glandular unit can therefore be regarded as the digestive pump, and the endodermoid unit - as its main valve.

In addition, digestive glands are often provided with auxiliary elements such as reservoir cells, stalks, and conductive cells.

Carnivorous glands operate under different digestive strategies . In some species digestive cycles take place only when prey is available to the trap, in other species the glands show a continuous digestive activity. The former strategy is employed by the snap-traps of *Dionaea* and *Aldrovanda*, where digestive fluid is secreted by all trap glands when prey is available and the trap shuts, or by the adhesive traps of *Drosera* and *Pinguicula*, where digestive fluid is secreted only by glands that are stimulated by entrapped prey. The latter strategy is employed by pitcher plants and by *Utricularia*, where the main volume of the digestive fluid is spontaneously secreted during the maturation of the trap. In this latter case the entrapment of prey often operates additional secretion of enzymes and leads to a decrease in the pH of the digestive fluid. We therefore see that digestive gland activity is usually stimulated by the presence of prey even if the trap is passive.

The pitcher epithelium of *Sarracenia* is composed of a glandular epidermis that continuously occupies the inner surface of the bottom zone of the pitcher, with an endodermoid sub-epidermis that constitutes a physical barrier of extracellular leakage of water and solutes. This unique surface-gland serves not only as a digestive gland but also plays a key role in helping associated fauna to coexist in the pitcher. The epithelium was shown to control the levels of oxygen, carbon dioxide and various other solutes in the digestive pool. The role played by associated organisms in prey breakdown and digestion is significant mainly in pitcher plants.

The structure of the cuticle covering the outer surface of digestive glands corresponds to the trapping strategy. When the fluid is secreted spontaneously, as in the pitcher plants, the cuticle also opens spontaneously during gland maturation. When the fluid is secreted only in response to trapping, the cuticle also opens only when stimulated by prey. Cuticular opening seems to develop as a result of wall stretching, that in turn is caused by an increase in the ionic content of the outer glandular cells. In *Dionaea* it was shown that a wave of chloride transport precedes cuticular opening, and this ion was shown to accumulate in turn in the various layers of the glands: first in the basal cells, then in the endodermoid cells and later in the glandular cells. Chloride ions were followed under the electron microscope and were seen to move from one cell to another both via plasmodesmata, that serve as plasmatic connections between cells that bridge across cell walls, and via the tangential cell walls that are located between endodermoid cells and the basal cells or glandular cells. In the basal cells chloride is accumulated in special organelles.

The uptake of digestion products from the gland surface is an active, energy consuming process, in which ATPase is involved. Some products are immediately consumed or metabolized in the gland itself, whereas others are transferred to other plant organs.

The digestive glands of carnivorous plants are interesting not only because of the special nature of the plants that carry them, but also because these structures secrete enzymes to the plant surface as the result of simple external chemical signals, in contrast to most other cases in the plant kingdom where stimulated secretion of enzymes is restricted to internal structure only. This quality of the digestive glands makes them an ideal model for research of glandular mechanisms in plants.

In vitro Cultivation and Experiments with Carnivorous Plants

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Porter (1940) reported germination and growth of sterile sown *Nepenthes maxima*. This work marks the very starting point of growing carnivorous plants *in vitro*, published only a few years after the final

establishment of plant organ cultures. Since then protocols have been developed for cultivating many genera of carnivorous plants *in vitro*, including: *Aldrovanda*, *Byblis*, *Cephalotus*, *Darlingtonia*, *Dionaea*, *Drosera*, *Drosophyllum*, *Genlisea*, *Heliamphora*, *Nepenthes*, *Pinguicula*, *Sarracenia*, and *Utricularia*.

However, the purposes for growing carnivorous plants *in vitro* are quite diverse. It is useful to subdivide these in the following categories:

- commercial mass propagation
- *ex situ* conservation
- physiological examination under sterile conditions, especially for understanding the nutrition of carnivorous plants
- study and production of secondary metabolites.

The applied techniques and the exploited mechanisms for reaching a particular goal are consequently as different as the purposes themselves. For the first two categories clonal propagation is achieved using techniques which minimize somaclonal variation e.g. the shoot tip culture or the single node technique. Organ cultures are used for the third category, whereas undifferentiated fast growing cell cultures are preferred for the production of natural products.

In our laboratory, we have established *in vitro* cultures of several carnivorous plants and their close non-carnivorous relatives in the order Nepenthales (incl. Polygonaceae, Plumbaginaceae, Nepenthaceae, Ancistrocladaceae, Dioncophyllaceae, Drosophyllaceae, and Droseraceae) for the purpose of studies on their secondary metabolism. The members of this group are marked by their ability to produce acetogenic quinones like plumbagin, 7-methyljuglone, or emodin. Furthermore, the families Ancistrocladaceae and Dioncophyllaceae (incl. *Triphyophyllum peltatum*) are notable for containing the unique naphthylisoquinoline alkaloids (Bringmann & Pokorny 1995) investigated in our group.

First experiments with callus cultures have shown that acetogenic metabolite production can be elicited by exogenous stimuli.

The carnivorous syndrome of one of the above mentioned species, *viz. T. peltatum* has hitherto not been demonstrated conclusively because the uptake of organic matter was not proven experimentally. For this reason labelled alanine (an amino acid commonly found in animal protein) was fed to the insect-trapping organs of *T. peltatum* during a field trip to the Taï National Park in Ivory Coast (Bringmann & al. 1996). After GC/MS analysis of extracts from different parts of fed and control plants, incorporation and redistribution of the label was demonstrated unambiguously. *T. peltatum* is a part time carnivorous plant with all required attributes.

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The Effect of *Bacillus cereus* on the Digestion of Prey by Carnivorous Plants

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Carnivorous plants catch and digest insects. This digestion of prey is due to enzymes produced by the carnivorous plants, to enzymes produced by bacteria, or a combination of both, depending on the species. Carnivorous plants rarely secrete all the enzymes needed for total digestion of prey (Juniper 1989, p.190;