Carnivory in *Byblis* Revisited II: The Phenomenon of Symbiosis on Insect Trapping Plants

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Introduction

When people think of carnivorous plants, they mostly think that those little "killers" catch and digest anything they are able to overwhelm. However, carnivorous plants benefit many arthropods, including ants, true bugs, small crawfish, mosquito-larvae and spiders. Furthermore, numerous bacteria and fungi profit from the presence of the captured prey. In some cases the benefit is through sheer robbery, for example when ants steal the prey from a sundew trap. Other times, the ants live on the plant and defend it from herbivores. As they go about their lives, the ants drop mineral rich feces on the leaves or inside the pitchers. This is a case of classic symbiosis in which both sides benefit by the partnership. (The plant also benefits from the more rapid processing of prey into nutrients. This deters fungal development, which is a considerable danger especially for plants that use glue traps but that do not produce enzymes.) This kind of symbiosis is exploited by the non-carnivorous tobacco plant (*Nicotiana tabacum*) which has gluey regions that protect the plant from herbivores. These zones are cleaned by resident true bugs (*Engitatus tenuis*). An analogous cleaning symbiosis is well known from cleaning stations in coral reef habitats, where specialized shrimp and fish clean parasites off much bigger species.

Other relationships occur which are borderline-symbiotic. For example, a small red crawfish (*Geosesarma malayanum*) raids *Nepenthes ampullaria* pitchers. It uses its claws to crush and consume the drowned prey in a wasteful way. The crushing speeds digestion, which compensates for the loss of part of the prey. This situation would be a true symbiosis only if the crawfish were specialized to coexist with the carnivorous plant population.

It is necessary to understand the details of symbiosis because a new discussion about carnivory in plants is beginning. This is important for plants (perhaps even including tobacco) which use glue traps. The results of recent investigations about the plant-arthropod mutualism in *Roridula gorgonias* and about the enzyme production on *Byblis liniflora* are discussed below.

Is *Roridula* Carnivorous?

Roridula is a South African genus containing two shrubby species which bear stalked glands that produce an effective India rubber-containing glue. The carnivorous status of species in *Roridula* has been debated ever since Charles Darwin first suggested they were carnivores (1875). Work by Marloth (1910) and Lloyd (1935) countered Darwin's conclusions because the sticky shrublets do not have the sessile glands that produce proteolytic enzymes and which absorb nutrients (as does *Drosophyllum*). *Roridula* was repeatedly shown to be unable to produce digesting

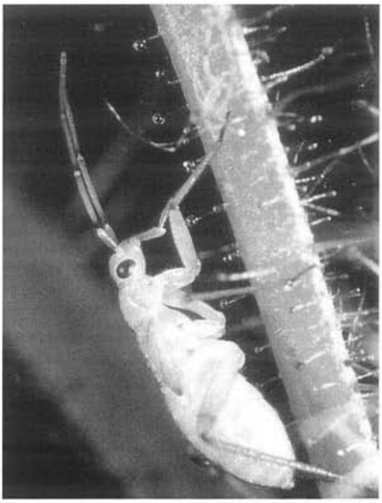

Figure 1: Symbiotic bug on *Roridula gorgonias*. Photo by Matthias Schmidt.

enzymes, so it was theorized that these plants (that have the strongest glue of all the insect-trappers) only benefited from the captured prey when nutrients from the decaying prey washed into the soil. Capsid bugs (Miridae) which live on the plants were postulated as representing another loss to the plant because, astonishingly, they freely move on the plant and steal the immobilized insects. Furthermore, some species of spiders use their webs to avoid the plant's glue and feed upon the Capsid bugs and arthropods stuck to the plant. But in spite of all this, Darwin's theory remained popular and *Roridula* continues to be grown by carnivorous plant enthusiasts.

During 1991 to 1996 I raised two plants of *Roridula gorgonias* in my living room in Weil am Rhein, Germany. They were 1.2 m tall, and had a good population of *Pameridea* bugs. The bugs remained on their host plant and only on rare occasions the adults used their wings for a reconnaissance of our house (no persons were attacked!). On sunny days, when I moved the plants to my balcony, the bugs did not try to escape. During the winter I fed the bugs with beetle larvae from pet shops, and in the summer the plants caught enough flies and wasps for the bugs. When arthropods were captured in abundance, the bug population grew so large the plant was nearly suffocated by their feces (in nature the bug population is moderated by spiders. By feeding the plant in moderation, there were fewer feces and they gradually became paler and paler until they practically disappeared (this happened even indoors). One year the plants were so vigorous they produced sixty beautiful pink flowers! This is documented in my first English-language video (1994), in which I suggested it was an example of a true symbiosis. I soon became involved in the heated discussion regarding the carnivorous status of *Roridula*. I maintained that *Roridula* is a true carnivorous plant even though it does not have enzymes that can dissolve its captured prey. I think the nutrition is not absorbed via soil fertilization but much more effectively through the predigested feces of its *Pameridea* partners. I think the definition of true carnivorous plants (that is, trapping of prey, digestion of prey by proteolytic enzymes, and absorbing the nutrients) should include the passive digestion by true symbiosis, as long as the nutrients are absorbed.

Supporting evidence appeared in 1996, when Ellis and Midgley published detailed and highly interesting examinations. They used a method developed by Dixon *et al.* (1980), who traced the ^{15}N nitrogen uptake in *Drosera erythrorhiza*. Yeast was combined with ammonium sulfate tagged with ^{15}N, and this mixture was fed to fruit flies (*Drosophila melanogaster*) for five days. Ellis and Midgley tested plants in the field and in the laboratory, both with and without *Pameridea* bugs present. The fruit flies were placed on the plants, and eaten by the

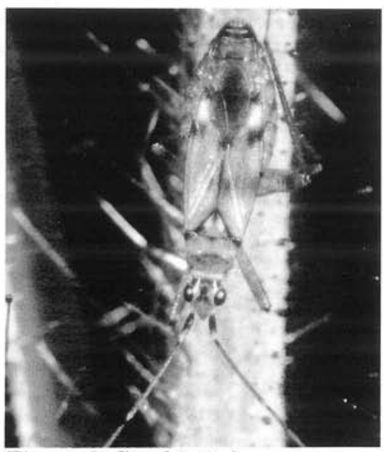

Figure 2: Symbiotic bug on *Roridula gorgonias*. Photo by Matthias Schmidt.

Pameridea bugs. Several leaves of the plants were later removed, cleaned of impurities, and their ^{15}N isotope content was analyzed. The plants with resident bugs showed a clearly higher ^{15}N content, particularly in newly formed leaves. This confirms the *Roridula-Pameridea* symbiosis. *Roridula* seems to absorb the feces via stomata, as do many other non-carnivorous plants. *Roridula* clearly benefits from its captured arthropods more efficiently than it would by soil fertilization. However, it is truly carnivorous?

Are *Byblis* and *Darlingtonia* Carnivorous?

Near Perth Australia, China (1953) reported Capsid bugs on carnivorous plants, specifically *Setocornis bybliphilus* on *Byblis gigantea* and two *Cyrtopeltis* species on tuberous *Drosera*. Unfortunately, during our visit there in 1991, my wife Irmgard and I saw no Capsids on *B. gigantea*, and the tuberous *Drosera* were dormant. In May 1995, while filming *B. liniflora* near Kununurra, North Australia for our latest video (1995), we immediately found numerous bugs living on them. The similarity of their behavior to that of *Pameridea* bugs on *Roridula* was amazing. Although they were a little smaller, they had the same dotted pattern on their back (typical for the family Miridae), the same appetite for the plant's prey, and the phenomenal ability to use the glue drops as a cooling agent without becoming entrapped. We filmed a smaller Miridae bug on *Drosera ordensis* and two more species on *Drosera indica* variants near Darwin.

Like mosquito larvae living in *Nepenthes* pitchers, I thought the bugs we were observing must have some kind of defense against proteolytic enzymes produced by the host plants. However, I discovered that bugs living on *Byblis liniflora* may not require such protection. In a series of simple experiments using photographic film to test carnivorous plants for enzymes, I examined several *Drosera* species, *Byblis liniflora*, and *Roridula dentata* (Hartmeyer, 1997). Enzymes were detected by their ability to digest the gelatin layer of the photographic film. While all the sundews were shown to produce enzymes (as expected), none of the trials detected enzyme production in *Byblis liniflora*! Those plants capable of digesting the gelatin protein on photographic film can also digest animal protein. Conversely, a plant unable to digest the gelatin layer on film is also unable to digest animal protein. Recall that *Byblis liniflora* has sessile glands for nutrient absorption which *Roridula* lacks. However, these results suggest the *Byblis-Setocornis* mutualism (and probably also the *Byblis-Cyrtopeltis* mutualism) may be much more similar to the *Roridula-Pameridea* mutualism than previously believed. Although Bruce (1905) reported on digestive enzymes in *Byblis gigantea*, the fact that none were found in *Byblis liniflora* recently sheds serious doubt on the carnivory of the genus.

Incidentally, enzymes are not produced by *Darlingtonia californica* or some *Heliamphora* species. Are they not carnivorous? Carnivorous plant enthusiasts need not despair—there is hope for their Cobra Lilies and expensive Pitcher Plants. Both genera have symbioses with arthropods. Along these lines, numerous associations between carnivorous plants and animals are featured in a recent documentary (Carow, 1996). Just enlarge the definition of carnivory to include this situation!

Conclusion

The production of enzymes should not be a prerequisite for a plant to be considered carnivorous—a symbiosis with another digesting agent should be sufficient. In the past, symbioses were mistakenly considered strange exceptions, but now it is apparently a widespread syndrome with carnivorous plants. Indeed, with some plants it is an integrated part of the digestive system! All the plants commonly considered carnivorous but which do not produce enzymes have symbioses with arthropods. I hope these new examinations of *Byblis liniflora* and *Roridula gorgonias* trigger interesting discussions on the subject.

Plant	Arthropod	Occurrence
Byblis gigantea	*Setocornis bybliphilus*	Perth, Australia
Byblis liniflora	*Setocornis / Cyrtopeltis* species	Kununurra & Cairns, Australia
Darlingtonia californica	*Metriocnemus edwardsi*	USA
Drosera erythrorhiza	*Cyrtopeltis droserae, C. russelli*	Perth, Australia
Drosera pallida	*Cyrtopeltis droserae, C. russelli*	Perth, Australia
Drosera stolonifera	*Cyrtopeltis droserae, C. russelli*	Perth, Australia
Drosera indica varieties	*Setocornis / Cyrtopeltis* species	Kununurra & Darwin, Australia
Drosera ordensis	A tiny Miridae species	North Australia
Heliamphora	Several mosquito larvae	Venezuela
Nepenthes bicalcarata	*Camponatus schmitzi* *Misumenops nepenthicola* *Thomisus nepenthiphilus* Mosquito larvae	Borneo
Various *Nepenthes*	Several mosquito larvae	Asia, Australia, Madagascar, Seychelles
Roridula dentata	*Pameridea marlothii*	South Africa
Roridula gorgonias	*Pameridea roridulae*	South Africa
Sarracenia flava	*Sarcophaga*	USA
Sarracenia purpurea	*Wyeomyia smithii*	USA, Canada

Table 1: Examples of plant-animal mutualism in carnivorous plants and allies

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