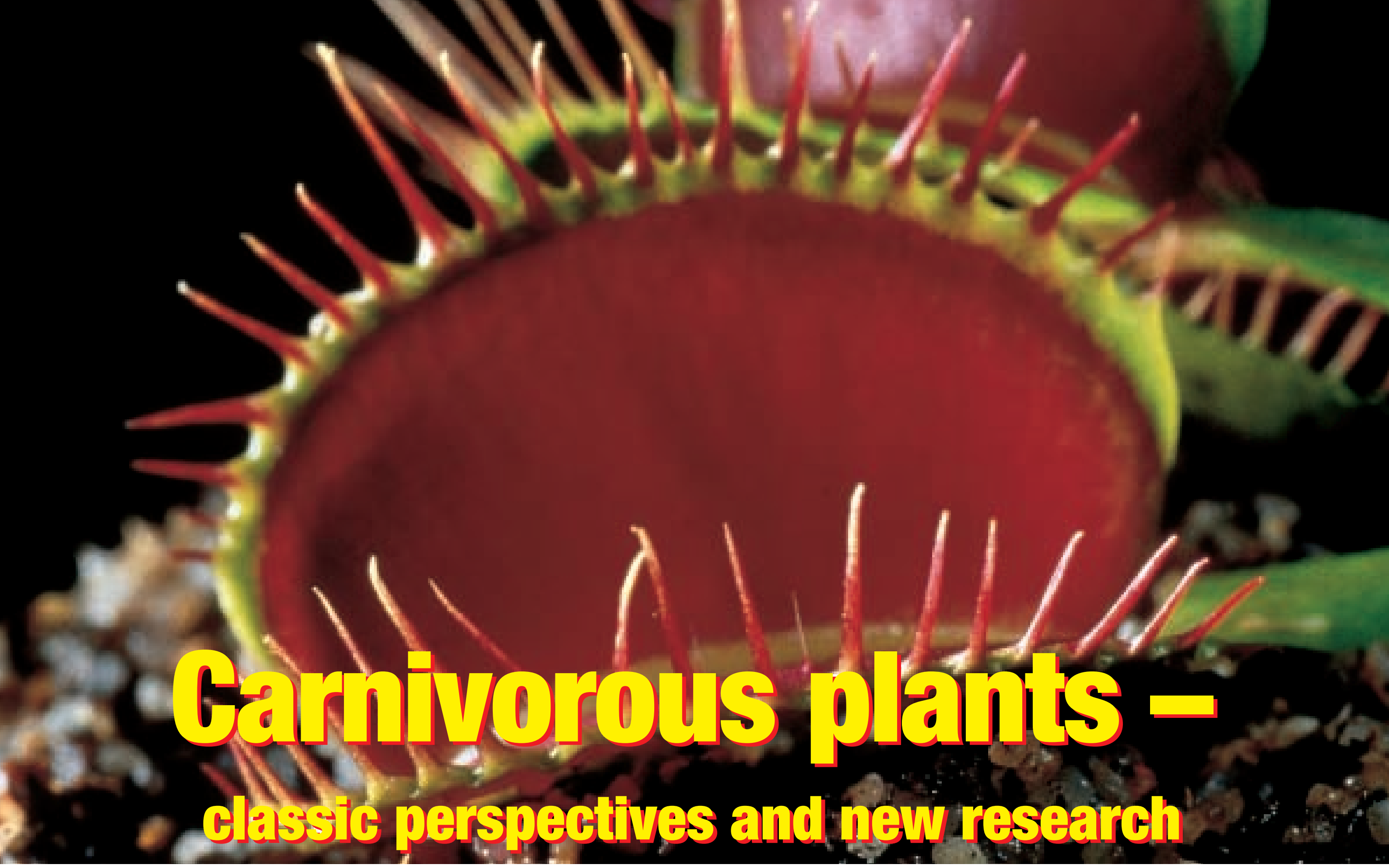

Carnivorous plants – classic perspectives and new research

Barry Rice
The Nature Conservancy, Davis, USA

The ranks of known carnivorous plants have grown to approximately 600 species. We are learning that the relationships between these feeders and their prey are more complex, and perhaps gentler, than previously suspected. Unfortunately, these extraordinary life forms are becoming extinct before we can even document them!

Carnivorous plants are able to do four things: they attract, trap, digest and absorb animal life forms. While these four abilities may seem remarkable in combination, they are, individually, quite common in the plant kingdom. All plants that produce flowers for the purpose of summoning pollinators are already skilled at attracting animals. Many plants trap animals at least temporarily, usually for the purposes of pollination. Digestion may seem odd, but all plants produce enzymes that have digestive capabilities – carnivorous plants have only relocated the site of enzymatic activity to some external pitcher or leaf surface. Finally, absorption of nutrients is something that all plants do (or, at least, all that survive past the cotyledon stage). Carnivorous plants have simply combined these conventional plant traits into a novel foraging strategy.

Types of traps

The Venus flytrap (*Dionaea muscipula;* title image) is the best known carnivorous plant. It has a ground-hugging rosette of leaves that look and function like hinged, foothold bear traps. A detailed study reveals a fascinating array of refinements in its hunting technique. Rapid leaf closure is triggered when the scrabbling of prey bends hairs on the leaf-lobe surface. But, in order to weed out false signals, the trigger hairs must be bent, not once, but two or more times in rapid succession. In effect, the plant can count! When the trap first closes, the lobes fit together very loosely, the marginal spines interweaving to form a botanical jail. Prey items that are too small to be worth digesting can quickly escape, and the trap will reopen the next day. But, large prey remain trapped, and their panicked motions continue to stimulate the trigger hairs. This encourages the traps to seal completely, suffocating the prey, and to release digestive enzymes. (Children who feed dead flies to their pet Venus flytraps are often disappointed when, the next day, the uninterested plants open their traps and reject the inanimate morsels – only live prey stimulate the leaves enough to complete the digestion process.) After about one week, the leaves reopen to reveal the crispy exoskeleton that survived the digestion process.

While *Dionaea muscipula* is but one species, we know of about 600 other carnivorous plants in 17 genera across ten different plant families. With so many species, it should be no surprise that the bear-trap approach is not the only trick that carnivorous plants use! In Table 1, carnivorous genera are listed along with their primary methods of prey capture. The diversity of techniques these plants employ is impressive.

The simplest kind of trap is the pitfall. In this, the plants create a chamber (in basic form, a funnel or vase) into which prey plummet. Digestive enzymes in the bottom of the vase perform the expected function, and nutrients are

Title image: The red maw of the Venus flytrap (Dionaea muscipula) *beckons!*

Table 1. Types of carnivorous plants

Genus	Common Name	Trap Type
Aldrovanda	waterwheel plant	bear trap
Byblis	rainbow plant	sticky flypaper
Cephalotus	Albany pitcher plant	pitfall
Darlingtonia	cobra lily, California pitcher plant	sticky flypaper
Dionaea	Venus flytrap	bear trap
Drosera	sundew	sticky flypaper
Drosophyllum	dewy pine	sticky flypaper
Genlisea	corkscrew plant	lobster pot
Heliamphora	sun pitcher	pitfall
Nepenthes	tropical pitcher plant	pitfall, sticky flypaper
Pinguicula	butterwort	sticky flypaper
Roridula	(none)	sticky flypaper
Sarracenia	trumpet pitcher	pitfall, lobster pot
Triphyophyllum	(none)	sticky flypaper
Utricularia	bladderwort	suction trap

absorbed into the plant. Yet even this simple carnivorous leaf is often modified with innovations to improve the trap's efficacy. The trap walls may be covered with downward pointing hairs or waxy, slimy surfaces. Enticing odours or beguiling pseudo-floral pigmentation patterns may attract prey. Strategically placed nectaries may be situated directly over the pitfall opening to encourage browsing insects to wander to the locations of maximal peril (*Nepenthes bicalcarata;* Figure 1a). The structure of the pitcher may be modified with overhanging ledges to frustrate insects trying to climb to safety. Some pitfall traps are equipped with transparent windows that illuminate the pitcher interior – this fools insects into believing the shining digestive fluid is a portal to freedom. Once the prey have fallen into the pit, they find themselves in more than just a bath of weak enzymes – pitcher fluid has been found to contain wetting agents, toxins, and even mild anaesthetising agents! Genera of pitcher plants occur throughout the world: *Sarracenia* (Figure 1b) and *Darlingtonia* in North America, *Heliamphora* in South America, *Cephalotus* in Australia, and *Nepenthes* (mostly) in southeast Asia, but with a few species found elsewhere. Two New World bromeliad genera *Catopsis* and *Brocchinia* are also suspected of being carnivorous.

Another carnivorous tactic is to develop leaves with glandular, sticky surfaces. These leaves may emit either a sugary or fungal smell, with different smells attracting different prey. Mucous-exuding glands give the plant the appearance of being coated with delicious nectar. On some genera, these glands are perched high upon tentacles; on others (i.e., *Pinguicula;* Figure 2a) the glands are sessile at the leaf surface. Once prey lands upon the leaves, their legs and wings become mired, and escape is impossible. Struggle only ensures their death, as mucus coats and suffocates them. Digestion occurs on the spot, and the leaf may even curl over the prey to increase the number of digestive glands contacting the invertebrate morsel. The genera of these sticky-leafed carnivores include *Byblis, Drosera* (Figure 2b), *Drosophyllum, Pinguicula, Roridula* and *Triphyophyllum*

Kingdom Plantae has yet other devious machinery to use against Animalia. *Aldrovanda* is an aquatic sister genus to the Venus flytrap. *Genlisea* is a lobster-pot aquatic (having entered, prey cannot find the escape hatch), while *Utricularia* (Figure 3) has evolved more than 220 species of carnivores that use bizarre suction traps to draw tiny aquatic organisms into their bug-thirsty, digestive bladders (Figure 3b).

Some species, dissatisfied with convention, combine techniques. *Sarracenia psittacina* is in a genus of pitfall carnivores, but its traps are tilted sideways. It appears to be mostly harmless except during periodic floodings, when it captures aquatic animals using a lobster pot technique. Meanwhile, *Nepenthes inermis* and a few other species of pitcher plants have slimy inner trap walls, and function as sticky trap plants.

In a surprising step towards botanical disarmament, one bladderwort species (*Utricularia purpurea*) may have abandoned its carnivorous congeners, as it seems its bladders may primarily be used to house algae and zooplankton in a mutualist relationship. Evolution leads to constant innovation!

Prey spectrum

Various organisms are captured and eaten by carnivorous plants. The list includes arthropods, such as insects, arachnids, millipedes, centipedes, annelids and crustaceans, as well as slugs and snails, and even small vertebrates such as amphibians and reptiles. A few dead rodents have even been found in *Nepenthes* pitchers, but these captures are certainly incidental and rare. This diverse array of prey presents a quandary for lexicographers, who cannot decide what to call these plants. None of the proposed words work, neither 'carnivorous' (insects do not contain meat) or 'insectivorous'

Figure 1. (a) The fierce pair of spines on Nepenthes bicalcarata are actually only nectaries to attract prey. (b) Sarracenia leucophylla – a North American pitcher plant – growing in Alabama.

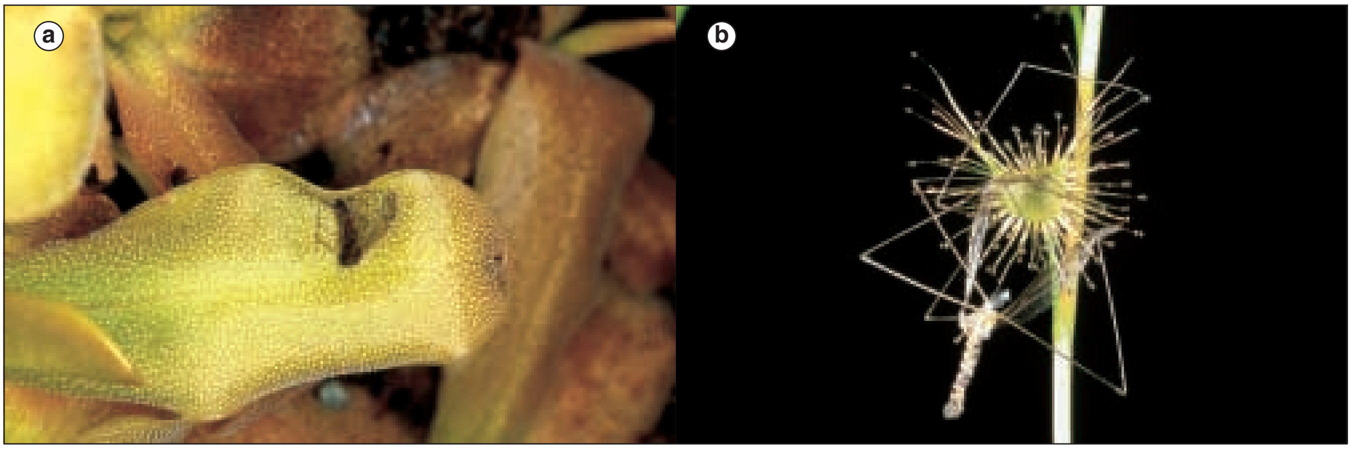

Figure 2. (a) A gnat is absorbed into the slimy leaf of the butterwort Pinguicula macroceras subsp. nortensis. (b) The small leaves of the Australian sundew Drosera auriculata can trap comparatively large prey.

(centipedes are not insects). Even 'animal-eating' is too restrictive a term, since some carnivorous plants (*e.g., Genlisea*) delight and perhaps even specialise in consuming protozoa.

Why are they carnivorous?

With such a large number of carnivorous plant species, it should be no surprise that they live in a wide variety of habitats. But carnivorous plant habitats share an important characteristic – they all hunt in habitats that are deficient in some essential nutrients, nutrients that are readily available in animal tissues. It is this environmental stress that gives carnivorous plants a selective advantage. By diverting resources into making specialised structures, such as prey-trapping leaves, the plants benefit by harvesting nitrogen and other nutrients from captured prey. In contrast, in a nutrient rich environment, the carnivorous approach is not a valuable strategy. In fact, carnivorous plants are so specialised for low nutrient conditions that they cannot survive in nutrient-rich habitats. (Specialist horticulturists know that one of the fastest ways to kill their prized carnivorous gems is to fertilise them!)

Examples of nutrient-poor ecosystems that are friendly to carnivorous plants include epiphytic habitats (using other plants for structural support) in tropical moist forests, seasonally wet acidic or neutral pH deserts, and a wide variety of acidic wetlands such as peat bogs, marshes, swamps, wet savannahs and fens. A frequent indicator for habitats suitable for carnivorous plants is the presence of *Sphagnum* moss. This moss tends to buffer the pH to highly acidic levels that favour carnivorous plants. (Among other effects, high acidity reduces decomposition rates so few nutrients are available.)

Carnivores are not picky in terms of temperatures – tropical to boreal habitats are all populated by carnivorous plants. Marine or brackish habitats are the only major ecosystem type not penetrated by these hungry botanicals, no doubt because of the high availability of nutrients in such conditions.

Such a wide variety of habitats means that carnivorous plants are widely distributed, more than most people suspect. They are found on every continent (except Antarctica), and their global centres of diversity include southeastern Asia (*Nepenthes*), southeastern USA (*Sarracenia*), western Australia (*Drosera* and *Utricularia*), northern South America (*Heliamphora*), and southern Mexico/central America (*Pinguicula*).

Figure 3. (a) A cultivar bladderwort flower, Utricularia calycifida 'Asenath Waite'. (b) Aquatic bladders of Utricularia intermedia.

New research

Traditional botanical studies are still active (new species are being described each year), and ecologists are broadening (and complicating!) our understanding of carnivorous plants. We are learning that, instead of capturing anything small enough to fit into their leaves, some carnivorous species specialise in specific prey types. *Nepenthes* are particularly adept in this dimension – *Nepenthes albomarginata* may specialise only on foraging termites, while the 'most scatological' award must surely go to *Nepenthes lowii* (Figure 4). This plant may not be strictly carnivorous at all. It produces edible exudates on its pitcher lids that are irresistible to sunbirds, and as the birds feast they excrete into the pitchers, much to the plant's coprophagous satisfaction. Another innovative species is *Nepenthes ampullaria*. This plant is noteworthy for producing clusters of ground pitchers that carpet the ground. These pitchers may function in part to capture detritus raining from the forest canopy.

Of particular research interest is the notion that non-plant accomplices may be cooperating with the carnivores. For example, the digestion in many of the pitcher plant genera may be performed, at least in part, by bacteria or other inquiline fauna (lodgers), such as larval flies, mosquitoes and even tadpoles. Such organisms help digest the prey and excrete useful nitrogenous compounds into the pitcher fluid. Some scavenging organisms, such as spiders (*Misumenops nepenthicola* and *Thomisius nepenthephilus*) or diving ants (*Camponotus schmitzi*), plunge into their friendly *Nepenthes* pitchers to retrieve large prey items. Perhaps without the intervention of these opportunistic feeders, nutrient overload could occur, which would damage the pitcher through over-feeding. The mutualism between ants and *Nepenthes bicalcarata* (Figure 1a) is so advanced that the tendril supporting the pitcher is hollow and inflated, providing excellent nesting cavities for the ant allies.

Another kind of mutualism is exemplified by the case of Capsid bugs (*e.g., Cyrtopeltis* and *Setocornis* species), which safely navigate the adhesive glands of *Drosera* and *Byblis* sundews to eat the prey captured on the sticky leaves. The bugs apparently produce excrement that contains useful nitrogenous compounds. Indeed, when deprived of these bugs, some carnivorous *Byblis* species are completely incapable of translating captured prey into absorbable nutrients. *Roridula* (a genus of South African plants) was temporarily removed from the list of carnivorous species when it was noted that its glandular leaves were resinous and not mucosal. It is apparently carnivorous after all, as long as you are willing to allow the mutualism with assassin bugs.

Figure 4. Nepenthes lowii – an avian lavatory – cultivated in California.

Not all carnivores appreciate foragers, however. It is possible that the leaf-curling of some *Pinguicula* around prey may be, in part, to jealously protect the prey from thieving kleptoparasites. Might it be that the dramatic leaf curling seen in so many *Drosera* species is not intended to help digest the prey, but rather is primarily to protect the food items from theft?

Laboratory research has of course been active, with particularly active investigations directed towards understanding the molecular mechanisms of nutrient uptake, the importance of carnivory for growth, and the nature of the digestive juices secreted by carnivores.

Even research into the history of carnivorous plant botany has been active, if in a particularly bawdy direction. The logic behind the coining of the common name 'Venus flytrap' has been essentially inexplicable. The explanation concocted by its discoverers – New World botanists and their cohorts in England – was that its flowers were as beautiful as the goddess, Venus, was. The plant's small, drab, white and green flowers do not corroborate this unlikely explanation. Furthermore, the poorly Latinised version of this name (by botanists who certainly could do better) added to the confusion (*Dionaea muscipula* means 'Aphrodite's mousetrap' – suggesting that it is a catcher of mammalian prey and not of insects). Recently Nelson and McKinley (1990) revealed the smutty secret. Those puritanical naturalists of Botany's past envisioned – in the plant's quivering red lobes, sensitive behaviour and attractive qualities – similarities to female genitalia. The Goddess of Love was invoked, and the jest was immortalised with the Latin name. (The official explanation about the attractive flowers was simply a cover story to protect the delicate sensibilities of the drawing room ladies.) Later, William Bartram (a participant in the conspiracy) was so bold as to waggishly write in his *Travels* … of this 'sportive vegetable' that seduced incautious insects with its 'incarnate lobes'.

Carnivores in captivity

Carnivorous plants are not easy to grow for the casual horticulturist. Even Darwin noted that he was unsuccessful with his Venus flytraps. However, with just a small amount of research, representative species of most of the carnivorous genera can be grown with only minor pain.

Horticultural interest in carnivorous plants rises and falls – the first noteworthy peak was in the Victorian era when *Nepenthes* and orchids both were grown (and more often killed) by the voracious plant hunters and their financing nurseries in Great Britain. The tide of interest is high once again, and this time the internet has helped increase communication among scattered, isolated enthusiasts. In addition, the membership numbers in carnivorous plant organisations are rising. The most prominent group is the International Carnivorous Plant Society (ICPS), which produces a fine quality journal* called *Carnivorous Plant Newsletter*, which includes comments on cultivation, conservation, new carnivorous cultivars and even peer reviewed scientific papers, such as new taxon descriptions.

** The author is coeditor for Carnivorous Plant Newsletter!*

Figure 5. Another of the few remaining prime habitats for Sarracenia being destroyed in Florida.

Conservation

Carnivorous plants are greatly threatened by human activity, for, while they are not directly targeted by humans as a desirable resource, they are strongly damaged by our incidental activities. Humans have tried a number of methods to 'improve' or 'reclaim' their habitats. Wetlands are drained (Figure 5), forests are slashed and burned, lands are fertilised, natural wildfires are suppressed – all of these activities are harmful to carnivorous plant habitats.

Simultaneously, nutrient-rich pollutants are allowed to seep from industrial or agricultural sources into biologically rich areas dismissed as 'wastelands'. The nutrient flux from these sources alters the soil and water chemistry so much that the carnivorous species are poisoned while the non-carnivorous native and non-native species overwhelm the ecosystem. The extirpation of the remarkable *Aldrovanda vesiculosa* (an aquatic version of the Venus flytrap) from most of its range in Europe and Japan is one example of this process.

Frequently, the effects of pollutants kill the sphagnum moss in wetlands. (The importance of sphagnum moss in these environments cannot be overstated – the moss dominates the wetland biomass, and creates the hydrological and habitat structure that defines the ecosystem.) When nutrient levels rise, the sphagnum rapidly dies and the entire structure of the habitat collapses.

The effects of habitat conversion by development, agricultural fragmentation of once continuous plant ranges, altered hydrology, pollution, modified fire regimes, invasive species, and poaching by the nursery trade and private enthusiasts all conspire to make conservation of carnivorous plant species extremely challenging and, perhaps, not particularly successful. The poorly understood effects of imminent global climate change do not make the future look very encouraging.

The horticultural community has become increasingly interested in conservation, and organisations like the ICPS and the British CPS have conservation grant programmes. However, the relationships between horticulturists and conservation groups are not always easy – numerous poaching events have poisoned the good will of many conservation workers. Still, innovative programmes are being implemented.

Field studies and laboratory research continue to reveal new information about these plants. However, this botanical legacy is disappearing. In the USA, the vast majority of the wetlands have been destroyed. Conservationists hoping to capture the genetic variety of carnivorous plants are too late – the cake has already been consumed, and only the crumbs remain. The fate of the remaining carnivorous plant communities are not at all certain – will these fragmented populations throughout the world survive the present era of anthropogenic extinctions? Will they survive the effects of global climate change? We will see (or rather, our children will). These plants, which require clean and unspoiled habitats to survive, are the fabled canaries in the coal mine – their fate is our own.

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(Further reading suggestions are listed on our website at www.iob.org/biologist.asp)

Websites

www.sarracenia.com
The author's web site, includes an extensive 'Frequently Asked Questions' area and photographic gallery.

www.carnivorousplants.org
The International Carnivorous Plant Society, which publishes Carnivorous Plant Newsletter.

www.labs.agilent.com/bot/cp_home
Jan Schlauer's taxonomic database of all carnivorous plant Latin names, cultivar names, and synonyms. Includes illustrations.

Barry Rice *completed his PhD in Arizona in 1995. He works as an invasive species scientist for The Nature Conservancy, a nonprofit conservation organization. His interest in carnivorous plants originated in 1985 when he decided to grow Venus flytraps he found captive in a corner flower shop. His interest has continued, and while he is still active in horticulture, most of his spare time is spent doing fieldwork, plant photography, and coediting the International Carnivorous Plant Society's journal. He is currently working on promoting a number of carnivorous plant conservation initiatives.*
PO Box 72741
Davis, CA 95617
USA
Barry@sarracenia.com