

What Are the Nearest Noncarnivorous Relatives of the Carnivorous Plants?

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How many times did the carnivorous syndrome arise in plants? Do Croizat's ideas of a single origin of carnivorous plants have any merit? Is the Sarraceniales of Engler which groups *Sarraceniaceae*, *Droseraceae*, and *Nepenthaceae* together a natural group? The Nepenthales of Cronquist includes the same three families as Engler's Sarraceniales but the Nepenthales of Takhtajan excludes *Sarraceniaceae*. Which expert should we believe? Are the families of carnivorous plants natural ones? Does *Heliamphora* belong in the *Sarraceniaceae*? Does *Dionaea* belong in the *Droseraceae*? Finally, what are the nearest noncarnivorous relatives of the various groups of carnivorous plants?

For many of the carnivorous plants these problems have been hard to answer until now because of the extreme modification and possible parallel evolution of the vegetative parts of the plants and the possession of very similar rose like flowers by so many of the plants. There has been a tendency to place them together because they are carnivorous and to be conservative about placing them with other plant groups but they are ordinary flowering plants (albeit ones with extraordinary feeding habits) and must be more closely related to some noncarnivorous plants than they are to others.

Until fairly recently authority ruled when it came to plant groupings above the genus level. That is still so today but methods are being developed which appear to be able to provide an objective estimate of the degree of relatedness of plants at the family level and above.

This article is based on information already published in Albert, V., S. Williams and M. Chase (1992) *Carnivorous Plants: Phylogeny and Structural Evolution*. *Science* 257: 1491-1495.

As a plant physiologist interested in comparative physiology of the *Droseraceae* I have always wanted to know what the closest noncarnivorous relatives of these plants are. Several authorities (Takhtajan, Thorn and Dahlgren) have suggested that there is a relationship to the order Saxifragales but Cronquist, who when he died last year was the greatest botanical authority in the USA, suggested a relationship to the Violales and placed the group in a different subclass than the other three botanists. My chance to have a hand in solving the mystery came when I spent my sabbatical last year working at University of North Carolina at Chapel Hill (UNC) with Victor Albert, Hal Hills and Mark Chase, using methods involving cladistic analysis of DNA sequences. While the results cannot yet be considered the last word, they indicate that answers to many of the questions can be found and give a very good estimate of what they are likely to be.

The methods are fairly simple but require some explanation. Consider that the information in a gene is information, just as the information in a book is. The cells faithfully copy the information each time they divide, passing the information on from generation to generation. If we view cells as illiterate scribes who copy manuscripts without knowing their meaning we expect the scribes to make typos or errors in the manuscripts. These errors are in turn faithfully copied later. In some instances the editor (natural selection) eliminates certain passages which prevent the cell from working properly but many of the errors survive editing and leave a record of the history of the gene. Since all plants descended from a plant with an error will faithfully

copy the error, it is simpler (or “more parsimonious”) to assume that an error arose once than that it occurred several times. Teachers often use the principle of parsimony when they assume that two term papers with identical spelling and grammatical errors in the same awkward sentences had a common origin!

Using the record of typos we could predict which manuscripts were copied from a common source and make a reconstruction of the order in which the text of the manuscripts deviated from each other. The result can be drawn as a genealogical tree with hypothetical “ancestral” manuscripts at the nodes and real ones at the tips of the branches. This is just what the scientists in Mark Chase’s lab at UNC were doing with the DNA from the chloroplast gene *rbcl*, only their tree included 500 species of seed plants from cycads and ginkgo to orchids and asters. The tree they obtained is reasonable in the sense that it is much like the traditional classification system and that most groups that are considered natural ones by the majority of taxonomists were consistent with the DNA data. There were also some surprises but even these when viewed carefully often made sense in terms of morphological and phytochemical characteristics of the plants.

When I started to look for a sabbatical project which would use DNA data to infer which group of carnivorous plants was most closely related to *Drosera*, Joe Mazrimas told me that he had sent a number of plants to Victor Albert and Mark Chase. I called Vic and Mark and arranged to join them in their research. They had already sequenced *Drosera*, *Nepenthes*, *Sarracenia*, *Roridula*, *Pinguicula* and *Utricularia* and included them in the universal seed plant tree mentioned above. When I began working with Vic and Mark the tree had 250 species instead of 500 and it was just beginning to look as if a sensible tree could be generated from the data that was rapidly gathering in laboratories around the world.

As far as the carnivorous plants go it seemed logical enough that *Pinguicula* and *Utricularia* were right together and that they were near the Scrophulariales which have very similar flowers. It was also interesting that *Drosera* and *Nepenthes* were together and a bit strange that they were near such plants as spinach and amaranth and not Saxifragaceae where many people have thought they belonged. It was still unclear how much the method could tell us about the relationships of the taxa we were interested in. Don Schnell generously supplied the first samples I worked with and Steve Smith who was nearby in Climax NC provided a lot of material that allowed a good start. Rob Gardener of the Carolina Botanical Garden was also a great help but the bottleneck on plant material really ended when Don Schnell suggested that I get in contact with Ron Gagliardo who has numerous carnivorous plants in tissue culture. Ron was located at North Carolina State a short distance away and was very cooperative. Much of the work with *Drosera* was possible because of Ron’s generosity. *Drosophyllum* from Joe Mazrimas and *Darlingtonia* from Peter D’Amato helped round out the genera which Vic had not been able to get hold of previously. Generous donations were also made by John DeGreef and Gordon Snelling.

As we added more species of carnivorous plants to the study, the universal tree also gradually grew from 250 species to 475 species and finally to 500. At this point several relationships became clear.

The DNA data indicated that *Drosera* is distantly related to the order Caryophyllales (a group which includes carnations, spinach, amaranth, pokeweed and cactus) and that it is more closely related to the Plumbaginaceae (which includes the woody ornamental plumbago), Polygonaceae (the family which includes buckwheat and rhubarb) and to *Nepenthes*. *Plumbaginaceae* have sticky mucilage secreting hairs which are quite similar to those of *Drosophyllum*, *Drosera* like flowers and plumbagin, a naphthaquinone common to *Drosera*, *Drosophyllum*, *Dionaea*, *Aldrovanda*, *Nepenthes* and *Tripyophyllum*.

The data indicate that *Sarracenia* (except for being a dicot) was not even remotely

related to either *Drosera* or *Nepenthes*, where it has sometimes been placed, but instead it is a relative of the Ericales, the acid loving group that includes several parasitic plants as well as rhododendron, blueberries and cranberries. The data indicated *Roridula* is fairly closely related to *Sarracenia* and, of course, *Darlingtonia* and *Heliamphora* are even more closely related. The position of *Roridula* was a complete surprise to me since Francis Lloyd had declared that it was not a carnivorous plant in 1929 but since it seems to be related to *Sarraceniaceae* it is clearly of interest whether or not it is carnivorous. The whole question of carnivory of *Roridula* should be reinvestigated.

As might be expected the DNA data placed the members of the *Lentibulariaceae* (*Utricularia* near *Pinguicula*) together and confirmed their relationship with the Scrophulariales which also as has been proposed previously. *Proboscidea*, a sticky haired non-carnivorous plant with bilaterally symmetrical (zygomorphic) flowers is more distant but also fairly closely related to *Utricularia* near *Pinguicula*.

When *Byblis* too turned out to be near *Utricularia* and *Pinguicula* in the tree it startled us. The flower of *Byblis* looks radially symmetrical (actinomorphic) as opposed to bilaterally symmetrical and it did not seem that it should be placed here. However the *Byblis* flower is not strictly radially symmetrical since the stamens hook downward. The hairs of flypaper leaves of both *Pinguicula* and *Byblis* look nearly identical. The exact position of *Byblis* is still a bit unclear. It may be only remotely related to *Utricularia* and *Pinguicula* or it may be fairly closely related. More data needs to be analyzed to determine its exact position.

The data place *Cephalotus* all by itself. It is not particularly close to any other group of carnivorous plants. Its closest relatives are a number of plants endemic to Australia, New Zealand and Chile. It is remotely related to *Oxalis*, the common lawn and greenhouse weed.

Brocchinia is a bromeliad. As expected, the bromeliads formed a branch within the monocots in the study with 500 taxa. We did no further work on it but there is a report by Givnish, Systema Smith and Hahn (1992, American Journal of Botany 79:145 [abstract #416]) that DNA restriction site studies (which are a different method than our rbcL sequencing studies) show it to be related to the bromeliads *Brewcaria*, *Lindmania*, and *Navia* which with *Brocchinia* are all native to the Guyana Shield. This cluster of genera is most closely related to *Fosterella*, a mesophytic Andean genus. All are in a clade with the subfamily Pitcairnioideae (Bromeliaceae).

The work with DNA is in its infancy and changes in some details of what is described above are likely. The combination of cladistic analysis and DNA sequencing is a powerful tool and I believe within a few years we will have a much firmer understanding of the relationships of carnivorous plants with other plants than we have had in the past.

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