Observations on Life Strategies of *Genlisea*, *Heliamphora*, and *Utricularia* in Natural Habitats

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In December 2001 I travelled through Venezuela. I expected to visit Mt. Roraima during my travels, and since I was particularly interested in the carnivorous flora in this area, I arrived with as much laboratory equipment as I could bring (Figure 1). I especially hoped that my microscope would let me study the prey captured by *Genlisea*. In this paper, I report on a few novel observations and interpretations that resulted from this trip.

Prey of *Genlisea roraimensis*

In a recent paper, Barthlott *et al.* (1998) presented laboratory observations which suggested that *Genlisea* are specialists in capturing and digesting protozoa. My own observations with cultivated *Genlisea* show they capture many nonprotozoan prey (Studnicka, 1996). This is in agreement with Lloyd, who noted that Brazilian *Genlisea* captured "copepods, and the like, small water spiders, nematodes, and plenty of other forms" (Lloyd, 1942). A weakness of both my research and the work reported by Barthlott *et al.* (1998) was that our research programs both were based on cultivated plants. As such, I was curious to observe what *Genlisea* plants captured in their native habitats in South America.

This interest led me to visit Roraima with a small microscope in my backpack. My microscope can easily detect protozoa in wet soil samples, and I have used it to examine the often-numerous protozoa that occur in the soil of cultivated *Genlisea*. If protozoa were common in either the wild *Genlisea* traps at Roraima or their habitats, I was confident I could detect them easily. During my investigations, my two assistants and I made three interesting observations. First, when we looked for protozoa in association with the *Genlisea*, none were observed within the traps. Second, we found that protozoa were very rare in the moist soil where *G. roraimensis* grew. Since I have used this equipment to detect protozoans in other wet soil samples, I can confidently conclude that the soil we studied on Roraima had very low populations of protozoa. Third, we did observe living, mobile nematodes within the *Genlisea* trap vesicles.

I believe the *Genlisea* traps are indeed well-deserving of the name "eel-traps" because they apparently capture eel-like nematodes in the wild. While protozoans may be caught by *Genlisea* (although this was not observed), my observations suggest the multicellular, massive nematodes such as those found in the soil where *Genlisea* were growing would be a more significant prey (Figure 2).

It should be noted that we did not see dead nematodes in the *Genlisea* traps. I do not think this is contrary to my hypothesis that they are being captured and digested, because dead nematodes are extremely difficult to detect in the complex internal structures in *Genlisea* traps—only by moving and waving are the nematodes easily seen. However, it cannot be ruled out that the nematodes may be living

Figure 1: A "laboratory for microscopy" on the top of Roraima, in the location *El Hotel II*. The author making sections of *Genlisea* traps. Photograph by Ines Esterkova.

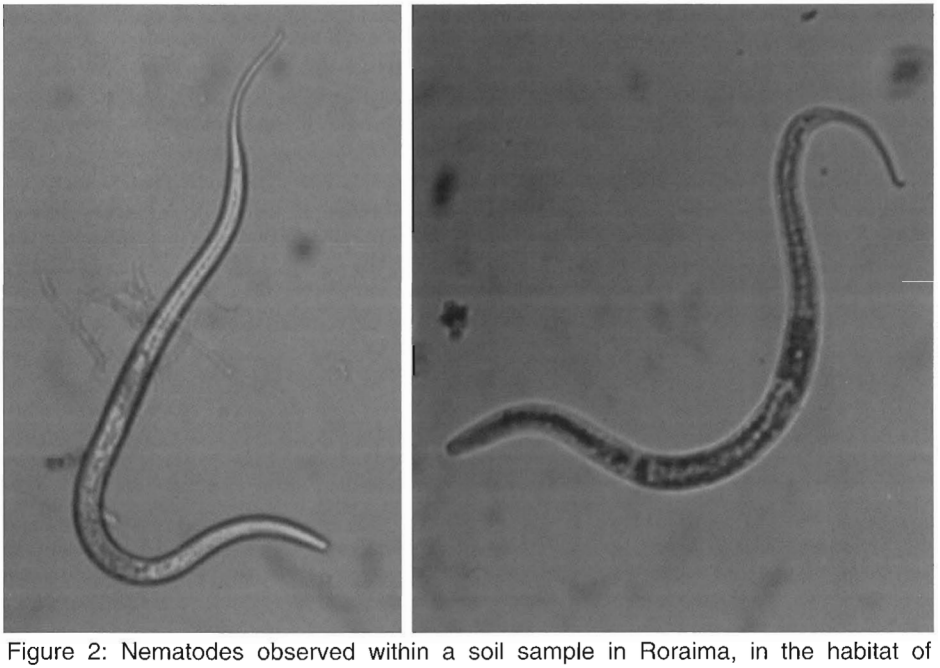

Figure 2: Nematodes observed within a soil sample in Roraima, in the habitat of *Genlisea roraimensis*. Photographs by the author.

in the *Genlisea* traps, contributing to a food web by digesting other captured prey items. (Since the nematodes are not likely to be removing the prey items from the *Genlisea* traps, it would not seem appropriate to refer to them as kleptoparasites.)

It is interesting to note that Barthlott *et al.* (1998) do mention that field observations in Africa did detect the presence of more than nine species of protozoa in *Genlisea stapfii*. It is very possible that the different species of *Genlisea* have different preferences in prey, and this may be a fruitful avenue for future field research (Studnicka, 1996). It is even possible that protozoans caught are of little nutritive value to the plants, or may even act as kleptoparasites.

Heliamphora nutans as a Deadly Habitat for Mosquitoes

It is well known that each *Heliamphora* pitcher bears a small, usually cup-like lid appendage. This appendage has extrafloral nectaries that produce sweet nectar that has been observed to attract ants and other foraging insects (Lloyd, 1942; Bütschi, 1989; Baumgartl, 1993). During our trip on Mt. Roraima we examined the contents of *H. nutans* traps with surprising results. Our observations showed that the majority of the organic material trapped in *Heliamphora* pitchers consisted not of animal prey, but rather of decaying plant leaves that had fallen into the traps. This humus supports a pitcher-bound ecosystem of life forms—in all the pitchers we examined, we found living aquatic mosquito larvae. (Occasionally we found dead mature mosquitoes.) No other insects were found in the pitchers.

So it seems that female mosquitoes successfully visit *Heliamphora nutans* pitchers to lay their eggs, and survive to escape. Furthermore, the eggs hatch and the larvae develop nicely in the pitchers. They are part of a vigorous ecosystem which transforms the dead leaves into assimilable nutrients for the plant. Is *Heliamphora nutans* carnivorous at all? I think so. First, prey are attracted by the hood appendage. Second, I think that at least a fraction of the mosquito larvae may never successfully leave the pitcher upon maturity. For when the larvae pupate and metamorphize into adults, the newly emerged mature mosquitoes may not all successfully escape the narrow traps, especially since it would be their first-ever attempts at flight. The slightest aerobatic mistake would result in their plunging back into the pitcher fluid to be digested, and could account for the dead mosquitoes we found in the trap (although we are not positive the mosquito larvae and the dead mature mosquitoes found are the same species).

Apparently, the *Heliamphora* pitchers are complicated ecosystems that include detritus, algae, microorganisms, and mosquitoes. This special adaptation lets *Heliamphora nutans* thrive in an otherwise hostile environment.

Utricularia and *Brocchinia* Relationships

It is often observed in the literature that *Utricularia humboldtii* on Auyántepui and Cerro Neblina grows in the fluid filled basins of bromeliads, such as *Brocchinia* spp. (Bütschi, 1989; Rivadavia, 1999; Taylor, 1989). I have made field observations that suggest that, at least in the area of Mt. Roraima where *Utricularia humboldtii* thrives and grows to nearly giant proportions, bromeliad urns may be at most a secondary habitat for the bladderwort.

Brocchinia species are widespread and frequent in the areas near Mt. Roraima. A large population of *B. tatei* grows in the cloud forest at the mountain's base (Figure 3), while at least several more specimens occur on the top of the plateau itself. Below the cloud forest, in the margins of the Gran Sabana, the wet meadows contain many more *Brocchinia* plants (*B. reducta* or *B. hechtioides*—the exact identification is not yet certain). However, even though *Utricularia* are found in all these habitats, we found no cases of *U. humboldtii* living in the *Brocchinia* urns!

Figure 3: *Brocchinia tatei* rosettes about 1 m in diameter are numerous in the cloud forest in the basal cone of Roraima. Nevertheless, no *Utricularia humboldtii* grows there. Photograph by the author.

Figure 4: Dense structure of the grassland community of grasses, including *Rhynchospora* species (Cyperaceae). Note that the leaves of the *U. humboldtii* are up to 114 mm wide, a sign of optimal growing conditions. Photograph by the author.

It has been suggested that the long, arching aerial stolons that *U. humboldtii* produces enable the plant to navigate from one bromeliad urn to another (Taylor, 1989) or other parts of the same bromeliad urn (Rivadavia, 2001). However, in the apparent absence of a close relationship between *U. humboldtii* and bromeliads in the area of Mt. Roraima, I propose an alternate purpose for these stolons—I believe they simply let the plant hop from one suitable pool of water to another. This interpretation is particularly supported by the structural nature of the native grassland tussock communities. These tussock communities appear to be ideal for *U. humboldtii*—I have seen huge colonies of plants, growing to comparatively giant size, i.e. leaves up to 11.4 cm (4.5 inches) wide. They are dominated by dense bunches of plants (including *Rhynchospora* spp., *Orectanthe* spp.), as well as *Phragmipedium* spp (Figure 4). The dense growths of these plants break the wetland into a patchy matrix of pools, and prevent *Utricularia* from spreading from one pool to the next. Only by producing the tall aerial stolons, which arch over the tussocks of interfering vegetation, can the *Utricularia* seek suitable new habitats.

This case is an interesting contrast with another bladderwort-bromeliad pairing. I studied *Utricularia reniformis* and the bromeliad *Vriesea atra* in Serra dos Órgãos, Brazil, in 2000. In this situation, a close relationship between the two species was plainly visible. But while the advantage to the *Utricularia* was obvious, it is not clear if the *Vriesea* benefited from the relationship.

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Literature Reviews

Bradford, J.C. & Barnes, R.W. 2001, Phylogenetics and Classification of Cunoniaceae (Oxalidales) Using Chloroplast DNA Sequences and Morphology. Systematic Botany 26: 354-385.

This paper is interesting because it proposes a "new" hypothesis on the closest relative of *Cephalotus*, the systematic position of which is still somewhat enigmatic. Earlier studies have assigned Cephalotaceae to the order Oxalidales (Cunoniales) without any convincing affiliation. In this study the ordinal position is confirmed, and sequence homology comparisons of the trnL-trnF-region of the chloroplast genome (rbcL homology comparisons being inconclusive) suggest a sister relationship between Cephalotaceae and Brunelliaceae, the clade with these two being in turn sister to Cunoniaceae. The similar floral morphology of these families has already been