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Carnivorous Plants with Hybrid Trapping Strategies

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Recently I wrote a general book on carnivorous plants, and while creating that work I spent a great deal of time pondering some of the bigger issues within the phenomenon of carnivory in plants. One of the basic decisions I had to make was select what plants to include in my book.

Even at the genus level, it is not at all trivial to produce a definitive list of all the carnivorous plants. Seventeen plant genera are commonly accused of being carnivorous, but not everyone agrees on their dietary classifications—arguments about the status of *Roridula* can result in fistfights![1] Recent discoveries within the indisputably carnivorous genera are adding to this quandary. *Nepenthes lowii* might function to capture excrement from birds (Clarke 1997), and *Nepenthes ampullaria* might be at least partly vegetarian in using its clusters of ground pitchers to capture the dead vegetable material that rains onto the forest floor (Moran *et al*. 2003). There is also research that suggests that the primary function of *Utricularia purpurea* bladders may be unrelated to carnivory (Richards 2001). Could it be that not all *Drosera*, *Nepenthes*, *Sarracenia*, or *Utricularia* are carnivorous? Meanwhile, should we take a closer look at *Stylidium*, *Dipsacus*, and others? What, really, are the carnivorous plants?

Part of this problem comes from the very foundation of how we think of carnivorous plants. When drafting introductory papers or book chapters, we usually frequently oversimplify the strategies that carnivorous plants use to capture prey. For example, the following classification scheme of carnivorous plant strategies probably looks familiar:

Snap traps (or bear traps): *Aldrovanda, Dionaea*.
Flypaper plants: *Byblis, Drosera, Drosophyllum, Pinguicula, Roridula, Triphyophyllum*.
Pitfall traps: *Brocchinia, Catopsis, Cephalotus, Darlingtonia, Heliamphora, Sarracenia, Nepenthes*.
Suction traps: *Utricularia*.
Lobster pot traps (or eel traps): *Genlisea*.

However, as happens in all simple classification systems for living organisms, there are examples that span categories. These are cases where carnivorous species have hybrid strategies in capturing prey. In this paper I will describe a few of them.

Flypaper-pitfall hybrids

The genus *Nepenthes* has more species than any other genus of pitfall carnivores, so it is not a surprise that some of its members have evolved into forms that use extraordinary strategies to obtain valuable nutrients.

Nepenthes inermis is an interesting highland species from Sumatra that has funnel-shaped pitchers that lack a peristome. The tiny pitcher lid of this species is little more than a thin strap held high above the pitcher. It was long assumed that this *Nepenthes* was simply another pitfall carnivore. But is it? Why is the inner surface of the pitcher coated with a thin layer of mucilaginous slime? Clarke (2001) reviews various observations and ideas that have been presented for this species, and concludes that *Nepenthes inermis* pitchers probably function as hybrid flypaper-pitfall traps. Insects are attracted to the pitchers, perhaps because of their bright green color or aromatic fragrance. But instead of foraging on a peristome, the insects become mired on the sticky surface on the inner surface of the pitcher. Gravity then causes the captured prey to slowly slide down the pitcher surface until they enter the bath of fluid in the lower portion of the pitcher. A depressing end for the insects, indeed!

[1]In this paper, I will accept as “carnivorous” those plants that do not produce their own enzymes, but which may use associates or commensals to complete the digestion process.

Figure 1: Inside a *Darlingtonia* pitcher, looking out. Notice how difficult it would be to reach the entrance corridor once prey find themselves inside the pitcher. The treacherous pitfall is at the far right. Note how dark the escape aperture is, when compared to the illuminated pitfall. Photograph made in natural light.

Figure 2: The entrance corridor into a *Nepenthes ampullaria* pitcher.

Lobster pot-pitfall hybrids

Pitfall traps and lobster pot traps have many commonalities. Both types of traps rely upon the prey entering a chamber from which they cannot escape. The key difference between these trap strategies is in how the prey are conveyed to their doom. In pitfall traps, the prey errs by losing its grip on a slippery or otherwise challenging surface, and in this temporary lapse of navigational control it plummets—in accordance with Newton's law of gravitation—into a chamber from which it cannot escape. In contrast, a lobster pot works by producing obstacles that effectively act as one-way valves, much like the turnstiles that guide the traffic flow of human commuters at public transportation facilities. Prey enter the trap under their own powers of movement (instead of being ushered in by gravity, as in a pitfall trap).

Erect *Sarracenia* are exemplars of respectable pitfall traps. Once an insect topples into a *Sarracenia* pitcher its options for escape are limited by the exceedingly slippery pitcher walls. Even victims with wings are in great danger, since nearly all flying insects fly in a mostly-lateral direction—in order to fly out of a pitcher, an insect must be skilled at flying vertically in very cramped quarters. Gravity takes its toll, and the plant receives its meal.

However, one species—*Sarracenia psittacina*—is clearly not a pitfall plant. The pitcher of this species is tilted at 45° to the horizontal, or very often is perfectly horizontal. If held at such angles, conventional *Sarracenia* traps would be essentially harmless. But the pitcher opening in *Sarracenia psittacina* is uniquely modified. Instead of gaping like a hungry mouth, the trap opening is shaped as a lateral entry tunnel that provides access to a large, globose, internal cavity inside the pitcher trap (see Back Cover). Once an insect passes through the tunnel and drops into the internal cavity, escape is extremely difficult. This escape route is very small, and is also very hard to get to because its opening is held high above the floor of the pitcher cavity. These two attributes of the escape route— small size and difficulty of access—are classic lobster pot features.

Meanwhile, another passage is presented to the prey; one much easier to enter, and so very inviting. This tube is lined with long hairs that point ever deeper into the trap, and which allow entry but prohibit exit. But woe to the insect that enters this passage: *Ergo insectum moriturum*!

Clearly, Slack (1979) was correct when he listed *Sarracenia psittacina* as a lobster pot, along with *Genlisea*. But is this the only case of a lobster pot carnivore masquerading as a pitfall plant? Consider *Darlingtonia californica*. In strategic structure, it is almost identical to *Sarracenia psittacina*—the only significant difference is that the trap is rotated ninety degrees so the pitcher tube is once again vertical, as is usual in a pitfall plant. Prey, mostly daytime foragers, land on the fanglike appendages dangling under the pitcher orifice. These insects crawl up and through a cylindrical entry corridor with confidence because the inside of the pitcher is brilliantly illuminated by the glassy windows on the pitchers.[2] Climbing into the pitcher, the insects clamber to the end of the entry corridor and vault over the edge, dropping a short distance onto the flat floor of the expanded pitcher head. Now, the only real escape lies in backtracking, but this would be difficult because it would require scaling the steep outer edge of the entry corridor, which has an overhanging ledge[3] (see Figure 1). Flying insects are unlikely to escape aerially because the pitcher roof, confusingly sealed with transparent windows, is nearly as bright as the daytime sky, while the real avenue of escape—directly downwards through a comparatively small opening—is relatively dark because it points down towards the ground.

Meanwhile, another avenue is easily accessed. Brightly illuminated with glassy windows, it is the descending pitcher tube that leads to death by drowning, and a hoard of hungry *Metriocnemus* larvae…

Darlingtonia, then, has the two key attributes of a lobster pot: a small portal that is difficult to find again once entered and which is difficult to access even if found. Are there any other examples of lobster pot-pitfall traps? Possibly, depending upon how much you wish to blur the boundaries. The peristomes of both *Nepenthes ampullaria* and *N. aristolochioides* are modified so that the entry

[2]While the fenestrations in *Sarracenia* pitchers are translucent at best, in *Darlingtonia* they are truly, and remarkably, as perfectly transparent as a paper-thin sheet of mica.

[3]There is, however, a small gap in the *Darlingtonia* entry corridor, and lucky is the insect that can find it!

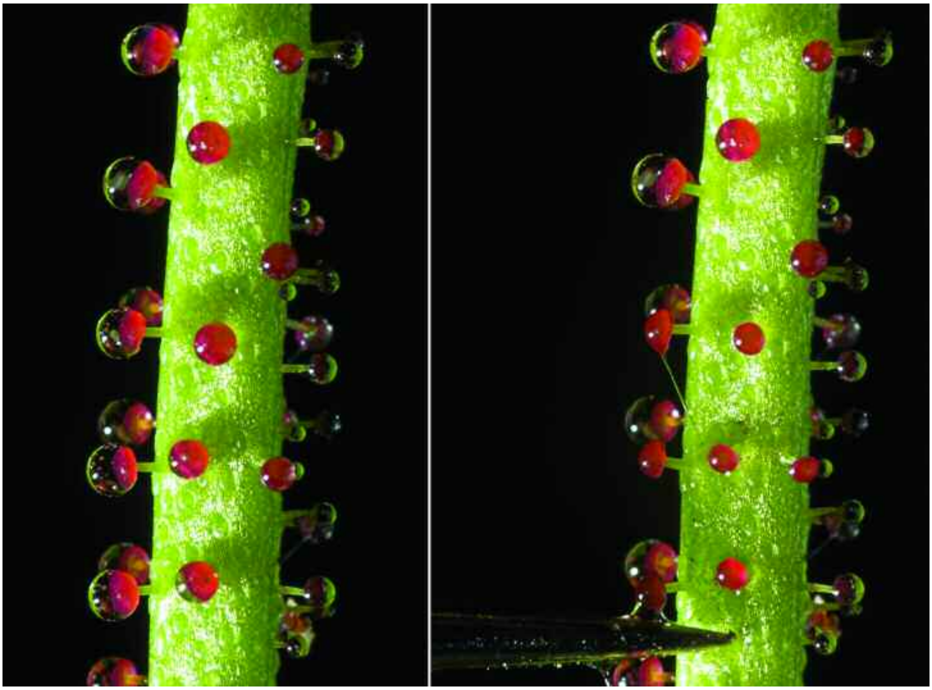

Figure 3: Left: A fresh *Drosophyllum* leaf with the mucous glands and sessile digestive glands easily visible. Right: The same leaf, swept with the tip of a metal pin. Notice how mucus is transferred onto the pin.

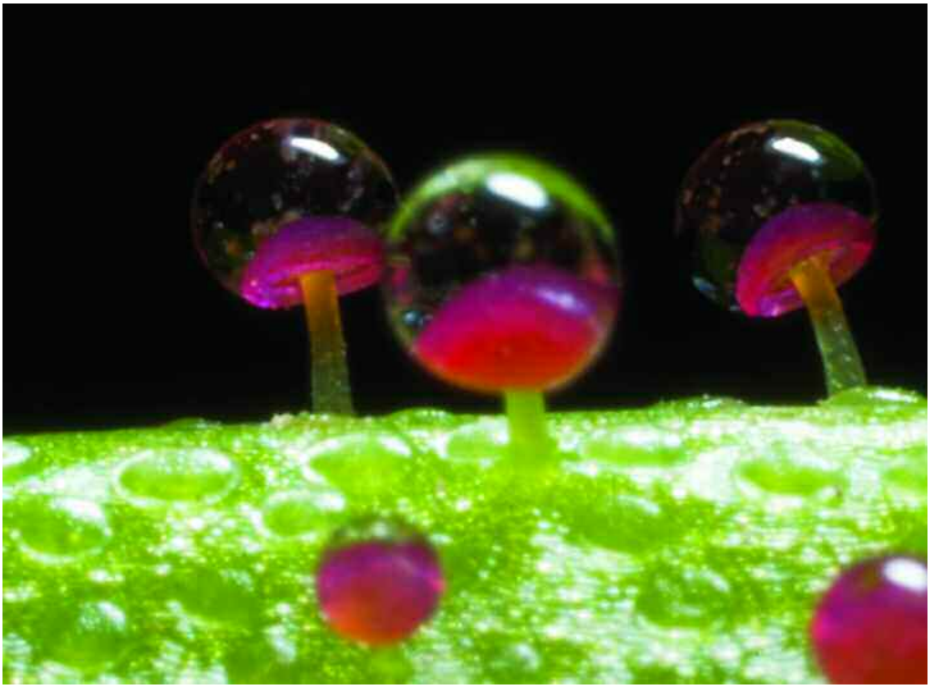

Figure 4: Extremely high power imagery showing the mushroom-like shape of *Drosophyllum* mucous glands.

into the pitcher is transformed into an entry corridor (see Figure 2), much as in *Darlingtonia* or *Sarracenia psittacina*. The peristomes of other *Nepenthes* species, such as *N. jacquelineae* or *N. mirabilis* var. *echinostoma* give their pitchers a bit of lobster pot flavor, too. Even *Cephalotus* pitchers have, interior to their peristomes, a second ledge which impedes the escape of prey. But at this point, the suggestion of a lobster pot is probably stretching the definition. Even if one were to concede that the peristome structures of *Nepenthes* pitchers have a retentive function that is effective because it has an element of the lobster pot strategy, these are still gravity-driven pitfall traps…mostly.

Another flypaper-pitfall hybrid

Flypaper plants capture prey by generating sticky droplets on the leaves. Bugs contacting these droplets cannot escape. The adhesive glue from each gland acts like a rope, tying the prey to the gland tip, and thus to the leaf. As a necessary result, so obvious it may first escape your notice, is the simple fact that while prey may struggle and thrash, they eventually succumb very close to the point of original leaf contact.

Drosophyllum lusitanicum, the large glandular plant from Portugal, Spain, and Morocco, uses a different strategy. Stalked glands cover the leaf surface, and the plant appears to be yet another passive flypaper. And indeed, tiny prey that are trapped by leaves adhere to these glands as in a conventional flypaper. But when *Drosophyllum* captures much grander prey, a new strategy emerges.

When a large insect lurches against a *Drosophyllum* mucous gland, an extraordinary event occurs. Instead of forming a long strand binding the prey to the gland, the entire load of mucus is neatly transferred onto the prey (see Figure 3). *Drosophyllum* gland heads have an interesting mushroom-shape unlike any *Drosera* glands, and this shape may be key in effectively transferring the mucus (see Figure 4). The insect responds by blundering into another gland, which again transfers its burden of mucus onto the prey. The bewildered insect moves about the leaf as it tries to rid itself of the unwanted mucus. *Drosophyllum* leaves spend the majority of their lives oriented vertically, or are at least steeply ascending. This ensures that the struggling, ever-more-beslimed insect is guided gravitationally down the length of the leaf. After several glands have been contacted, the prey is sufficiently coated with slime so it can no longer breathe: it suffocates (or drowns), ironically perched in an aerial location on a threadlike leaf. The sessile glands then contribute to the digestion process by releasing additional fluids.

Drosophyllum therefore differs from conventional flypaper plants in that it uses gravity to drop the prey downwards, until it is surrounded by fluid in which it drowns. This exact sentence could be used to describe a pitfall carnivore such as *Nepenthes*. Indeed, the trap of *Drosophyllum* is in essence a pitfall-flypaper, even though there is no pit!

The previous examples of carnivorous plants with hybrid foraging strategies show how our simple classification schemes are inadequate. Nature often creates situations that confound our attempts at simple analyses. Be very cautious, I say, when labeling one carnivore a "pitfall trap" and another a "flypaper plant." And in the same way, we must remember that some plants may blend the boundaries between carnivory and noncarnivory. We must keep our eyes open for these intermediate cases, and prepare ourselves for long arguments about carnivory! As for me, I've recently obtained a few *Stylidium* plants, and will be watching them very carefully!

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