

Evolution of carnivorous and paracarnivorous plants

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Albert, V.A., Williams, S.E., and Chase, M.W., 1992. **Carnivorous plants: phylogeny and structural evolution.** *Science*, 257: 1491-1495.* Historically, inferences about the evolution of carnivorous plants were based primarily on morphology, especially trap type. This study by Albert et. al. was the first to examine the evolution of carnivory using molecular tools, and sampled 100 plants across 72 families, including 13 carnivorous genera. Their phylogeny indicates at least seven separate origins of carnivory, and demonstrated multiple convergences of generalized trap form in distantly related taxa.

Plant carnivory in the strict sense is a relatively rare ability which requires a suite of adaptations. This phylogeny contained several genera that met some, but not all of the criteria used to define carnivory. These taxa whose carnivorous status has been questioned (“paracarnivores”) are especially useful in understanding the evolution of the carnivorous lifestyle.

Anderson, B., Midgley, J.J., 2002. **It takes two to tango but three is a tangle: mutualists and cheaters on the carnivorous plant *Roridula*.** *Oecologia*, 132: 369–373. The genus *Roridula* (Roridulaceae) consists of two species endemic to nutrient-poor areas of South Africa. The plant has an obligate, species-specific digestive mutualism with two species of *Pameridia* (Hemiptera), which feeds on trapped prey and defecates on the leaves.

In this paper, Anderson et. al. demonstrated that *Roridula* absorbs ~70% of its total nitrogen in this manner. This study also found that the population density of *Pameridia* was negatively correlated with the density of the spider *Synaema marlothi*. *S. marlothi* feeds on both trapped prey and *Pameridia*, and Anderson et. al. proposed that *S. marlothi* was a “cheater” in that it exploited the trapping efforts of the plant, reduced the population of the mutualist, but apparently did not offer the plant any benefit in return.

Anderson, B., Midgley, J.J., 2003. **Digestive mutualism, an alternate pathway in plant carnivory.** *Oikos*, 102: 221–224. This paper proposed widening the definition of carnivorous plants to include those that digest their prey indirectly through obligate and host-specific mutualisms. Specifically, *Roridula*.

Anderson, B., 2005. **Adaptations to foliar absorption of faeces: a pathway in plant carnivory.** *Annals of Botany*, 95: 757-761. The leaves of all terrestrial plants are coated with a waxy cuticle, which acts as a protective barrier. Many carnivorous plants have specialized

absorptive glands which permit the uptake of dissolved prey; these glands are absent in *Roridula*. To investigate the method of absorption in *Roridula*, the dye neutral red was applied to foliage, and was found to be absorbed through unusual cuticular gaps, which the author used to strengthen the argument for defining *Roridula* as carnivorous.

Anderson, B., Midgley, J.J., 2007. **Density-dependent outcomes in a digestive mutualism between carnivorous *Roridula* plants and their associated hemipterans.** *Oecologia* 152:115–120.* Although the digestive mutualism between *Roridula* and *Pameridia* was described in 1996, this study is the first to note that *Pameridia* not only feeds on trapped prey but also sucks the plant sap of *Roridula*. This important detail was omitted from previous studies, which focused on the mutual benefits of this relationship.

Through manipulative experiments, Anderson 2007 found that the growth rate of *Roridula* was highest under conditions of intermediate *Pameridia* densities. The growth rate at high densities resembled that of plants without *Pameridia*, indicating that the increased herbivory on *Roridula* by *Pameridia* may neutralize added nutritional benefits.

This finding caused the authors to revise the role of the spider previously described as a “cheater” of the mutualism in Anderson 2000. The coevolution of mutualisms imply long term stability. In mutualisms that contain some element of antagonism, predators such as this may be important in adding stability to the system.

Barber, J.T., 1978. ***Capsella bursa-pastoris* seeds: Are they "carnivorous"?** *Carnivorous Plant Newsletter*, 7: 39–42. This short essay suggested that *C. bursa-pastoris* (shepherd's purse) should be examined for carnivory. The researchers were studying mucilage of submerged seeds when they noticed that mosquito larvae appeared to be attracted to the seeds, where they became stuck to the mucilage and died. Although some proteolytic enzyme activity was detected in the mucilage, no publications have since reported further tests and the carnivory of *C. bursa-pastoris* remains unsupported.

Barthlott, W., Porembski, S., Seine, R. and Theisen, I., 2007. **The Curious World of Carnivorous Plants.** Timber Press, 224p. This book had excellent photos of the corkscrew traps of *Genlisea* that I used in my presentation.

Burger, A. E., 2005. **Dispersal and germination of seeds of *Pisonia grandis*, an Indo-Pacific tropical tree associated with insular seabird colonies.** *Journal of Tropical Ecology*, 21(3):263–271. This morbid study investigated the claims that the seeds of *P. grandis* are adapted to trap and kill seabirds for the added nutritional benefit of germinating near a decomposing corpse. This notion is based on numerous reports of dead birds who apparently died after being entangled by the sticky infructescence. The researchers however found that any possible benefit

to germinating plants was outweighed by the damage done by scavenging crabs that were attracted to the decomposing birds, and could not be considered as adapted for carnivory.

Clarke, C.M., 1997. **Nepenthes of Borneo**. *Natural History Publications (Borneo), Kota Kinabalu*. 207 pages. Unfortunately this is the only published account of the unusual relationship between *Nepenthes lowii* and birds. *Nepenthes* is one of the most diverse and specialized genera of carnivorous plants, but this species appears to supplement its diet with the droppings of birds, which it apparently attracts with specialized food rewards. The author suggests *N. lowii* may be evolving away from carnivory and towards coprophagy; however more observations are needed to confirm this phenomenon. This author also describes the tendril domatium of *N. bicalcarata*, which harbor ants that also supplement the carnivore with their accumulated wastes.

Darnowski, D.W., Carroll, D.M., Płachno, B., Kabanoff, E., and Cinnamon, E. (2006). **Evidence of protocarnivory in triggerplants (*Stylidium* spp.; Stylidiaceae)**. *Plant Biology*, 8(6): 805-812. Comparisons of herbarium sheets showed similar numbers of insects stuck to *Stylidium* as those on sticky carnivorous plants. Endogenous protease activity was also detected (I misstated this in my talk). The sticky hairs of this genus are concentrated not on the leaves but on the floral parts, which is commonly thought of as a defense mechanism against crawling nectar-robbing insects such as ants. However, if the absorption of nutrients from prey is detected, *Stylidium* may well be reclassified as a carnivorous plant, if only slightly.

Dolling WR, Palmer JM. 1991. ***Pameridea* (Hemiptera: Miridae): predaceous bugs specific to a highly viscid plant genus *Roridula***. *Systematic Entomology*, 16: 319–328. This was the first paper to note the occurrence of *Pameridea roridulae* on *Roridula gorgonias*, which was found exclusively on this plant.

Ellis AG, Midgley JJ. 1996. **A new plant–animal mutualism involving a plant with sticky leaves and a resident hemipteran**. *Oecologia*, 106: 478–481. *Roridula* has long been suspected of carnivorous capabilities. However, although the leaves are covered with sticky hairs which trap numerous insects, the method of digestion and absorption were unknown. When Dolling 1991 described *Pameridia* it was originally thought to be a kleptoparasite of *Roridula*, intercepting the nutrients within trapped prey before it could be absorbed by the plant.

Ellis 1996 quantified the nutritional role that *Pameridia* feces plays by using flies which were raised on yeast containing the stable isotope ^{15}N . The labeled flies were applied directly to the leaves of *Roridula*. Plants which were allowed access to the hemipterans were found to have a more than a fivefold increase in ^{15}N when compared to plants from which hemipterans were excluded. This finding led the authors to conclude that there existed a mutualistic relationship in which *Pameridia* benefitted from the trapped prey, and *Roridula* benefitted from the indirect

digestion of nutrients. This study is the first report of a mutualism between a carnivorous plant and an invertebrate.

Ellison, A.M., Gotelli, N. J., Brewer, J. S., Cochran-Stafira, D. L., Kneitel, J. M., Miller, T. E., Worley, A. C., Zamora, R., 2003. **The evolutionary ecology of carnivorous plants.** *Advances in Ecological Research*, 33: 1-74. In 2000, the Ecological Society of America hosted a symposium where ecologists were asked to suggest areas of future carnivorous plant research, reviewed here. For my talk I was interested in the possible use of phytotelma to study inquiline community assembly, food web dynamics, and the stability of digestive mutualisms.

Givnish, T. J., Burkhardt, E. L., Happel, R. E., Weintraub, J. D., 1984. **Carnivory in the bromeliad *Brocchinia reducta*, with a cost/benefit model for the general restriction of carnivorous plants to sunny, moist, nutrient-poor habitats.** *The American Naturalist*, 124 (4): 479-497. This paper explained that although *B. reducta* was not shown to produce enzymes, it hosted a community of phytotelma inquilines which perform digestion by proxy. *B. reducta* grows in nutrient-poor areas alongside other carnivores, has a highly modified pitcher shape, and has been found to contain large numbers of drowned insects; however it is often considered a paracarnivore due to digestive mutualism.

Hess, S., 2005. **Evidence of zoophagy in a second liverwort species, *Pleurozia purpurea*.** *The Bryologist*, 108(2), pp. 212-218. I mentioned the fact that small arthropods and nematodes had been found trapped in a folded thallus structure of several liverwort species, although this has not been investigated further.

Plachno, B.J., Adamec, L., Lichtscheidl, I. K., Peroutka, M., Adlassnig, W. and Vrba, J., 2006. **Fluorescence labeling of phosphatase activity in digestive glands of carnivorous plants.** *Plant Biology*, 8:813–820. The most difficult criteria that defines a carnivore is endogenous production of enzymes. This is the first study that conclusively demonstrated endogenous production, rather than the existence of surface enzymes which may be a result of contamination. Unfortunately, the enzyme studied was phosphatase, which would be useful in liberating phosphorus from animal corpses, but is also used in the conversion of ATP into ADP and may simply indicate increased metabolic activity.

Radhamani, T.R., Sudarshana, L., and Krishnan, R., 1995. **Defence and carnivory: Dual role of bracts in *Passiflora foetida*.** *Journal of Biosciences*, 20(5): 657-664. This study did find protease activity in the glandular hairs on the bracts of *P. foetida*, which is the most common enzyme used to define carnivory. However, there is no mention of sterilizing the bract surface or otherwise demonstrating that production was endogenous, nor was absorption found. This may simply be another case of a sticky floral defense against nectar-robbars.

Rachmilevitz, T. and Joel, D.M. (1976). **Ultra structure of the calyx glands of *Plumbago capensis* Thumb. in relation to the process of secretion.** *Israel Journal of Botany*, 25:159-168. I mentioned that this species has also been investigated for carnivorous activity; however again, the sticky hairs are found only on the floral parts.

Rees, W. A. and Roe, N. A., 1978. ***Puya raimondii* (Pitcairnioideae, Bromeliaceae) and birds: an hypothesis on nutrient relationships.** *Canadian Journal of Botany*, 58: 1262-1268. Many species of *Puya* have extremely sharp outwardly pointing spines, supposedly to deter herbivores. This paper observed that the spines of the bird-pollinated *P. raimondii* pointed inward towards the rosette. This treelike (>10m) Andean bromeliad is found above treeline and several bird species also use the rosette as a nest site, where the inward pointing spines appear to provide stability to the nest.

These birds are also trapped by the spines and killed, and Rees 1978 counted a total of 44 dead birds in only 17 individual plants. Additionally, the leaves were reportedly curved into a trough shape, which may allow *P. raimondii* to benefit from the added nutrients provided by runoff of accumulated nest debris, droppings and dead birds.