The Search for all of the victims and all of the killers

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Carnivorous plants often claim the name "insectivorous" for the simple reason that most carnivorous traps usually contain insects, and, even when not insects, trapped prey are usually close cousins of the insects from within the Phylum Arthropoda. An example of this is when bladderworts (*Utricularia* spp.; Lentibulariaceae) trap crustaceans such as amphipods and copepods, which are arthropods, like insects. Indeed, Darwin's book on the carnivorous plants recognizes this fact with its title Insectivorous Plants (Darwin 1875). Splitting open a pitcher from *Sarracenia leucophylla*, as an example, usually reveals one chitinous arthropod exoskeleton after another.

There are, of course, examples of carnivorous plants preying on other groups in the Kingdom Animalia, such as the trapping of vertebrates (Phylum Vertebrata) by genera such as *Sarracenia* (e.g. Butler *et al*. 2005), and rotifers of Phylum Rotifera can be found in the aquatic traps of *Utricularia* (e.g. Kurbatova & Yershov 2009).

The ubiquity of arthropods as prey and the noticing of vertebrates can be explained by two facts. First, the arthropods are the largest, and, by several measures, the most successful phylum on Earth. They may not build steel bridges or conduct controlled studies, but they shine for the sheer number of species and individuals found on Earth. So, no wonder that the land plants have fed so much on such abundant prey.

Second, the vertebrates are often noticed because they are in our own phylum and we tend to notice our own kind first. Also, given the size, strength, and complex nervous systems of vertebrates, trapping these animals or obtaining nutrients from them in some other way seems especially impressive and, thus, noteworthy. Thus, as an example, we notice newts in *Sarracenia purpurea* traps (Butler *et al*. 2005).

All of this raises the question: what about the many other phyla of animals? Are they the subject of trapping by carnivorous plants? From that flows the further question: could a look at these phyla, not known to be trapped by carnivorous plants, point out targets to search for new carnivorous plants?

There are well over 30 phyla of animals (Sadava *et al.* 2012; Mason *et al.* 2017; Table 1), the majority of which are at least partly marine and not known as prey for plants. One might also add the untrapped classes and orders within phyla that have been recognized as prey for carnivorous plants. For example, consider the cephalopod mollusks: the squids, the octopuses, and their relatives, which have not been recorded as plants' prey, though their cousins in the same phylum have.

Given that life started in the seas, it is no surprise that the greatest number of animal phyla can be found in those seas. This makes for abundant prey. It is also important to recall that many animal phyla, such as the mollusks, may have members which are sessile, and hard or impossible to trap as adults, but which have motile larvae which could serve as prey for carnivorous plants.

Some of this lack of trapping could have to do with the relative lack of land plants having returned to marine or brackish habitats (Table 1). Those plants that have returned to salty water

Table 1. Some phyla of animals (based on Sadava *et al.* 2012; Mason *et al.* 2017).

Phylum	Marine/Estuarine Members
Sponges (multiple phyla)	Many
Ctenophora	All
Placozoa	All
Cnidaria	Many
Orthonectids	All
Rhombozoans	All
Chaetognatha	All
Bryozoa	Many
Entoprocta	Most
Platyhelminthes	Many
Gastrotricha	Some
Rotifera	Many
Nemertea	Most
Brachiopoda	All
Phoronida	All
Annelida	Many
Mollusca	Many
Kinoryncha	All
Loricifera	All
Priapulida	All
Nematoda	Some
Nematomorpha	None
Tardigrada	Some
Onychophora	None
Arthropoda	Many
Xenoacoelomorpha	Some
Echinodermata	All
Hemichordata	All
Tunicata	All
Lancelata	All
Vertebrata	Many

are all angiosperms—there are no salt-water examples of gymnosperms, fern allies, or non-vascular land plant groups (Cook 1996; Table 2). The few truly marine angiosperms, such as seagrasses, have simple bodies and no obvious traps, and there are not that many angiosperms in brackish habitats, either. Salt-water habitats have probably been overlooked for this reason as well as the reason that the insects and mammals that receive so much attention as prey for known carnivorous plants are comparatively rare in these salt-water habitats.

But what about seaweeds? (From the outset, it should be made clear that this paper is a speculative one, designed to argue that certain organisms may be carnivorous. The paper aims to point the direction for new research and to argue from first principles why these organisms probably exist. It does not provide hard data and is, thus, more theoretical.)

Why might seaweeds include carnivorous plants? (These could be referred to as salt-water carnivores.) First, it should be noted that the Green and Red Algae, including familiar edible oceanic plants like sea lettuce (*Ulva lactuca*) and dulse (*Palmaria palmata*) are part of the Plant Kingdom, based on molecular and other studies of the last few decades (Sadava *et al*. 2012; Mason *et al.* 2017). It could also be argued that only the Green Algae can be considered "plants," given their close connection to the land plants which include the recognized carnivorous plants. Any search among the Green Algae for carnivores could usefully and easily include a check of the Red Algae for carnivory. Given their general nature as photoautotrophs, this would probably be an interesting related work for carnivorous plant workers.

The Brown Algae include seaweeds such as kelp and evolved separately from the Plant Kingdom. They are more closely related to organisms such as the single-celled

Table 2. Aquatic flowering plants in marine, estuarine, brackish waters (from Cook 1996 except *Taylor 1989, and personal observations in Great Marsh near Chestertown, Maryland, USA).	
Family	**Genera**
Apiaceae	*Lilaeopsis, Oenanthe*
Araceae	*Cryptocorne*
Cymodoceaceae	*Amphilbolis, Cymodocea, Halodule, Syringodium, Thalassodendron*
Droseraceae	*Aldrovanda*
Eriocaulaceae	*Eriocaulon*
Hydrocharitaceae	*Euhalus, Halophila, Thalassia*
Juncaginaceae	*Triglochin*
*Lentibulariaceae	**Utricularia*
Najadaceae	*Najas*
Poaceae	*Coleanthus, Paspalum*
Potamogetonaceae	*Ruppia*
Primulaceae	*Samolus*
Zannichelliaceae	*Althenia, Lepilaenia, Zannichellia*
Zosteraceae	*Heterozostera, Phyllospadix, Zostera*

diatoms and the decomposers known as watermolds (Mason *et al.* 2017). These are not plants, though they are photoautotrophs like plants and have evolved many similar forms to those of the Green and Red Algae. For this reason, any search for marine carnivorous plants among the Green Algae might at the same time also look among the photoautotrophic Brown Algae for carnivory as an interesting connected study.

Based on the fossil record, seaweeds, including the Green Algae, which can be called "plants," have existed for at least three times as long as the flowering plants, giving them plenty of time to evolve the carnivorous syndrome.

What factors might be important in searching for salt-water carnivorous plants and for carnivorous activity among other seaweeds? First, consider that turbulence is important for terrestrial carnivores which either live in areas with low turbulence in the air or place their traps where delicate prey will not be blown away by turbulence, as with sundews. Their leaves are often low to the ground in a zone with poorly stirred or unstirred air or found among other vegetation that lowers or eliminates turbulence. Also, bladderworts usually have their traps in waters with little or no turbulence or movement, and the rare exceptions, especially the rheophytic bladderworts, stop making traps in very turbulent water (Adamec *et al.* 2015).

Turbulence is likely to be an issue for salt-water photoautotrophs, including plants, especially due to the near-constant action of marine tides. Personal observations made it clear that this is even true in the relatively protected habitat found in estuaries. Thus, salt-water carnivores would need to reduce turbulence in some way. This could come in the form of traps with pits or tunnels, similar to terrestrial carnivores like *Sarracenia* or *Genlisea*, which prey could enter, allowing an internal trapping mechanism to work in an internal low-turbulence environment.

Another possibility would be for seaweeds to be part-time carnivores if they were stranded above the water and, thus, out of the turbulence generated by tides. These could be sticky on their surfaces, trapping and quickly digesting prey between tides. Seaweeds, plants and non-plants alike, generate abundant mucilage which could be used in this way as it is used by *Drosera* and *Pinguicula*.

A third possibility would be for salt-water carnivores to be found in places where the density of growth lowered turbulence. One possible habitat like this could be the Sargasso Sea off Bermuda, where the dense growth of seaweeds, especially *Sargassum*, provides a nursery for young animals, potential prey, and lowered turbulence due to the density of seaweed growth.

In any case, the search for salt-water carnivores among plants and other photoautotrophs should also look at habitats which are similar to those of terrestrial and fresh water carnivorous plants: ones with high light intensity and low nutrient availability. The high light in these habitats provides enough energy for carnivorous plants to make their complicated traps while performing the normal daily activities seen in all plants. This would require low-turbidity salt-water habitats for carnivory in seaweeds, including those accepted as plants.

Low nutrient levels provide the selective pressures for carnivores to have evolved their carnivorous structures. There are many low-nutrient salt-water habitats, such as the previously mentioned Sargasso Sea. These would be analogous with the bogs and tepuis where so many terrestrial carnivorous plants are found.

So, it seems probable that salt-water carnivores exist: it's time to go looking for the killers.

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