HOW EXCLUSIVE ARE CARNIVOROUS PLANTS?

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We tend to think that carvinorous plants belong to an exclusive club. Alone amongst the rich variety of plant life, only a few hundred fungi and flowering plant species are thought to be carvinorous, and of these we are mostly familiar with the flowering CPs. It is hardly surprising — the bizarre and often highly sophisticated traps of these plants have set them far apart from anything else we know of. Or have they?

Charles Darwin (1875) suspected that many plants bearing adhesive glands might turn out to be carnivorous, amongst them *Saxifraga umbrosa, Primula sinesis, Pelargonium zonale, Erica tetralix,* and *Mirabilis longifolia*, but (uncharacteristically) he did not take his suspicions any further. Probably the most influential review of the likelihood of carnivory outside our traditional concepts was Francis Lloyd's opening chapter in his classic book *The Carnivorous Plants*, published in 1942. In this he briefly mentioned a whole host of various insect-trapping devices in a quite extraordinary range of plant species — and yet he either dismissed or passed over all of them. It is probably thanks to Lloyd that we have settled for such a meagre number of carnivorous plant species.

One outstanding problem, though, is to define exactly what a carnivorous plant is, and I'll return to this question later on. What I want to consider first is the *potential* scope for widening the carnivory membership in the plant kingdom.

Adhesive traps

One of the commonest carnivorous plant traps is the sticky leaf trap, which glues its prey down while digesting it. This type of trap is present in many flowering plants (*Drosera, Drosophyllum, Pinguicula, Triphyllum*) and also hundreds of fungal species. But there are many more flowering plants which bear sticky hairs on parts or the whole of their shoots, as pointed out by Darwin; a few examples are given in Table 1. Aha, you might say — these sticky hairs are there to protect the plant from herbivorous insect predators, particularly crawling ones. Yes, this is no doubt true, but then the same equally applies to *Drosera, Drosophyllum* et al.; the essential difference, though, is that the plants in Table 1 (and others like them) have not been properly investigated. However, this is not true for a few forgotten species.

Apart from Charles Darwin, most of the early classic scientific work was carried out by Germans, so it came as a great surprise to me to stumble upon an intriguing Italian paper in *Biological Abstracts* entitled "Ricerche anatomofisiologiche sulla *Petunia violacea* e sulla *Petunia nyctaginiflora* come piante insettivore." Even

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Nepenthes had a coastal distribution during the Cretaceous.

Having written all this, I remind the reader that the foregoing is speculative and based on the assumption that CP distribution was determined mainly by continental drift. Long distance dispersal may have played a part in the matter. One wonders though, that if *Drosera* was spread about in such a manner, why then were *Byblis* and *Cephalotus* not so affected.

REFERENCES

Nikitin, P. A. 1927. Interglacial occurrence of *Aldrovanda vesiculosa* L. New Phytologist 26:58-59.

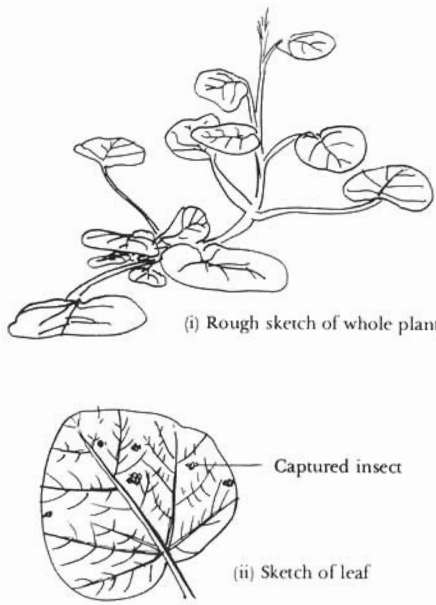
Raven, P. H. and Axelrod, D. I. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Garden 61:539-673.

TABLE 1. Examples of sticky hairs borne on the shoots of higher plants not traditionally considered carnivorous.

Organ(s) on which hairs are borne	Example of species
Leaves	*Erica glandulosa*
Stem	*Aeonium canariense*
Whole inflorescence	*Geranium madeirense*
Leafy bracts around flower	*Platylepis glandulosa*
Pedicel, corolla and calyx of flower	*Linnoea borealis*
Ribs of calyx	*Plumbago europea*
Entire foliage	*Primula glutinosa*

with my complete lack of the Italian language, I grasped that there was something very interesting in this. A call to the Science Museum Library located the paper by Zambelli, and started a fascinating paper chase, for cited in this paper were references to two other papers on insectivory in *Martynia lutea* (Mameli, 1916) and *Lychnis viscaria* (Mameli and Aschieri, 1920). All three papers were written by botanists at the University of Pavia, in the 1910s and 1920s, and translation of salient parts of each paper* revealed that both mucilage and digestive enzymes were detected in the secretions from the hairs of all four species. Furthermore, all these species readily captured and killed insect visitors, which, at least in the case of *Martynia*, attracts midges and other detritus-feeding flies by giving off a stinking odor. Figures redrawn from the paper are shown in figure 1.

Why did Lloyd omit these investigations (and many of the other useful references they cited) from his book, particularly as his literature research appears to be otherwise exceptionally thorough? To be fair, Lloyd did cite the earlier work of Fermi and Buscaglione (1899), who found that *Martynia* and many other genera could not digest animal matter; but the answer to why he did not include the later research which superseded this reference is a mystery. What is clear, though, is that we have taken Lloyd's book as definitive of all pre-1942 work, and that the Italian work has become lost in the course of time.



(i) Rough sketch of whole plant

(ii) Sketch of leaf

Figure 1. *Martynia lutea*

A more recent series of papers has described an even more intriguing discovery. John Barber of Tulane University, New Orleans, has shown that *seeds* of *Capsella bursa-pastoris* (Shepherd's purse), and probably most other Cruciferae seeds, behave like full-grown carnivores (refer to Barber, 1978). Not only do they trap, digest and absorb insect life, but they also release an attractant which lures mosquito larvae. The benefit to the seed's nutrition appears to be all the more important, since seeds of *Caspella* are very small, with consequently small food reserves; in addition, the germinating seedlings often

(iii) Leaf Glands (After Mameli, 1916)
(Magnification not known)

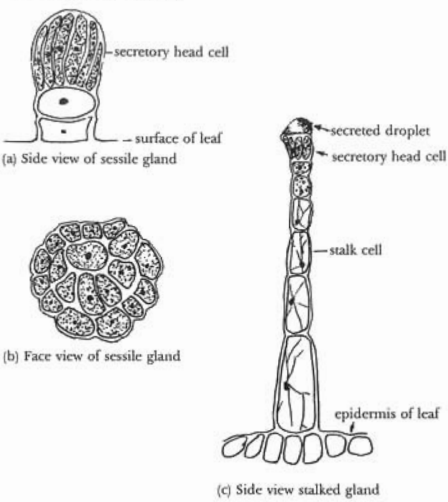


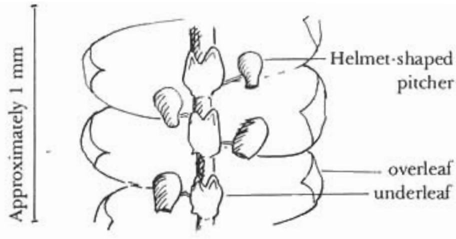
Figure 1. *Martynia lutea*

develop in nutrient deficient environments. (Perhaps the digestion of the prey also releases heat, so that the seeds germinate more readily).

Water-holding organs

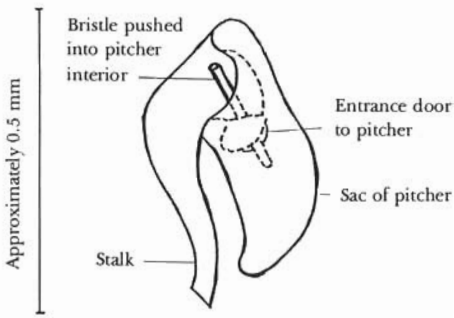
Another 'classic' carnivorous plant trap is the water-filled leaf pitcher; unwary animals are lured into them, fall in, and drown. Various types of water-holding structures are present in a wide variety of other plants, particularly in those plants having no contact with the ground but having independent means of nutrition — the epiphytes. Because of their aerial disposition, most epiphytes suffer from irregular water supplies, and have evolved various sorts of pitchers to collect and store rainwater.

Many of these water-holding pitchers are also ideal for trapping animals as well as rainwater. For example, the leaf lobes of many leafy liverworts (a group of lower plants resembling mosses) are cup-shaped, and readily catch rainwater trickling down the bark of a tree or whatever structure they are supported on. Microscopic single-celled organisms are often found swimming inside the leaf lobe pitchers, but do not seem to come to



Frullania tamarisci, viewed from below
(Drawn after Watson, 1971)

Colura calyptrifolia (after Muller, K. 'Rabenhorst's Krytogamen-Flora von Deutschland, Osterreich und der Schweiz VI', Edn. 3 Lieferung 9 (1957), Akad. Verlag. Geest & Partig, Leipzig)



Leaf lobe pitcher of *Pleurozia*
(Drawn after Stephani, F., 'Hepatiques insectivores', Rev. Bryol. 13:97-99 (1886))

Figure 2. Leafy liverwort pitchers

any harm inside them. However, the leaf lobes of two largely tropical genera, *Colura* and *Pleurozia* developed into astonishingly sophisticated pitchers (figure 2). The narrow entrance to each slipper-shaped pitcher is closed off by two flaps, one of which is rigid and one which is flexible. Should an animal pass into one of these pitchers it would have to push the flexible flap inwards, but once inside the pitcher the flap would spring back and seal off the entrance. Whether minute animals are trapped in this way is simply not known, but modern authorities such as Schuster (1966) regard the function of the pitchers as primarily for storing water, although Watkins (1971) says a carnivorous function is plausible.

Other epiphytic pitchers are generally much larger than those of the leafy liverworts, and as well as rainwater, collect dead leaves, insect carcasses, and other organic debris. Whether the animals become trapped and killed in such pitchers is not clear, even though their remains are almost certainly of nutritional value to the plant. For example, in the elaborate pitchers of *Dischidia rafflesiana* adventitious roots grow into the accumulated organic matter so as to extract useful food. Living animals are also found in many pitchers, such as in the cup-shaped leaf bases ('cisterns') of *Billbergia pallidflora* (cistern plant) (Van Oye, 1923). That most other members of the pineapple family, the Bromeliaceae, also have cup-shaped water-storing organs is certain, but some sort of symbiotic relationship with aquatic animals is quite possible.

Water-holding structures are not exclusive to epiphytes. *Dipsacus sylvestris* (the common teasel) has long been suspected of having carnivorous habits, as its leaf and flower bracts are very effective rainwater traps, often containing an abundance of insect bodies. Francis Darwin (son of Charles) noted that beetles caught in the teasel's bracts appeared to die quicker than in ordinary rainwater (F. Darwin, 1877), and Christy (1923) thought that the bract water stupefies its prey before it drowns. Unfortunately neither scientist provided more conclusive evidence for its carnivory.

There are many more water-holding devices just as likely to perform a carnivorous or 'quasi-carnivorous' function, and some of these are included in Table 2.

Another intriguing type of pitcher is that of the ant-plants, in which an ant population lives within the plant, protecting it from attack by herbivores and/or overgrowth by vines. Fred Rickson, of Oregon State University, Corvallis has recently shown that cohabiting ants of the ant-plant *Hydnophytum formicarum* actually *feed* the plant with insect remains they have previously captured, and that these remains are absorbed into the plant (Rickson, 1979). Although this type of nutrition does not strictly qualify as carnivory, since the animal food is trapped and killed by the ants (not the plant), it shows an uncanny resemblance to proper carnivory: degraded animal matter is absorbed into both types of plants. Since

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TABLE 2. Examples of water-holding structures, which may also serve a carnivorous function.

Organ	Description	Examples
Leaf lobe	Cup- or slipper-shaped pitchers	*Frullania, Colura*
Pocket leaves	Rosette of leaves surrounding a funnel-shaped cavity holding water and organic debris	*Asplenium nidus*, members of the Bromeliaceae
Mantle leaves	Leaves pressed against a stem so as to be able to collect water and organic debris (into which roots grow)	*Drynaria*
Cisterns	Urn-shaped cups formed from vertical leaves	*Billbergia*
Leaf and floral bracts	Cup-shaped pitchers	*Dipsacus sylvestris*
Pitcher leaves	Hollow pitchers which collect water and organic debris (into which roots grow)	*Dischidia rafflesiana*

PLATE VI – Explanation of Illustrations

Figs. 1-9: *Aldrovanda vesiculosa.*

Fig. 1.	Cross-section through the midrib of the leaf with a tactile bristle. X140.
Fig. 2.	Sensitive hinge of a live tactile bristle. X480.
Fig. 3.	The same after treatment with Javelle water; the delicate outer walls of the hinge cells are greatly swollen.
Fig. 4.	The same after treatment with $ZnCl_2$-I_2 solution. The varying intensity of the violet coloring is indicated by the varying gray tints. The swollen outer walls of the hinge cells remain colorless.
Figs. 5-7.	Plasmodesmata between the hinge cells and the mechanical cells of the tactile bristle bordering on the base. After treatment with I_2-KI solution and dilute sulfuric acid and staining with toluidine blue. X approx. 1200.
Fig. 8.	The same with much less swelling of the transverse wall.
Fig. 9.	The base of the tactile bristle. X530.

Figs. 12 and 13: *Drosophyllum lusitanicum.*

Fig. 12.	Cross-section through two cells of the epidermal glandular layer of a stalked gland. The cuticle has fine pores. After treatment with Javelle water. X approx. 600.
Fig. 13.	Surface view of two cells of the epidermal glandular layer. After treatment with Javelle water.

Fig. 15: *Drosera rotundifolia.*

Figs. 15a and b.	Isolated protoplasts of the lateral glandular cells of a parietal tentacle as seen from the side. On the upper side a row of plasma appendages which project into the peripheral pits. After swelling of the membrane with dilute sulfuric acid. X approx. 900.

Fig. 20: *Drosera longifolia.*

Fig. 20.	Isolated protoplast of an apical glandular cell. After treatment with dilute sulfuric acid and staining with toluidine blue. X approx. 1000.

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Hydnophytum is also an epiphyte, it is quite likely that it materially benefits from its insect meals. Ironically, *Nepenthes bicalcarata* is also an ant-plant as its pitcher-supporting tendrils are hollow and provide shelter for the ants which burrow into them.)

Discussion & conclusions

The likelihood of discovering carnivory amongst many more plant species than currently recognised looks very promising. Although this article has only made brief mention of sticky and pitcher traps, there are many other promising candidates with other types of traps worth considering, many of which were included in Lloyd's introductory chapter in his book (Lloyd, 1942).

Yet since the publication of Lloyd's book, only *one* new genus, *Triphyophyllum*, has been officially added to the list of plant carnivores (Green, Green and Heslop-Harrison, 1979). Why has so little progress been made on this front?

One of the reasons is probably the uncertainty of what *exactly* a carnivorous plant is. The main criteria may be as follows (although there is at least one exception to every point):

1. Attracts animals to a trap.
2. Traps and kills the animal victims.
3. Secretes a digestive juice onto the prey.
4. Absorbs the products of digestion into the plant.
5. The plant derives material benefit from its animal nutrition.

Another reason for not investigating more species is that proving carnivory, as outlined in the above criteria, requires considerable time, facilities, and money. For example, absorption of digestion products is best shown by using radioactively labelled compounds fed directly or indirectly (through animals) into the plant, and this technique needs stringent safety facilities as well as sophisticated apparatus.

Perhaps there is also a reluctance amongst enthusiasts to extend the 'status' of carnivory too far. After all, the conventional carnivores were largely established by scientific investigation over 50 years ago — why should we spend time and money on testing out completely new species?

To my mind the most exciting results could come from investigating crop plants. Darwin made mention of the sticky glands of *Nicotiana tabcum* (tobacco), but there are other surprising possibilities, amongst them the sticky leaf glands of a wild tomato *Lycopersicon hirsutum* and of some species of wild potato (e.g., *Soolanum tuberosum*). Both the tomato and potato glands have been extensively studied, but surprisingly only their insecticide activity has been sought after (e.g., Williams *et al.*, 1980, Gibson, 1978 respectively).

Given the chance, we might be on the threshold of a renaissance in carnivorous plant research with prizes as every bit as great as those that Charles Darwin and his contemporaries grabbed. Above all we must keep open minds, perhaps even regarding these plants as having *degrees* of carnivory, rather than *in toto*.

References

Barber, J. T. *Capsella bursa-pastoris* seeds. Are they carnivorous? Carniv. Pl. Newsletter 7:39-42 (1978).

Christy, M. The common teasel as a carnivorous plant. J. Bot. 61:33-45 (1923).

Darwin, C. *Insectivorous Plants*. J. Murray, London (1875).

Gibson, R. W. Resistance in glandular-haired wild potatoes to flea beetle. Am. Potato J. 55:595-599 (1978).

Green, S., Green, T. L. and Heslop-Harrison, Y. Seasonal heterophylly and leaf gland features in *Triphyophyllum* (Dioncophyllaceae), a new carnivorous plant genus. Bot. J. Linn. Soc. 78:99-116 (1979).

Lloyd, F. E. *Carnivorous Plants*. Wlatham, Massachusetts (1942), reprinted by Dover Publications, (1976).

Mameli, E. Richerche anatomiche, fisiologiche e biologiche sulla *Martynia lutea* Lindl. Atti. Ist. Bot. dell'Universita di Pavia, Series II, 16:137-188 (1916).

Mameli, E. and Aschieri, E. Richerche anatomiche e biomiche sul *Lychnis viscaria*. Atti. Ist. Bot. dell'Universita di Pavia, Series II, 17:119-129 (1920).

Rickson, F. R. Absorption of animal tissue breakdown products into a plant stem — the feeding of a plant by ants. Am. J. Bot. 66:87-90 (1979).

Schuster, R. M. *The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian. Vol. 1.* Columbia Univ. Press, New York and London (1966).

Watkins, E. V. *The Structure and Life of Bryophytes*, 3rd edition, p. 40. Hutchinson, London (1971).

Williams, W. G., Kennedy, G. G., Yamamoto, R. T., Thacker, J. D., Bordner, J. 2-tridecanone: a naturally occurring insecticide from the wild tomato *Lycopersicon hirsutum* f. *glabratum*. Science 207:888-889 (1980).

Zambelli, E. Ricerche anatomofisiologiche sulla *Petunia violacea* e sull *Petunia nyctaginiflora* come piante insettivore. Atti. Ist. Bot. dell'Universita di Pavia, Series IV, 1:75-87 (1929).

Van Oye, P. De micro fauna en flora der bladtrechers van Bromeliaceae. Natuurwetenshapp. Tijdschr 5:179-182 (1923).

Additional Note: If anyone has photos of any of the potential carnivores mentioned in this article or others also likely to be carnivorous, I would be *very* grateful to have loan of them to make copies. All material will be promptly returned and remuneration made for costs.

* If anyone would care to volunteer translating further parts of the papers I would very much like to hear from them!