■ Opinion

Carnivorous plants and UV-radiation: a captivating story?

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Carnivorous plants are "different", and this fascinates people. The "appetite" of carnivorous plants has, on occasion, taken on mythical proportions. In "The Day of the Triffids" giant, man-eating plants go on a rampage, while in "Ice Age 3: Dawn of the Dinosaurs" a carnivorous plant gobbled up an entire mammoth. On a slightly less violent note, we have observed that carnivorous plants on our University College Cork recruitment stand help attract high school students during open days, giving us a chance to advertise our undergraduate degree in plant biology. A psychologist could probably write a PhD thesis on the fascination of humans with carnivorous plants. However, let me just say that if you are interested in these plants, you are in good company. Back in 1875, Charles Darwin wrote "Insectivorous Plants", a book focussing heavily on *Drosera sp* (sundew) (Fig. 1A). In fact, Charles Darwin was so fascinated by these carnivorous plants that he once stated that "at this present moment, I care more about the *Drosera* than the origin of all the species in the world" (Darwin 1860). I surmise that Charles Darwin's interest in carnivorous plants was inspired by his family. In fact, Dr. Erasmus Darwin, his grandfather, was already investigating how the tentacles of *Drosera* species respond to stimuli (Cheers 1992). Another carnivorous plant aficionado was Joseph Hooker (of Bentham and Hooker taxonomic fame) who as director of Kew Gardens, London, was able to collect carnivorous species from across the world. Hooker studied the digestive system of carnivorous plants and concluded that "a substance, acting as a pepsin is given off from the inner wall of a pitcher [of a *Nepenthes sp*], but chiefly after placing the animal matter in the acid fluid" (Cheers 1992). Taken together, these early observations summarise the main characteristics of carnivorous plants: their ability to capture and digest prey (insects, arthropods, and even small mammals) for the purpose of plant nourishment. In fact, there is not a lot else that the different taxa of carnivorous plants share. The nearly 600 species of carnivorous plants that occur across nine families and different taxa are not necessarily closely related. Indeed, there is strong evidence that carnivory in plants has evolved independently on at least nine separate occasions (Givnish 2014). Their trapping structures are highly diverse, and these include the sticky leaves and/or responsive tentacles (like those observed by Erasmus Darwin), pitfall traps or pitchers with digestive juices (as studied by Joseph Hooker), hinged-trapping leaves in *Dionaea sp* (Venus fly trap) and bladder-traps in *Utricularia sp* (bladderwort). In general, there is good understanding of the actual mechanical responses involved in capturing prey as well as the subsequent digestive processes involved in extracting nutrients from the prey. What is typically less clear is why any insect (or other prey) would venture near the trapping-structure of a carnivorous plant. Secreted nectar, scent and trap

Figure 5.1: *Drosera rotundifolia* plants in visible light (A) and under UV radiation (B) showing reflectance of tentacles. Copyright O. Holovachov (http://www.holovachov.com).

shape and colour are often listed as key attractants for insects (Joel et al. 1985), with in some cases flowers emitting different scents as the trapping-structure to avoid potential pollinator-prey conflicts (Ho et al. 2016). Yet, it has also been suggested that UV-radiation plays a role in prey attraction (Joel et al. 1985). In fact, in 2012/2013 several major news outlets reported that "These Carnivorous Plants Glow Under Ultraviolet Light to Attract Prey" (Smithsonian.com, December 11, 2013), "Carnivorous Plants Glow to Attract Prey" (National Geographic, February 25, 2013), and "Carnivorous plant species glow blue to lure prey" (BBC Nature, February 19, 2013). These stories referred to strong UV-induced fluorescence, which was reputed to attract prey, and an example of which is shown in figure 2. Here, I will explore the evidence for a role of UV-radiation in attracting prey, and identify some of the gaps in our understanding of this putative role of UV-radiation.

It has long been known that floral patterns of UV-reflection or absorbance play a key role in pollination biology (Brock et al. 2016; Cronin and Bok 2016). Such floral UV patterns are common. Indeed, the *UV4Plants bulletin* (Issue 1, 2016) displayed a photograph which showed UV-patterns in dandelion flowers. These patterns are thought to contribute to attracting or deterring of specific insects, serve as plant-species specific markers and/or as orientation cues. Joel et al. (1985) noted the conceptual similarities between flowers attracting pollinators and carnivorous plants attracting prey. Using UV-photography, Joel et al. (1985) surveyed UV-patterns in the trapping structures of carnivorous plants. The authors took their photos under natural sunlight conditions using filters that transmit between 305 and 385 nm. Their study showed that various carnivorous plants have "conspicuous UV patterns" on or near their traps. The pitchers of *Heliamphora* display a clear UV-reflecting entrance to the beaker-structure. In contrast, *Sarracenia* pitchers contain UV-absorbing nectar, while in *Drosophyllum* species the old leaves are UV-reflecting, whilst the young, carnivorous leaves in the centre of the plant are UV-absorbing and appear

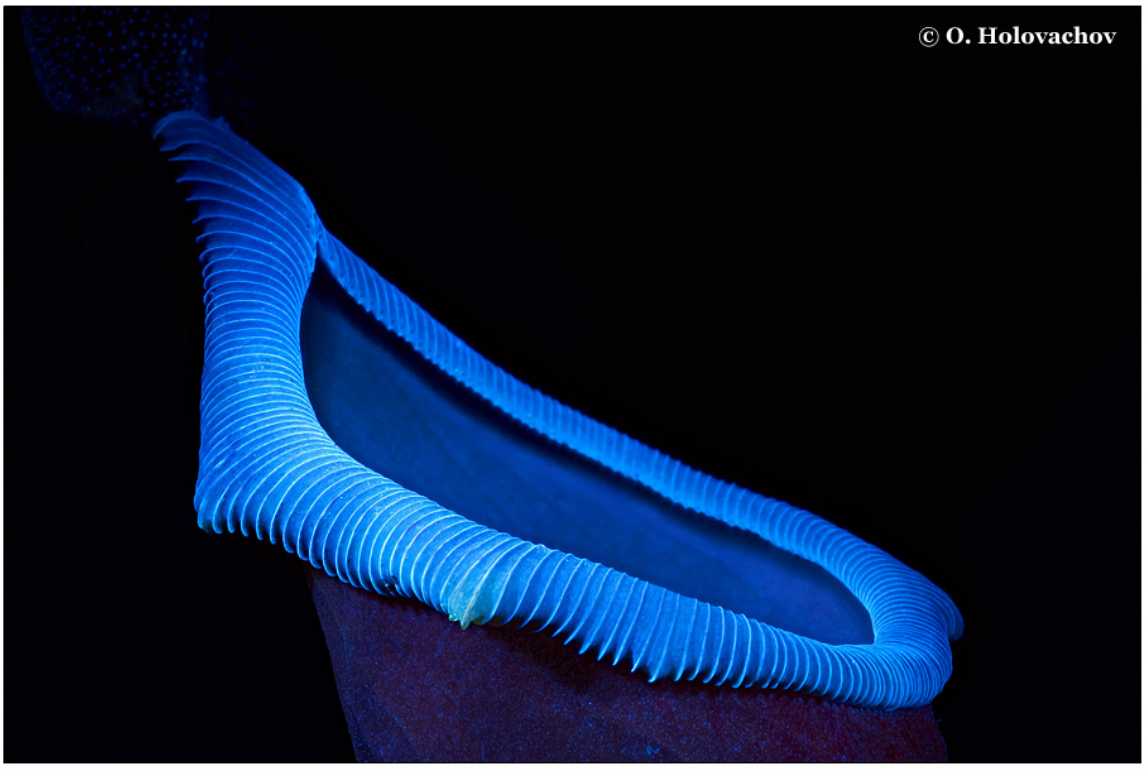

Figure 5.2: Blue fluorescence emitted by the rim of a *Nepenthes alata* beaker. Copyright O. Holovachov (http://www.holovachov.com).

as a relatively dark environment. A recent photograph of UV-reflectance in *Drosera rotundifolia* by Oleksandr Holovachov shows reflectance of tentacles (Figure 1B). Kurup et al. (2013) took the study of UV-patterns a step further by scanning the fluorescence of trapping structures using a densitometer. Kurup et al. (2013) focussed on blue fluorescence, following excitation with 366 nm radiation. In this context it is worth pointing out that the technology used by Joel et al. (1985) showed reflectance and absorbance in the UV-B and UV-A part of the spectrum, while Kurup et al. (2013) measured UV-induced blue fluorescence. Not surprisingly, different UV-patterns were noted by the two groups. Thus, technology plays a key role in what UV-pattern is observed, and this is a major consideration when interpreting the literature. Kurup et al. (2013) explored the blue fluorescence of *Nepenthes sp* peristomes (the ring of tissue that surrounds the entrance to the digestive tube). The authors stated that "The peristomes of *Nepenthes* species flashed like well-designed blue fluorescent tracks".

The markings in or near traps have been hypothesised to have a functional role in prey capture (Joel et al. 1985; Kurup et al. 2013). Moran, Clarke, Greenwood, et al. (2012) showed that an insectivorous species of *Nepenthes* displayed a distinct colour pattern compared to a closely related species that harvests tree-shrew excreta. Light does play a role in creating this pattern. Shading experiments by Moran, Clarke, and Gowen (2012), showed that reductions in visible and UV light resulted in a substantial decrease in the capture of *Drosophila* by *Nepenthes aristolochioides* pitchers. However, these results were interpreted in the context of light

(of all wavelengths) transmitted through the translucent pitcher, rather than as a specific role for UV-patterns. Kurup et al. (2013) experimentally tested whether UV-induced blue fluorescence has a functional role in prey capture. The authors found that removal of the peristome (rim) from *Nepenthes* pitchers led to a dramatic decrease in captured prey. Masking the peristome with acetone-extracts had a similar negative effect on prey capture. These results might be interpreted as supporting a role of UV-induced fluorescence in prey-capture (which is exactly what popular scientific journals did), but are far from conclusive. Clearly, excising tissue will not just remove UV-induced fluorescence, but also cells that are important for the production of nectar and scent, while causing massive tissue disruption. Similarly, acetone-extracts will have multiple effects on cells and tissues. Furthermore, basic photobiological questions should be asked concerning UV-induced blue fluorescence. How realistic is it that the sensitivity of the insect eye is such that it can perceive small changes in UV induced blue fluorescence, against a background of solar blue radiation? In this context, it is also important to be aware of the background of blue autofluorescence emitted by cell-wall-bound ferulic acid and other plant secondary metabolites following excitation with UV wavelengths (Buschmann et al. 2000; García-Plazaola et al. 2015). Thus, although pictures of UV-induced blue fluorescence look great, doubts remain concerning the functional role of such fluorescence. In fact, these doubts also apply to the common UV-induced blue fluorescence in, for example, flowers. Holovachov (2015) states that "despite considerable research efforts, the function of ultraviolet-induced visible fluorescence in the world of plants remains poorly understood", and indeed is unlikely to play a key role in the interactions between insects and plants.

Phenomena such as UV-reflectance, and UV-absorbance are more likely candidates for attracting insect prey. Both UV-reflectance, and UV-absorbance are known to be involved in the well characterised process of pollinator attraction in flowers (Guldberg and Atsatt 1975; Silberglied 1979). Unfortunately, the monitoring of UV reflectance and absorbance is often subject to technical limitations. UV-enabled cameras are equipped with filters that transmit in the UV-range of the spectrum, thus omitting the visible wavelengths. Yet, changes in UV absorbance and reflectance need to be interpreted in terms of the contrast with other wavelength zones. Exploring whether UV-radiation per se has a role in carnivory can be straightforward, for example by comparing prey capture in the presence or absence of UV-radiation. However, interpreting the precise role of UV radiation is complex as any UV-effect can be mediated either through the insect (i.e. vision) or through the plant (i.e. absorbance or reflectance). If the duration of the experiment is long enough, UV acclimation responses will further modify the biochemical make-up of the plant, and therefore potential UV-patterns. Clearly, prising apart the complex interaction between prey and carnivorous plant will be highly complex. Nevertheless, the application of the principles and terminology of photobiological research and UV-manipulation, as commonly practised in the UV4Plants community, can potentially contribute to the understanding of the role of UV radiation in prey capture. Exploring the wavelength dependency of UV reflectance and absorbance vis-á-vis insect vision can consolidate the link between these processes; for instance, local excitation with UV lasers can trigger local UV-reflectance whilst avoiding a direct effect on the insect. The use of artificial "model traps" together with the application of UV-absorbing pigments can similarly be used to experimentally test attraction traits. Nevertheless, it is unlikely that such work will generate more than "correlations" between UV-exposure and prey capture. Genetic manipulation is a more likely

strategy to conclusively proof a role for UV radiation in prey capture. Manipulation of UV-patterning through, for instance, breeding (Moyers et al. 2017), or manipulation of the spectral vision of the prey, for example of the model species *Drosophila melanogaster* (Feiler et al. 1992), are both realistic. Studies using genetically modified material should be able to reveal the relative importance of UV patterns, relative to other attractants such as secreted nectar, scent and trap shape and colour.

For now, UV-patterns exist, caused by UV-reflectance, UV-absorbance and UV-induced blue fluorescence. But although the story of UV-and carnivorous plants may be captivating, the truth about the functional role of UV-patterns is still to be captured!

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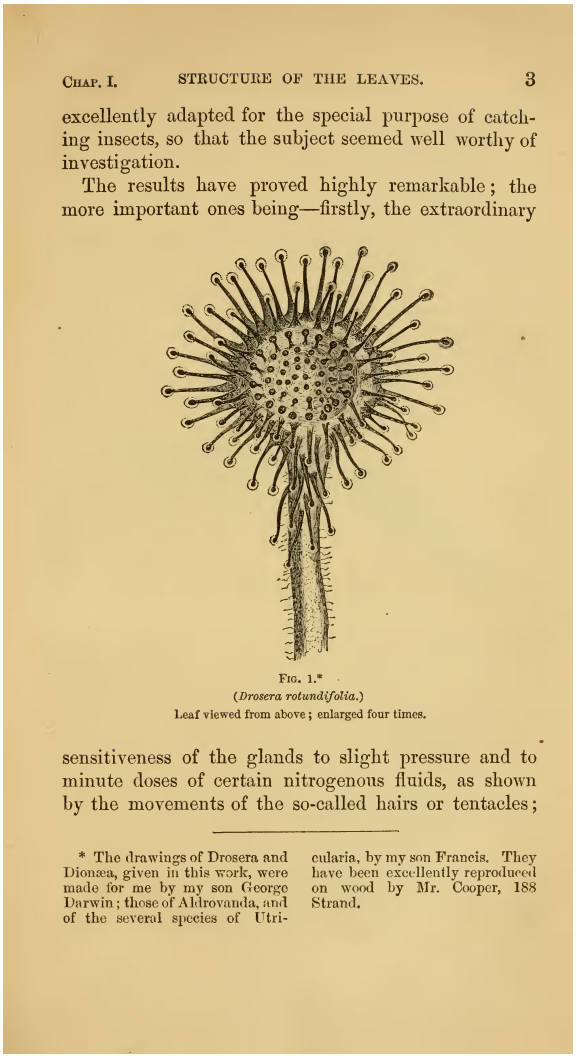

CHAP. I. STRUCTURE OF THE LEAVES. 3

excellently adapted for the special purpose of catching insects, so that the subject seemed well worthy of investigation.

The results have proved highly remarkable; the more important ones being—firstly, the extraordinary

FIG. 1.*
(*Drosera rotundifolia.*)
Leaf viewed from above; enlarged four times.

sensitiveness of the glands to slight pressure and to minute doses of certain nitrogenous fluids, as shown by the movements of the so-called hairs or tentacles;

* The drawings of Drosera and Dionæa, given in this work, were made for me by my son George Darwin; those of Aldrovanda, and of the several species of Utricularia, by my son Francis. They have been excellently reproduced on wood by Mr. Cooper, 188 Strand.

Figure 5.3: Page 3 from the book *Insectivorous plants* (Darwin 1875).

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