WHAT EXACTLY IS A CARNIVOROUS PLANT?

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We all find carnivorous plants fascinating, beautiful, and interesting. But just what is a carnivorous plant? What are the attributes that transform a mundane vegetable into a hungry killer? For a long time I preached that a plant is carnivorous if it attracts, captures, digests, and absorbs prey. This four-point definition seemed to work.

In 2009 I was asked to write a scientific review of carnivorous plants for a technical volume (Rice 2010). I used this opportunity to review prior definitions of carnivory in plants. The first carefully stated definition I could find had two parts: (1) a plant must have at least one adaptation for attraction, capture, or digestion of prey, and (2) that the plant must be able to absorb the nutrients from the prey (Givnish *et al*. 1984). Juniper *et al*. (1989) also offered a definition with two criteria—the possession of both traps and digestive organs. To the common four-point definition (attract, capture, digest, and absorb), Schnell (2002) added that a carnivorous plant must clearly benefit from the obtained nutrients.

Why is it so difficult to easily define what we mean by carnivorous plants? The problem is rooted in two underlying issues: paracarnivory, and hunting inefficiency.

Paracarnivorous Plants

Paracarnivorous plants are those that have some, but not all, of the characteristics of a carnivorous plant. The situation is exemplified by the two species in the genus *Roridula* (Anderson 2005; Anderson & Midgley 2002). These plants have sticky, prey-capturing leaves. *Roridula* species live in nutrient-poor habitats with *Drosera* and *Utricularia*, so clearly being carnivorous would give them access to valuable resources. However, the sticky fluids on their leaves are resin-based (not mucus-based), and as such cannot transmit digestive fluids from the plant to the prey, nor can they transmit nutrients from the prey back to the plant. Accordingly, *Roridula* was classified noncarnivorous by Lloyd (1942) and many subsequent authors (Schlauer 2002; and others).

Is this classification appropriate? Many studies have shown that creatures captured by the leaves of *Roridula* are consumed by capsid insects that live on the plant, and that feces from these insects are absorbed by the plant through specialized gaps in their waxy cuticle (Anderson 2005). With this in mind, should *Roridula* be considered carnivorous? I believe the answer is clearly “yes”.

A common objection to a carnivorous classification for *Roridula* is based in the fact the plants do not produce their own digestive enzymes. But is this objection valid? Many animals have microbes in their digestive tracts, which facilitate in digestion. Termites provide a famous example of this. Although termites eat wood, they cannot digest it. The enzymes that digest their meals are produced by protozoa and bacteria that live in the termites’ digestive tracts. Just as I consider termites to be organisms that eat and digest wood (albeit in a mutual relationship with microbial life), I consider *Roridula* to be a carnivorous plant.

Although the species of *Roridula* are carnivorous because of their symbiotic relationships with insect allies, the mere occurrence of capsid insects on a plant does not mean it is carnivorous. Yes, capsids are frequently found on *Drosera* and *Byblis* in Australia (Hartmeyer 1996; Lowrie 1998).

However, I have also observed them on many other plants, including *Brugmansia*, *Helianthus*, *Ibicella*, and *Stylidium* (Rice 2008; pers. observation). These plants may simply be suitable hunting grounds for the carnivorous capsids, and may not partake in the meals.

Another interesting parallel can be drawn between *Roridula* and *Darlingtonia* (the pitcher plant of western North America). While *Darlingtonia* has evolved a variety of exquisite characters to encourage the capture of prey, the plants in this genus do not produce digestive enzymes. Instead, *Darlingtonia* plants rely upon a suite of commensals such as the ravenous larvae of *Metriocnemus edwardsii* midges (Rice 2006). I look at *Darlingtonia* and I see a carnivorous plant. But really, the only difference between *Darlingtonia* and *Roridula* is one of topology—in *Darlingtonia*, the enzyme producing commensals live internally in pitcher fluids, while in *Roridula* the enzyme producing commensals live on the surface of the plant. This is not the kind of difference that would separate carnivorous from non-carnivorous plants.

Considering the issue of digestive enzymes further, it is useful to look at other intermediate cases in the realm of pitcher plant genera. There is no doubt that many (*Cephalotus*, *Nepenthes*, *Sarracenia*, *etc.*) produce digestive enzymes. However, even in these cases some of the digestion is performed by commensal organisms ranging in size and complexity from bacteria, to arthropods, and even vertebrate associates (Bradshaw & Holzapfel 2001; Clarke 1997, 2001; Gibson 1999, 2001; Rice 2006; Schnell 2002). As noted, *Darlingtonia* does not produce digestive enzymes, nor do any of the *Heliamphora* except possibly *H. tatei* (Jaffé *et al.* 1992). Meanwhile, the pitchers of *Sarracenia purpurea*—which are unique in the genus for persisting for approximately two years—produce digestive enzymes for only a tiny fraction of their lives (Gallie & Chang 1997).

All this being said, it is important to draw the line between those plants that are only occasionally and incidentally involved in the death and decay of animal life, and those that are truly carnivorous. Adopting an overly-generous definition—such as including all plants that absorb decaying animal products through their roots—would result in the classification of nearly all plants as carnivorous. Chase *et al.* (2009) use this definition, noting that "nearly all plants are capable of a degree of carnivory." This approach errs in being excessively lax, just as requiring a plant to produce its own digestive enzymes for inclusion in the ranks of carnivory is excessively strict.

Hunting Inefficiencies

Another reason it is difficult to define plant carnivory is that even the most indisputably ravenous of carnivorous plants are very poor hunters! Who among us hasn't spent many long minutes watching insects crawling about on the surface of a *Dionaea* plant, only to see it eventually leave without ever having touched a trigger hair? Who hasn't watched flies, wasps, or ants feed endlessly on the nectar under the lid of a *Sarracenia* or *Nepenthes* plant, before flying safely away? The fact is that most of the creatures that visit carnivorous plants leave safely enough, perhaps even the better for having supped on delicious nectar.

The main reason this issue is important, is that it attacks one of the very pillars of carnivorous plant definitions—do carnivorous plants really attract prey? Clearly, plants such as *Sarracenia*, *Heliamphora*, and *Darlingtonia*, which have nectar-producing glands at key locations on their traps, are quite adept at luring prey to the trap openings. But for the most part, the "attractive properties" of carnivorous plants are taken as a matter of faith—it has been demonstrated for only a small fraction of the so-called carnivorous plants.

For example, *Drosera* and *Pinguicula* are undisputably classified as carnivorous. Yet the only studies comparing the attracting effects of *Drosera* and *Pinguicula* to comparably sized inert traps

(Antor & García 1994; Harms 1999; Watson *et al.* 1982; Zamora 1990, 1995) failed to show any significant active luring by such plants (Ellison & Gotelli 2009)! Many of the carnivorous plants might not lure prey at all—and if we exclude these from the ranks of carnivory, our definition might eliminate many carnivorous plants; at risk are *Drosera*, *Pinguicula*, *Utricularia*, *Genlisea*, *Byblis*, as well as others.

That even the most active of carnivorous plants are poor hunters means that it is difficult to separate the poor but hungry hunters, from the plants that do not seek animal flesh at all!

A New Definition for Plant Carnivory

So how does one define "carnivorous plants?" One approach is to create a definition and then examine the plant kingdom, asking which satisfy your definition. Another approach is to examine

Table 1. Carnivorous families, genera, and species counts. Note that carnivory in the plant world has evolved separately at least five times. Some of these groups, which contain carnivores of distinctly different strategies, probably represent additional cases where carnivory has developed independently (Ellison & Gotelli 2009, and sources therein).

Group 1: Caryophyllales		
Dioncophyllaceae	*Triphyophyllum*	1
Droseraceae	*Aldrovanda*	1
	Dionaea	1
	Drosera	187
Drosophyllaceae	*Drosophyllum*	1
Nepenthaceae	*Nepenthes*	128
Group 2: Ericales		
Roridulaceae	*Roridula*	2
Sarraceniaceae	*Darlingtonia*	1
	Heliamphora	18
	Sarracenia	11
Group 3: Lamiales		
Byblidaceae	*Byblis*	7
Lentibulariaceae	*Genlisea*	21
	Pinguicula	96
	Utricularia	225
Group 4: Oxalidales		
Cephalotaceae	*Cephalotus*	1
Group 5: Poales		
Bromeliaceae	*Brocchinia*	2
	Catopsis	1

the world of plants, observe the syndrome of carnivory, and then craft a definition that includes the plants that seem to fit the role. Following the latter philosophy, I proposed (Rice 2010) the following definition, which seems quite sensible:

1) Clear adaptations to capture prey are present. Such adaptations may include specialized structures (*i.e.*, basic traps such as glandular tentacles or pitcher trap) and/or enhancements to improve the luring and capture of prey (*i.e.*, extrafloral nectaries, attractive UV or pigmentation patterns, odors, hairs that guide prey, *etc.*).

2) A mechanism is present by which prey are degraded into a form that can be assimilated by the plant. The digestive mechanism may be enzymes produced by the plant, decomposition by bacterial activity, or other organisms in a mutualist relationship with the plant (*i.e.*, arthropods as in the cases of *Darlingtonia* and *Roridula*).

3) A pathway is available that allows nutrients to be absorbed into the plant, thus contributing to the plant's competitive and reproductive fitness.

Simply stated, the definition is that a plant must have traps, a digestion mechanism, and a nutrient pathway that benefits the plant.

Using this definition, the families, genera, and species counts for each of the seventeen genera of carnivorous plants of the world are given in Table 1. The picky reader may wish to refer to my web site (Rice 2007), where I maintain more updated species lists than the one above, which is frozen in time.

Plants currently excluded from my list, either because they do not fit my definitions or as yet have inadequate evidence supporting their possible carnivory, include *Aracamunia*, *Capsella*, *Colura*, *Dipsacus*, *Ibicella*, *Paepalanthus*, *Passiflora*, *Philcoxia*, *Proboscidea*, and *Stylidium*. Time may add these to my list.

Does the above definition and resulting species list make sense to you? If not, spend time generating your own definition of "carnivorous plants." It is a pleasant diversion, an interesting exercise, and surprisingly challenging!

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