HELIAMPHORA: THE NATURE OF ITS NURTURE

by
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Considerable question of whether Heliamphora is truly carnivorous has arisen lately. These doubts largely have been related to accounts of short visits to various tepuis, usually in the 'dry" season, in which the visitors decry the paucity of anything for a respectable CP to eat. I used quotes around "dry" because these visitors will attest to the nightly cold, hard rains and heavy morning fog often lasting until past noon. The "dry" season is generally February to March.

As a result of trying to figure out how these pitcher plants get along with little to trap, and apparently no enzymes anyway, some novel proposals have been put forward on how they do survive. One recent one (Clayton, 1994) suggested that dust carried on prevailing winds from African deserts and then washed into the pitchers by rain provided nourishment, at least for the upland stands of pitcher plants since those occurring in the lowlands of the Gran Sabana had access to plenty of insects. This is an intriguing concept. It is certainly true that studies have shown that varying amounts of African desert dusts are carried to the New World daily. But before we assign the role of dustbin to Heliamphoras, let us examine some other evidence.

In October, 1970 Brewer-Carias, a dentist in Caracas who is also a naturalist, spent several days on top of Cerro de la Neblina (Mountain of the Mists) some 10,000 feet above the rain forest floor. Observing the tall *H. tatei* all day long, he noticed a steady stream of mosquitoes being trapped by the pitchers. The modified hood, called a spoon in this genus, was highly colored and developed in bright light and had a noticeable fragrance and abundant nectar production. He noted that the mosquitoes were attracted to the spoon initially and then fell into the pitchers. Often, several mosquitoes at once approached the spoon, became tangled, and fell into the pitcher. While he was up there, Brewer-Carias also determined the nature of the mechanical water level maintenance system of the pitchers. So here, we have observation of abundant flying insects being allured to and trapped by the pitchers.

In January and February of 1985, Renner spent 20 days on Cerro de la Neblina for the purpose of studying floral biology of *H. tatei* and other plants, particularly pollination mechanisms. Up until that time, it had been assumed that a paucity of insect life atop tepuis indicated that birds were the most likely pollinators. On the contrary, Renner effectively observed that an abundant bee fauna, particularly bumblebees on this 10,000 foot tepui, were the main pollinators of this species. In fact, the poricidal anther dictates that bee "buzzing" is necessary to release pollen. As we have observed in cultivated *Heliamphora* spp., pollen is not spontaneously shed. While Renner's observations pertain to pollination and not nutrition, they again testify to abundant insect life on this tepui.

So, what about other species on other tepuis? The answer is in a highly seminal paper (Jaffe, et al., 1992) written by four botanist who live in Venezuela. These people spent nine years studying all five *Heliamphora* spp. on eleven tepuis. Studies were conducted in the field as well as on plants in the lab. Proteolytic properties of fluid from open and unopened pitchers was measured using azoalbumin. Nutrient absorption was measured by ion extinction in solutions of phosphorus and potassium added to pitchers, and use of radio labeled amino acids. During field observations, numbers and kinds of arthropods in the area were enumerated by netting as well as those captured by pitchers. This double census is vital since a different ratio of captured vs. ambient arthropods indicates preferential capture by possible luring. Similar studies on other pitcher plant genera have been flawed by not including the double census.

Vegetation on tepuis varies a great deal, something that can only be appreciated by visiting as many as these authors did. Roraima and Kukenan, for example have very sparse vegetation, very small pitcher plant populations compared to other tepuis, and few arthropods. Auyan, by contrast, has a robust vegetation, including forests of shrubs and trees to 3-10 m.

The workers confirmed Brewer-Carias' observation concerning the attractive value of the spoon. They also noted that tall pitchers (eg *H. tatei*) captured flying insects (mostly mosquitoes and other dipterids) while the remaining four smaller species captured prodigious quantities of ants, and the occasional large biomass beetle or scorpion. Mature but young pitchers have the highest quantity of freshly captured prey, while older pitchers were less active. *H. tatei* pitchers have waxy scales on the inside which break loose and cause prey to lose footing. Once the leaf opens, it fills with rainwater in addition to whatever fluid was inside prior to opening, and level is maintained by one of two leveling devices (pore or wing-channeling). After a few days of relatively dry weather, pitcher contents tend to dry with decrease in water level and prey-catching ability. Artificial addition of water causes capture to resume promptly. In addition to water absorption by roots, pitchers also absorb rain water foliarly. Water in the pitcher has a low surface tension, suggesting a wetting agent, which results in insects sinking and drowning sooner than if placed in pure water controls.

It was discovered that one species, *H. tatei* , does produce intrinsic enzymes secreted into pitcher fluid, but only in some stands on some tepuis. These enzymes were discovered on azoalbumin tests on sterile fluid aspirated from unopened pitchers.

Numbers of prey captured were of course proportional to total numbers of potential victims present, being very few on Roraima vs many on Auyan. Commensals also inhabited pitchers (similar to *Sarracenia* and *Darlingtonia* , including similar genera such as *Wyeomyia* and *Metriocnemus*). Occasionally, *Utricularia* spp. were seen growing in pitchers! Potassium, phosphorus and amino acids were all absorbed.

The authors conclude after these extensive studies that heliamphoras are indeed highly developed carnivorous plants and quite active in this respect where numbers of prey allow. The lack of instrinsic enzymes in four of the five species does not detract when one considers the situation with *Sarracenia purpurea* and *Darlingtonia* . In the former, rain-filling of pitchers is also very vital (hood erect). Bacteriolysis and activity of commensals contribute to digestion where intrinsic enzymes are lacking. Given the overwhelming evidence for carnivory generally in the genus, survival in spartan environs such as Roraima must depend on seasons and years richer in prey than others are. Furthermore, studies with sarracenias have indicated that pitchers are relative gluttens given the opportunity, and only a very small portion of what they actually catch is necessary to maintain the plant.

The paper by Jaffe is a "must read" for all those with a serious interest in *Heliamphora* carnivory and other aspects of physiology.

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Oxygen budget in the traps of ***Utricularia australis***

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Suction traps of the aquatic bladderwort *(Utricularia)* species are 1-5 mm wide bladders, the walls of which consists of only two layers of cells (see Lüttge, 1983, p. 501-504; Juniper et al., 1989, p. 64-71). During suction of a prey (firing), their luminal volume is increased by more than 40 % (Lüttge, 1983, p. 502). In aquatic bladderworts, the light-green traps contain chlorophyll and are capable of photosynthesis. Frequently, older traps become pigmented and their colour is rose to black (Knight, 1992). How prey is digested in *Utricularia* traps remains unclear, although microorganisms were shown to play a role (Juniper et al . 1989, p. 195).

The small volume of the traps together with their respiratory activity and that of the prey may cause the prey to die from anaerobiosis as recently hypothesized by Dr. Laurie E. Friday (Cambridge Univ.. U K.). Direct evidence is, however, lacking. Animals caught in the traps may stay alive for a certain period: Hegner (1926) investigated feeding of *Utricularia* traps by protozoa and observed that they had died after 75 min.

The aim of this study was to evaluate the oxygen budget in *Utricularia australis* traps based on measured values of their photosynthetic and respiration rates.

Utricularia australis R.Br. was cultivated outdoors or collected from a fishpond near the town of Trebon (Czech Republic). Net photosynthetic rate (PN) and dark respiration rate (DR) were estimated in a closed stirred chamber (8.6 ml) at a temperature of 22° C as linear parts of current response of a fine O_2-sensor in 20-min periods of light or darkness. The irradiance was 70 W.m^{-2} (400-700 nm). The experimental solution contained 1.04 mM $NaHCO_3$ and 1 mM KCI. and had a PH of 7.4. Thus, the initial $C0_2$ concentration was about 0.1 mM. Three groups of mature empty traps of different age and colour (32-51 traps) were selected (Table I). The pigment responsible for the dark colour of the traps was a red anthocyanin as was shown in diluted HCl. In other experiments (Table II), DR of intact empty traps,