Evolution -- the Lamiales Carnivores

The carnivorous plant genera *Byblis*, *Genlisea*, *Pinguicula*, and *Utricularia* along with the murderous *Ibicella* and *Proboscidea* are in the plant order Lamiales (Wikipedia). *Byblis* is placed in its own family Byblidaceae. *Genlisea*, *Pinguicula*, and *Utricularia* are in their own family Lentibulariaceae. *Ibicella* and *Proboscidea* are placed in the family Martyniaceae consisting of 5 genera.

Close relatives of the Lamiales carnivores include the families Bignoniaceae (Trumpet Creeper, *Jacaranda*, *Catalpa*), Pedaliaceae (Sesame), Verbenaceae (*Verbena*, *Lantana*), Lamiaceae (Mint), and over a dozen others. We don't know which of these are sister clades to the carnivorous families because the divergence happened too long ago and too quickly to be resolved with current DNA testing. The fast evolving genes don't resolve divergences that old and the slowly evolving genes did not change enough during the short time period in which the Lamiales originally differentiated. A number of authors choose the Pedaliaceae (Wikipedia) as a sister of convenience to the Lentibulariaceae because the plants in that family tend to have sticky leaves.

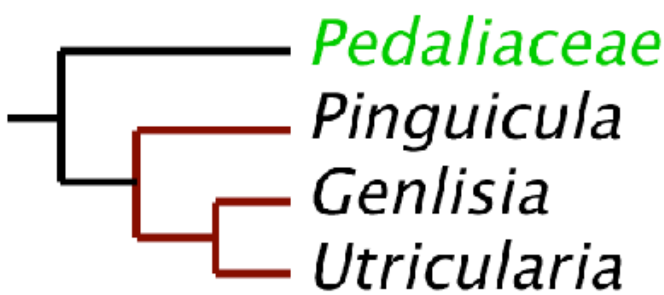
Pinguicula lusitanica. Notice how the leaves curve in.

There is not much to say about the evolution of *Byblis* at this point. In the DNA phylogenies it tends to fall in with families of plants that used to be considered part of the Scrophulariaceae and not close to the other carnivores. It has a unique design for its glands and appears to have evolved carnivory independently of the the other carnivores.

Utricularia nephrophylla from Brazil. The purple disks are the traps which are modified leaves, the long white strands are stems, and the green things are photosynthetic protuberances that some people call or get confused with leaves. The plant has no roots. If you would see this plant in the wild all you would see are the green protuberances and maybe a few of its cute flowers.

The Martyniaceae murderous plants are closer to the Lentibulariaceae carnivores but definitely not sisters. Comparing the glands of these plants it is also apparent they are not directly related.

DNA testing of the Lentibulariaceae carnivores provides an interesting history of the group.

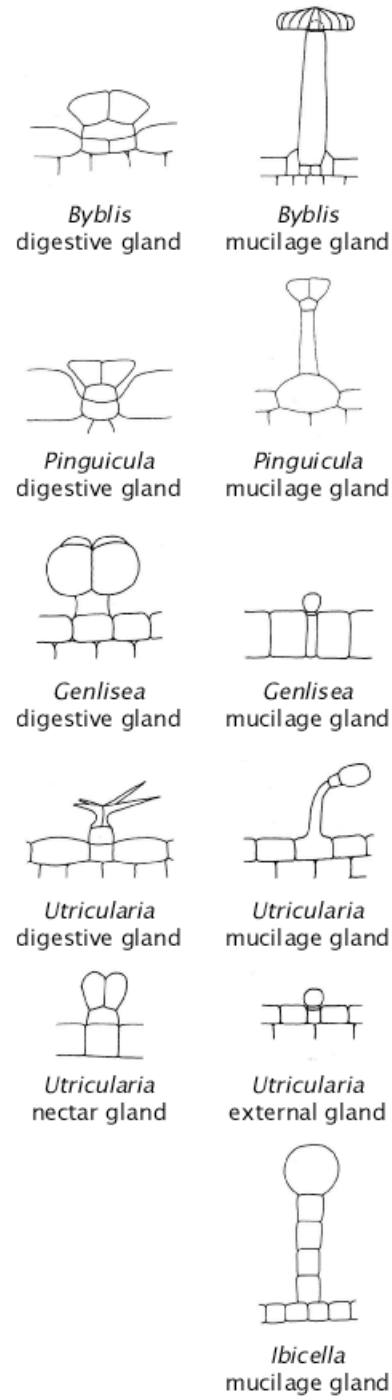


DNA cladogram of the Lentibulariaceae carnivores (in black) with a non-carnivorous relative in green. The length of the lines horizontally are NOT proportional to genetic changes.

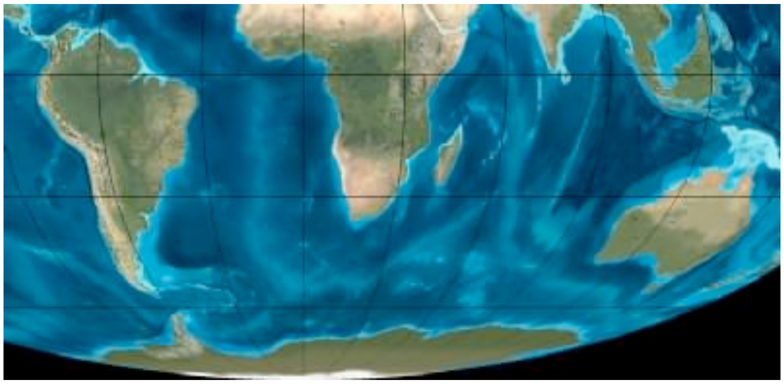
We have a flypaper carnivore basal in the clade and closely related to a pigeon trap carnivore and that is in turn related to a suction trap carnivore. This does NOT mean *Pinguicula* gave rise to *Genlisea* and *Genlisea* gave rise to *Utricularia*. What it says is at some point in the past *Pinguicula* and the *Genlisea*/*Utricularia* clade had a common ancestor. At a later time the *Genlisea* and *Utricularia* clade split. We can confirm this interpretation looking at the digestive glands of the three genera. Plachno, et al. (2005) has a summary of digestive gland fine-structural characters. There is a general *Pinguicula* to *Genlisea* to *Utricularia* trend. You can assign some characters to the common ancestor of the family Lentibulariaceae and some to the ancestor of the *Genlisea*/ *Utricularia* clade. However, other characters are only found in *Genlisea* or found in *Pinguicula* and more derived *Genlisea* but not primitive *Genlisea*.

Was the common ancestor of the Lentibulariaceae carnivorous? The Muller *et al*. papers listed below discuss the milestones in the evolution of the Lentibulariaceae carnivores. Since all three genera have superficially similar, vascularized digestive glands that also function to absorb nutrients it is likely the last common ancestor of the group was already a carnivore. It probably looked similar to *Pinguicula lusitanica*. That is it hugged the ground and the leaves rolled in but did not have as developed digestive or mucilage glands. After the split with the *Genlisea*/ *Utricularia* ancestor, the proto-*Pinguicula* further developed the digestive and mucilage glands. The ancestor that lead to *Genlisea*/ *Utricularia* probably formed pitcher-like leaves. Some *Pinguicula* species today will occasionally produce leaves that look like small horizontal pitchers. However those pitchers are peltate while the traps of *Genlisea* and *Utricularia* are rolled (see image of a *Utricularia* trap at right). The rolled leaves would have allowed the proto-*Genlisea*/ *Utricularia* to utilize a different resource if they were were buried or otherwise subsurface. The common ancestor may have had forked leaves since both genera have forked traps. In the *Genlisea* clade the trap elongated and the forks spiraled. In the *Utricularia* clade the trap shortened, folded back, and developed the sophisticated trap door mechanism at the leaf fork.

Jobson, et al. (2003) did a DNA study of 75 species of the Lentibulariaceae (there are more than 340 species in the family!) which was expanded for *Pinguicula* by Cieslack et al. (2005). Within the genus *Pinguicula* they found the non-hybernacula-forming warm temperate species to be basal (*P. lusitanica* and *P. crystalina* from Europe, *P. antactica* from southern South America, and the SE USA species). Most of the temperate Eurasian and North American hybernacula-forming *Pinguicula* fall into a single large clade of closely related species. The exceptions are the northeast Asian and Arctic *P. ramosa*, *P. villosa*, and *P. varigata* which form a clade and *P. alpina*. The Eurasian, hybernacula-forming *P. alpina* is



Drawings not to scale of digestive glands from Proc. 4th Intl. Carniv. Pl. Conf. pages 63-73 (PDF) reproduced from other sources. Muller et al. (2006) say "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."



Miocene "Satellite view" of the southern continents. Note Antarctica is ice free along the coast. Who knows what the flora of Antarctica consisted of and whether there were seasonal bird migrations with carnivore seeds between their toes between Antarctica and the other southern continents. Portions of map, © Ron Blakey, Northern Arizona University Geology.

basal to a clade consisting of the Mexican and Caribbean species. Forming a hybernacula or producing succulent, non-carnivorous leaves allows the Mexican and Caribbean species to survive in regions with distinct dry seasons.

However, *P. alpina* as we know it can not be the direct ancestor of the central American species. Besides the fact that *P. alpina* has a number of unique specializations not found in its relatives, it has the wrong number of chromosomes. Caspar and Stimper (2009) list chromosome numbers for 82 *Pinguicula* taxa. Most Mexican *Pinguicula* are diploids (x=11, 2n=22) while *P. alpina* is a tetrapoid with a different base number (x=8, 2n=32). The *Pinguicula* ancestral base number is x=8. Most of the non-Mexican *Pinguicula* are diploid, tetraploid, octoploid, and hexadecaploid x=8 (2n=16, 32, 64, 128) with a few interesting exceptions. Based on chromosome numbers in combination with the DNA data there are no clear candidates currently extant that appear to be directly ancestral to the Mexican species.

Cieslack et al. (2005) interpret the phylogeny to indicate *Pinguicula* originated in a humid subtropical environment and later developed specializations for surviving freezing or drying. Caspar and Stimper (2009) concur on this view based on the current locations of various chromosome variants. This is different from Jobson, et al. (2003) which placed the cold temperate species basal. Cieslack et al. (2005) tested more species giving them a better picture of the genus. Even with the extra species their analysis did not show strong confidence in the split between warm temperate and the cold temperate species. Even more testing may help here or *Pinguicula* invaded cold temperate or mountainous regions early on in which case the lack of confidence may reflect a close association. With the testing it may be difficult to trace any of these events if the key species in Europe were wiped out 14.8 million years ago as a result of the Nordlinger Ries impact [Wikipedia] and mid-miocene extinction event [Wikipedia].

Trap of the *Utricularia alpina* x *U. campbelliana* hybrid produced by Miroslav Studnicka. With the more primitive terrestrial *Utricularia* traps you can see how the trap develops and the relationship to the *Genlisea* trap. The trap is essentially a folded leaf that bifurcates. If you stretched this trap out you would have the basic shape of the *Genlisea* trap. Of course the *Utricularia* trap and the *Genlisea* trap each have major details the other doesn't have. Image © Bartosz Jan Plachno, Jagiellonian University, Cracow, Poland.

Utricularia inflata is fully aquatic native to North America. The pink disks are the traps. The plant uses its stems for photosynthesis.

Pinguicula medusina hybernacula. The hybernacula allow the plant to survive the tropical dry season in southern Mexico.

Genlisea is found today in tropical South America, Africa, and Madagascar. At this point the DNA phylogenies are equivocal about the paleogeography of *Genlisea*. There appear to have been multiple exchanges between South America and Africa/ Madagascar.

Utricularia is found world-wide today but it appears the bulk of the diversification within the genus happened in South America although the most basal species are found in Australia. The main line of *Utricularia* species is terrestrial. Multiple times *Utricularia* invaded other habitats and continents. Besides bogs and fens it can be found on rock face seeps, stream sides, as an attached aquatic, and suspended aquatic. This diversity is reflected in the fact that 225 species have been described so far.

-- John Brittnacher

Pinguicula lusitanica is found in Europe.

Genlisea hispidula is found in Africa.

Utricularia bisquamata flower. This is a terrestrial species found in Africa.

For a more detailed discussion please see the following articles and articles they reference.

Muller, K. and Th. Borsch and L. Legendre and I. Theisen and W. Barthlott (2002) Evolution of carnivory in the Lentibulariaceae: considerations based on molecular, morphological, and physiological evidence. Proc. 4th Intl. Carniv. Pl. Conf. pages 63-73 (PDF)

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

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

Cieslack, T., J. S. Polepalli, A. White, K. Muller, T. Borsch, W. Barthlott, J. Steiger, A. Marchand, and L. Legendre (2005) Phylogenetic analysis of Pinguicula (Lentibulariaceae): chloroplast DNA sequences and morphology support several geographically distinct radiations. American Journal of Botany 92(10):1723–1736.

Plachno J. B., Kozieradska-Kiszkurno M., Swiatek P. (2007) Functional ultrastructure of *Genlisea* (Lentibulariaceae) digestive hairs. Ann. Bot. 100:195-203

Casper, S. Jost and Rosemarie Stimper (2009) Chromosome numbers in *Pinguicula* (Lentibulariaceae): survey, atlas, and taxonomic conclusions. Plant Syst. Evol. 277:21–60.

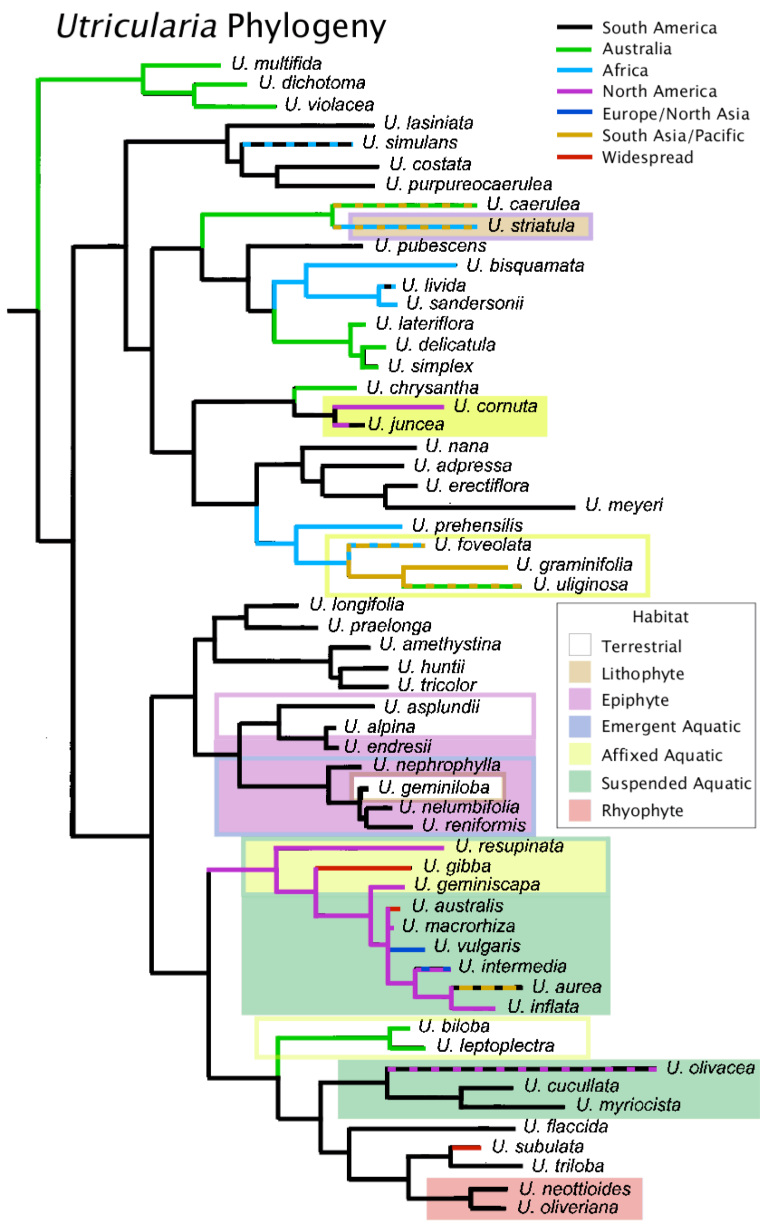

Figure modified from:

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Rice, Barry A. (2006) Growing Carnivorous Plants. Timber Press, Portland, OR, USA.