especially bladderworts *(Utricularia)*: fuzzy arberian morphology complements classical morphology. Annals of Botany 88, 1173 – 1202.

Saint-Hilaire, A. (1833) Voyage dans le district des Diamans du Brésil. Paris: Librairie-Gide.

Salamin, N., Hodkinson, T. R., and Savolainen, V. (2002) Building supertrees: an empirical assesment using the grass family. Systems Biology 51, 136 – 150.

Sanderson, M. J. and Donoghue, M. J. (1994) Shifts in diversification rate with the origin of angiosperms. Science 264, 1590 – 1593.

Sanderson, M. J. and Donoghue, M. J. (1996) Reconstructing shifts in diversification rates on phylogenetic trees. Trends in Ecology and Evolution 11, 15 – 20.

Sanderson, M. J. and Wojciechowski, M. F. (1996) Diversification rates in a temperate legume clade: are there "so many species" of *Astragalus* (Fabaceae)? American Journal of Botany 83, 1488 – 1502.

Sanderson, M. J. (2003) r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. Bioinformatics 19, 301 – 302.

Savolainen, V. and Goudet, J. (1998) Rate of gene sequence evolution and species diversification in flowering plants: a re-evaluation. Proceedings of the Royal Society B, Biological Sciences 265, 603 – 607.

Schnepf, E. (1960) Zur Feinstruktur der Drüsen von Drosophyllum lusitanicum. Planta 54, 641 – 674.

Schnepf, E. (1961) Struktur und Funktion der Golgi-Elemente in Insektivoren-Drüsen. Berichte der Deutschen Botanischen Gesellschaft 74, 269.

Seine, R. and Barthlott, W. (1994) Some proposals on the infrageneric classification of *Drosera* L. Taxon 43, 583 – 589.

Seine, R., Porembski, S., Balduin, M., Theisen, I., Wilbert, N., and Barthlott, W. (2002) Different prey strategies of terrestrial and aquatic species in the carnivorous genus *Utricularia* (Lentibulariaceae). Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 124, 71 – 76.

Sirova, D., Adamec, L., and Vrba, J. (2003) Enzymatic activities in traps of four aquatic species of the carnivorous genus *Utricularia*. New Phytologist 159, 669 – 675.

Slowinski, J. B. and Guyer, C. (1989) Testing the stochasticity of patterns of organismal diversity: an improved null model. American Naturalist 134, 907 – 921.

Slowinski, J. B. and Guyer, C. (1993) Testing whether certain traits have caused amplified diversification: an improved method based on a model of random speciation and extinction. American Naturalist 142, 1019 – 1024.

Stapf, O. (1906) Lentibulariaceae. In Flora of Tropical Africa IV, Vol. 2 (Thiselton-Dyer, W. T., ed.), Ashford, Kent: Reeve, pp. 468 – 499.

Stopp, K. (1958) Notiz über die Dehiszenzweise der Kapselfrüchte von *Genlisea hispidula* Stapf. Beiträge zur Biologie der Pflanzen 34, 126 – 142.

Taylor, P. (1955) Lentibulariaceae. In Flora of West Tropical Africa, 2nd ed., Vol. 3 (Hutchinson, J. and Dalziel, J. M., eds.), London: Crown Agents for Oversea Governments and Administrations, pp. 375 – 381.

Taylor, P. (1967) Lentibulariaceae. In Botany of the Guayana Highland, Vol. 7 (Maguire, B. et al., eds.), Memoirs of the New York Botanical Garden 17, pp. 201 – 228.

Taylor, P. (1972) Lentibulariaceae. In Flore d'Afrique Centrale (Zaire – Rwanda – Burundi), Vol. Spermatophytes, Meise: Jardin botanique national de Belgique, pp. 1 – 62.

Taylor, P. (1973) Lentibulariaceae. In Flora of Tropical East Africa, Rotterdam: Balkema, pp. 1 – 26.

Taylor, P. and Fromm-Trinta, E. (1983) Una nova espécie para o género *Genlisea* St.-Hil., Sect. *Tayloria* (Lentibulariaceae): *Genlisea uncinata* P. Taylor and Fromm-Trinta. Bradea 3, 365 – 368.

Taylor, P. (1988) Lentibulariaceae. In Flora Zambesiaca, Vol. 8, London: Royal Botanic Gardens, pp. 9 – 42.

Taylor, P. (1989) The genus *Utricularia*: a taxonomic monograph. In Kew Bulletin Additional Series XIV. London: Royal Botanic Gardens.

Taylor, P. (1991) The genus *Genlisea* St. Hil. – an annotated bibliography. Carnivorous Plant Newsletter 20, 27 – 33.

Vintejoux, C. and Shoar-Ghafari, A. (1997) Secretion of mucilages by an aquatic carnivorous plant: *Utricularia neglecta* L. (Lentibulariaceae). Acta Botanica Gallica 144, 347 – 351.

Williams, S. E., Albert, V. A., and Chase, M. W. (1994) Relationships of Droseraceae – a cladistic analysis of *rbc*L sequence and morphological data. American Journal of Botany 81, 1027 – 1037.

Wolfe, A. D., Datwyler, S. L., and Randle, C. P. (2002) A phylogenetic and biogeographic analysis of the Cheloneae (Scrophulariaceae) based on ITS and *mat*K sequence data. Systematic Botany 27, 138 – 148.

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