

# Carnivorous Plants

**Wolf-Ekkehard Lönig**, *Max-Planck-Institute for Plant Breeding Research, Cologne, Germany*

**Heinz-Albert Becker**, *Max-Planck-Institute for Plant Breeding Research, Cologne, Germany*

Carnivorous plants include some 500 plant species of various angiosperm orders and families that – by enormously different and ingenious trap mechanisms – catch small animals (mostly insects) and subsequently digest them.

## Introduction and History

The idea that plants – being the quintessence of peaceful organisms standing at the basis of the food chain of life – could themselves catch and eat animals, appeared so improbable to most botanists and other researchers that from the first descriptions in the fifteenth and sixteenth centuries (*Pinguicula* by Auslasser, 1479; *Sarracenia* by de Lobel, 1576; *Utricularia* also by de Lobel, 1591) it took several hundred years for the carnivorous nature of these plants to be generally recognized. Ellis first suggested carnivory for *Dionaea* to Linné in a letter of 1769 (which suggestion Linné rejected), Roth surmised the same for *Drosera* in 1780, Bartram for *Sarracenia* in 1791, and Korthals for *Nepenthes* in 1839/1842. The years 1861 and 1868 brought the first discoveries of the trap functions in *Aldrovanda* (de Lassus) and *Utricularia* (Holland), respectively. The first digestive enzyme was determined by Hooker 1874 in *Nepenthes*. However, in 1875, the idea of carnivorous plants was still rejected as scientific rubbish ('wissenschaftlicher Plunder') by Regel, director of the botanic garden of St Petersburg – the same year that Charles Darwin published his book on *Insectivorous Plants* in London. The following years brought an explosion of research papers (see Further Reading for the historic details; e.g. Schmucker and Linne-mann, 1959; Juniper *et al.*, 1989; Slack, 2001; Braem, 2002). Apart from the angiosperms, there are about 50 species of carnivorous fungi.

## Habitats

Although most carnivorous plant species prefer or even depend on acid, peaty and boggy (low-nutrient) soils, their victims providing especially nitrogen, several species are also found in other environments. *Utricularia vulgaris*, for example, lives in meso-eutrophic waters (pH between 5 and 8) of the northern hemisphere and 'in both Africa and India some *Utricularia* species are commonly found in rice cultivations' (Taylor, 1989, p. 45), and thus may even be considered as invaders of a more or less artificial non-oligotrophic environment. *Pinguicula* avoids extremely poor soils and occurs also in mineral rich habitats. *Drosophyllum* is restricted to dry locations. Almost all car-

## Introductory article

### Article Contents

- Introduction and History
- Habitats
- Functional Morphology and Anatomy of Different Trap Types
- Nutrition and Digestion
- Systematics and the Origin of Carnivorous Plants
- Economically and Horticulturally Important Species

doi: 10.1038/npg.els.0003818

nivorous plants demand open habitats and cannot cope with prolonged shady environments. Except in *Roridula* there is no mycorrhiza in carnivorous plants, even in locations where all other species are strongly mycotrophic (high-moor bogs). Many Australian *Drosera* species occur not only in swamps and heathlands (as expected), but also in open forests, some also in loam soils of watersheds, sandy clay soils of *Eucalyptus* woodlands and others.

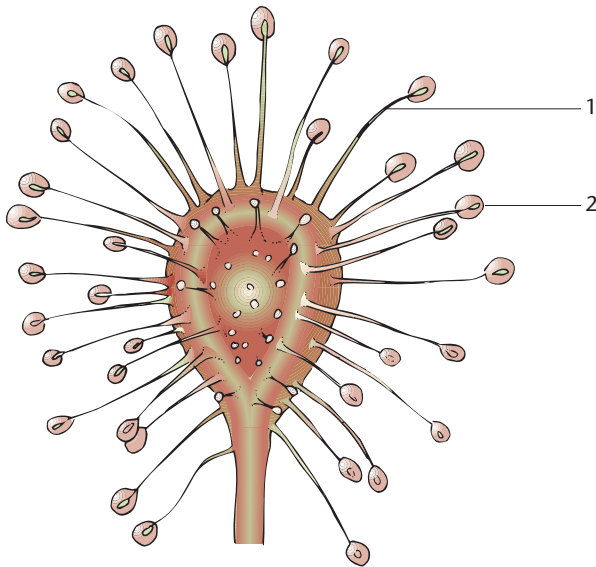
## Functional Morphology and Anatomy of Different Trap Types

The general problem for a sessile organism to access mobile prey was biologically answered by an amazing variation of different trap types. They are commonly classified by the physical properties of the trapping mechanism in adhesive-, pitcher-, snap- and suction traps. Even those traps appearing to display a relatively simple design constitute highly morphologically and functionally specialized organs belonging to the most intricate structures of the plant kingdom. Most of the traps are leaf-derived structures which have undergone astonishing metamorphoses to perfectly functioning hunting mechanisms in addition to being photosynthetically active.

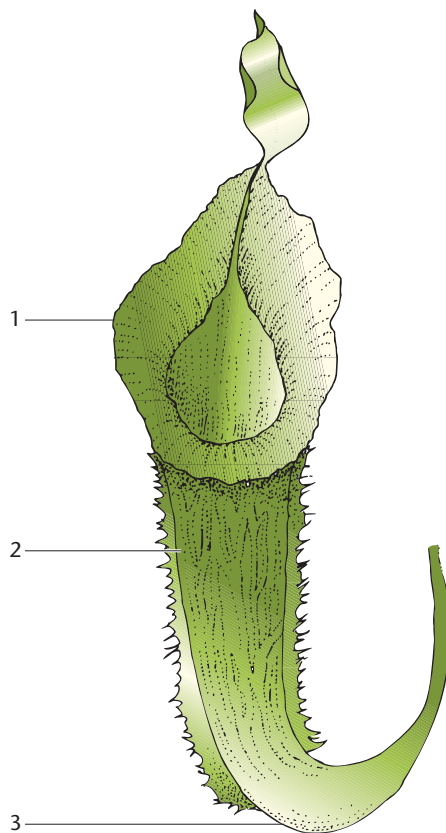
To give an overview of the diversity of the mechanisms one example for each trap type is discussed in the following text.

The basic principle of the adhesive type is glue in the form of a sticky mucilage. As depicted in **Figure 1**, the stalked glands of the Droseraceae are present as glistening droplets, which are surmised to participate in the attraction of insects. As soon as an insect touches the droplets, and by its rescue attempts is attached to more of them, the glands increasingly bend to the centre of the trap where the insect finally is fully immersed and digested.

Slipperiness, as an opposite physical principle to stickiness, allows pitchers like *Nepenthes* (**Figure 2**) to successfully capture small animals. A waxy zone starts below the



**Figure 1** Stalked trapping glands (1) of a *Drosera* leaf. Once insects have touched the glistening droplets (2), each attempt to escape increases the number of attachments. Subsequently the stalked glands bend to the centre of the leaf where the prey is digested.

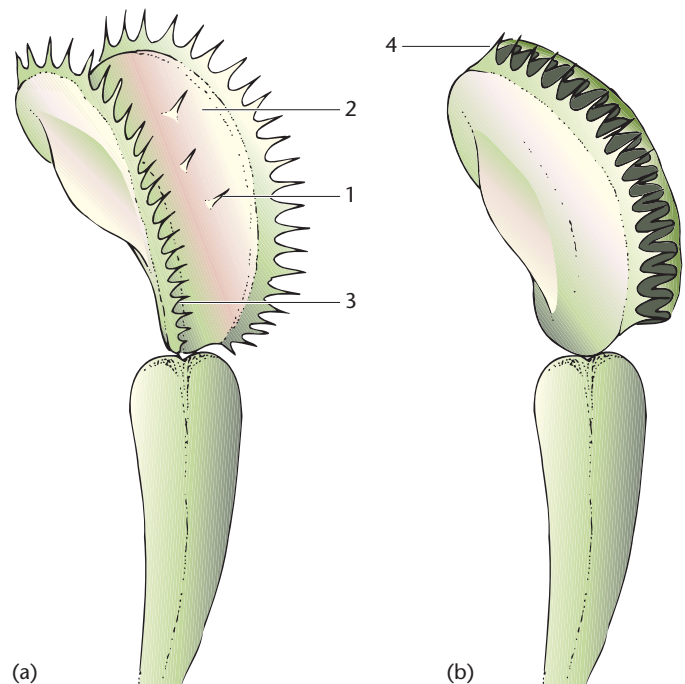


**Figure 2** As typical pitchers, *Nepenthes* (drawn according to a photograph of Schmucker and Linnemann) attract insects by the often brilliantly coloured ribbed rims and the nectar glands between the ribs (1). Reaching the slippery internal waxy zone (2) just below, the prey drops into the digestion fluid (3) at the base of the pitcher lumen.

upper rim, which is often T-shaped to hinder vertical escapes from inside the trap. Slippery material makes it impossible for the insects to climb the walls vertically to escape through the entrance. They finally fall into the digestion fluid at the bottom of the pitcher and are dissolved and digested.

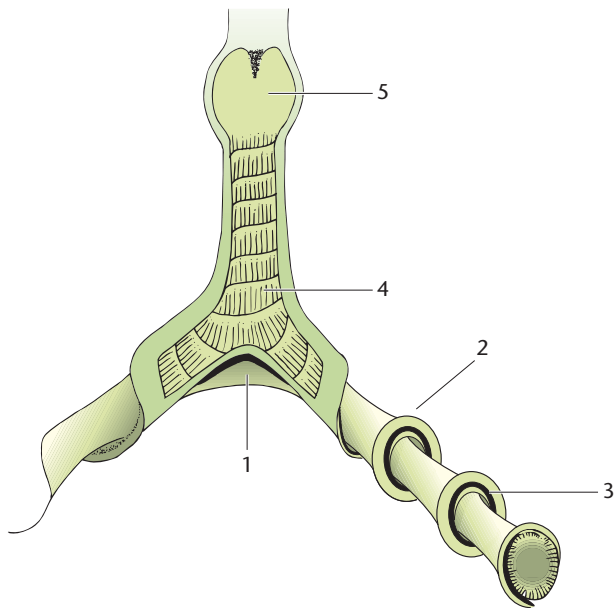
A high degree of functional motility can be observed for *Dionaea* types, the so-called Venus flytraps (**Figure 3**). The two lobes of the leaf lamina are connected at the central rib by a mobile hinge. At each lobe three or four sensor hairs function to trigger a receptor potential which is transmitted as an action potential to the effector where the closure of the trap is triggered. The prey is retained by the marginal teeth, which are interlocked in the closed phase, and the insect is finally digested by glands surrounding the trigger hairs. A similar design is found in the aquatic *Aldrovanda*. However, instead of prong-like teeth, it displays, among further features, folded margins and the trap is much smaller (2 mm).

Another type of aquatic trap is found in *Genlisea*, the 'corkscrew plant'. Its design and hunting technique are different from both the aquatics *Aldrovanda* and *Utricularia*, the latter being one of *Genlisea*'s close relatives (see below). At their distal end the trap of *Genlisea* consists of a two-pronged fork leading to a slitlike mouth between the



**Figure 3** (a) A *Dionaea* flytrap (redrawn according to Juniper *et al.*) begins to operate when a trigger hair (1) on the leaf lamina (2) is mechanically stimulated. An electric potential is transmitted to the hinge of the mid-rib (3), inducing rapid closure. (b) In the closed state the trapped prey is prevented from escaping by the interlocked teeth (4). (c) The trap of *Dionaea muscipula*: note the three trigger hairs on the lobes of the leaf lamina and the long marginal teeth which are interlocked in the closed phase. Photograph by Maret Kalda, MPI, Cologne.

branches, the mouth continuing in a spiral the full length down each branch. Upwards a necklike cylinder leads into a hollow bulb constituting the digestive chamber which in

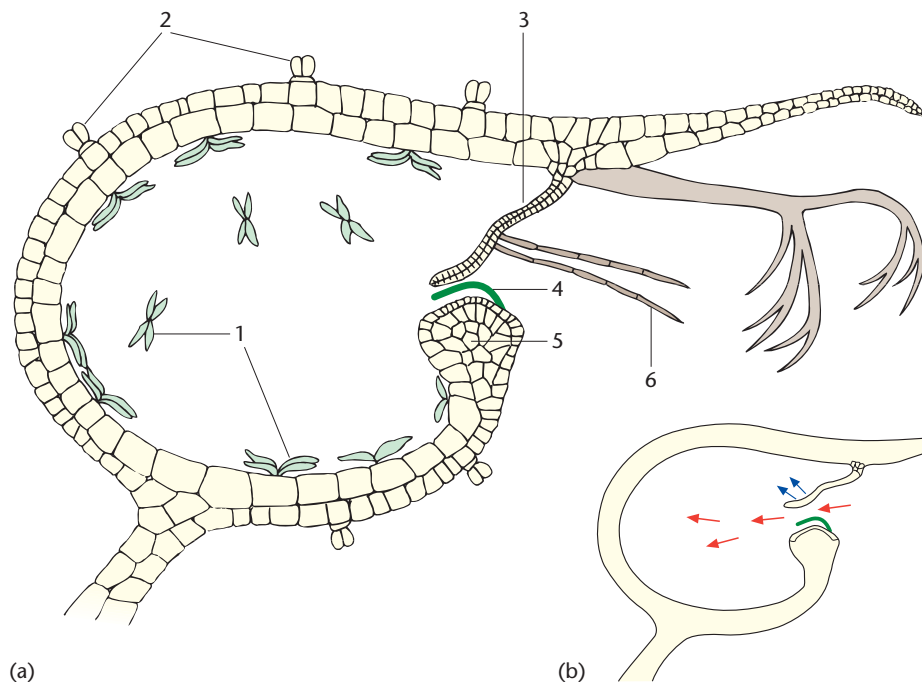


**Figure 4** The *Genlisea* trapping device (redrawn according to Pietropaolo; slightly altered): The mouth (1) and its elongations into the two spiral arms (2) provide the entrances (3) for small aquatic animals as nematodes or copepods. The prey is directed by detaining hairs (4) and most probably also by negative hydrostatic pressure to the bulb (5), where they are finally digested.

turn is connected with the proximal cylindrical footstalk (**Figure 4**). In addition to small copepods and nematodes, *Genlisea* traps also accumulate soil particles. Suction appears to be involved to assist in drawing in the prey and soil particles.

Highly specialized suction traps as depicted in *Utricularia* (**Figure 5**) are also adapted to water as surrounding medium. The trap is set by negative hydrostatic pressure. Glandular structures outside and inside the bladder were shown to be involved in water transport from the lumen to the surrounding medium. When a potential prey (e.g. a copepod, cladoceran, ostracod) stimulates the antennae of the trap door, the latter is opened and the trap walls, being under negative pressure, expand rapidly sucking in water through the door opening. The prey is sucked in concomitantly and the door quickly returns to its former state. The opening process is estimated to take less than 2 ms and the entire firing process – stimulation, door opening, and closing – lasts about 30 ms and is thus one of the fastest movements in the plant kingdom.

In addition to the main characteristics of the physical trapping mechanisms, the traps of most carnivorous plants exhibit accessory features suitable for attracting small animals. Different trap types increase their efficiency by colours, olfactory stimuli and further anatomical devices (windows, detaining hairs, slippery material). Moreover, apart from the trapping devices there are some additional deviations from the general angiosperm design principle:



**Figure 5** (a) The internal four-armed glands (1) and the external globe-shaped glands (2) are involved in the generation of the strong negative hydrostatic pressure in the trap of the bladderwort *Utricularia* (redrawn according to Lloyd and Schmucker and Linnemann; altered). When the trap is set, the door exhibiting a hinge region (3) is attached to the velum (4) on the horseshoe-formed abutment (5). The trigger hairs (6) function as highly sensitive levers. (b) When the trigger hairs (**Figure 5a, b**) are touched, they bend the distal part of the entrance and the door is rapidly opened (6). To ease the tensions between the negative hydrostatic pressure of the lumen and the adjoining water, both the latter and the prey are speedily sucked in.

*Utricularia* does not develop any roots, and *Genlisea* has ‘root-leaves’, so that genuine roots are missing here, too.

## Nutrition and Digestion

The basic question which has been debated for more than a century is whether the insects and other small invertebrates, as well as some fish fry, are really essential for normal development of carnivorous plants or whether they can also persist and flourish without prey. Regarding the observation of many authors that the species investigated can normally grow and flower under laboratory conditions, it has been objected that such environments do not reflect their special natural habitats and thus cannot provide the solution to this problem.

The conventional view is that carnivorous plants are clearly benefiting from digestion of small invertebrates and fish fry. This, however, could not be corroborated by recent painstaking investigations in *Utricularia purpurea*. The return of nitrogen and phosphorus from an overall investment of 25 – 50% in bladder formation proved to be less than 1% in the cases investigated. One hypothesis is that *Utricularia* plants benefit more from living communities of microorganisms and associated detritus, i.e. by mutualism, than from carnivory. The open question is, however, to what extent the results can be generalized for other *Utricularia* species or for other carnivorous plant genera. Conversely, writers like Schnell (2002, p. 20) are convinced ‘that carnivorous plants do indeed benefit from their unique adaptations by exhibiting more rapid and enhanced growth, more prolific flowering and seed set, and a better ability to maintain and even improve their competitive edge within their habitats’.

Carnivorous plants digest their prey by means of enzymes such as acid phosphatase, proteases, peptidases, esterases and chitinase. Also, ribonuclease and deoxyribonuclease and still others have been detected. An amylase is found in *Aldrovanda*. For several carnivorous plant species more investigations are necessary to corroborate and enlarge earlier findings.

Usually the same glands producing the enzymes are also responsible for the absorption of the digested materials.

## Systematics and the Origin of Carnivorous Plants

### Systematics

The following 11 families and 21 genera altogether with about 500 species of carnivorous plants can presently be distinguished (species numbers in brackets followed by geographical distribution):

### Sarraceniaceae (pitchers)

- *Sarracenia* (9): Atlantic North America
- *Heliamphora* (5): Guyana, Venezuela
- *Darlingtonia* (1): California

### Nepenthaceae (pitchers)

- *Nepenthes* (80): southeast Asia, Australia, Madagascar

### Dioncophyllaceae (adhesive traps)

- *Triphyophyllum* (1): southwestern Ivory Coast, Liberia, Sierra Leone

### Cephalotaceae (pitchers)

- *Cephalotus* (1): southwest Australia

### Droseraceae ((a) snap traps, (b) adhesive traps: sticky tentacles)

- *Drosophyllum* (1) (b): Portugal
- *Drosera* (110) (b): cosmopolitan
- *Dionaea* (1) (a): North and South Carolina and Northern Florida, USA
- *Aldrovanda* (1) (a): Old World (‘submerged water-plant’)

### Roridulaceae (adhesive traps: sticky glands on stems)

- *Roridula* (2): southeast Africa

### Byblidaceae (adhesive traps: sticky glands on stems)

- *Byblis* (2): Australia

### Lentibulariaceae ((a) adhesive traps: sticky glands on leaves, (b) suction-traps: bladders with trap-door entrances, (c) complex alimentary canal)



- *Pinguicula* (30) (a): northern temperate zone
- *Genlisea* (25) (b?)(c): tropical South America
- *Utricularia* (species numbers given vary between 214 and 280) (b): cosmopolitan
- *Polypompholyx* (4) (b): South America, Australia
- *Biovularia* (2) (b): tropical South America, Cuba

## Martyniaceae (adhesive traps)

- *Ibicella* (1): southern USA, Mexico

## Bromeliaceae (pitchers)

- *Brocchinia* (1): Venezuela, Guyana
- *Catopsis* (1): Florida to Brazil

## Eriocaulaceae (pitchers)

- *Paepalanthus* (1): Serra de Cipo, Brazil

## The origin of carnivorous plants

Since this topic has constituted a set of most absorbing and controversial questions of carnivorous plant research for about 130 years ('the evolution of leaves with trap systems from noncarnivorous ones is mysterious, and there are no widely accepted hypotheses' – Rivadavia *et al.*, 2003, p. 123), we have invested a correspondingly detailed examination of these problems in the following paragraphs.

Although the carnivorous nature of *Roridula* sp., *Paepalanthus bromelioides* and *Brocchinia reducta* is still doubted by some authors, most writers agree that the nine fully substantiated families belonging to six different plant orders already clearly show that carnivory in plants must have arisen several times independently of each other. In a scenario of strong convergence based on morphological data the pitchers might have arisen seven times separately, adhesive traps at least four times, snap traps two times and suction traps possibly also two times. Nevertheless, such conclusions have been questioned by some authors as perhaps 'more apparent than real' (Juniper *et al.*, 1989, pp. 4, 283), discussing the origin of all carnivorous plant families from one basic carnivorous stem group (Croizat had already dedicated a larger work to this hypothesis in 1960).

The independent origin of complex synorganized structures, which are often anatomically and physiologically very similar to each other, appears to be intrinsically unlikely to many authors so that they have tried to avoid the hypothesis of convergence as far as possible. Yet, molecular comparisons have corroborated the independent origin of at least five of the carnivorous plant groups.

However, *Dionaea* and *Aldrovanda*, which according to most morphological investigations were thought to have arisen convergently, are now placed very near each other 'and this pair is sister to *Drosera*' (Cameron *et al.*, 2002, p. 1503). Nevertheless, since none of the genes studied so far is known to be expressly involved in structure formation of the traps, more information will probably be gained by the discovery and comparison of genes directly participating in trap formation. Although Cameron *et al.* approach Croizat's hypothesis mentioned above, there is no question that several similar trap devices arose independently of each other.

Also, several authors have discussed the question whether the modern synthesis (selection of mutations 'with small or even invisible effects on the phenotype' – Mayr) could provide a sufficient explanation of the many convergently arisen synorganized trap mechanisms. Darwin in 1875 examined several basic points on how the origin of some carnivorous structures could perhaps be envisioned by a process of gradual evolution. However, most authors have remained critical. The following questions and statements posed by Nachtwey in 1959 concerning the origin of *Utricularia*'s trap still have not been answered satisfactorily at the beginning of the twenty-first century and may illustrate some of the principal problems of the origin of carnivory in plants. After a careful description of the structures and functions of the trap, Nachtwey raised the question of how the origin from a leaf tip should be envisioned and went on to ask (pp. 99/100): 'Which nondirectional mutation should have occurred first in a normal leaf tip and subsequently displayed any selective advantage? Without an advantage it would have been lost as trivial. The modern synthesis strongly emphasizes that mutation and selection have to cooperate to generate new structures. So, by which blind mutations should the suction trap have originated?' And regarding the problem of further evolutionary stages the writer continues: 'Even a perfect suction trap displaying the astonishing ability to rapidly catch animals would have no advantage in the struggle for life because the prey would not be digested. Conversely, the production of highly effective digestive juices would be of no avail for the tip of a leaf as long as it could not capture the prey, which is absolutely necessary. But even if suction trap and digestive juices cooperated, nothing would be gained in the struggle for life. The dissolved proteins must also be absorbed and metabolized to species-specific proteins. The formation of the suction trap requires the perfect cooperation of many different genes and developmental factors. At the end a benefit is reached in the struggle for life, but not by any evolutionary stage.' Nachtwey concluded that none of the contemporary evolutionary theories was able to answer these questions, proposing that the answer might lie outside the present scientific paradigms.

Although other scenarios could possibly be envisioned and some objections raised against Nachtwey's reflections (perhaps unknown functions of nascent structures, per-

haps minor uptake of organic compounds by leaves without digestive and absorbent glands), the problem appears to have been aggravated by the recent discoveries that the well-being of *Utricularia purpurea* appears to be largely independent of its prey (see details under nutrition and digestion above).

Juniper *et al.*, who favour the functional proposition of Schnell quoted above, also agree with Nachtwey on the intricacy of the evolutionary problem, stating that ‘no adequate evolutionary sequence can yet be constructed even to present a speculative path for the origin of what appears to be a relatively homogeneous group’ (1989, p. 43). As for this problem, they continue that *Utricularia* ‘is a complex bit of mechanism and offers, as yet, an intractable problem in evolution’ (1989, p. 117). The latter writers generally favour a more or less saltational model for the origin of carnivorous plants, a view shared by some other biologists as a general model for the origin of large numbers of morphological species and genera in the living world.

Yet, even authors preferring ‘gradual evolutionary change through unimaginable aeons of time’ (Slack, 2001, p. 19) admit the depth of the origins problem for carnivorous plants: ‘Unfortunately this is a question which we cannot hope to answer without suitable fossil evidence, and one can offer a mere hypothesis’ (Slack pp. 18/19). Moreover, it appears to be hard even to imagine clearcut selective advantages for all the thousands of postulated intermediate steps in a gradual scenario, not to mention the formulation and examination of scientific (i.e. testable) hypotheses for the origin of the complex carnivorous plant structures examined above.

The reader is further invited to consider the following problem. Charles Darwin provided a sufficiency test for his theory (1859, p. 219): ‘If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down.’ Darwin, however, stated that he could ‘not find out such a case’. Biochemist Michael J. Behe (1996, p. 39) has refined Darwin’s statement by introducing and defining his concept of ‘irreducibly complex systems’, specifying: ‘By *irreducibly complex* I mean a single system composed of several well-matched, interacting parts that contribute to the basic function, wherein the removal of any one of the parts causes the system to effectively cease functioning.’

Some biologists believe that the trap mechanism(s) of *Utricularia* and several other carnivorous plant genera (*Dionaea*, *Aldovanda*, *Genlisea*) come at least very near to ‘such a case’ of irreducible complexity. It is to be hoped that future research will fully clarify these questions.

## Economically and Horticulturally Important Species

There is hardly any large garden centre that does not offer at least some carnivorous plant species, most often *Dionaea muscipula* and pitcher plants (including several *Nepenthes* hybrids). Mass production by tissue culture for the market includes *Dionaea*, *Drosera*, *Heliamphora*, *Nepenthes*, *Pinguicula*, and *Sarracenia*. Several popular books have been dedicated to the cultivation of carnivorous plants and most scientific books provide the reader with at least a chapter on the cultivation of these plants. Much information on the topic of economically and horticulturally important species can also be found in *The Carnivorous Plant Newsletter*, the official publication of the International Carnivorous Plant Society.

Also relevant economically is the long history of *Drosera* in western herbal medicine. After a range of different uses from at least the sixteenth century onwards, the drug consolidated about 1900 as a remedy against the common cold (ingredient in many cough syrups), as well as bronchitis, asthma and other respiratory problems (it is thought to have a relaxing effect on the bronchial musculature).

## Summary

Carnivorous plants constitute a fascinating group of mostly independently arisen organisms. Their true nature was unrecognized for centuries by most botanists and other researchers, and they still present many open scientific questions concerning habitats, functional morphology, systematics and especially the origin of species. They do not fit into any narrow scheme of botanical ideas, but display, perhaps, the most strongly developed ‘nonconformist’ features of the entire plant world: (1) instead of being eaten they lure, catch and eat small animals by ingenious trap mechanisms; (2) similar complex anatomical and physiological structures are often found in unrelated families; (3) they present the most captivating problems for systematics and evolution; and (4) in spite of their often problematic culture, they enjoy increasingly popularity in cultivation worldwide. Moreover, some species also appear to contribute to human health. Future investigations will help to elucidate some of the problems mentioned above.

## Further Reading

- Albert VA, Williams SE and Chase MW (1992) Carnivorous plants: phylogeny and structural evolution. *Science* **257**: 1491–1495.
- Becker H-A, Saedler H and Lönig W-E (2002) Transposable elements in plants. *Encyclopedia of Genetics*, (Eds in Chief: S Brenner and JH Miller), vol. 4, pp. 2020–2033. San Diego: Academic Press.
- Behe M (1996) *Darwin’s Black Box: The Biochemical Challenge to Evolution*. New York: The Free Press.

- Braem FG (2002) *Fleischfressende Pflanzen*, Augsburg, Germany: Naturbuch Verlag/Weltbild Verlag. [Provides a useful list of e-mail addresses on carnivorous plant sources as well as carnivorous plant societies.]
- Cameron K M, Wurdack KJ and Jobson RW (2002) *Aldrovanda* is sister to *Dionaea* (Droseraceae): molecular evidence for the common origin of snap-traps among carnivorous plants. *American Journal of Botany* **89**: 1503–1509.
- Croizat L (1960) *Principia Botanica*. Caracas, Venezuela (published by the author).
- D'Amato P (1998) *The Savage Garden. Cultivating Carnivorous Plants*. Berkeley, CA: Ten Speed Press.
- Darwin C (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.
- Darwin C (1875) *Insectivorous Plants*. London: John Murray.
- Erickson R (1978) *Plants of Prey in Australia*. Perth, Australia: Lamb Paterson.
- Goebel K (1889, 1891, 1893) *Pflanzenbiologische Schilderungen*, 3 vols. Marburg, Germany: N G Elwert..
- Jolivet P (1987) *Les Plantes Carnivores*. Collection 'Science et Découvertes'. Monaco/Paris: Editions du Rocher Jean Paul Bertrant Éditeur.
- Juniper BE, Robins RJ and Joel DM (1989) *Carnivorous Plants*. London: Academic Press.
- Labat J-J (2000) *Plantes Carnivores. Comment les cultiver facilement*. Stuttgart: Edition Ulmer.
- Lönnig W-E (2001) *Gregor Mendel, der Wasserschlauch (Utricularia) und die Evolution*. Köln, Germany: Naturwissenschaftlicher Verlag.
- Lönnig W-E (2001) Natural selection. In: Craighead WE and Nemeroff CB (eds) *The Corsini Encyclopedia of Psychology and Behavioral Sciences*, 3rd edn, vol. **3**: pp. 1008–1016. New York: John Wiley.
- Lönnig W-E and Saedler H (2002) Chromosome rearrangements and transposable elements. *Annual Reviews of Genetics* **36**: 389–410.
- Lowrie A (1987, 1989, 1999) *Carnivorous Plants of Australia*, 3 vols.. Nedlands: University of Western Australia Press.
- Lloyd FE (1942) *The Carnivorous Plants*. Waltham, MA: Chronica Botanica Company.
- Mayr E (1970) *Populations, Species and Evolution*. Cambridge, MA: The Belknap Press of Harvard University Press.
- Nachtwey R (1959) *Der Irrweg des Darwinismus*. Berlin: Morus Verlag.
- Pietropaolo J and Pietropaolo P (1996/2001) *Carnivorous Plants of the World*. Portland, OR: Timber Press. [Provides a useful list of email addresses on carnivorous plant sources as well as carnivorous plant societies.]
- Richards JH (2001) Bladder function in *Utricularia purpurea* (Lentibulariaceae): Is carnivory important?. *American Journal of Botany* **88**: 170–176.
- Rivadavia F, Kondo K, Kato M and Hasebe M (2003) Phylogeny of the sundews, *Drosera* (Droseraceae), based on chloroplast *rbcL* and nuclear 18S ribosomal DNA sequences. *American Journal of Botany* **90**: 123–130.
- Schmucker T and Linnemann G (1959) Carnivorie. In: Ruhland W (ed.) *Handbuch der Pflanzenphysiologie*, vol. XI: *Heterotrophie*, pp. 198–283. Berlin: Springer-Verlag.
- Schnell D (2002) *Carnivorous Plants of the US & Canada*. Portland, OR: Timber Press.
- Slack A (1986) *Insect-eating Plants and How to Grow them*. London: Alphabooks.
- Slack A (2001) *Carnivorous Plants*, (Sec Ed. Marston Magna) Yeovil, UK: Marston House.
- Taylor P (1989) *The Genus Utricularia*, A Taxonomic Monograph. Kew Bulletin. Additional series XIV. Royal Botanic Gardens, Kew. London: Her Majesty's Stationery Office.
- Williams SE, Albert VA and Chase MW (1994) Relationships of Droseraceae: a cladistic analysis of *rbcL* sequence and morphological data. *American Journal of Botany* **81**: 1027–1037.