9F. Carnivory

1. Introduction

Since the classic work of Charles and Francis Darwin (1875, 1878) well over a century ago on the carnivorous habit of *Drosera*, considerable information has accumulated on the significance of captured animal prey in the nutrition of carnivorous plants. **Carnivory** includes the catching and subsequent digestion of the freshly trapped prey. This is a common form of nutrition in the animal kingdom, but is rare in plants, with only about 800 species from 10 families (Table 1). Carnivorous plants are distributed worldwide, but they are generally restricted to sunny, wet, nutrient-poor environments. This distribution pattern suggests that, under these conditions, carnivory has a major **benefit** for plant survival. The major benefits will be **nutritional** (Ellison 2006). The restricted distribution of carnivorous plants, however, also suggests that the **costs** of the carnivorous habit exclude carnivores from most habitats. These costs include a reduced **photosynthetic capacity** of carnivorous tissues (Mendez & Karlsson 1999, Ellison & Farnsworth 2005).

2. Structures Associated with the Catching of the Prey and Subsequent Withdrawal of Nutrients from the Prey

Carnivorous plants invariably have highly specialized structures, such as **adhesive hairs** or **emergences** [e.g., in *Pinguicula* (butterwort), *Drosera* (sundew) and *Byblis* (rainbow plant)], bladder-like **suction traps** [in *Utricularia* (bladderwort), **"lobster-pot"** or **eel traps** [in *Genlisea* (corkscrew plant)], **snapping traps** [in *Dionaea* (Venus' fly trap) and *Aldrovanda* (waterwheel plant)], or **pitfalls** [e.g., in *Nepenthes* (pitcher plant), *Sarracenia* (pitcher plant), and *Cephalotus* (Albany pitcher plant)] (Fig. 1, Table 1). The pitfall traps mostly contain water and are an ecological niche for protozoa, algae, and numerous small animals, of which some (e.g., the larvae of many Diptera) are exclusively associated with this habitat.

Although it is strictly speaking not a carnivorous species, *Capsella bursa-pastoris* (shepherd's purse) has a mucous layer that surrounds the germinating seeds, which has the capacity to catch and digest nematodes, protozoa, and bacteria (Barber 1978). Other **protocarnivorous** species include *Geranium viscosissimum* (sticky purple geranium), *Potentilla arguta* (glandular cinquefoil), which are common in the Pacific Northwest of the United States, and *Stylidium* species (trigger plants) in Australia (Darnowski et al. 2006). Many "sticky" plants show proteinase activity on their glandular surfaces. They digest proteins that are trapped on these surfaces and subsequently absorb and translocate the breakdown products (Spomer 1999). Sticky plants have glands on their shoot surfaces that exude mucilage. This may have evolved as a defense against small arthropod herbivores. The mucilage hinders their movement, trapping them on the surface, where they die. Carnivorous species with adhesive surfaces [e.g., *Drosera* (sundew), *Byblis* (rainbow

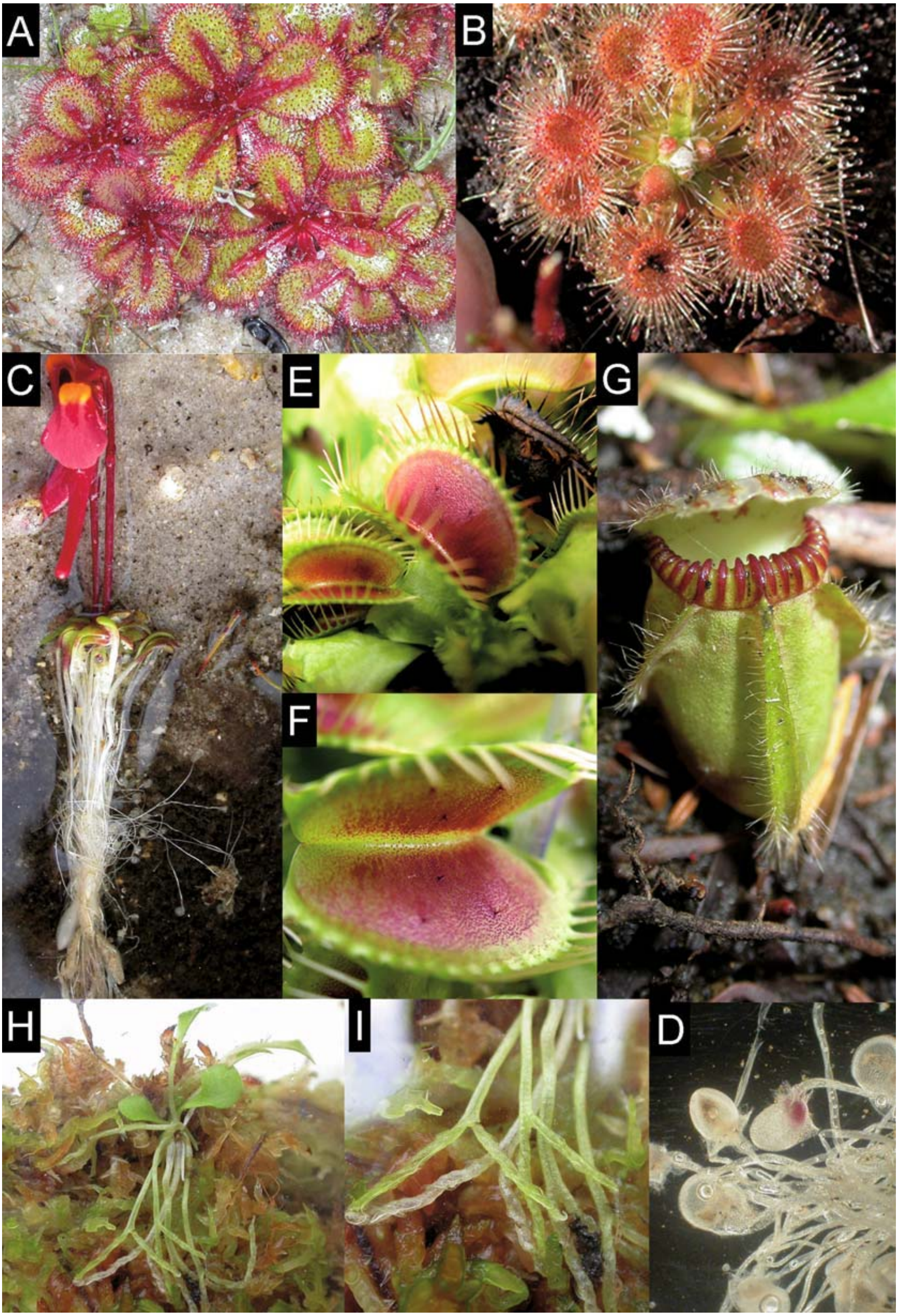
A
B
C
E
G
F
H
I
D

Table 1. Carnivorous plant families and genera with their geographical distribution and trapping mechanisms.

				Trapping mechanism					
Family	Genus	*N*	Geographical distribution	Eel trap	Suction trap	Snapping trap	Pitfall pitcher	Adhesive trap	Movement involved
Nepenthaceae	*Nepenthes*	70	Madagascar, Seychelles, Sri Lanka, Assam, S. China, Indochina, Malaysia, N.E, Australia, New Caledonia				x		
Sarraceniaceae	*Sarracenia*	8	Atlantic N. America				x		
	Heliamphora	5	Guyana Highlands				x		
	Darlingtonia	1	California, Oregon				x		
Dioncophyllaceae	*Triphyophyllum*	1	W. Africa					x	
Droseraceae	*Drosera*	90	Worldwide					x	x
	Dionaea	1	N. and S, Carolina			x			
	Aldrovanda	1	Central Europe, Asia, N.E. Australia, Africa			x			x
Drosophyllaceae	*Drosophyllum*	1	W. Mediterranean					x	x
Byblidaceae	*Byblis*	5	Australia, New Guinea					x	
Roridulaceae	*Roridula*	2	S. Africa					x	
Cephalotaceae	*Cephalotus*	1	S.W. Australia				x		
Lentibulariaceae	*Pinguicula*	46	Northern hemisphere					x	x
	Genlisea	21	Central America, tropical and S. Africa, Madagascar	x					
	Utricularia	*c.* 200	Worldwide		x				x
Stylidiaceae	*Stylidium*		W. Australia						

Sources: Lüttge (1983), Mabberley (2000), Anderson & Midgley (2002), Darnowski et al. (2006).
Note: *N* is the number of species in each genus.

plant), *Roridula* (fly bush), and *Pinguicula* (butterwort)] probably evolved from glandular or "sticky" protocarnivores (Juniper et al. 1989). Examples of protocarnivores include tropical bromeliads and *Dipsacus* (teasel), which have primitive "pitfalls" (Christy 1923).

Some carnivorous plants attract their prey by the production of nectar at the edge of the trap. This nectar is actively secreted and the carbon costs of this process may amount to 4–6% of the plant's total carbon budget (Pate 1986, as cited in Karlsson et al. 1991). The extrafloral nectar also contains a range of amino acids, so there are also N costs (Dress et al. 1997). In addition, the carnivorous plants secrete adhesive substances by special glands [e.g., *Drosera* (sundew) and *Pinguicula* (butterwort)]. All carnivorous plants are green and capable of C_3 photosynthesis. Hence, carbon is unlikely to be a major element to be withdrawn from their prey, although it is certainly incorporated. Carnivorous species naturally occur on nutrient-poor, wet, acidic soils, with the exception of *Pinguicula* (butterwort), which grows on a chalky substrate. Most species have a poorly developed root system, and many are considered

Figure 1. (continued) Examples of carnivorous plants with different trapping structures. (A, B) *Drosera* tubaestylus and *Drosera* pulchella with adhesive hairs. (C, D) intact plant of *Utricularia menziesii* and detail of the trap of *Utricularia multifida* (bladderwort), with bladder-like suction traps. (E, F) *Dionaea muscipula* (Venus' fly trap), with snapping trap and trigger hairs. (G) *Cephalotus follicularis* (Albany pitcher plant), with pitfall. (H) *Genlisea violacea* (corkscrew plant) with lobster-pot or eel traps. (A, B, C, and G: photo H. Lambers; D: courtesy M.W. Shane, School of Plant Biology, the University of Western Australia, Perth, Australia; E and F, courtesy M.C. Brundrett, School of Plant Biology, the University of Western Australia, Perth, Australia; H and I, reproduced with permission from http://www.exoticaplants.com/database/cps/genlisea/page/violacea.htm).

TABLE 2. Response to feeding in the natural habitat of a mineral nutrient supplement or insects (16 *Drosophila* flies per plant) to members of a natural population of the annual *Drosera glanduligera* (pygmy sundew).

	No *Drosophila* applied		*Drosophila* applied	
	No mineral nutrients applied	Mineral nutrients applied	No mineral nutrients applied	Mineral nutrients applied
Biomass (mg DM)	4.4	7.1	13.3	11.0
N concentration (mmol g^{-1} DM)	1.1	0.8	1.5	1.3
Total N (µmol plant^{-1})	4.9	5.7	19.9	14.2
P concentration (µmol g^{-1} DM)	26	17	22	33
Total P (nmol plant^{-1})	114	124	299	368

Source: Karlsson & Pate (1992).

nonmycorrhizal (Sect. 2.2. of Chapter 9A on symbiotic associations; Adlassnig et al. 2005). It is generally assumed that carnivory is an adaptation to nutrient-poor soils and that inorganic nutrients are largely derived from the prey. There is a positive effect of supplementary feeding with prey on growth, even when this is done in the plant's natural habitat (Thum 1988, Zamora et al. 1997). However, this growth response to prey addition also occurs at high soil nutrient levels, which suggests that nutrients may not be the only mechanism by which carnivory enhances growth (Karlsson et al. 1991).

N is a major element withdrawn from the prey (Ellison & Gotelli 2001, Millett et al. 2003). Relatively tall, erect, or climbing *Drosera* (sundew) species may derive approximately 50% of all their N from insect feeding, whereas species with a rosette habit derive less N from insects (12–32%, depending on site) (Schulze & Schulze 1990). Carnivorous plants are likely to derive other elements from their prey as well, in particular **P** (Pate & Dixon 1978, Karlsson & Carlsson 1984, Ellison 2006) (Tables 2 and 3). For *Nepenthes mirabilis* (pitcher plant), *Cephalotus follicularis* (Albany pitcher plant), and *Darlingtonia californica* (pitcher plant) the maximum fraction of N that is derived from insects is 62, 26, and 76%, respectively (Schulze et al. 1997). When insects are scarce (e.g., in the extremely nutrient-poor habitat of the tuberous sundew *Drosera erythrorhiza* (red ink sundew) in Western Australia), the input of N from the catch of arthropods by the glandular leaves may be very small. Isotopic tracer studies (^{15}N; Sects. 2.4 and 3.6 of Chapter 9A on symbiotic associations) show that 76% of all N in the prey is transferred to the plant in *Drosera erythrorhiza* (red ink sundew), but this constitutes only 11–17% of its total N requirement in its natural environment (Dixon et al. 1980). In this habitat, specialized small beetles that do not stick to the glandular emergences compete with the plant for food by consuming the prey stuck to the leaf hairs. The glandular emergences might therefore function primarily to deter herbivores. The efficiency of insect capture in *Sarracenia purpurea* (northern pitcher plant) (i.e., the number of captures per number of visits by potential preys) is also very low: less than 1% (Newell & Nastase 1998). These examples illustrate the importance of quantitative assessments in determining the actual significance of the carnivorous habit in acquiring nutrients from a prey in a natural habitat.

TABLE 3. The effect of feeding *Utricularia gibba* (bladderwort) with *Paramecium* on Mg and K deficiency.

	Internodes		
Media	Number (% of control)	Length	Number of bladders formed
Complete medium (= control)	100	100	
Complete plus feeding	96	104	
Complete minus Mg^{2+}	38	33	85
Complete minus Mg^{2+} plus feeding	53	42	151
Complete medium (= control)	100	100	66
Complete plus feeding	136	139	86
Complete minus K^{+}	72	52	66
Complete minus K^{+} plus feeding	100	83	104

Source: Sorenson & Jackson (1968).

3. Some Case Studies

This section presents some more detailed ecophysiological studies of carnivorous plants.

3.1 Dionaea Muscipula

One of the most fascinating traps is that of *Dionaea muscipula* (Venus' fly trap), which is a species endemic on sandy soils in the central south-eastern coastal plain of North America (Fig. 1F). The trap consists of two lobes that are attached to a petiole. There are three **"trigger hairs"** on each lobe (Fig. 1F). Mechanical stimulation of these hairs leads to rapid closure of the trap. This is one of the fastest movements known in plants and is sufficiently rapid to catch even the most alert insects (Hodick & Sievers 1988, 1989). One of the six hairs inside the trap must be stimulated twice within 20 s; stimulation of two different hairs within the same time frame has the same effect (Fig. 2). Touching of one of the hairs leads to an **action potential** , which is propagated over the surface of one of the lobes (Fig. 3). At least two action potentials are required to close the trap. **Ca** in the cell wall is a prerequisite for any action potential to develop. In the absence of available Ca [e.g., when it is experimentally bound by a strong chelator (EGTA)], no action potential is produced. Inhibitors of the cytochrome path, uncouplers (Sect. 2.3.3 of Chapter 2B on plant respiration), and compounds that block Ca channels (e.g., $LaCl_3$) also inhibit the trap's excitability. We do not yet know what role, either direct or indirect, Ca plays in the signal transduction that leads to the closure of the trap.

Trap closure involves an increased **wall extensibility** of the lower epidermal cells (Table 4). Increased extensibility of the lower epidermis, in combination with the **tissue tension** (Sect. 4 of

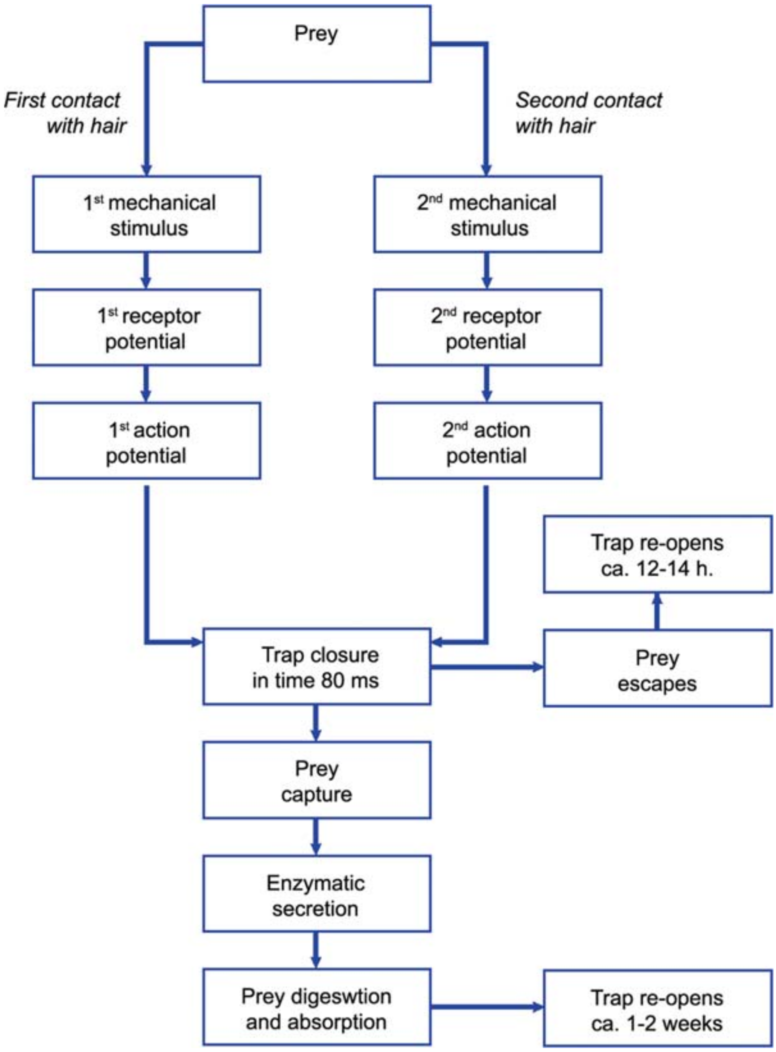

Figure 2. A scheme of the events after stimulation of the hairs of *Dionaea muscipula* (Venus' fly trap). The time elapsed between the first and second stimulus cannot exceed 20 s (after Jacobson 1965).

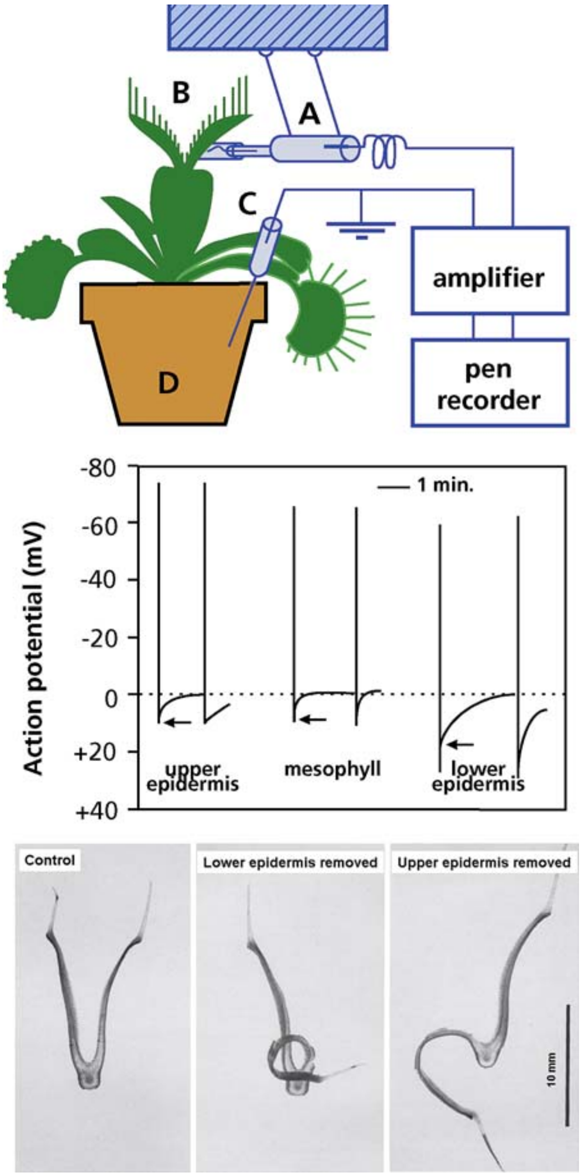

FIGURE 3. (*Top*) A scheme of the experimental design to determine action potentials from the surface of *Dionaea muscipula* (Venus' fly trap). One electrode (A), suspended by a thread pendulum to maintain electrical contact with the leaf (B) during movement. The reference electrode (C) is inserted into the substratum and earthed. (*Middle*) Extracellular recordings of action potentials during trap closure (arrows). Trigger hairs (not shown), the upper and lower epidermis, as well as the mesophyll produce action potentials. (*Bottom, a*) Cross-section of the Venus' flytrap, left intact. (*Bottom, b*) Similar cross-section, but with the lower epidermis of the right-hand lobe removed, forcing the lobe to curl inward, illustrating what happens when the cells of the lower epidermis suddenly expand upon triggering of the sensitive hairs, as during trap closure. (*Bottom, c*) Similar cross-section, but with the upper epidermis of the left-hand lobe removed, forcing the lobe to curl outward, illustrating what happens when the cells of the lower epidermis slowly expand during growth, as during trap re-opening (Hodick & Sievers 1988, 1989).

Chapter 3 on plant water relations), leads to trap closure. The tissue tension is due to the relatively elastic walls of the mesophyll cells ("swelling tissue"), compared with that of the epidermal cells. The presence of the relatively rigid upper and lower epidermal cells prevents the cells in the swelling tissue from reaching full turgor while the trap is open. The changes in extensibility that allow closure of the trap are not due to cell-wall acidification, as is the case when auxin induces similar changes in cell-wall properties (Sect. 2.2.2 of Chapter 7 on growth and allocation).

Closure of the trap occurs in two steps. The first step is a movement triggered by **mechanical** stimulation. If this is not followed by **chemical** stimulation, the trap gradually opens, due to the growth of the upper epidermis. If a chemical stimulus (in the form of chemical compounds from the hemolymph of the trapped insect) does occur, then the trap closes tightly and special glands begin to secrete **hydrolases** (e.g., proteases, phosphatases, DNAase) and fluid (Table 5). Trap opening is a much slower process, requiring extension (growth) of the upper epidermis (Fagerberg & Howe 1996). The opening

Table 4. The relative extensibilities of the upper and lower sides of the trap of *Dionaea muscipula*, measured as reversible (elastic) and irreversible (plastic) extension, induced by the application of a constant load for 10 minutes.

	Upper side	Lower side
Trap closed		
Elastic extensibility	3.5	6.9
Plastic extensibility	1.6	11.4
Trap closed and then paralyzed		
Elastic extensibility	nd	8.1
Plastic extensibility	nd	12.6
Trap open and then paralyzed		
Elastic extensibility	3.5	2.7
Plastic extensibility	1.8	1.8

***Source*: Hodick & Sievers (1989).**

***Note*: Tissue strips were extended perpendicularly to the midrib (nd = not determined). In some of the experiments, the trap was paralyzed with $LaCl_3$, which blocks Ca^{2+} channels and prevents excitability in whole leaves.**

and closing of the trap can occur only a few times, until both the upper and the lower epidermis have achieved their maximum length.

Snapping traps such as in *Dionaea muscipula* occur in only one other genus: the aquatic *Aldrovanda* (waterwheel plant). Molecular studies have shown that *Aldrovanda* is sister to *Dionaea* , and that the pair is sister to *Drosera* . Snap-traps are derived from adhesive traps and have a common ancestry among flowering plants (Cameron et al. 2002).

Table 5. The effect of chemical compounds normally present in the hemolymph of the prey, on the secretion of digestive fluids by *Dionaea muscipula*.

N-compound	Protein secretion % of control	Volume secretion % of control
Whole fly (*Calliphora*)	100	100
Uric acid	63	107
Ammonia	44	121
Glutamine	20	94
Urea	9	27
Phenylalanine	–	16

***Source*: Robins (1976).**

***Note*: Data are expressed as a percentage of the values found for whole flies.**

3.2 The Suction Traps of *Utricularia*

The genus *Utricularia* (bladderwort), with over 200 species, is the most widespread of all carnivorous plants (Juniper et al. 1989). Many species from this rootless genus are aquatic or hygrophytic plants, occurring in nutrient-poor shallow water or flooded soil. Small bladders are produced on the shoots, either in water or in wet soil (Fig. 1C,D). A single trap is an ovoid bladder, up to 10 mm in length, with an entrance and a stalk (Fig. 4). The ventral part of the trap wall in the entrance forms the **threshold**. The inner surface of the trap is covered by four-armed hairs (quadrifids), which secrete **enzymes** that digest the captured prey. The inner surface of the threshold is covered by two-armed hairs (bifids), which mainly play a role in the movement of water out of the bladder lumen. Both types of hairs consist of a basal cell, a middle cell (which is a **transfer cell**), and terminal secretory cells. In the posterior part of the pavement epithelium there are hairs with terminal cells, whose cuticles ("velum") seal up the trap door. Commonly, there are glandular hairs near the trap entrance; these hairs produce mucilage for prey attraction. Thus the trap contains several types of hairs that are specialized to perform quite different functions (Fineran 1985, Płachno & Jankun 2004).

Small animals (e.g., *Daphnia* species) touch one of the hairs of a trap door, causing the "door" to snap open inward. The inside of the trap has a lower **hydrostatic pressure** than the outside, so water flows in when the trap opens, carrying the prey with it (Fig. 4). Then the trap door closes again. The entire process takes 10–15 ms. The role of the hairs might be that of a "lever", but action potentials may also play a role. The low hydrostatic pressure inside the bladder is the result of active transport of Cl^- from the lumen of the bladder to the cells that surround it (across membrane A in Fig. 5). Na^+ follows down an electrochemical potential gradient. Active transport is probably via "two-armed glands" (Fig. 5). Transport of NaCl to the cells that surround the lumen of the bladder causes a gradient in water potential between the lumen and these cells. As a result, water flows from the lumen to these cells causing an increase in turgor which in turn promotes the transport of Na^+, Cl^-, and water out of the cells in the direction of the medium that surrounds the bladder. Suction traps only occur in *Utricularia* species.

Digestion of the prey in the bladders of *Utricularia* species requires the secretion of **enzymes** , as in other carnivorous plants (Sirová et al. 2003). Apart

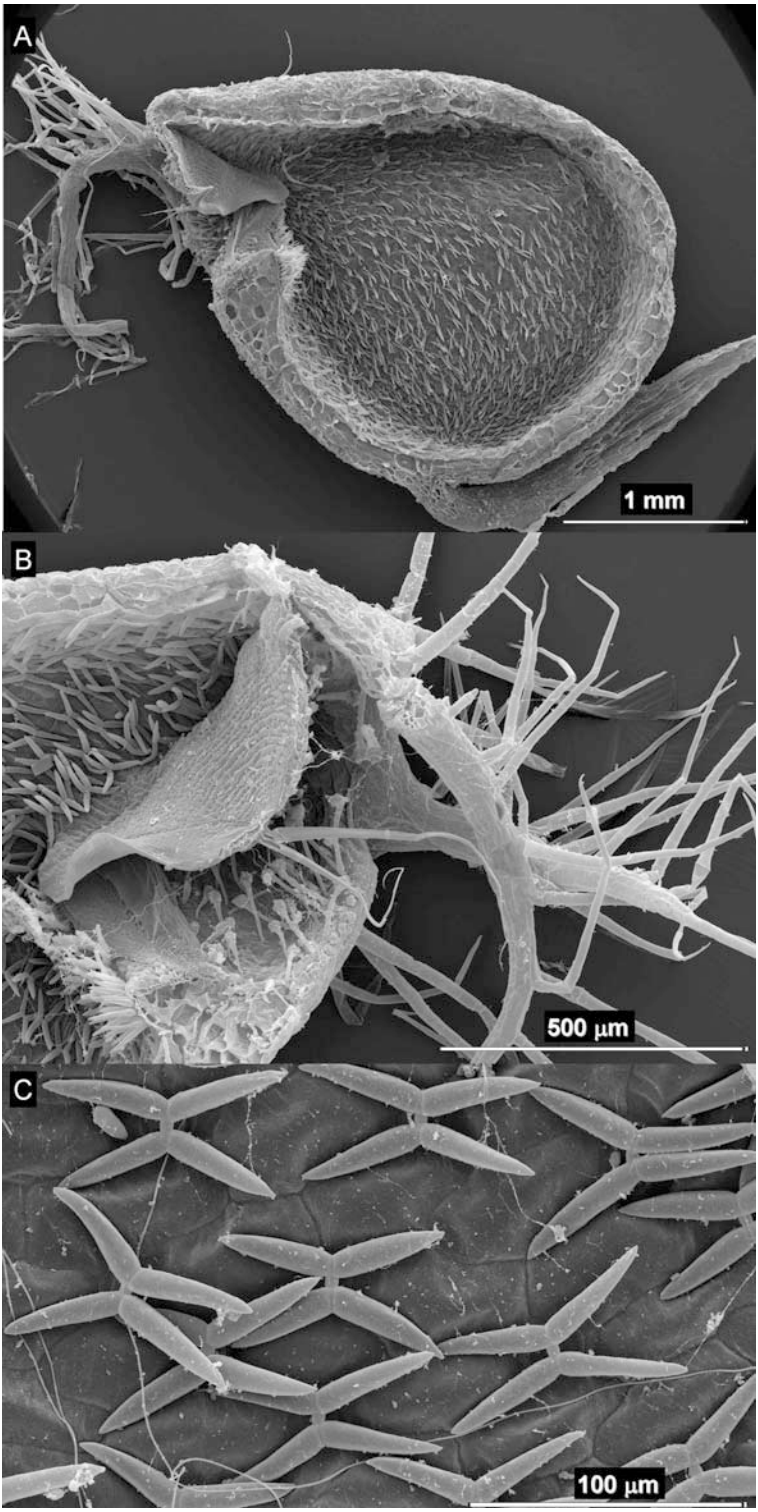

FIGURE 4. (*Top*) Median section through a trap of *Utricularia intermedia* , showing antennae above the trap door at the left and numerous quadrifid (four-armed) and bifid (two-armed) hairs inside the lumen of the trap. A stalk attaches the trap to the rest of the plant (Płachno & Jankun 2004). Copyright Polish Academy of Science. (*Bottom, left*) Detail of the trap door showing two sensitive hairs attached to the door, pointing toward the outside solution. Note the bifid hairs attached to the threshold of the door, and the quadrifid hairs at all other locations surrounding the lumen. (*Bottom middle*) Higher magnification view of quadrifid hairs. (*Bottom right*) Higher magnification view of quadrifid hairs (courtesy B.J. Płachno, Department of Plant Cytology and Embryology, The Jagiellonian University, Cracow, Poland).

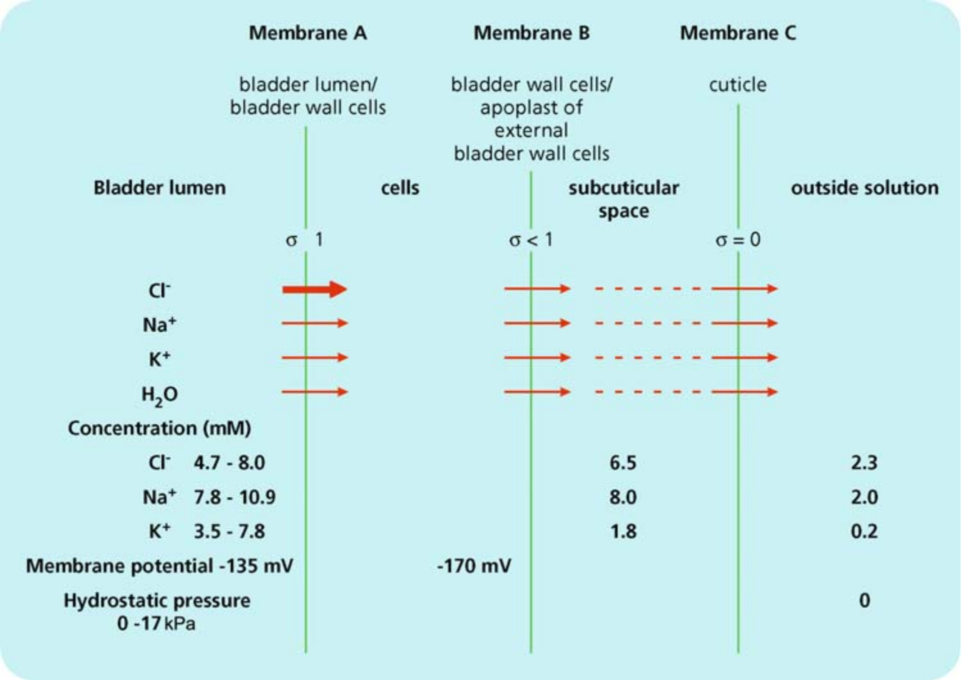

FIGURE 5. A model of solute and water flow in the resetting of the bladder of *Utricularia* species. Heavy arrow: active transport; thin arrows: passive transport; dotted lines connecting the arrows: bulk flow of solution through the subcuticular space to the outside. The values of ionic concentrations and pressure in the bladder lumen show the range between triggered and reset bladder. The potential difference in the lumen, apart from a very rapid change at the time of triggering, is constant during resetting (Sydenham & Finlay 1975).

from captured prey, bladders also harbor communities of living algae, zooplankton, and associated debris. Bladders of *Utricularia purpurea* in the Everglades of South Florida, where plants invest an average of 26% of their biomass in bladders, capture only a few aquatic microinvertebrates. It has therefore been suggested that the major benefit of bladders to the plant may be a mutualism with the community inside the bladder, rather than a predator–prey interaction (Richards 2001).

Molecular studies have shown that *Genlisea* is sister to *Utricularia* , and that the pair is sister to *Pinguicula* (Jobson et al. 2003). *Genlisea* attracts protozoa chemotactically, trapping them in its subterranean leaves (Barthlott et al. 1998); it also traps a range of other small organisms (Płachno et al. 2005).

3.3 The Tentacles of *Drosera*

The organs of adhesive traps such as those of *Drosera* (sundew, (Fig. 1A,B) and *Pinguicula* (butterwort) can also move after mechanical and/or chemical triggering. The tentacles (emergences) on the leaves function in catching and digestion of the prey, so that the tentacles, or even the entire leaf, may surround the prey as a result of their movement. Some of these (faster) movements are triggered by **action potentials** (Williams & Spanswick 1976). Two action potentials within 1 minute are required to trigger bending of a tentacle. The slower movements require a chemical stimulus (Williams 1976).

Digestion of the prey by carnivorous plants requires specific digestive enzymes, including **chitinases** , which hydrolyze the chitin in arthropod skeletons (Matusikova et al. 2005). Some of these enzymes are produced by the plant, in response to chemical stimuli from the prey, but it is likely that some hydrolytic enzymes are also produced by microorganisms, and that the carnivorous plant takes advantage of the presence of such microorganisms (Chandler & Andersson 1976).

Species with adhesive or flypaper traps belong to different families (Table 1), and some of them are closely related to species with different trapping mechanism, offering clear examples of **divergent evolution** (Albert et al. 1992).

3.4 Pitchers of *Sarracenia*

Sarracenia purpurea (northern pitcher plant), which is common to North America, has modified leaves that form open, fluid-containing pitchers. Secretions produced at the lip of the pitcher attract insects, some of which fall into the pitcher, drown, and are subsequently digested. During the early development of the plant, the pitcher produces traps with large, flat phyllodes that initially do not function well as traps and are primarily photosynthetic organs. At a later developmental stage of the plant, large, fully developed traps are produced. These traps can live for over a year, but most of the prey is caught within the first 50 days after the trap opens. Like other carnivorous plants, *Sarracenia purpurea* produces **hydrolytic enzymes** . Expression of protease, RNAase, DNAase, and phosphatase is partly developmentally controlled; it is also induced by the addition of nucleic acids, protein, or reduced N to the fluid in the trap (Gallie & Chang 1997). This suggests that hydrolase expression is induced upon perception of the appropriate chemical signals, which could improve the cost: benefit ratio of the carnivorous habit.

Though morphologically and functionally similar, pitcher plant genera belong to three distinctly separate families (Table 1). In particular, *Cephalotus follicularis* (Albany pitcher plant, Fig. 1G) is phylogenetically very distant, belonging to its own genus and family. This offers another fascinating example of **convergent evolution** (Adams & Smith 1977, Albert et al. 1992).

3.5 Passive Traps of *Genlisea*

A passive type of trap that is only found in the genus *Genlisea* (corkscrew plant) is the "**lobster-pot**" or "**eel trap**" (Barthlott et al. 1998). *Genlisea violacea* forms a rosette of small photosynthetic, green leaves that are attached to subterranean white traps, which are highly modified carnivorous leaves (Fig. 6). The Y-shaped traps are 2–15 cm long and about 1 mm thick. The hollow arms of the trap open into a hollow tubular neck, with an inner diameter of 200–500 mm. The tube ends in a slightly dilated vesicular cavity. The entire central cavity of the arms and neck is filled with water and lined with hairs pointing toward the vesicle. As such, *Genlisea* traps function as "eel traps". Microscopically small preys are attracted to enter the traps, and, due to the inward-pointing hairs, are led toward the vesicle. Here, **enzymes** are secreted, and the prey is digested. The traps of *Genlisea* attract and catch protozoa (Barthlott et al. 1998; Płachno et al. 2005, 2007), but the kind of prey it traps depends on the food that is available, and *Genlisea* is fairly opportunistic in its feeding behavior (Płachno et al. 2005).

Based on a similarity to traps of *Utricularia* , it has been suggested that there might also be active water flow in *Genlisea* traps. However, *Genlisea* traps lack bifid glands that would be responsible for water pumping as in *Utricularia* traps. There is virtually no water in the traps of *Genlisea* species, showing that the traps are passive (Adamec 2003).

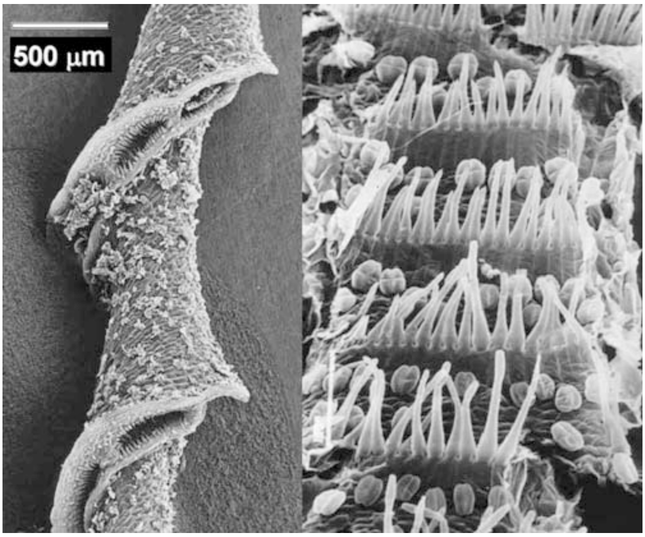

Figure 6. Passive trap of *Genlisea margaretae* . (*Left*) Scanning electron micrograph showing detail of a single trap; note the inward-pointing hairs. (*Right*) Higher magnification scanning electron micrograph of the inside of the tube. Courtesy W. Barthlott, University of Bonn, Germany.

4. The Message to Catch

Carnivory is a rare trait in the plant world, predominantly associated with nutrient-poor habitats which is why carnivorous species are relatively common in ancient, severely nutrient-impoverished landscapes of Western Australia, South Africa, and the Pantepui Highlands. Another center of diversity is the south-east of the United States, especially on nutrient-poor lateritic or sandy soils. There are **benefits** of the carnivorous habit, in that the prey provides an extra source of nutrients ("fertilizing effect"). There are also **costs** associated with secreting nectar, slime, and enzymes, but these would seem relatively small. The larger costs of the carnivorous habit are probably a reduced photosynthetic capacity, which would exclude carnivorous species from nutrient-rich sites where competition for light is important.

Carnivorous plants with adhesive surfaces probably evolved from protocarnivorous "sticky" glandular plants. Protocarnivory is much more widespread than carnivory. If glandular crops with protocarnivorous capabilities were engineered, these could reduce the need for pesticides and even require a somewhat lower fertilizer input. The various trapping mechanisms of carnivorous plants offer great examples of both **convergent** and **divergent evolution**.

References

Adamec, L. 2003. Zero water flows in the carnivorous genus *Genlisea* . *Carniv. Plant Newslett.* **32:** 46–48.

Adams, R.M. & Smith, G.W. 1977. An S.E.M. survey of the five carnivorous pitcher plant genera. *Am. J. Bot.* **64:** 265–272.

Adlassnig, W., Peroutka, M., Lambers, H. &. Lichtscheidl, I.L. 2005. The roots of carnivorous plants. *Plant Soil* **274:** 127–140.

Albert, V.A., Williams, S.E., & Chase, M.W. 1992. Carnivorous plants: phylogeny and structural evolution. *Science* **257:** 1491–1495.

Anderson, B. & Midgley, J. 2002. It takes two to tango but three is a tangle: mutualists and cheaters on the carnivorous plant *Roridula*. *Oecologia* **132:** 369–373.

Barber, J.T. 1978. *Capsella bursa-pastoris* seeds. Are they "carnivorous"? *Carniv. Plant Newslett.* **7:** 39–42.

Barthlott, W., Porembski, S., Fischer, E., & Gemmel, B. 1998. First protozoa-trapping plant found. *Nature* **392:** 447.

Cameron, K.M.,Wurdack, K.J., & Jobson, R.J. 2002. Molecular evidence for the common origin of snap-traps among carnivorous plants. *Am. J. Bot.* **89:** 1503–1509.

Chandler, G.E. & Andersson, J.W. 1976. Studies on the nutrition and growth of *Drosera* species with reference to the carnivorous habit. *New Phytol.* **76:** 129–141.

Christy, M. 1923. The common teasel as a carnivorous plant. *J. Bot* . **61:** 33–45.

Darnowski, D.W., Carroll, D.M., Płachno, B.J., Kabanoff, E., & Cinnamon, E. 2006. Evidence of protocarnivory in triggerplants (*Stylidium* spp.; Stylidiaceae). *Plant Biol.* **8:** 805–812.

Darwin, C. 1875. Insectivorous plants. Murray, London.

Darwin, F. 1878. Experiments on the nutrition and growth of *Drosera rotundifolia* . *J. Linn. Soc. Bot.* **17:** 17–23.

Dixon, K.W., Pate, J.S., & Bailey, W.J. 1980. Nitrogen nutrition of the tuberous sundew *Drosera erythrorhiza* Lindl. with special reference to catch of arthropod fauna by glandular leaves. *Aust. J. Bot.* **28:** 283–297.

Dress, W.J., Newell, S.J., Nastase, A.J., & Ford, J.C. 1997. Analysis of amino acids in nectar from pitchers of *Sarracenia purpurea* (Sarraceniaceae). *Am. J. Bot.* **84:** 1701–1706.

Ellison, A.M. 2006. Nutrient limitation and stoichiometry of carnivorous plants. *Plant Biol.* **8:** 740–747.

Ellison, A.M. & Farnsworth, E.J. 2005. The cost of carnivory for *Darlingtonia californica* (Sarraceniaceae): evidence from relationships among leaf traits. *Am. J. Bot.* **92:** 1085–1093.

Ellison, A.M. & Gotelli, N.J. 2001. Evolutionary ecology of carnivorous plants *Trends Ecol. Evol.* **16:** 623–629.

Fagerberg, W.R. & Howe, D.G. (1996) A quantitative study of tissue dynamics in Venus' fly trap *Dionaea muscipula* (Droseraceae). II. Trap reopening. *Am. J. Bot.* **83:** 836–842.

Fineran BA. 1985. Glandular Trichomes in *Utricularia* : a review of their structure and function. *Isr. J. Bot.* **34**: 295–330.

Gallie, D.R. & Chang, S.-C. 1997. Signal transduction in the carnivorous plant *Sarracenia purpurea* . Regulation of secretory hydrolase expression during developmentand in response to resources. *Plant Physiol.* **115:** 1461–1471.

Hodick, D. & Sievers, A. 1988. The action potential of *Dionaea muscipula* Ellis. *Planta* **174:** 8–18.

Hodick, D. & Sievers, A. 1989. On the mechanism of trap closure of Venus flytrap (*Dionaea muscipula* Ellis). *Planta* **179:** 32–42.

Jacobson, R.L.1965. Receptor response in Venus's fly-trap. *J. Gen. Physiol.* 49: 117–129.

Jobson, R.W., Playford, J.,Cameron, K.M., & Albert,V.A. 2003. Molecular phylogenetics of Lentibulariaceae inferred from plastid *rps* 16 intron and *trn* L-F DNA sequences: implications for character evolution and biogeography. *Syst. Bot.* **28:** 157–171.

Juniper, B.E., Robins, R.J., & Joel, D.M. (1989.) The carnivorous plants. Academic Press, London.

Karlsson, P.S. & Carlsson, B. 1984. Why does *Pinguicula vulgaris* L. trap insects? *New Phytol.* **97:** 25–30

Karlsson, P.S. & Pate, J.S. 1992. Contrasting effects of supplementary feeding of insects or mineral nutrients on the growth and nitrogen and phosphorus economy of pygmy species of *Drosera* . *Oecologia* **92:** 8–13.

Karlsson, P.S., Nordell, K.O., Carlsson, B.A., & Svensson, B.M. 1991. The effect of soil nutrient status on prey utilization in four carnivorous plants. *Oecologia* **86:** 1–7.

Lüttge, U. (1983) Ecophysiology of carnivorous plants. In: Encyclopedia of plant physiology, N.S. Vol. 12C, O.L. Lange, P.S. Nobel, C.B. Osmond, & H. Ziegler (eds). Springer-Verlag, Berlin, pp. 489–517.

Mabberley, D.J. 2000. The Plant-book. A portable dictionary of the higher plants. Cambridge University Press, New York.

Matušíková, I., Salaj, J., Moravčíková, J., Mlynárová, L., Nap, J.-P, & Libantová, J. 2005. Tentacles of in vitro-grown round-leaf sundew (*Drosera rotundifolia* L.) show induction of chitinase activity upon mimicking the presence of prey. *Planta* **222:** 1020–1027.

Mendez, M. & Karlsson, P.S. 1999. Costs and benefits of carnivory in plants: insights from the photosynthetic performance of four carnivorous plants in a subarctic environment. *Oikos* **86:** 105–112.

Millett, J. Jones, R.I., & Waldron, S. 2003. The contribution of insect prey to the total nitrogen content of sundews (*Drosera* spp.) determined in situ by stable isotope analysis New Phytol. **158:** 527–534.

Newell, S.J. & Nastase, A.J. 1998. Efficiency of insect capture by Sarracenia purpurea (Sarraceniaceae), the northern pitcher plant. *Amer. J. Bot.* **85:** 88–91.

Pate, J.S. & Dixon, K.W. 1978. Mineral nutrition of *Drosera erythrorhiza* Lindl. with special reference to its tuberous habit. *Aust. J. Bot.* **26:** 455–464.

Płachno, B.J. & Jankun, A. 2004. Transfer cell wall architecture in secretory hairs of *Utricularia intermedia* . *Acta Biol. Crocov. Ser. Bot.* **46:** 193–200.

Płachno, B.J., Adamus, K., Faber, J., and Kozłowski, J. 2005. Feeding behaviour of carnivorous *Genlisea* plants in the laboratory. *Acta Bot. Gall.* **152** : 159–164.

Płachno, B.J., Kozieradzka-Kiszkurno, M. & Swiatek. P. 2007. Functional ultrastructure of *Genlisea* (Lentibulariaceae) digestive hairs. *Ann. Bot.* **100:** 195–203.

Richards, J.H. 2001. Bladder function in *Utricularia purpurea* (Lentibulariaceae): is carnivory important? *Am. J. Bot.* **88:** 170–176.

Robins, R. J. 1976. The nature of the stimuli causing digestive juice secretion in *Dionaea muscipula* Ellis (Venus's flytrap). *Planta* **128:** 263–265.

Schulze, W. & Schulze, E.-D. 1990. Insect capture and growth of the insectivorous *Drosera rotundfolia* L. *Oecologia* **82:** 427–429.

Schulze, W., Schulze, E.-D., Pate, J.S., & Gillison, A.N. (1997) The nitrogen supply from soils and insects during growth of the pitcher plants *Nepenthes mirabilis*, *Cephalotus follicularis* and *Darlingtonia californica*. *Oecologia* **112:** 464–471.

Sirová, D., Adamec, L., & Vrba, J. 2003. Enzymatic activities in traps of four aquatic species of the carnivorous genus *Utricularia* . *New Phytol.* **159:** 669–675.

Sorenson, D.R. & Jackson, W.T. 1968. The utilization of paramecia by the carnivorous plant *Utricularia gibba* . *Planta* **83:** 166–170.

Spomer, G.G. 1999. Evidence of protocarnivorous capabilities in *Geranium viscosissimum* and *Potentilla arguta* and other sticky plants. *Int. J. Plant Sci.* **160:** 98–101.

Sydenham, P.H. & Findlay, G.P. 1975. Transport of solutes and water by resetting bladders of *Utricularia Aust. J. Plant Physiol.* **2:** 335–351.

Thum, M. 1988. The significance of carnivory for the fitness of *Drosera* in its natural habitat. 1. The reactions of *Drosera intermedia* and *D. rotundifolia* to supplementary insect feeding. *Oecologia* **75:** 472–480.

Williams, S.E. 1976. Comparative sensory physiology of the Droseraceae–the evolution of a plant sensory system. *Proc. Am. Phil. Soc.* **120:** 187–204.

Williams, S.E. & Spanswick, R.M. 1976. Propagation of the neuroid action potential of the carnivorous plant *Drosera*. *J. Comp. Physiol. A: Neuroethol. Sens. Neur. Behav. Physiol.* **108:** 211–223.

Zamora, R., Gomez, J.M. & Hodar, J.A. 1997. Responses of a carnivorous plant to prey and inorganic nutrients in a Mediterranean environment. *Oecologia* **111:** 443–451.