

THE PATH TO PLANT CARNIVORY

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There is a considerable amount of interest in the pages of CPN on the subject of CP evolution. In a recent exchange of correspondence with Dr. Juniper, he sent me a rough draft of a chapter he authored for a forthcoming biology textbook. I would like to share some of his ideas with our readers hoping that it might stimulate further ideas on the subject.

A discussion of the evolution of any CP is purely speculative, simply because there isn't any scientific evidence of plant material still in existence from the ancient ages. Most carnivorous plants are herbs which are too soft-bodied to survive the activity of microorganisms in the soil for scientists to locate and study. There are even plants existing today that have most, but not all the "necessary" carnivorous mechanisms, so that they are either into or out of the carnivorous habit.

Some assumptions we can make on their evolution is that being flowering plants, the carnivorous habit had to begin sometime after the Upper Cretaceous period at the end of the Mesozoic era about 100 million years ago.

If one looks at a typical representation of an evolutionary tree (as one appears in CPN 7:18 (1978)), there are six independently developed places where CP are found at widely separated places in the natural order of things:

ORDER

GENERA

- | | |
|--------------------|---|
| 1) SARRACENALES | N & S American Pitcher plants |
| 2) NEPENTHALES | <i>Nepenthes</i> , <i>Drosera</i> , <i>Dionaea</i> , <i>Drosophyllum</i> <i>Aldrovanda</i> |
| 3) VIOLALES | <i>Triphyophyllum</i> |
| 4) SAXIFRAGALES | <i>Byblis</i> , <i>Cephalotus</i> |
| 5) SCROPHULARIALES | <i>Pinguicula</i> , <i>Utricularia</i> , <i>Biovulria</i> <i>Polypompholyx</i> , <i>Genlisea</i> , <i>Martynia</i> |
| 6) BROMELIALES | <i>Brocchinia</i> , <i>Catopsis</i> |

As one looks at the list above, the plant order Scrophulariales have asymmetric flowers and are regarded relatively more advanced than other groups having radial or symmetrical flowers which tend to cluster together in an evolutionary sense. The trapping mechanisms, however, do not fall so easily into such typical categories. No matter how we analyze this chart, the CP fall into a polyphyletic scheme and it's not easy to come up with viable relationships to one another.

Most of the carnivorous plants we know today exhibit 7 features in order to be successful in their habitat:

- | | |
|------------|-----------|
| 1. Attract | 5. Digest |
| 2. Trap | 6. Absorb |
| 3. Retain | 7. Use |
| 4. Kill | |

It is Dr. Juniper's opinion that it is not necessary to assume that any one of these individual features has a common origin in evolution. In fact, many of these features occur uniquely or occasionally grouped in plants living today that do not rely on carnivory. For example:

Flowers attract.
Root caps secrete mucilage.
Flowers temporarily trap pollinators.
Germinating seeds secrete digestive enzymes.
Plant leaves absorb surface nutrients.

In CP, several features develop in a certain limited area of the plant, and these features are expressed there to an EXTREME EXTENT.

Since there are no intermediates in the fossil record of carnivores, we are forced to speculate on the path to plant carnivory by looking at analogous structures from non-carnivorous plants. This report will concentrate on the *Nepenthes* trap and the *Dionaea* trigger hair.

THE NEPENTHES PITCHER

There are many examples of flowers of non-carnivorous genera that trap insects even though true carnivorous plants never use the floral structure for this purpose. The tropical flowering plant, *Dischidia*, has a modified leaf in which ants may temporarily live. Other examples are the ornamental *Croton* and *Ficus bengalensis* whose leaf tips form small pockets or pitchers with no obvious purpose. Wild plants can undergo large modifications or adaptations in a few generations with examples of doubling flowers, fasciated stems, fused fruits or multiple meristems. These modifications may be due to selector genes that undergo duplications and mutations in large segments and become part of the inheritance package in subsequent generations.

The waxy surface within the pitcher and just below the nectar-secreting glands under the peristome lip is a wax-secreting epidermal surface which appears to have no exact parallel in any other known plant. Insects find it difficult to adhere to these waxy scales because the scale pulls away very easily when a claw of an insect attempts to take hold. When the waxy scales are removed with chloroform solvent, insects can once again escape by climbing out of the pitchers. This crystalline wax is secreted only by cells in this area during pitcher development and presents an effective barrier to insect escape. Once it is used up by flaking off the walls, the wax is not replaced so that old pitchers often are seen to allow insects to escape.

Epicuticular waxes in plants are usually present for water retention, sunlight protection, dew condensation or frost damage protection. It may protect the plant from plant pathogens and insect predation. In general, we do not see plant surface wax in more primitive plants as a device to impede the movement or adhesion of harmful insects. However, there are two species of fern that do have a powdery wax that seems to be there as a mechanism to impede insects attacking the sori (the propagation mechanism) of one *Ceropteris triangularis* and the petiole and rachis of *Phlebodium aureum*.

Other examples of the general defensive role of wax on the pedicel, especially of the type that is crumbly, soft and non-adhesive, exists in other angiosperms. The *Dahlia*, *Narcissus*, *Blood-Lily* and *Amaryllis* are some examples of this. *Sarracenia* and *Dionaea* also have waxy-coated pedicels but *Drosera* has a glandular-flowering stem and this is an example of how nature 'plays the cards'. It is not difficult to see how this wax has become adapted to a specific restraining role in *Nepenthes* and *Brocchinia reducta*.

THE DIONAEA TRIGGER HAIR

One view to explain the purpose of leaf hairs or glands of various sorts which may impede or kill insects is that they are purely defensive structures. They do not exist because of selection towards carnivory but remain in *Roridula* where the tentacles on the leaves trap insects but there are no absorbing glands to make use of the nutrients. This plant may be obtaining its nutrients indirectly. Older leaves fall to the soil with their prey which are slowly broken down into nitrogenous nutrients by soil microorganisms and later absorbed by the roots of the plant.

PLANT CARNIVORY (Continued)

The well-known, rock garden herb- Catchfly-belonging to over 400 species of the *Silene* genus secrete an adhesive fluid from their glands which trap insects. Several species of the Nightshade genus *Solanum* have glandular hairs which rupture into releasing a sticky substance when aphids attack the plant and glues these insects to the leaf. This may prevent virus diseases from spreading from plant to plant. The leaf surfaces of the tobacco plant *Nicotiana glauca* trap insects in a similar manner. The pubescent calyx, with stalked glands on the upper part of *Plumbago capensis* often catch aphids.

A gland bearing leaf, then, can be readily transformed as a teratoma into a pitcher. Plants that bear trichomes, which usually are branched hairs or bristles on the leaf surface, are capable of absorbing simple nutrients. Charles Darwin tested many plants and found that 2 species of the *Saxifraga*, which is distantly related to *Drosera*, could absorb organic matter from raw meat and solutions of nitrate and ammonia. Another non-carnivorous example is the Bromeliad family where trichomes in the tank cells absorb at least 2 amino acids from a solution in contact with the leaf. Absorption of nutrients is not a problem in the evolutionary sense.

GLANDS

Examples of secretory and absorptive glands in the plant world are not restricted to carnivorous plants. In the fern, *Isoetes*, there are organs which secrete a mucilaginous layer of fluid containing protein in the basal regions of the microphylla, and this organ's function once had an extracellular lytic activity analogous to the glands from CP. In *Cephalotus*, there is evidence of an ancestral stomatal pore that developed into a simple absorptive gland. The epidermal glandular cells of *Nepenthes* may also have a stomatal origin. When glands developed over evolutionary time, various functions also showed up a specialization for mucilage or enzyme secretion. *Drosera* is an exception in that the tentacle retained both functions of capture and digestion. In the leaf base, there are sessile glands probably involved in the transport of the digestive fluid. They may have been derived from ancestral stomata which is a very tentative idea, but may be the basis for the digestive glands of all the carnivorous species.

The evolution of what appeared first in *Sarracenia*, *Nepenthes* and *Dionaea* is the question of nectar-secreting glands or enzyme-secreting types. *Darlingtonia* is an example of a primitive carnivore where there are nectar glands, but no glands in the digestive zone that appear to secrete enzymes. Perhaps, this dichotomy in function is the present day example of an intermediate stage in the development of a highly adapted CP species.

Nectar glands secrete dilute fluids based on the exudation of phloem contents and need to become more concentrated to be an enzyme secretion gland. However, a contrary example was pointed out by Dr. Juniper when he observed that nectar-secreting glands in the rim of the pitcher of *Sephalotus* only appear in the mature pitcher and not in juvenile pitchers. Both plants function successfully in capturing and digesting prey.

Drosophyllum is a single example of how its glands may have evolved over a period of time from being first a simple lure, then a trapping glue, a drowning mechanism, an enzyme medium and finally a hygrometer to absorb moisture from the air. Are there any CP specimens living today which can suggest a possible evolutionary sequence? Most biologists concur that there are 4 CP which may be closely related: *Drosophyllum*, *Drosera*, *Dionaea*, and *Aldrovanda*.

We can speculate that the primitive carnivore looked something like a modern *Pinguicula*. *Drosophyllum* diverged early from this primitive beginning because of pressure to develop glands capable of maintaining its water balance during dry spells on the Iberian coast. Then *Drosera* diversified over the entire earth developing a tentacle that is both nastic and tropic in function. Also, this led to a more economical use of enzymes and mucilage required to trap and digest prey. The gland head went to the prey, and not the prey going to wasteful and copious amounts of mucilagenous fluid.

In the beginning, a CP plant could have started out glandless and we see a modern example of this trait today in a mutant *Drosera erythrorhiza* as shown in CPN 9(1):11 1980. Although this plant totally lacked stalked glands, it had lost the ability to absorb nutrients but did have sessile glands in the leaf base.

Dionaea development perhaps came about by fusion of the tentacles of the leaf margin, however, a study of the leaf venation pattern suggests tentacles were lost and that each lobe developed by expansion of a *Drosera* leaf. In the intermediate stage, this pre-*Dionaea* leaf must have retained 3 or 4 tentacles on each lobe which today are called sensory hairs. There is a striking physiological resemblance between the stalked glands of *Drosophyllum*, the tentacles of *Drosera*, the trigger hairs of *Dionaea* and the bristles of *Aldrovanda*. There is a structure termed the endodermoid cell layer which is present in the stalked gland, tentacle and trigger hair of their respective species. This structure is indicative of a secretory ancestry. If *Drosera erythrorhiza* can grow sometimes without tentacles, it can grow with some of its tentacles modified to form cilia around the edge of the *Dionaea* leaf!

There are no intermediate species that can lead us to the possible origin of *Aldrovanda* but it is known that *Dionaea* frequently is found submerged in flooded areas a part of the year. It's interesting that even under several inches of water it is capable of trapping prey.

In conclusion, none of the features of carnivorous plants are exclusive but actually shown to be partly inherited during polyphyletic evolution. A few of these features are ancient with analogues found even in the fern family. The spectrum of all the features in one plant undoubtedly evolved because of the "relentless grind of pest pressure."

After completing Dr. Juniper's report, it occurred to me that there may be a living example of an intermediate plant which has characteristics between *Dionaea* and *Drosera rotundifolia*. This plant was recently described in 1985 as *Drosera falconeri* Kondo & Tsang and is a member of the petiolaris group. The plant resembles *Dionaea* in having small scaly bulbs encased in the petiole bases, the petioles are oblanceolate and the leaves are arranged in basal rosettes. The roots are blackish-brown and the leaf blades are circular and rather flat with the surface covered with glandular trichomes, but the rim having longer tentacles encircling it. The trap is reddish-orange in color and when the new leaf first emerges, it is folded along a midrib closely resembling a newly growing leaf of *Dionaea*. I have not observed if a mature leaf blade folds in half when an insect is trapped, but that would be an interesting similarity to *Dionaea*. The plant was discovered in 1980 by Doug Falconer and sent to Peter Tsang who reported this discovery in the pages of CPN 9(2):46 1980.

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